**TELLUS**

# Environmental controls on the CO₂ exchange in north European mires

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## ABSTRACT

Net CO₂ exchange measured under well-mixed atmospheric conditions in four different mires in Sweden and Finland
were used to analyse which factors were controlling photosynthesis and respiration. The parameters of a light response
function showed strong seasonal variations with similar behaviour for all mires. The half-monthly nighttime respiration
rates in the central part of the growing season were about two times higher in the southernmost, warmest site, Fäje,
as compared to the northernmost, coldest site, Kaamanen. However, Kaamanen had high photosynthesis rates, and
this in combination with the long daylight periods in the middle of the summer caused Kaamanen to have the largest
net ecosystem exchange (NEE) during the summer period. Fäje that showed the highest productivity had also the
highest respiration and therefore, the lowest NEE during summer. Correlation between half-monthly components and
different environmental variables showed the highest correlation between the components themselves. Thereafter came
temperature except for Fäje where water table depth (WTD) explained most of the variance both for detrended and
temperature-normalized components. All sites showed dependencies between WTD and the respective components
during drying up periods. Temperature sensitivity was higher for productivity than for respiration indicating that CO₂
uptake would increase during global warming.

## 1. Introduction

The net carbon balance in mire ecosystems is composed by several significant exchange processes (Waddington and Roulet, 2000; Clair et al., 2002; Billet et al., 2004), that is, the land–atmosphere exchange of CO₂ (Lafleur et al., 2003; Aurela et al., 2004) and CH₄ (Granberg et al., 2001; Nilsson et al., 2001), respectively, and carbon transport with water recharge and water discharge (Kortelainen et al., 1997; Elder et al., 2000; Billet et al., 2004). The land–atmosphere exchange of CO₂ is composed by the uptake through photosynthesis and the loss through respiration. These two processes represent normally by far the two largest C-fluxes in the mire ecosystem and the difference

between the two represent the net ecosystem exchange of CO₂ (NEE). The ecosystem respiration is further composed by heterotrophic and autotrophic respiration, respectively. Understanding the main environmental controls of the different components that constitutes the NEE is one crucial step to understand and to predict the net carbon exchange of mires under a changing environment (Bubier et al., 2003).

Both seasonal and annual estimates of NEE vary considerably within mires (Alm et al., 1997; Waddington and Roulet, 2000; Bubier et al., 2003), between mires (Arneth et al., 2002; Moore et al., 2002) as well as for a particular site between years (Lafleur et al., 2003; Aurela et al., 2004; Sagerfors et al., 2007). The variation in NEE is controlled by both site specific factors, that is, state factors, determining the mire type and by temporally variable factors. The more site specific factors are, for example, topography, geochemistry and climate while the more temporally variable factors are plant phenology and meteorological

variables, that is, air temperature, precipitation, humidity and radiation. The long-term average NEE for any mire should be mostly related to the state factors while seasonal and annual variations in NEE should be controlled by phenological and meteorological factors.

The master variables controlling the development of mire type is the origin of water and the availability of nutrient (e.g. Ivanov 1981; Hilbert et al., 2000; Belyea and Baird, 2006). Ombrogenic mires, that is, those that only receive water through precipitation are always nutrient poor due to a limited availability of mineral nutrients. Minerogenic mires that receive water also from the surrounding mineral soils, develops into oligotrophic or eutrophic types depending on the nutrient conditions of the catchment. These hydrogeochemical differences among mires also results in different responses to variations in the water balance. The mire plants are also differently adapted with respect to optimal water table depth (WTD, Clymo, 1984). Depending on mire type and relative distribution of the microtopographical features, with different optimal average WTD, the effect of changed water table level on NEE, photosynthesis and respiration, respectively, will most probably be quite different (Belyea and Clymo, 2001; Belyea and Baird, 2006).

The long-term average peat carbon accumulation rate is known to differ between mire types being higher in bogs than in fens (Tolonen and Turunen, 1996; Turunen et al., 2002). However, the coupling between mire type and NEE is less obvious. Based on growing season measurements and modelling, both photosynthesis and respiration increased from bogs over poor fen, intermediate fen to rich fen. The NEE over the growing season was however effectively zero in the bog and rich fen, respectively, while the poor and intermediate rich fen represented a significant C uptake (Bubier et al., 1999).

The mire C exchange is shown to be affected by temperature (Arneth et al., 2002), ground water level (Silvola et al., 1996), plant biomass, growth and radiation availability (Bubier et al., 1998), and these relations are commonly used to infer the effects of a changing climate on the mire C exchange. Several of these variables are however more or less strongly correlated which makes interpretations of the true causal relationships difficult. For example, on a seasonal time scale air temperature, plant phenology and productivity and to a lesser extent the water table are most often correlated. All of these factors also affect photosynthesis as well as respiration.

The aim of this paper is to resolve the causal relationships between the $CO_2$ exchange components [NEE, gross primary productivity (GPP) and ecosystem respiration] and some environmental variables in mires of different nutrient status. The abiotic variables used are air temperature ($T_a$), photon flux density (PPFD), vapour pressure deficit (VPD) and WTD, all of which are master variables in controlling either photosynthesis or ecosystem respiration. To accomplish these analyses we have used complete annual cycles of eddy covariance data from four northern mires in Scandinavia.

*Fig. 1.* Map of Scandinavia showing the locations of the four sites.

## 2. Material and methods

In this study, four northern peatlands supported within the scope of Nordic Centre for Studies of Ecosystem Carbon Exchange and its Interactions with the Climate System (NECC), two in Sweden and two in Finland (Fig. 1), were investigated with respect to exchange of $CO_2$ between land surface and atmosphere. The sites represent a diverse range of peatland types and climate zones, ranging from cold temperate in the south to subarctic in the north. There are other comparable peatland sites in the same geographical region from which eddy correlation measurements of $CO_2$ exchange are available (Johansson et al., 2006). However, the sites chosen for the purpose of the present comparison all share exactly the same methodology for eddy correlation measurements (closed-path $CO_2$ analysers as opposed to open-path) and for consistency this study is therefore restricted to the four sites listed below.

### 2.1. Site description

Geographic location and climate of the sites are described in Table 1. The southernmost site, Fäjemyr (hereafter denoted 'Fäje'), is an ombrotrophic, eccentric bog dominated by dwarf shrubs (*Calluna vulgaris* L. Hull*, Erica tetralix* L.), sedges (*Eriophorum vaginatum* L.) and *Sphagnum* mosses (mainly *Sphagnum magellanicum* Brid., *Sphagnum rubellum* Wils.), and a sparse dwarf pine cover (*Pinus sylvestris* L.). The flux tower (measurement height: 3.4 m) is located ca. 290 m from the edge of the southern part of the bog. The source area consists mainly of a mosaic of hummocks, lawns and carpets with a lower occurrence of hollows fairly evenly distributed over all wind directions. The winters are characterized by intermittent snow cover, but mostly there is some period with a continuous snow cover. The snow depth rarely exceeds a few decimetres. Site details and instrumentations are described in Lund et al. (2007).

