Effects of N and P fertilization on the greenhouse gas exchange in two nutrient-poor peatlands

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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$_2$O 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, probably associated with rapid growth of nutrient-limited soil microorganisms. No treatment effect was seen on the CH$_4$ exchange, while N$_2$O emissions peaks were detected in N fertilized plots indicating the importance of taking N$_2$O into consideration under increased N availability. In a longer term, increased nutrient availability will cause changes in plant competitive patterns. The related effect on the future net greenhouse gas exchange is likely dependent on the mixture of nutrients being made available and which plant functional types that benefit from it, in combination with other changes related to global warming.

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 15–30 g C m$^{-2}$ yr$^{-1}$ (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 bacteria, while part of it is consumed in the aerobic surface zone by methanotrophic bacteria (Whalen, 2005). The current 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\(_2\)O) 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).

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 kg N ha\(^{-1}\) yr\(^{-1}\), and found enhanced decomposition rates under higher N deposition. This was explained by 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). 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\(_2\)O 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 \(R_{\text{eco}}\) 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) report 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 fertilization 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 all greenhouse gases (CO₂, CH₄, N₂O), 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. We hypothesize that we will observe: (1) increased CO₂ component fluxes (GPP, Reco) in response to N addition in Storflaket and P addition in Fäjemyr; (2) limited effects on CH₄ exchange; and (3) increased N₂O 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 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 mm, respectively. The wet and dry N deposition in the area is estimated to ca. 15 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 rather 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 m) close to Abisko Scientific Research Station. Long-term mean annual temperature and precipitation are −0.8°C and 304 mm, respectively. The mire is underlain by permafrost with an active layer of 60–70 cm in the study area in late summer (Åkerman
In this area, N deposition is ca. 2 kg N ha\(^{-1}\) yr\(^{-1}\) (Fig. 1), which indicates N limitation. 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 × 2 m) were randomly assigned one of the following four 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 the quotient between fertilization water concentration and soil water concentration was higher for N than for P. Nutrients were given as NH\(_4\)NO\(_3\) and NaH\(_2\)PO\(_4\) × H\(_2\)O 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\(^{-1}\).

### 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; one week in May, two weeks in June–July and one week in September. Greenhouse gas flux measurements in connection to the fertilization events were performed on day 0, 1 (fertilization day), 2, 4, 7 and 14, in order to explore particularly short-term effects.
summer 2006, aluminium collars (depth: 20 cm) were inserted in each plot. The collars had grooves that were filled with water during GHG flux measurements to avoid gas leakage. Transparent chambers (40×40 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$_2$O 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$_2$O 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) 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 significant fluxes was high ($r^2=0.89$, $n=11$) with a close to 1:1 relationship between GC and Innova (regression equation: $\text{GC}=0.94\text{Innova}+0.088$). 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 $R_{\text{eco}}$ during two minutes; and (3) darkened chambers measurements of CH$_4$ (and N$_2$O in Fäjemyr) during ca. 25 min.

2.4 Ancillary measurements

In connection to 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 perfo-

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rated 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. 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 to 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 in time adjacent measurements with transparent and darkened chamber, respectively. For CH₄ and N₂O 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. GHG 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);

\[ GPP = \frac{b_0 \times PPFD \times T_s}{b_1 + PPFD} \]  

(1)

\[ R_{eco} = \exp(b_0 + b_1 \times T_s + b_2 \times WTD) \]  

(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 (Fig. 2). Respiration fluxes were significantly higher than CL (two-sided Dunnett test: \( p < 0.05 \)) on day 1 (fertilization day) for HNP plots in spring, for LN and HN plots in summer, and for LN and HNP plots in autumn. Respiration fluxes were also significantly higher for HN plots on day 2 in autumn. In Fäjemyr, \( R_{eco} \) was significantly higher for HN, HNP and P plots on day 1 in autumn. No such effect was seen in the GPP or \( CH_4 \) fluxes 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 \( \mu g N_2O \text{ m}^{-2} \text{ h}^{-1} \) were detected. In total six fluxes exceeded 100 \( \mu g N_2O \text{ m}^{-2} \text{ h}^{-1} \), where five out of six occurred in N plots. Average \( N_2O \) fluxes during the measurement period were 24.4, 10.9, −16.1 and −6.1 \( \mu g N_2O \text{ m}^{-2} \text{ h}^{-1} \) for 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-ANOVA) are shown in Table 1, and estimated marginal means (average fluxes adjusted for covariates, if any) in Table 2. 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 2). In summer, all nutrient addition treatments had higher CO$_2$ uptake rates on average compared to control, while in spring and autumn the rates in HN plots were similar to CL plots. There was no significant treatment effect for $R_{\text{eco}}$ (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 CH$_4$ fluxes (p=0.091), where HN and P plots had on average higher rates than CL plots, while the HNP plots had counter-intuitively lower rates.

