Tellus (2007), 59B, 826–837
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TELLUS

CO_2 exchange of a sedge fen in southern Finland—the impact of a drought period

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(Manuscript received 15 January 2007; in final form 5 July 2007)

ABSTRACT

Eddy covariance (EC) measurements of net ecosystem CO_2 exchange (NEE) were conducted on a boreal sedge fen in southern Finland (61°50′N, 24°12′E) during a 1.5-yr period covering two summers in 2004–2005. The EC data were complemented by chamber measurements, which enabled the partition of the daytime NEE into respiration and photosynthesis. A special emphasis was put on the hydrometeorological responses of CO_2 exchange during a drought period in July 2005. A mean CO_2 efflux of 0.009 mgCO$_2$ m^{-2} s^{-1} was observed during mid-winter (January–February), while the night-time respiration during the two Julys averaged 0.09 mgCO$_2$ m^{-2} s^{-1}. During both years the mean midday uptake in late July was about -0.16 mgCO$_2$ m^{-2} s^{-1}. An annual CO_2 balance of -188 gCO$_2$ m^{-2} was observed in 2005. A slightly higher net sink of -219 gCO$_2$ m^{-2} was estimated for 2004. The drought period experienced in July 2005 caused a clear depression in the daily NEE values. From the combined analysis of EC and chamber measurements it was concluded that this was mainly due to increased respiration, but evidence was also found of suppressed photosynthesis due to a high VPD.

1. Introduction

Northern peatlands constitute a vast store of carbon accumulated from the atmosphere, mostly during the Holocene (Gorham, 1991; Turunen et al., 2002). The carbon balance of a peatland ecosystem is highly dependent on both temperature and hydrological conditions (Silvola et al., 1996; Bubier et al., 2003), and it has been suggested that this carbon pool is unstable in a changing climate (IPCC, 2001). According to global climate models, climate warming will be accompanied by more frequent and more severe droughts in some regions (IPCC, 2001). While in Finland the precipitation is predicted to increase 5–40% by the 2080s (Jylhä et al., 2004), most of the precipitation increase is suggested to take place in winter, while the summers would stay nearly unchanged (Ruosteenoja et al., 2005). Furthermore, the increased potential for evapotranspiration due to the higher temperatures and more intense but less frequent precipitation events would actually also lead to more frequent and severe summer droughts in Finland (Ruosteenoja et al., 2005).

In wetlands, dry conditions usually increase the soil respiration by deepening the aerobic layer, but at the same time they decrease the ecosystem uptake by suppressing photosynthesis (Gorham, 1991; Arneth et al., 2002; Moore, 2002; Bubier et al., 2003). High temperatures further increase soil and plant dark respiration (e.g. Silvola et al., 1996). Several field studies have demonstrated these effects on the growing season CO_2 balances of different wetland ecosystems (Shurpali et al., 1995; Alm et al., 1999; Griffis et al., 2000; Bubier et al., 2003). On the other hand, warmer conditions during the growing season may benefit the photosynthetic potential of the vegetation (Shaver et al., 1998; Griffis and Rouse, 2001). In addition, warmer springs will probably increase the length of the growing season, which is suggested to have a major effect on the annual CO_2 balance (e.g. Myneni et al., 1997; Griffis et al., 2000). In some cases such increments in the net uptake may overshadow the sink-reducing effects on the annual balances, especially when no severe drought is observed (e.g. Aurela et al., 2004). Despite the wide range of short-term studies on these hydrometeorological responses of the carbon dynamics in wetlands, there still remain open questions about their net effect on the annual balances of different wetland ecosystems. More long-term CO_2 flux measurements are thus required for improving the estimates of regional carbon budgets.

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DOI: 10.1111/j.1600-0889.2007.00309.x

The micrometeorological eddy covariance (EC) method has proved a highly useful tool for estimating the CO_2 exchange on an ecosystem scale. During the last decade, EC measurements have become more popular, especially on forests (Baldocchi, 2003), but some long-term CO_2 flux measurements were also started at the end of the 1990s on wetlands (Lafleur et al., 2003; Aurela et al., 2004). During the last few years, an increasing number of annual CO_2 balances have been reported for wetlands (e.g. Corradi et al., 2005; Sottocornola and Kiely, 2005; Lund et al., 2007; Sagerfors et al., 2007), but taking into account the diversity of wetland ecosystems, the coverage of different wetland types in different climatic conditions must still be considered limited.

While the EC method enables continuous measurements of areally averaged CO_2 fluxes and is thus suitable for long-term balance assessment, it fails to provide species-specific information on the CO_2 exchange in different parts of the ecosystem. However, the EC data can be complemented by chamber measurements (Silvola et al., 1996; Alm et al., 1999; Tuittila et al., 2004), which provide data on a much smaller spatial scale. With direct measurements of daytime respiration, the chamber method also enables a better partition of the daytime net ecosystem exchange (NEE) into gross photosynthesis (*GP*) and respiration (*R*).