Siikaneva is an oligotrophic fen located on the border of southern and middle boreal vegetation zones. Vascular plants are relatively scarce and dominated by sedges (*E. vaginatum*, *Carex rostrata* Stokes and *Carex limosa* L.). The moss layer is a continuous

*Table 1.* Site information for the NECC peatland sites used in the analyses

| Site name | Coordinates | Data year | Annual temperature (°C) | Annual precipitation (mm) | Peatland type | Dominating vegetation species | Peat depth (m) | EC system (gas analyser, sonic anemometer) |
|---|---|---|---|---|---|---|---|---|
| Fäje | 56°15′ N, 13°33′ E | 2005.08–2006.07 | 6.2 (January: −2.4, July: 15.1) | 700 | Temperate, ombrotrophic bog | *E. vaginatum, C. vulgaris, E. tetralix, S. magellanicum, S. rubellum* | 4–5 | LI-6262, Gill R3 |
| Siikaneva | 61°50′ N, 24°11′ E | 2005 | 3.0 (January: −7.4, July: 15.5) | 713 | Boreal, oligotrophic fen | *E. vaginatum, C. rostrata, C. limosa, S balticum, S. majus, S. papillosum* | 2–4 | LI-7000, Metek USA-1 |
| Degerö | 64°11′ N, 19°33′ E | 2002 | 1.2 (January: −12.4, July: 14.7) | 523 | Boreal, oligotrophic mixed mire | *E. vaginatum, V. oxycoccus, A. polifolia, S. lindbergii, S. majus, S. balticum* | 3–4 | LI-6262, Gill R2 |
| Kaamanen | 69°08′ N, 27°17′ E | 2001 | −1.1 | 474 | Subarctic, mesotrophic fen | *L. palustre, E. nigrum, V. uliginosum, S. rubellum, D. fuscescens* | 1 | LI-6262, SWS-211 |

*Sphagnum* carpet dominated by *Sphagnum balticum* Russ. C. Jens.*, Sphagnum majus* Russ. C. Jens. and *Sphagnum papillosum* Lindb. The flux tower (measurement height: 3.0 m) is located in a position where the fetch is in the range of 200–400 m in all directions. The snow cover is normally continuous during winter. Site details are given by Aurela et al. (2007).

Degerö Stormyr (hereafter denoted 'Degerö') is a boreal, oligotrophic fen situated in northern Sweden on a highland between two major rivers, Umeälven and Vindelälven ca. 70 km from the Gulf of Bothnia. The mire consists of a complex system of interconnected smaller mires divided by islets and ridges of glacial till (Sagerfors et al., 2007). The vascular plant community within the fetch is dominated by *E. vaginatum, Vaccinium oxycoccos* L. *and Andromeda polifolia* L. The moss carpets are dominated by *S. majus*; lawns by *S. balticum* and *Sphagnum lindbergii* Schimp.; and hummocks by *Sphagnum fuscum* Schimp. Klinggr. and *S. rubellum*. The flux tower is located ca. 250 m from the border of the mire, and the measurement height is 1.8 m. The source area is dominated by patches of wet lawn and carpet plant communities with a narrow sector towards the southeast consisting of scattered pine trees. In winter, the snow depth normally reaches ca. 0.6 m. Details about the site and the instrumentation are given by Sagerfors et al. (2007).

Kaamanen is a subarctic, mesotrophic fen typical of the aapa mire region in northern Finland. This type of fen is composed of a mosaic of ridges and pools with a typical horizontal length scale of a few meters. The site has no permafrost, but thin lenses of ice may remain in the well-insulated hummocks until late summer. The prevailing mosses on the fen are *S. rubellum* and *Dicranum fuscescens* Turn. The hollows are partially covered by different sedges (*Carex* spp.). On the oligotrophic areas there is also a significant volume of shrubs like *Ledum palustre* L., *Empetrum nigrum* L. and *Vaccinium uliginosum* L. The fetch extends at least 300 m in all directions, except to the west of the flux tower where the fetch is only 80 m. All data with winds from the related 75° wind sector were therefore discarded. Measurement height is 5 m. The winter in this area is characterized by low temperatures, down to −30 °C and a significant snow pack during several months. A detailed description of site and measurements are given by Aurela et al. (1998, 2001).

At all sites, flux footprint calculations have shown that the fluxes emanate from the mire surfaces during near neutral and unstable atmospheric conditions (Aurela et al., 1998; 2001, 2007; Lund et al., 2007; Sagerfors et al., 2007). Most of the strongly stable conditions with footprints extending beyond the mire surfaces were removed using a friction velocity threshold ($u^* <$ 0.1 m s$^{-1}$, cf. below).

## 2.2. Measurements and data handling

The fluxes of CO$_2$ between mire and atmosphere were measured using the eddy covariance method. All four sites used closed-path gas analysers for the fast CO$_2$ concentration measurements

and sonic anemometers for the wind measurements. The flux calculations were made basically according to the so-called Euroflux methodology (Aubinet et al., 2000). Quality control and flux corrections of the eddy covariance data from each site were made by the respective principal investigators.

Meteorological parameters were measured nearby or on the same tower as where the eddy covariance measurements were made. Ground water level relative to the surface of the mires was measured continuously with pressure transducers or by a float and counter device (Degerö). Details about flux and meteorological measurements are given in Lund et al. (2007) for Fäje, by Aurela et al. (2007) for Siikaneva, by Sagerfors et al. (2007) for Degerö and by Aurela et al. (1998, 2001) for Kaamanen.

If several years of measurements were available, a year without extreme weather events was used in the detailed data analyses following below. To ensure reliable and comparable data sets, the same $u^*$-threshold was applied to all sites ($u^* = 0.1$ m s$^{-1}$) and only data above this threshold was used (both day and night) in the subsequent analyses. Growing season onset was defined as when average daily temperature rose above 5 °C for more than 3 d in spring (Eriksson, 1992), and was consequently ended when temperature fell below 5 °C in autumn.

## 2.3. High temporal resolution data

Measured CO$_2$ flux data from each site during the growing season was divided into a daytime (defined as PPFD $> 10$ $\mu$mol m$^{-2}$ s$^{-1}$) and a nighttime (PPFD $< 10$ $\mu$mol m$^{-2}$ s$^{-1}$) data set. For the growing season, the daytime data set was grouped into half-monthly periods, and for each period the following non-linear regression equation (Falge et al., 2001) was fitted to determine the parameters $F_{csat}$, $R_d$ and $\alpha$:

$$\text{NEE} = -(F_{csat} + R_d)(1 - e^{\frac{-\alpha Q}{F_{sat} + R_d}}) + R_d, \tag{1}$$

where $F_{csat}$ is the CO$_2$ uptake at light saturation; $R_d$ is the dark respiration rate; $Q$ is the incoming PPFD and $\alpha$ is the initial slope of the light response curve.

The nighttime data set during the whole data year was likewise grouped into half-monthly periods, and for each period the following equation (e.g. Lloyd and Taylor, 1994) was fitted to the data;

$$\text{NEE}_{night} = R_0 e^{T_{an} \cdot \tau}, \tag{2}$$

where $R_0$ is the base respiration; $T_{an}$ is air temperature and $\tau$ is the temperature sensitivity. For these regressions the software package Matlab R14 (The Mathworks Inc., Natick, USA) was used.

## 2.4. Low temporal resolution data

The main components of the net CO$_2$ exchange, ecosystem respiration ($R_{eco}$) and gross photosynthesis (GPP) were estimated for half-monthly periods accordingly:

1. The GPP was modelled using eq. (1) with measured half-hourly PPFD as input by subtracting the corresponding respiration ($R_d$), and then summed per half-monthly period.