In Storflaket, both GPP (p=0.001) and $R_{\text{eco}}$ (p=0.018) had statistically significant treatment effects. Nitrogen plots had the highest rates of both GPP and $R_{\text{eco}}$, while average flux rates in P plots were similar to CL plots (Table 2). There was a strong tendency that fertilization decreased NEE in Storflaket (p=0.056), because GPP increased more than $R_{\text{eco}}$. The CH$_4$ fluxes 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 $R_{\text{eco}}$ and GPP in each plot in Fäjemyr; $r^2$ values range between 0.72–0.95 and 0.65–0.96 for $R_{\text{eco}}$ and GPP, respectively (Table 3). Soil temperature was always a significant variable in explaining $R_{\text{eco}}$. Water table depth was significant in 13 out of 16 plots, constantly showing a negative correlation with $R_{\text{eco}}$, indicating that lowered water table leads to increased respiration rates.

The resulting sums of the time series modelling of GPP and $R_{\text{eco}}$ in each plot be-
between March and November 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 adding the average flux. This procedure removes the trend associated with shrubs, but does not affect the average fluxes.

The average sums of $R_{eco}$, $GPP$ and $NEE$ in all plots were 634, -509 and 125 g C m$^{-2}$, respectively (Fig. 3). 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 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 is 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*) add 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.

A short-term (hours to days) response in $R_{\text{eco}}$ 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 etc., the fresh C substrate pool became exhausted and the stimulating effect of increased nutrient availability ceased. Whether decomposition becomes suppressed in a longer term (Berg and McClaugherty, 2003) can not be seen in our data.

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 2). This may be because *Sphagnum* mosses represent the main part of the ecosystem CO$_2$ uptake during 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 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, also $R_{\text{eco}}$ 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 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 a longer 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 $R_{\text{eco}}$ 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 $R_{\text{eco}}$ 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 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 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 $R_{\text{eco}}$ is accurate. This propagates into the estimation of the growing season NEE in which 14 out of 16 plots acted as a CO$_2$-C source to the atmosphere.

No treatment effect was found for CH$_4$ emissions, but the positive correlation with sedges indicates a potential for increased CH$_4$ flux 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$_4$ fluxes may be associated with inhibition of CH$_4$ oxidation by methanotrophic bacteria. In HNP plots decreased flux can be due to decreased plant root exudation rates, because of alleviated nutrient limitation, leading to decreased substrate availability for methanogenic bacteria.

In addition to the gaseous C exchange, our data set indicates a strong possibility for increased N$_2$O emissions with increased N availability. Even though the flux measurements were performed at a low temporal resolution, several N$_2$O peaks were detected. This signifies the importance of taking N$_2$O exchange into account when considering N fertilization as a means of increasing C sequestration in ecosystems, since N$_2$O 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 \( R_{\text{eco}} \) were significantly increased in plots receiving additional N.

– Complex and nonlinear responses to nutrient addition were seen for the \( \text{CH}_4 \) exchange, while \( \text{N}_2\text{O} \) 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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Table 1. Statistics ($F$ and $p$ values) from the repeated measures analysis (RM-ANOVA) for treatment (between-subject) effects on CO$_2$ component fluxes ($NEE$, $R_{eco}$, $GPP$) and CH$_4$ fluxes in Fäjemyr and Storflaket. Shown are also $F$ and $p$ values for any significant covariates used in the analyses.

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| Storflaket            |      |        |          |      |        |
| $NEE$                 | 2.93 | 0.056  | –        | –    | –      |
| $R_{eco}$             | 4.28 | 0.018  | Vascular | 9.18 | 0.009  |
| $GPP$                 | 8.43 | 0.001  | Vascular | 11.7 | 0.004  |
| $CH_4$                | 0.57 | 0.690  | –        | –    | –      |
Table 2. Carbon dioxide component fluxes (NEE, $R_{\text{eco}}$, and GPP, mg CO$_2$ m$^{-2}$ h$^{-1}$) and CH$_4$ fluxes (mg CH$_4$ m$^{-2}$ h$^{-1}$) from Fäjemyr and Storflaket. Values are estimated marginal means (adjusted for covariates, if any) from RM-ANOVA.

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Table 3. Estimated parameters from Eq. (1) and Eq. (2) used to model seasonal time series of GPP and $R_{\text{eco}}$ in Fäjemyr. NS: Not significant (See Sect 2.5).

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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).
**Fig. 2.** Average $R_{eco}$ ($n=4$) rates 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. To increase visibility of the fertilization response with time y-axes scales differ between periods.
Fig. 3. Sum of modelled time series of $GPP$ and $R_{eco}$, detrended for shrubs, and $NEE$, 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.