In this study we report on the CO_2 exchange on a poor sedge fen in Southern Finland during a 1.5-yr period covering two summers in 2004–2005. The main aims of this study were to assess the annual CO_2 budget of the fen and to study the response of carbon exchange to hydrometeorological factors. Special emphasis was put on investigating the impact of a drought period experienced in July 2005. The annual CO_2 balance was determined based on eddy covariance data, but the simultaneous chamber measurements provided valuable supporting information for the analysis of the mechanisms behind the CO_2 exchange during the drought period.

2. Materials and methods

2.1. Study site

The measurement site is situated on a sedge fen in southern Finland (61°49.961′N, 24°11.567′E, 162 m a.s.l.). The oligotrophic Siikaneva fen belongs to the southern boreal zone (Ahti et al., 1968). The microtopography of the fen is relatively flat. Peat depth ranges from 2 m near the upland forest edge to almost 4 m at the centre of the site. The vegetation of the site, being dominated by different sedges (*Eriophorum vaginatum*, *Carex rostrata*, *C. limosa*) and a continuous *Sphagnum* carpet (*S. balticum*, *S. majus* and *S. papillosum*), is rather typical for such nutrient-poor mires in northern Europe (Gore, 1983). A maximum one-sided leaf area index (LAI) of 0.4 was observed for vascular plants in late July (Riutta et al., 2007; Wilson et al., 2007). The site is surrounded by Scots pine forest, and the homogeneous fetch suitable for eddy covariance measurements varies from 200 to 400 m in different directions. The mean annual temperature of the region is +3.3 °C, and the annual precipitation averaged 713 mm during the normal period of 1971–2000. A more detailed site description, including an aerial photograph of the site, is presented by Riutta et al. (2007).

2.2. Micrometeorological measurements

The CO_2 exchange was measured using the eddy covariance technique. The instrumentation included a USA-1 (METEK) three-axis sonic anemometer/thermometer and a LI-7000 (Li-Cor, Inc.) CO_2/H_2O gas analyser. The measurement height was 3 m and the length of the heated inlet tube for the closed-path CO_2 analyser was about 5 m. The mouth of the inlet tube was placed 20 cm below the sonic anemometer, the flow rate in the inlet tube varying from 4 to 6 L min^{-1}. Synthetic air with a zero CO_2 concentration was used as the reference gas. The micrometeorological sign convention, where negative fluxes and balances mean downward flux, that is, uptake by ecosystem, is used throughout the paper.

Supporting meteorological measurements including, for example, the air temperature (Vaisala, HMP) and humidity (Vaisala, HMP), soil temperatures (Campbell, 107) at various levels, water table level (WTL, PDCR1830), net radiation (Kipp&Zonen, NR LITE), and photosynthetic photon flux density (Delta-T), were collected by a Campbell 10X datalogger as 30-min averages.

2.3. Data processing

The fluxes were calculated as block averages with a 30-min averaging period. A double rotation of the coordinate system was performed according to McMillen (1988). The lag between the time series resulting from the transport through the inlet tube is taken into account in the on-line calculation of the flux quantities by maximizing the absolute value of the covariance in question. The air density correction related to the sensible heat flux was not needed (Rannik et al., 1997), but as the LI-7000 does not take into account humidity variations, a partial density correction was performed (Webb et al., 1980). Corrections for the systematic flux loss owing to the imperfect properties and setup of the sensors (insufficient response time, sensor separation, damping of the signal in the tubing and averaging over the measurement paths) were performed off-line using transfer functions with empirically determined time constants (Aubinet et al., 2000). Low-quality data were discarded using the stationarity and integral turbulence tests according to Foken and Wichura (1996). The data used for fitting the gap-filling model were screened using a 30% deviation limit, while a slightly higher tolerance (60%) was allowed for the data used for the long-term balance calculations. After additional screening for stable situations ($u_* < 0.1$ ms^{-1}) and outliers, the final data coverage was 39 and 55% for the stringent and looser conditions, respectively.

2.4. *Gap filling*

Due to the nature of eddy covariance measurements, there are always some gaps in the time series. The missing CO_2 flux data were filled using the parametrization

$$\mathrm{NEE} = \frac{PI\,\alpha\,Q\,GP_{\max}}{\alpha\,Q + GP_{\max}} + R_0\left\{1 + \frac{b_1}{1+\exp[(\mathrm{WTL}+b_2)/b_3]}\right\} \times \exp\left[E\left(\frac{1}{T_0} - \frac{1}{T_{\mathrm{air}}+T_1}\right)\right], \quad (1)$$

where Q is the measured photosynthetic photon flux density (PPFD), PI is an empirically determined effective phytomass index (Aurela et al., 2001), $GP_{\max}$ is the gross photosynthesis rate in optimal light conditions, α is the initial slope of NEE versus PPFD, R_0 is the rate of ecosystem respiration at 10 °C, T_{air} is the air temperature, $T_0 = 56.02$ K, $T_1 = 227.13$ K (Lloyd and Taylor, 1994), and the WTL (in cm) is defined as 0 at the peat surface. The model parameters E (in degree Kelvin), b_1, b_2 and b_3 (in cm) are fitted only once, while α, $GP_{\max}$ and R_0 are fitted in bi-weekly periods.