2. The daytime ecosystem respiration was then estimated by taking the difference between measured daytime NEE and modelled GPP for the respective period.

3. Total ecosystem respiration ($R_{eco}$) was calculated as the measured mean nighttime rate times night-length plus the estimated daytime respiration, and summed per half-monthly period. This means that in practice, the respiration rate at low $u^*$ values were replaced with the corresponding mean nighttime rates when $u^*$ was above the threshold value.

The above described scheme was used during the growing season. For the periods outside the growing season a simplified scheme was used, where $R_{eco}$ was estimated using the mean nighttime NEE rate summed over the half-monthly period. GPP was estimated as the difference between the measured daytime NEE and the estimated $R_{eco}$ times the day length, and summed per half-monthly period. This was justified since there was no or very low correlation between temperature and nighttime ecosystem respiration for periods outside of the growing season (cf. below), and, thus, there was no model available to estimate daytime respiration.

A regression analysis was made on the integrated half-monthly components (GPP and $R_{eco}$) during the growing season in order to assess the dependencies on the following environmental variables; air temperature ($T_a$), VPD, PPFD and WTD. Such analysis is hampered by the strong cross-correlation between the different environmental variables and by the strong seasonality in the processes governing the fluxes. In order to reduce such inadvertent influences the following steps were taken:

(1) Direct regression on the half-monthly components.

(2) Regression on de-trended components. GPP and $R_{eco}$ were normalized against potential solar radiation in order to reduce the effect of seasonality. In this way, the seasonal trend in flux components and environmental variables is removed. New variables were created in the following manner; the potential solar radiation for each half-monthly period for each site was used as a dummy variable with weights applied in such way that the sum of these new 'seasonal' variables and the sum of the respective components were made equal, that is:

$$GPP_{dummy}(i) = S(i) \left[ \frac{\sum_{i=1}^{n} GPP(i)}{\sum_{i=1}^{n} S(i)} \right], \qquad (3)$$

where $S(i)$ is the potential solar radiation against horisontal surface for half-month $i$ during the growing season. The residuals were then calculated as:

$$GPP_{res}(i) = GPP(i) - GPP_{dummy}(i) \qquad (4)$$

(3) Regression on component residuals normalized with respect to air temperature. The regression analysis on the residuals showed (cf. below) that the dominant control variable was temperature and in order to reduce this influence too, the residuals according to step (2) above, were normalized by dividing with the function value of the regression between the respective residual and the temperature (GPP$_{res\_norm}$).

The same method was applied to $R_{eco}$.

The method of separating measured NEE into respiration and GPP implies a combination of modelled and measured data. This means that neither $R_{eco}$ nor GPP are purely independent of the environmental variables that we later wish to analyse their dependencies to. There is, however, no way of circumventing this problem at the moment. However, the fluxes during nighttime represent the truly measured dark respiration of the whole ecosystem and it is thus interesting to analyse these data as well. The measured mean half-monthly nighttime respiration rates, $R_{night}$, were fitted to exponential growth function (eq. 2) and to the Lloyd and Taylor (1994) equation which previously has shown to give good results for other ecosystems (e.g. Lindroth et al., 2007):

$$R_{night} = R_{10} e^{308.56\left(\frac{1}{56.02} - \frac{1}{T-227.13}\right)}, \qquad (5)$$

where $R_{10}$ is the fitting parameter corresponding to the respiration rate at 10 °C and $T$ is the air temperature in K.

## 3. Results

### 3.1. Temporal variation of parameters and components

All sites show similar seasonal variation of parameters related to the light response function with maximum values occurring in the middle of the summer, around July (Fig. 2). In general, seen over the whole season, the southernmost site, Fäje, has the highest values and the northernmost site, Kaamanen, has the lowest vales. Concerning the seasonal variation of the light use efficiency parameter, $\alpha$, Fäje shows slightly different behaviour compared to the other sites with a secondary maximum late in the autumn (Fig. 2). It is also interesting to notice that Kaamanen has the highest $F_{csat}$ and $\alpha$ values in July of all sites, indicating very high capacity to take up $CO_2$ by photosynthesis during this part of the season especially since the respiration is lowest at that site. The variation of the dark respiration parameter, $R_d$ is largely a reflection of the air temperature differences between the sites (Fig. 3). The difference in climate between the sites is in accordance with the latitudinal differences with Kaamanen being the coolest site with the lowest mean daytime PPFD and VPD and Fäje being the warmest site which also has the highest radiation levels (Fig. 3).

The measured mean nighttime respiration rates ($R_{night}$) are very low from December to March at all sites (Fig. 4). The maximum respiration rates occur in July except for Kaamanen where
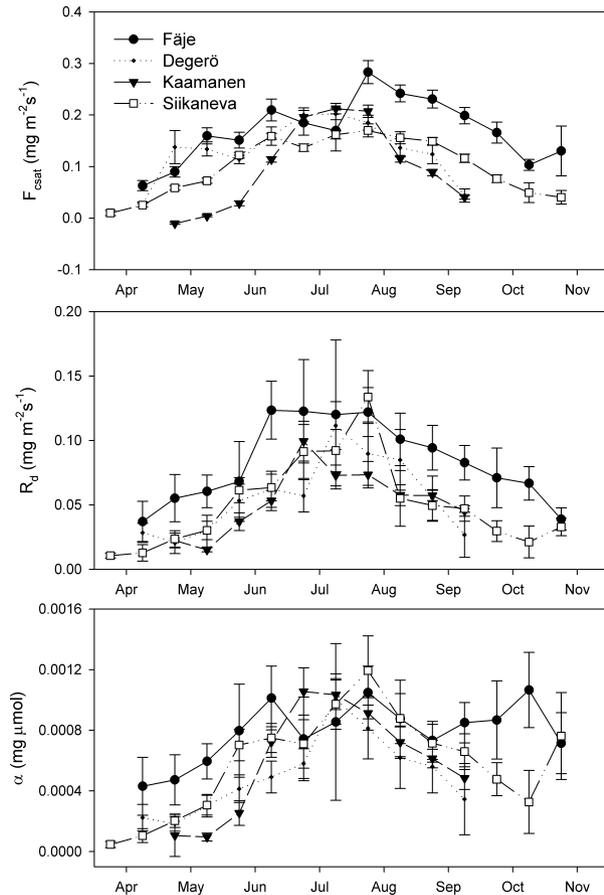
*Fig. 2.* Seasonal variation of the parameters of the light response function for the respective sites in $CO_2$ units. The values are half-monthly means with the error bar representing the 95% confidence interval.
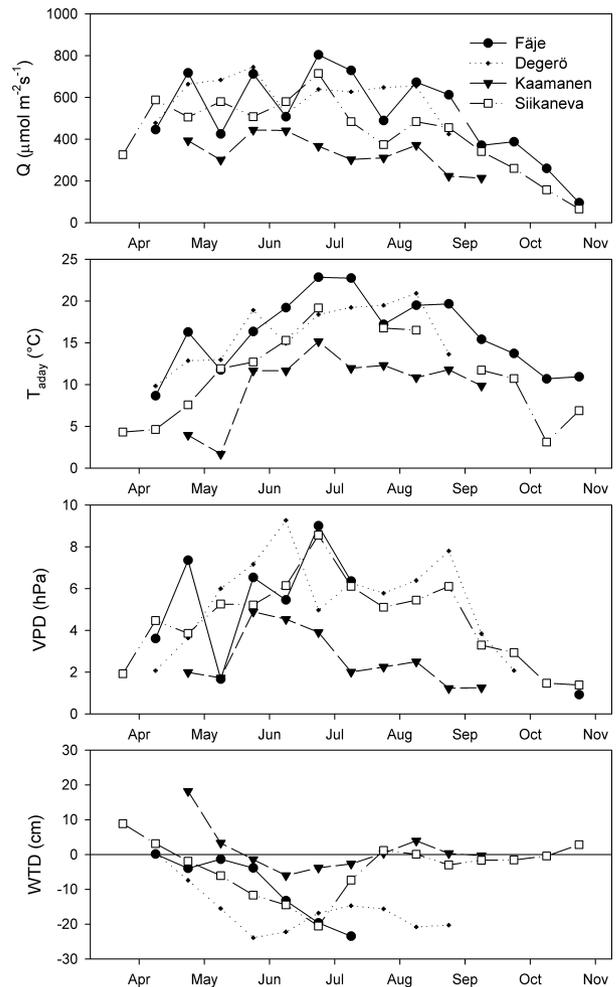


*Fig. 3.* The mean half-monthly daytime meteorological conditions and water table depth during the growing seasons at the different sites. $Q$ is photon flux density, $T_{aday}$ is the air temperature, VPD is vapour pressure deficit and WTD is water table depth.

the maximum occurs in first part of August. The respiration rates are higher in autumn than in spring, which is in good correspondence with the temperature pattern and the amount of living plant biomass. It is also a consistent pattern that when air temperature falls below zero, the respiration rates drops to their low wintertime values with very little variation remaining in spite of large variations in temperature (Fig. 4).

The mean nighttime rates during the heart of the growing season are highest in Fäje and lowest in Kaamanen; the rates being ca. two times higher on average in the former site during the heart of the growing season. The respiration rates at Siikaneva and Degerö were in between those of Fäje and Kaamanen but closer to the latter.

The cumulated half-monthly modelled GPP reaches its maximum values in July with similar values, about $-200$ g m$^{-2}$ per half-monthly period, for Fäje, Kaamanen and Degerö while the maximum occurs in August for Siikaneva at slightly lower value of $-175$ g m$^{-2}$ (Fig. 5). The onset of uptake is earliest in Fäje, around second part of March, then followed by Siikaneva

in first part of April, Degerö second part of April and finally Kaamanen in first part of May. The end of the uptake season follows reversed order with similar time delays between sites.

The cumulated half-monthly modelled ecosystem respiration ($R_{eco}$) is generally much higher at Fäje than at the other sites (Fig. 5) as was also shown by the nighttime rates (Fig. 4). Kaamanen has slightly lower respiration than Degerö and Siikaneva except during July–August when it is much lower, probably because of lower summer temperatures (cf. Fig. 3). The maximum in $R_{eco}$ occurs simultaneously with the maximum in uptake at all sites and there is very high and linear correlation between respiration and gross primary productivity with $r^2$ values ranging between 0.89 and 0.97 (Fig. 6).

The cumulated half-monthly NEE, which is directly measured by the eddy covariance systems at each site (the sum of respiration and gross primary productivity), shows a more complex
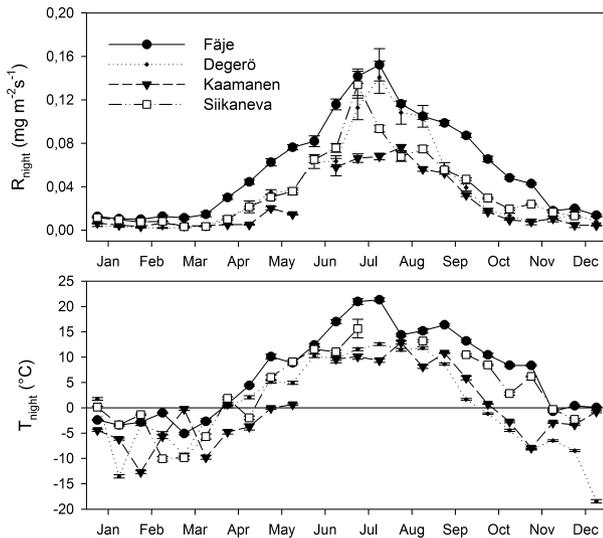
*Fig. 4.* Mean ± *SE* half-monthly measured nighttime $CO_2$ respiration rates for the different sites (top) and the corresponding mean nighttime air temperatures (bottom).



*Fig. 5.* Seasonal variation of cumulated half-monthly $CO_2$ fluxes; modelled gross primary productivity (top) and ecosystem respiration (middle) and measured net ecosystem exchange (bottom).

pattern than the individual components (Fig. 5). The northernmost site, Kaamanen, has the highest NEE occurring in July; while the southernmost site, Fäje has at the same time the lowest. Although the NEE is very high at Kaamanen in the middle of the summer, the period during which this system acts as a sink, with only three months with negative NEE, is much shorter than for the other sites.

The mean diurnal variation in NEE during the period May–September clearly shows the differences between the sites (Fig. 7). In May, Kaamanen is practically a source during the whole day while the other sites show significant net uptakes during daytime. The effect of the long daylight hours in Kaamanen is immediately visible in June when Kaamanen has the longest diurnal sink period. During July, Fäje and Degerö have the highest maximum net uptake rates in the middle of the day but also the highest respiration rates at night. The month of July provide a nice illustration to the importance of the balance between the two main components of the net flux as well as the importance of day length: In spite of having the highest uptake rates together with Degerö, Fäje has the lowest cumulated NEE values during this month (Fig. 5) because of its higher respiration rates and shorter day length than the other sites. In August, NEE is quite similar at all sites and then in September the differences are most pronounced.

### 3.2. *Relationships of flux components to environmental variables*

The fitting of the light response function to measured NEE during daytime according to eq. (1) gave generally quite good results with $r^2$ values typically between 0.7 and 0.9 during the central
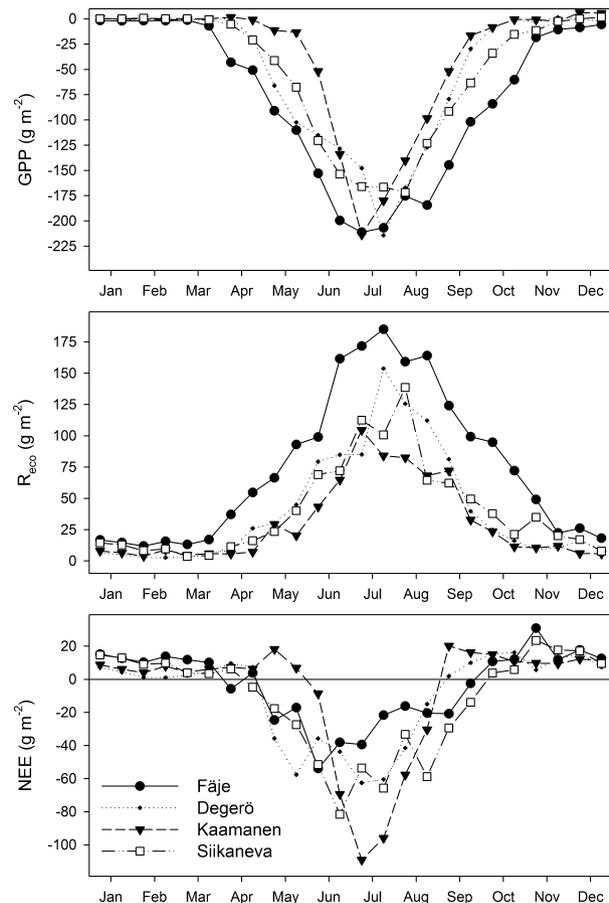
part of the growing season. The fits were lower in the beginning of the season and during bad weather conditions when there was little variation in either of the variables. An example of the relationship between NEE and PPFD is given in Fig. 8 for the period 1–15 July for the respective site. For this particular period, Kaamanen shows the highest light use efficiency, $\alpha$ (initial slope of the curve) as well as the highest $F_{csat}$. Both Siikaneva and Kaamanen have very low sensitivity to light for flux densities above ca 500 $\mu$mol m$^{-2}$ s$^{-1}$ while both Degerö and Fäje show slightly larger light sensitivity in this range.