2.5. *Chamber measurements*

In addition to the eddy covariance measurements, the CO_2 exchange was studied based on data collected with chambers. The chamber measurements were conducted at the same location on different vegetation types within the nearest 100 m of the EC measurement mast (Riutta et al., 2007). The measurements were conducted using both opaque and transparent chambers (60 cm × 60 cm × 31 cm), enabling the analysis of respiration and photosynthesis. The measurement system consisted of a climate-controlled chamber and a portable CO_2 analyser (EGM-3, PP Systems). CO_2 exchange measurements lasted 90–180 s depending on the flux rate. PPFD, chamber temperature, WTL next to the plot and soil temperatures were measured simultaneously. The measurements were conducted on 18 vegetated plots on a weekly or bi-weekly basis. In addition, respiration was measured with an opaque chamber on six bare peat plots in order to quantify the proportion of soil and plant-derived respiration from the ecosystem respiration. Their vegetation was removed prior to the measurements, and emerging plants were removed during the growing season when necessary.

In this study, the chamber data measured in the individual plant communities were upscaled by weighting the community-specific estimates by the area that the community represents within a 200-m radius of the measurement mast. Similarly the leaf area index, which was measured periodically on different plots, was averaged over the same area.

A plant-community-based CO_2 exchange model, derived from the chamber measurements, was utilized in this study to investigate the partitioning of NEE into respiration and photosynthesis. The model consists of separate parametrizations for GP and R of the different plant communities characteristic to the site (Riutta et al., 2007); it is similar to, but slightly more complicated than, the model used for data gap-filling in this work (eq. 1). Community-based parametrizations of the model were used for different vegetation types and for bare peat surfaces. In this work, we present the results separately for the two most important vegetation types, hummocks and *Eriophorum vaginatum* lawn that cover approximately 60% of the study site. The chamber measurements and the models are introduced in more detail by Riutta et al. (2007).

3. Results and discussion

3.1. *Meteorology*

The meteorological conditions during the measurement period can be characterized by comparing the data and the long-term averages at the nearby Juupajoki Hyytiälä weather station (61°51′N, 24°17′E) (Fig. 1). The annual average temperatures of 3.8°C (in 2004) and 4.4°C (in 2005) at Juupajoki were somewhat higher than the long-term average of 3.3°C (in 1971–2000), while the precipitation during both years, 727 and 703 mm, in 2004 and 2005, respectively, were quite close to the long-term average of 713 mm. However, there were some marked seasonal differences between the years. In spring (February–April) 2005, the precipitation was the lowest during the last 50 yr (data of the Finnish Meteorological Institute).

The maximum snow depths were 58 and 36 cm for 2004 and 2005, respectively. The long-term average is 59 cm; only twice during the last normal period was it lower than 36 cm. In March 2005, the thickness of the frozen peat layer varied between 5 and 30 cm at different locations. Due to the limited snow cover, the final snow melt at Juupajoki in 2005 had already occurred on 9 April. In 2004 the snow had melted by 21 April, closer to the long-term average of 30 April.

In 2004, June was cool, slowing down the phenological development, but July–August was slightly warmer than normal. In 2005, the May–June temperatures were close to the long-term averages, but the rest of the year (July–November) was markedly warmer than normal.

The summer of 2004 was relatively wet, but in August the precipitation was lower than that during the normal period. As a whole, the growing season of 2005 was also wetter than the average, but during the period 15 June–15 July the total precipitation was only 34 mm. In 2004, the water table depth never sunk below –5 cm, whereas during the drought period in July 2005 it fell to −25 cm.

The radiation data are consistent with the precipitation, showing that July 2004 was generally cloudier than July 2005. Despite the warm autumn of 2005, the permanent snow cover appeared at Juupajoki on the same day, 16 November, in both years.

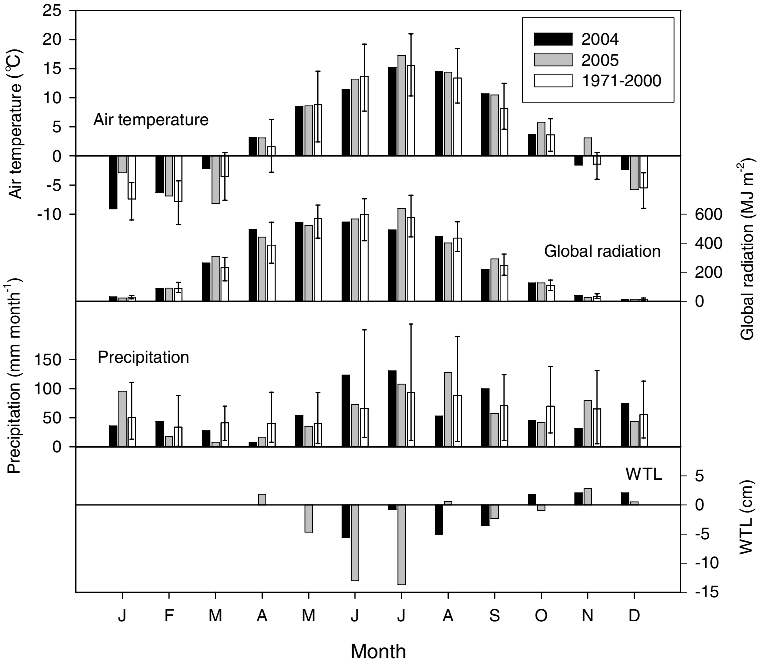

Fig. 1. The monthly mean values of temperature, global radiation, precipitation and WTL in 2004 and 2005, together with the long-term averages (1971–2000). The bar indicates the range of variation. The temperature and precipitation data were measured at the Juupajoki Hyytiälä weather station (61°51′N, 24°17′E), global radiation at the Jokioinen weather station (60°49′N, 23°30′E) and WTL at the Siikaneva fen.

3.2. CO$_2$ exchange

3.2.1. Seasonal cycle. The phenological development of the ecosystem can be illustratively presented as bi-weekly averaged diurnal CO$_2$ cycles (Fig. 2). The CO$_2$ efflux during the mid-winter period (January–February) was relatively stable, with an average rate of 0.009 mgCO$_2$ m^{-2} s^{-1}. The smallest fluxes were observed in March, just before the snow melt. The mosses and evergreen plants started photosynthesizing as soon as the snow was partially melted at the end of March. In April the uptake rate was already significant. Due to the earlier snow melt and more favourable early summer temperature conditions, the phenological development was faster in 2005 than in 2004. A somewhat higher LAI (Fig. 3) and consequently greater CO$_2$ uptake were observed in June 2005 (Fig. 2). The annual maximum rates of CO$_2$ uptake were observed in July and were followed by a slow decrease of fluxes towards autumn. Due to the warm autumn, the growing season continued further in 2005, and photosynthetical activity was still observed at the end of November.

The daytime maximum NEE was generally higher in 2005 than in 2004, but in July and in early August in 2005 the net uptake was somewhat suppressed (Fig. 2b). The bi-weekly mean diurnal cycles show that the differences in the CO$_2$ fluxes can mainly be explained by the differences in radiation conditions (Fig. 2b). Comparing the two measurement years, the higher PPFD is most of the time accompanied by a greater CO$_2$ uptake, and the CO$_2$ fluxes seem to follow the PPFD rather well even on a finer scale. In the first half of June, the radiation, temperature and humidity conditions were quite similar in both 2004 and 2005; the small difference in the CO$_2$ uptake is probably explained by the difference in the phenological state of the vegetation (Fig. 3). In the first half of July, on the other hand, the meteorological conditions differed markedly. The difference observed in PPFD would suggest that the uptake in 2005 should have been significantly greater than in 2004. However, this was the case only during the morning hours, while the opposite was observed during the afternoons (Fig. 2b). This afternoon depression was presumably caused by the hot and dry conditions. The mean mid-day uptake in moderate meteorological conditions in late July was about -0.16 mgCO$_2$ m^{-2} s^{-1} in both years (Fig. 2b), while the highest 30-min CO$_2$ uptake values were close to -0.3 mgCO$_2$ m^{-2} s^{-1} (data not shown).

3.2.2. Daily averages. The highest daily net uptake was observed in July 2004 (-6.3 gCO$_2$ m^{-2}d^{-1}) and in June 2005 (-6.4 gCO$_2$ m^{-2}d^{-1}) (Fig. 4). The daily CO$_2$ balances during winter were rather constant, with an average value of 0.8 gCO$_2$ m^{-2}d^{-1} during mid-winter (January–February). In March 2005 the net efflux was markedly lower, probably due to a cold period spanning from late February to mid-March. The soil temperature at -5 cm was very stable during mid-winter (from late December to February) varying within 0.1 °C close to zero. In March it fell rapidly by 0.3 °C, which change, even if small, may be critical for freezing of the layer in question.

The drought period in July 2005 is easily detected in the daily mean values of various components (Fig. 4). The WTL sank to -25 cm, which is rather low for a fen with a large catchment area, even though it would represent a quite normal or even low variation for a bog (Ingram, 1983). During the period of the minimum WTL, the temperature and the water vapour pressure deficit (VPD) were at their maximum (Figs. 2 and 4). These