The relationship between measured half-hourly nighttime NEE and temperature were very weak at all sites, except at Siikaneva where $r^2$ at the best reached 0.63 in May but more typically was in the range 0.3–0.4. Degerö showed practically no response to temperature at this time scale with all $r^2$ values below 0.1. However, when analysing the mean half-monthly nighttime rates versus temperature for the whole year, the relationship became very strong (Fig. 9). The Lloyd and Taylor (1994) equation gave marginally higher $r^2$ values than the simple two-parameter exponential growth function when fitted to all data (Fig. 9,

*Fig. 6.* Correlation between cumulated half-monthly modelled CO$_2$ flux components; ecosystem respiration versus gross primary productivity at the different sites.
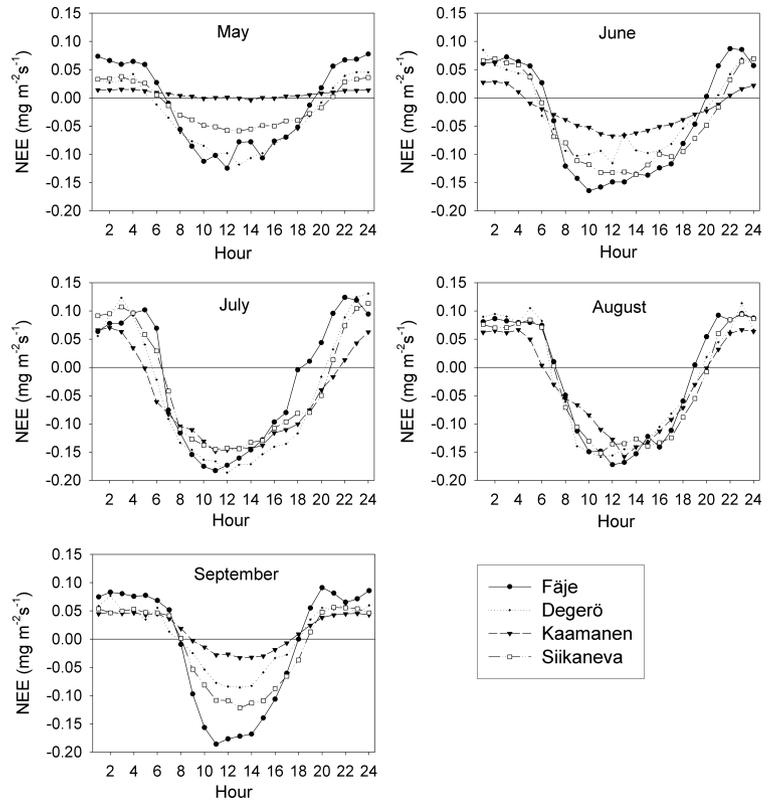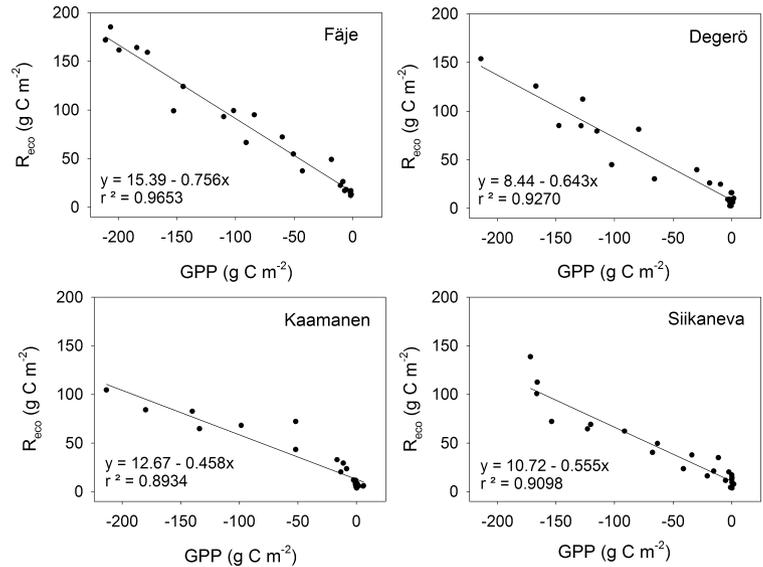


*Fig. 7.* The mean diurnal variation of the measured CO$_2$ NEE for the summer period at the different sites.

Table 2) but for individual site fits, the latter gave generally better results (Table 2). According to the latter equation, the temperature sensitivity, $\tau$, was lowest at Fäje and highest at Degerö while the opposite was true for the base respiration, $R_0$ (Table 2).

It was previously demonstrated (Fig. 6) that cumulated half-monthly ecosystem respiration ($R_{eco}$) and GPP were strongly correlated at all sites. The correlations between the respective components and the environmental variables $T_a$, PPFD, VPD and WTD, show that the correlation between the components themselves is actually stronger than between any of the component and the respective environmental variables (Fig. 10). The variable that shows the next strongest correlation is $T_a$ except for Fäje where $R_{eco}$ and WTD are more strongly correlated than $R_{eco}$ and $T_a$. It should be pointed out that the WTD was only available during a limited part of the growing season at Fäje, namely during the initial drying up in spring (cf. Fig. 3). It is,
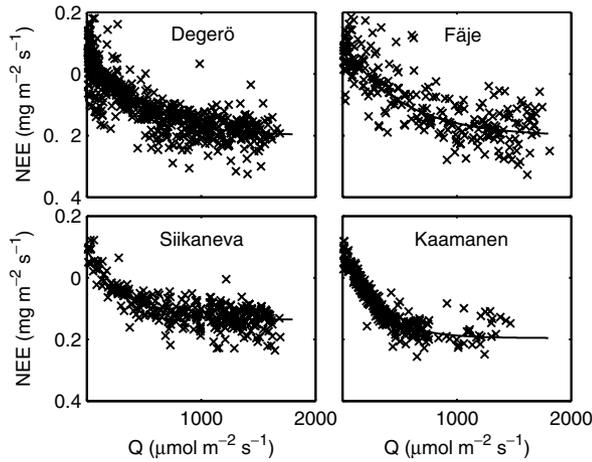
**Fig. 8.** Example of light response curves, measured $CO_2$ NEE versus photon flux density for all four sites for the period 1–15 July.
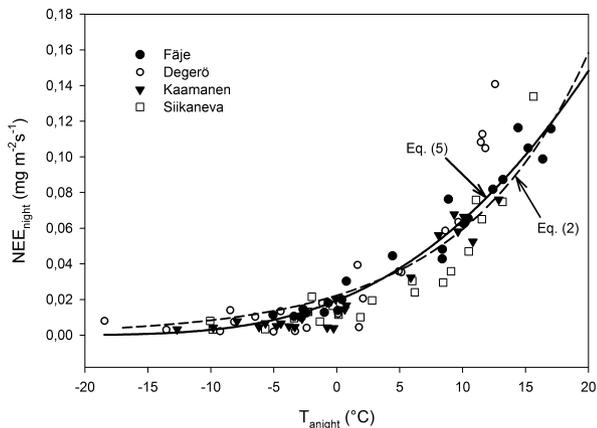


**Fig. 9.** Mean measured nighttime $CO_2$ respiration rates against the corresponding mean air temperature. Data from all sites fitted to the exponential growth function (eq. 2), respectively, to the Lloyd and Taylor (1994) eq. (5). Parameters in Table 2.