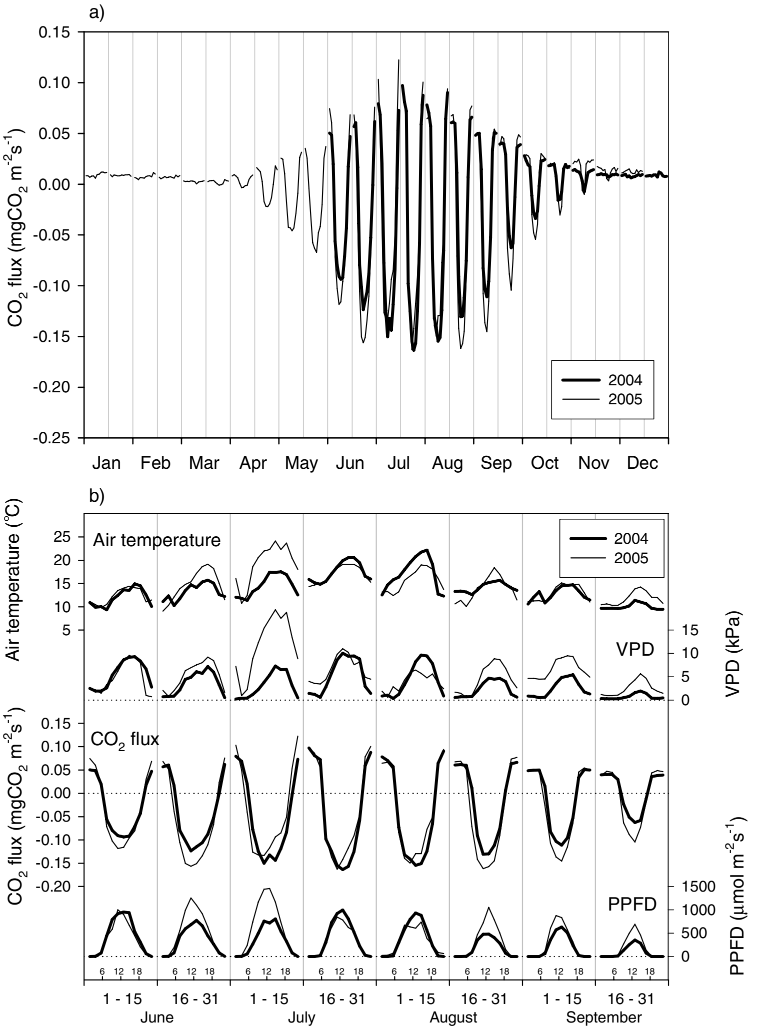

Fig. 2. (a) Successive half-monthly average diurnal cycles of CO$_2$ flux at Siikaneva in 2004–2005. (b) The same data from June to September together with air temperature, water vapour pressure deficit (VPD) and photosynthetically active radiation (PPFD).

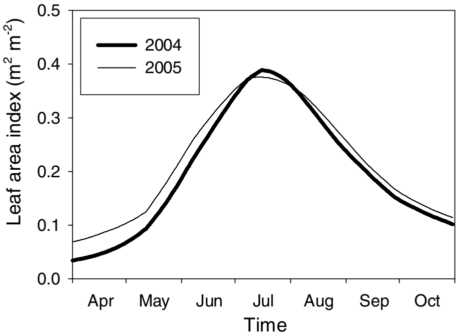

Fig. 3. Seasonal cycles of the leaf area index in 2004–2005 at Siikaneva.

hydrometeorological conditions caused a temporary but marked suppression in the daily net uptake in the first half of July 2005 (Fig. 4). The whole depression period in the NEE time series, however, is not explained by the drought. The lowest daily CO$_2$ rates were actually observed during the rainy days following the dry period, the decrease in uptake being caused by limited radiation. Whenever the daily average PPFD in July stayed below 150 μmol m^{-2} s^{-1}, the fen turned into a net source of CO$_2$ (Fig. 5). In moderate meteorological conditions (July 2004), the daily CO$_2$ balance is well correlated with the mean PPFD. During the drought period (July 2005), the maximum rates were rather similar, but the reductions due to the different stress factors caused significant scatter in the data.

3.2.3. Respiration and photosynthesis. Fig. 6 shows monthly averages of the respiration, mid-day NEE and the mid-day GP derived from the eddy covariance and chamber data. The EC respiration data have been obtained as the night-time efflux (PPFD < 10 μmol m^{-2} s^{-1}) while the chamber respiration is that measured during the daytime with an opaque chamber. The NEE and *GP* values are daytime averages (PPFD > 500 μmol m^{-2} s^{-1}) for both measurement methods.

The average *GP* is higher in 2005 than in 2004 throughout the summer, as observed by both methods. However, in July 2005 the NEE is somewhat lower than in 2004. This is probably due to

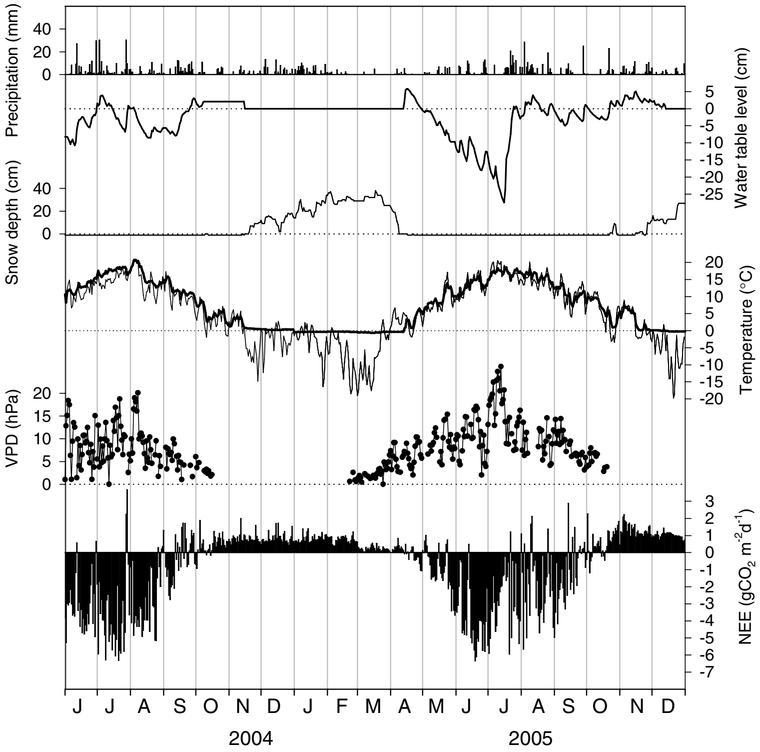

Fig. 4. Daily averages of water table level, snow depth, air (thin line) and soil (thick line) temperatures and net ecosystem CO$_2$ exchange (NEE) together with daily precipitation sum and mid-day water vapour pressure deficit (VPD) at Siikaneva.

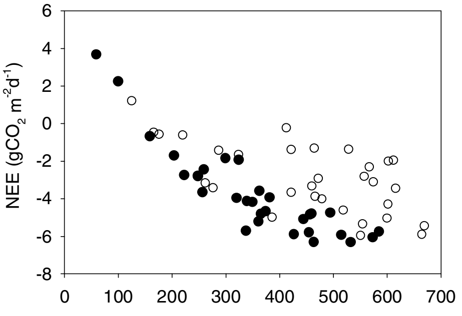

Fig. 5. Daily CO$_2$ balance (NEE) versus daily mean PPFD at Siikaneva in July 2004 (closed circles) and in July 2005 (open circles).

the drought period, which may also be detected in the increased respiration in July 2005. According to the EC measurements, the July average respiration was 0.081 and 0.095 mgCO$_2$ m^{-2} s^{-1} in 2004 and 2005, respectively. For the chamber data, the difference between the years is even larger. As a 2-week average, the respiration during the first half of July in 2005 is markedly higher than during any other period (Fig. 6).

The chamber observations were comparable to those obtained by the EC method, especially concerning the month-to-month and year-to-year variations (Fig. 6). On average, the chamber data showed somewhat smaller fluxes for both NEE and respiration. The same was observed by Riutta et al. (2007) for seasonal balances. It should be noted that there is a systematic temperature difference between the daytime chamber data and the night-time EC measurements. The influence of the drought period on the respiration was well seen by both methods, being especially pronounced in the chamber data.

The respiration from the bare plots was about 50% of that from the vegetated plots. Similar ratios have been obtained in earlier studies on fens (Moore et al., 2002; Crow and Wieder, 2005). During the first half of July 2005, the ratio was about 70%, suggesting that a large part of the respiration increment during that period was due to soil respiration. This seems rather logical, as the drought probably somewhat suppressed the metabolic activity of plants and thus also their dark respiration.

3.3. *Drought period*

3.3.1. Daytime NEE. As shown above, the daily CO$_2$ uptake was decreased during the drought period in 2005 (Fig. 4). Consistently with the daily averages, the daytime (PPFD > 800 μmol m^{-2} s^{-1}) NEE seems to depend on temperature, WTL and VPD (Fig. 7). In Fig. 7, we also compare the EC observations with the WTL and temperature (*T*) responses obtained from an NEE model that was fitted to the chamber data.

The relationships observed between NEE and these hydrometeorological components are not monotonic (Fig. 7). In warm and dry conditions (July 2005), the daytime uptake decreases with increasing temperature and decreasing WTL. In cooler conditions (July 2004), the daily uptake seems to increase with increasing temperature and decreasing WTL. Such a non-monotonic response is a result of the interaction between two opposite flux

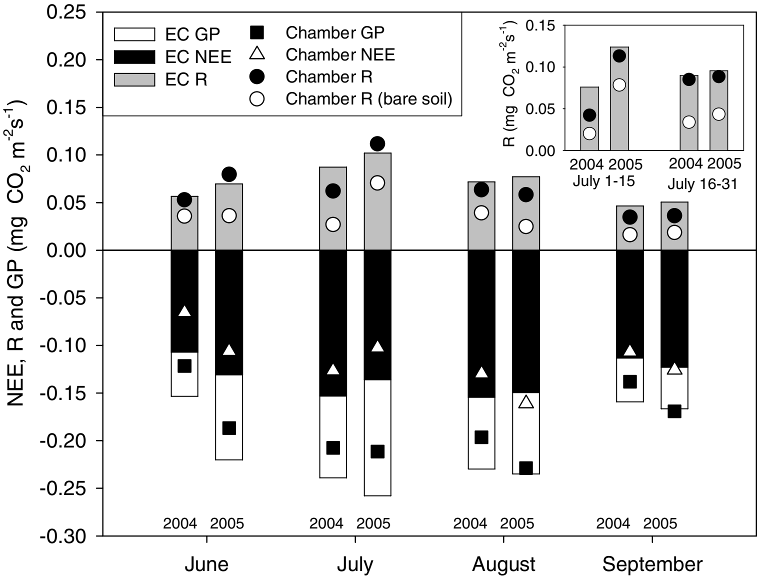

Fig. 6. Monthly averages of night-time respiration (*R*), daytime NEE and gross photosynthesis (*GP*) measured by eddy covariance (bars) and chamber (symbols) methods. The NEE and *GP* values are calculated from the daytime data (PPFD > 500 μmol m^{-2} s^{-1}). The EC respiration is obtained from night-time data (PPFD < 10 μmol m^{-2} s^{-1}), while the chamber respiration is measured during daytime using opaque chambers. Black and white circles represent chamber plots with normal vegetation and bare peat, respectively. In the insert, the respiration in July is divided into half-monthly periods.

components (respiration and photosynthesis), both of which have their own non-linear relationships with the factors in question.