**Fig. 10.** Relationship between the modelled components ecosystem respiration ($R_{eco}$) and gross primary productivity (GPP), their residuals ($R_{eco\_res}$ and GPP$_{res}$) and normalized values ($R_{eco\_res\_norm}$ and GPP$_{res\_norm}$) and the respective environmental variables; air temperature ($T_a$), photon flux density (PPFD), vapour pressure deficit (VPD), water table depth (WTDa) and water table depth only during the initial drying phase (WTDb).

however, interesting that GPP is more strongly correlated to $T_a$ than to PPFD and that the correlation between GPP and $T_a$ is even stronger than between $R_{eco}$ and $T_a$ at Fäje and Siikaneva. It is also observed that the temperature sensitivity is higher for GPP than for $R_{eco}$ at all sites; average slope of the linear regression is $-12.3 \pm 1.0$ (mean $\pm$ *SE*) for GPP and $7.6 \pm 1.9$ g m$^{-2}$ $^\circ$C$^{-1}$ for $R_{eco}$. The correlation between the components and VPD is also quite strong and at Siikaneva, it is for instance stronger than that to PPFD (Fig. 10). The problem with this kind of correlation analysis is the strong co-variation between the different environmental variables, which makes it difficult to judge which of the variables that really is in control and the fact that all variables including the independent ones, shows a strong and similar seasonal variability.

In order to reduce the effect of the seasonality, dummy variables for both $R_{eco}$ and GPP were created and then the residual between these dummy variables and the respective components
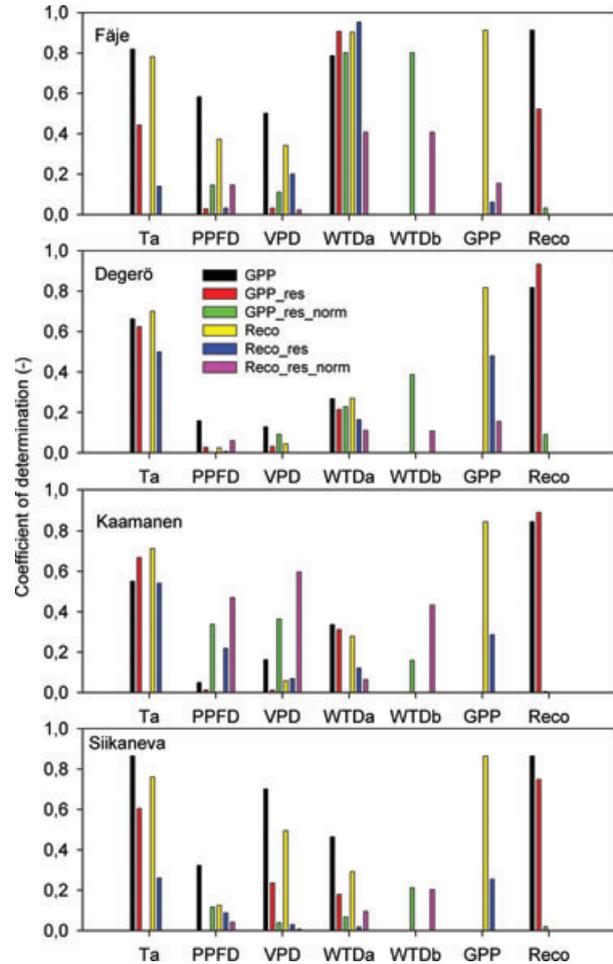
were calculated and correlated to the environmental variables. These new 'ecosystem respiration' and 'gross primary productivity' variables, cleared from seasonal variation, were denoted as $R_{eco\_res}$ and GPP$_{res}$, respectively. Again it turned out that the correlation between GPP$_{res}$ and $R_{eco\_res}$ was the strongest except for Fäje where WTD showed the strongest correlation (Fig. 10), similarly as for GPP. For $R_{eco\_res}$, $T_a$ showed the strongest correlation again with the exception of Fäje where WTD dominated. The temperature sensitivity was still higher for GPP$_{res}$ than for $R_{eco\_res}$. It should be noted that the correlation between the residuals and PPFD practically vanished at all sites indicating that the method of reducing the influence of the seasonal course on the correlations were successful.

*Table 2.* Regression results for half-monthly nighttime respiration rates versus the corresponding air temperatures for the two different eqs (2) and (5), respectively. $R_0$ (mg m$^{-2}$ s$^{-1}$) is the base respiration at 0 °C and $\tau$ is the temperature sensitivity in eq. (2) and $R_{10}$ (mg m$^{-2}$ s$^{-1}$) is the respiration rate at 10 °C in eq. (5)

|  | Parameters | Fäje | Degerö | Kaamanen | Siikaneva | All sites |
|---|---|---|---|---|---|---|
| Equation (2) | $r^2$ | 0.94 | 0.95 | 0.93 | 0.95 | 0.86 |
|  | $R_0$ | 0.026 | 0.012 | 0.015 | 0.010 | 0.022 |
|  | $\tau$ | 0.085 | 0.186 | 0.134 | 0.165 | 0.098 |
| Equation (5) | $r^2$ | 0.96 | 0.88 | 0.94 | 0.85 | 0.89 |
|  | $R_{10}$ | 0.063 | 0.083 | 0.058 | 0.058 | 0.064 |

In general, however, temperature still turned out to have a strong impact on both residual variables, and, in order to reduce also this influence, the residuals were normalized with respect to temperature (see Section 2.4). The components normalized for the respective temperature dependencies, now denoted $R_{\text{eco\_res\_norm}}$ and $GPP_{\text{res\_norm}}$, showed very low correlation with the remaining variables except for Kaamanen where VPD and PPFD showed relatively high correlations to both normalized variables and for Fäje where WTD continued to show high correlation (Fig. 10). In order to find out if the high dependency between WTD and both of the components at Fäje was an effect of just looking at the drying out phase, the regressions at the other sites were limited to the drying out phases at the respective sites and the correlation did indeed increase (Fig. 10).

## 4. Discussion

In an accompanying study of forest ecosystems situated in the same region as the mires studied here, the same approach was used to analyse the relationships between CO₂ fluxes and environmental parameters (Lindroth et al., 2007). The latitudinal as well as climatic range was similar in both studies. In the forests, the mean half-monthly $F_{\text{csat}}$ showed much larger variation between the forests as compared to the mires in this study. The maximum values in summer ranged between 5 and 24 $\mu$mol m$^{-2}$ s$^{-1}$ with the lowest values found for a mountain birch forest in northern Sweden (Abisko) and a thin pine forest in northern Finland (Sodankylä) and the highest for a beech forest in Denmark (Soroe). The corresponding maximum summertime values found here ranged between 4 and 7 $\mu$mol m$^{-2}$ s$^{-1}$. The corresponding maximum summertime values for the light use efficiency parameter, $\alpha$, were 30–70 mmol $\mu$mol$^{-1}$ for the forests and 20–27 mmol $\mu$mol$^{-1}$ for the mires, that is, lower in magnitude and with a more narrow range. The seasonal dynamics for the $\alpha$ parameter was also different; in the forests it increased steadily to a maximum in the middle of the summer and then it was fairly constant at this level throughout the growing season. The mires in this study showed a different pattern with an increase until mid-summer and then it decreased in the autumn. An exception was Fäje, that has a sparse cover of dwarf pines, where $\alpha$ behaved more like the forests. The dark respiration parameter, $R_d$, showed similar seasonal pattern as in forests (Lindroth et al., 2007) and the maximum values in the heart of the growing season were two to three times lower compared to those in the forests.

In general, the parameters of the light response function (eq. 1) from the mires reflected the latitudinal gradient (Fig. 2). Fäje, the southernmost site, had on average the highest values of $F_{\text{csat}}$, $R_d$ and $\alpha$, while Kaamanen had the lowest. However, during the summer months, Kaamanen showed similar values of $\alpha$ and $F_{\text{csat}}$, as the more southerly situated mires, likely due to the long daylight hours. It is also noticeable that Fäje had a less variable $\alpha$ than the other sites, indicating a high potential for CO₂ uptake throughout the growing season.

Obviously we should not expect that mires and forests behave the same when it comes to photosynthesis partly because of the species differences, but also because of the differences in water and nutrient regimes. At leaf level, both leaf nitrogen concentration and stomatal conductance are factors that have a strong control on photosynthesis and at stand level, the leaf area index (LAI) comes in as an additional very important factor (e.g. Schulze, 2006). In the forest study, it was shown that LAI explained much of the difference in the light response parameter values between the stands but unfortunately we cannot do the same analysis here because we are lacking accurate information on LAI from all sites. In Siikaneva, the LAI of the vascular plants was estimated to 0.4 (Riutta et al., 2007) and in Kaamanen to 0.7 (Aurela et al., 1998). If we add the photosynthetic active area of the leaves of the other species then it reasonable to assume an LAI of around 1 for Siikaneva and Kaamanen, and we can assume that the LAI of Degerö and Fäje is of the same order. If this assumption about LAI holds, then the mean value of the light response parameter for the summer period fits well with the relationship between summertime mean parameter values and LAI for the forests (Lindroth et al., 2007).

It is interesting to notice that the northernmost site, Kaamanen, reaches the same maximum half-monthly cumulated GPP as the southernmost site, Fäje during the peak of the summer (Fig. 5). This is probably partly an effect of the large difference in day length, with Kaamanen being situated above the arctic circle

and thus experiencing mid-night sun, while the daylight period at Fäje is only 72% and partly also due to environmental adaptation since the mean PPFD at that time in Kaamanen is only about half of that at Fäje (Fig. 3). The high GPP in Kaamanen also results in the highest half-monthly NEE of all sites since Kaamanen has the lowest ecosystem respiration ($R_{eco}$). Judging from the seasonal development of NEE (Fig. 5), it can be expected that Kaamanen would benefit most from a prolongation of the growing season. This is in line with results shown by Aurela et al. (2004) who analysed 6 yr of measurements from Kaamanen and found the highest correlation between annual NEE and date of snow-melt in spring.

In a study by Frolking et al. (1998) mid season data from six mires in Canada and USA and from one mire in northern Sweden was used to estimate parameters of a hyperbolic response function between NEE and PPFD. We compared the estimated parameters even if the hyperbolic functions used differed. Frolking et al. (1998) used the function by Ruimy et al. (1995) and the function used in this study followed Falge et al. (2001). The initial slope of the rectangular hyperbola ($\alpha$, the apparent quantum yield) averaged for all mire types in Frolking et al. (1998) was 0.00088 mg $CO_2$ $\mu$mol$^{-1}$ PPFD and separated on fen and bog, respectively, it was 0.0010 and 0.0007 mg $\mu$mol$^{-1}$, respectively. Their values compare well with the estimated values found in this study of $\sim$0.0008–0.0010 mg $\mu$mol$^{-1}$ (Fig. 2). Frolking et al. also found no difference in $\alpha$ between poor and rich fens, which are in accordance with our results with very similar mid-growing season average values between three of the four mires. The $\alpha$ value for the oligotrophic fen, Degerö, was probably slightly lower than for the other mires. The estimated average respiration values (Frolking et al. 1998) were 0.11 mg $CO_2$ m$^{-2}$ s$^{-1}$ for fens, with no difference depending on nutrient status, and 0.09 mg $CO_2$ m$^{-2}$ s$^{-1}$ for bogs, which deviates from the estimates in this study. The only bog in this study, Fäje, had the highest estimated respiration of around 0.12 mg $CO_2$ m$^{-2}$ s$^{-1}$, while the three fens averaged around 0.09 mg $CO_2$ m$^{-2}$ s$^{-1}$. One major difference between the two studies is that all mires but one studied by Frolking et al. (1988) are situated at lower latitudes (43°N–56°N) while the mires in this study ranged between 56°N and 69°N. The northernmost mire, the oligotrophic Storåmyran, (63°N) had the lowest estimated respiration of 0.05 mg $CO_2$ m$^{-2}$ s$^{-1}$ (Frolking et al. 1998). One major factor that might offset a potential relation between mire type and respiration is the latitude and its influence on air and soil temperature. The average respiration during the mid growing season from the four mires in this study increased with annual average temperature (or decreased with latitude, $r^2 = 1.0$, $n = 4$). (Due to differences in the hyperbolic model formulations the estimated $F_{csat}$ was not comparable)

Our correlation analysis suggests that both GPP and $R_{eco}$ are strongly dependent on WTD at one of the sites, Fäje (for which WTD data was only available during drying up phase), while the dependency is much weaker at the other sites except during dry-
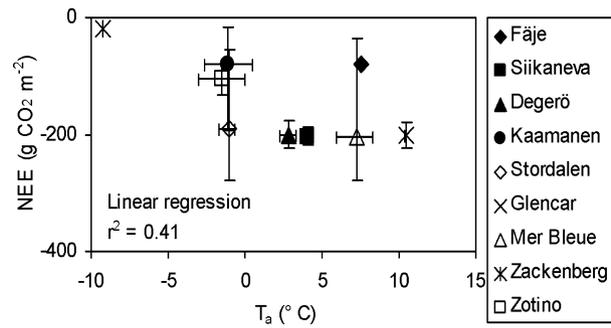


*Fig. 11.* Relationship between annual net ecosystem exchange and mean annual temperature for nine different northern hemisphere peatlands. Data from Kaamanen (Aurela, 2005), Fäje (Lund et al., 2007), Degerö (Sagerfors et al., 2007), Siikaneva (Aurela et al., 2007), Zackenberg (Nordstroem et al., 2001), Stordalen (Thomas Friborg, pers. comm.), Glencar (Sottocornola and Kiely, 2005), Zotino (Arneth et al., 2002) and Mer Bleue (Lafleur et al., 2003). Error bars depict range in NEE and $T_a$.