The respiration component typically has a monotonic response to *T* and WTL, with higher respiration in dryer and warmer conditions (Silvola et al., 1996; Bubier et al., 2003). The behaviour of the gross photosynthesis, on the other hand, is more complex. It has been shown for various species that gross photosynthesis has a non-monotonic temperature response (Crawford, 1989). A similar *GP* optimum has also been observed for the WTL response, especially for bryophytes (Tuittila et al., 2004). Dry conditions cause a stress for mosses, but a surplus of water may also decrease the photosynthesis by slowing down the gas transport to the chloroplast (Tuittila et al., 2004). It has been suggested that a similar behaviour may also be found for vascular wetland species (Riutta et al., 2007).

When calculating the WTL response with the chamber-based model in Fig. 7a, the temperature was kept constant (at the mean value for the period). Similarly, for the temperature response in Fig. 7b, WTL was kept constant. For both WTL and *T*, the model suggests that the decrease in daytime uptake under hot and dry conditions is partly due to the increase in respiration and partly due to the decrease in *GP* (data not shown). The EC results, which are independent of this model, show similar patterns. In the present case, no areal averaging was performed, so the absolute values of the model output are not directly comparable to the EC data, but the shape of the functions is. The optimum temperature for NEE was found to be about 20 °C, while for WTL the optimum was close to -10 cm. Interestingly, the optimum WTL at Siikaneva is at the same level as that found for the NEE on a lowland blanket bog in Ireland (Laine et al., 2007) and furthermore, similar to the estimated optimal WTL for maximum rate of peat accumulation occurring on a raised bog in the UK (Belyea and Clymo, 2001).

The influence of VPD was not included in the model based on the chamber data. The relationship between NEE and VPD seems to be more or less monotonic (Fig. 7c). NEE is independent of VPD for VPD < 15 hPa. In suboptimal VPD conditions (>15 hPa), NEE shows a linear decrease, with an average rate of 0.005 mgCO$_2$ m^{-2} s^{-1} hPa^{-1}.

3.3.2. Respiration. The daytime respiration and gross photosynthesis components are not obtained directly by the EC method. Parametrizations based on the night-time respiration are typically used for this partitioning. The night-time respiration shows a clear response to the air temperature and WTL over the summer (June–August) (Fig. 8). The night-time EC data are scattered, but the relationship with temperature is evident (Fig. 8a). The daytime respiration obtained by chamber measurements had a similar temperature response, although the base rate was somewhat smaller. A clear response was also found between the EC-based respiration and WTL at low water table levels, but in the normal WTL range (0 to -15 cm) no significant response was observed (Fig. 8b). However, in the case of the chamber data, WTL actually had a strong relationship with respiration within this range. This may be due to the fact that the WTL data for chambers are location-specific, while for the EC data WTL represents temporal variation of an areal average over variable microtopography and related plant communities. This kind of difference was observed for the CH$_4$ fluxes at Siikaneva, which correlated better with WTL variation between different microsites than with the temporal variation (Rinne et al., 2007).

3.3.3. Temperature response of NEE and R. The night-time EC data may be used to further study the actual temperature response of the daytime NEE, as it can be assumed that the night-time data do not include any effect of photosynthesis. The temperature response of night-time respiration was extrapolated to typical daytime temperatures using the respiration parametrization of

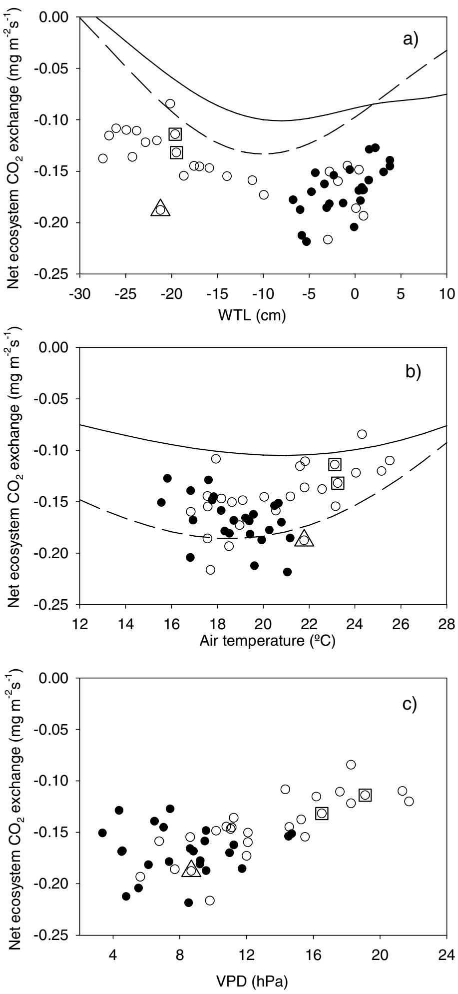

Fig. 7. Daytime (PPFD > 800 μmol m^{-2} s^{-1}) net ecosystem exchange (NEE) versus (a) water table level (WTL), (b) temperature and (c) water vapour pressure deficit (VPD) averages of the corresponding 30-min periods at Siikaneva in July 2004 (closed circles) and in July 2005 (open circles). In (a) and (b) the results of an NEE model fitted to the chamber data are presented for the two most important vegetation types, hummocks (solid thin line) and *Eriophorum vainatum* lawn (dashed thin line). The days analysed in Section 3.3.3 are marked by squares (5 and 9 July 2005) and a triangle (7 July 2005).