ing up phases. Kaamanen showed also relatively high sensitivity to WTD during the drying up phase, with similar explained variance as for Fäje for the seasonally and temperature normalized respiration (Fig. 10). Lafleur et al. (2005), also using the eddy covariance technique, did not find a strong relationship between ecosystem respiration and WTD at the bog Mer Bleue in Canada. This may be explained by the usage of different time scales; we analysed half-monthly averages while Lafleur et al. used daily averages. Most other studies have been made using chambers with measurements at a much smaller scale. Silvola et al. (1996) studied a large number of peatlands in southern Finland and found respiration to be sensitive to WTD at most sites with the highest sensitivity in dwarf shrub pine bogs (similar to Fäje in this study) and mesotrophic fens (e.g. Kaamanen in this study). Oechel et al. (1998) made a manipulation experiment in a wet sedge tundra ecosystem in Alaska and they found that respiration was highly sensitive to WTD but GPP was not. Bubier et al. (2003) made chamber measurements in a nutrient poor *Sphagnum* dominated peatland in the US and they also found quite large increase in respiration with decreasing WTD. The mean seasonal respiration increased with increasing WTD across mire sites from ombrotrophic to minerotrophic (Bubier et al. 1998). The sensitivity of respiration to WTD seems to be largest for relatively small changes and when the water table drops further, the sensitivity decreases again.

The strongest correlations in this study were however between the exchange components themselves. The cumulated half-monthly values of $R_{eco}$ constituted between 46 and 76% of cumulated half-monthly values of GPP for each of the mires ($r^2 > 0.89$). The strong dependency of $R_{eco}$ on GPP indicates that much of the respiration is autotrophic respiration. A similar dependency was found for ecosystem respiration on photosynthesis with data amalgamated from mires of varying nutrient

status from ombrotrophic to nutrient rich minerotrophic (Bubier et al., 1998). It was also interesting that temperature seems to have such a strong control on both respiration and gross primary productivity. In fact, after removal of the seasonal variation, GPP showed an even higher correlation to temperature than did $R_{\text{eco.}}$ At all sites, the temperature sensitivity was larger for GPP than for $R_{\text{eco}}$ indicating that an increase in temperature would most likely result in an increase in NEE, no other factors considered, for the systems studied here. This is also consistent with the general picture when comparing annual NEE for all mires on the northern hemisphere: there is positive but weak correlation between annual NEE and annual temperature (Fig. 11).

## 5. Conclusions

More and more peatland sites where eddy covariance technique is used to measure the CO$_2$ exchange between land and atmosphere are now being established around the world. Such data are particularly useful to analyse whole ecosystem exchanges and the responses to different kinds of environmental variables. In this study, we have tried to synthesize CO$_2$ flux data from four high latitude peatland sites of different types exposed to different climatic conditions. Our main conclusions are:

- The southernmost mire had the largest ecosystem respiration as well as the largest gross primary productivity while the opposite was true for the northernmost site. However, for the balance between the processes, the net ecosystem exchange, the picture appeared to be more complex.

- Apart from a high correlation between the two main components themselves, that is, respiration and photosynthesis, temperature was the single most important variable in explaining the variation in the component fluxes. Gross primary productivity was, also after detrending the inherent seasonal variation, found to be more sensitive to temperature than respiration for the actual sites.

- A changing climate, with effects on temperature and precipitation, will undoubtedly affect the flux components as well as the NEE and C balance in peatland ecosystems. In our present study, an increased temperature would increase the CO$_2$ uptake in all sites. However, it was also clear that if drying out phases become more abundant, which could be expected if changes in evapotranspiration are not balanced by changes in precipitation, the gross photosynthesis would decrease and the respiration increase. The sensitivity to water table depth varied between sites, with the highest sensitivity for a dwarf shrub type of bog.

- We are currently able to explain much of the variation in the main flux components, photosynthesis and respiration but many feedback effects exist and modelling is probably the only realistic way of handling all of the interactions in the mire–atmosphere system. It is of critical importance to reduce uncertainties in the associated processes, to be able to achieve reliable estimates of the CO$_2$ balance that are crucial for our understanding of the changes in the global carbon cycle.

## 6. Appendix: List of symbols

All mass units in CO$_2$.

| Name | Unit | Explanation |
|------|------|-------------|
| $\alpha$ | mg $\mu$mol$^{-1}$ | Light use efficiency; initial slope of light response curve (eq. 1) |
| $\tau$ | K$^{-1}$ | Coefficient of temperature response curve (eq. 2) |
| $F_{\text{csat}}$ | mg m$^{-2}$ s$^{-1}$ | Saturation value of light response curve (eq. 1) |
| GPP | g m$^{-2}$ | Modelled gross primary productivity summed per half-monthly period |
| GPP$_{\text{dummy}}$ | g m$^{-2}$ | Dummy variable for GPP for detrending of seasonal variation (eq. 3) |
| GPP_res | g m$^{-2}$ | Difference between GPP and GPP$_{\text{dummy}}$ (eq. 4) |
| GPP_res_norm | - | GPP_res normalized with respect to air temperature |
| NEE | mg m$^{-2}$ s$^{-1}$ | Measured mean net ecosystem exchange rate |
| NEE | g m$^{-2}$ | Measured NEE summed per half-monthly period |
| PPFD | $\mu$mol$^{-1}$ m$^{-2}$ s$^{-1}$ | Half-monthly mean photon flux density |
| $Q$ | $\mu$mol$^{-1}$ m$^{-2}$ s$^{-1}$ | Half-hourly photon flux density |
| $R_{\text{eco}}$ | g m$^{-2}$ | Modelled ecosystem respiration summed per half-monthly period |
| $R_{\text{eco\_res}}$ | g m$^{-2}$ | Difference between $R_{\text{eco}}$ and dummy $R_{\text{eco}}$ |
| $R_{\text{eco\_res\_norm}}$ | - | $R_{\text{eco\_res}}$ normalized with respect to air temperature |
| $R_{\text{d}}$ | mg m$^{-2}$ s$^{-1}$ | Intercept of light response curve (eq. 1); corresponds to the respiration rate at dawn and dusk |

| Name | Unit | Explanation |
|---|---|---|
| $R_{night}$ | mg m$^{-2}$ s$^{-1}$ | Measured mean nighttime respiration rate per half-monthly period |
| $R_0$ | mg m$^{-2}$ s$^{-1}$ | Base respiration coefficient; respiration rate at 0 °C (eq. 2) |
| $R_{10}$ | mg m$^{-2}$ s$^{-1}$ | Coefficient of Lloyd and Taylor equation; respiration rate at 10 °C (eq. 5) |
| $S$ | W m$^{-2}$ | Daily maximum potential global radiation (eq. 3) |
| $T$ | K | Half-monthly mean nighttime absolute air temperature |
| $T_a$ | °C | Half-monthly mean day or nighttime air temperature |
| $T_{an}$ | °C | Half-hourly mean nighttime air temperature |
| $u^*$ | m s$^{-1}$ | Friction velocity |
| VPD | hPa | Half-monthly mean vapour pressure deficit |
| WTD | cm | Half-monthly mean water table depth |

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