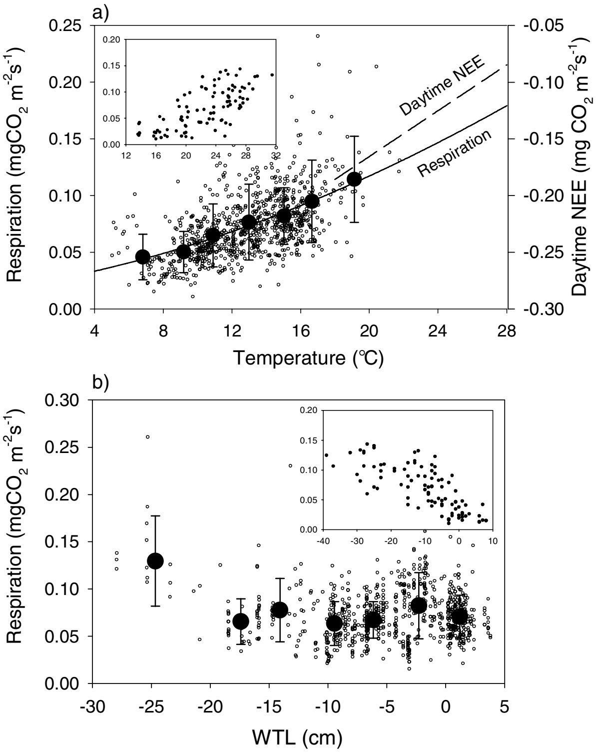

Fig. 8. Response of night-time respiration to (a) air temperature and (b) water table level (WTL) in the summers (June–August) of 2004 and 2005 at Siikaneva. Small open circles are the 30-min fluxes during both summers and black circles represent their class averages (2-°C and 4-cm classes, merged if less than 10 observations) with standard deviations. The corresponding chamber data are presented in the inserts. The modelled night-time respiration (solid line) and the linear regression between the 30-min daytime net ecosystem exchange (NEE) and air temperature (for $T > 20$ °C) (dashed line) are also shown.

eq. 1 (with $E = 257$ K and $R_0 = 0.07$ mgCO$_2$ m^{-2} s^{-1}) (Fig. 8a). This was compared with the linear regression between *T* and the observed daytime NEE (cf. Fig. 7b). This regression was derived from the 30-min EC data in the temperature range of $T >$ 20 °C in order to minimize the effect of the nonlinearity of the temperature response. A comparison of these curves (in the temperature range of 20–26 °C) indicates that the increase in the night-time respiration covers about 75% of the decrease in the daytime NEE. This implies that during the drought period, most of the NEE depression originated from enhanced respiration rather than from a depression of photosynthesis. This conclusion is in a good agreement with the monthly mean *R*, NEE and *GP* data, which show that the respiration during the first half of July 2005 was markedly higher than during the same period in 2004 or in August 2005 (Fig. 6).

3.3.4. VPD response of NEE. Due to the lack of *GP* measurements, we cannot directly estimate the influence of photosynthesis on the daytime NEE depression. However, assuming that VPD does not have any impact on respiration, only on photosynthesis, the NEE response to VPD provides some information. In practice, as VPD is highly correlated with *T*, and they are usually, at least over growing season, both correlated with WTL, it is difficult to distinguish the effects of different components. However, during the drought period there was an incident with a rapid change of weather as a hot and dry airmass was temporarily replaced by humid and slightly cooler air. On July 7, 2005, the VPD was markedly lower than on the previous and subsequent days (Fig. 7). For WTL and air temperature, on the other hand, no such great change was observed. On that day, the net CO_2 uptake was markedly greater than on the surrounding days. There was a heavy rain shower on the evening of July 7, but the humid

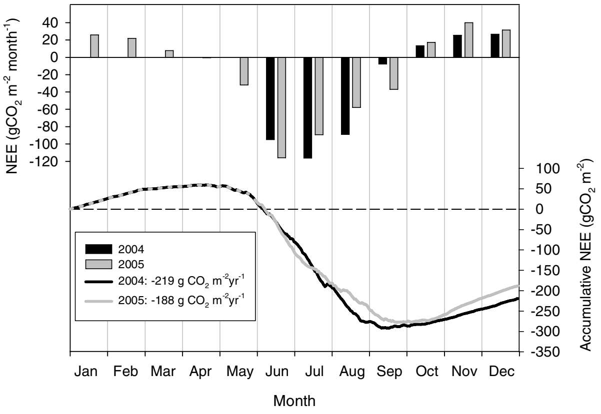

Fig. 9. The average monthly balances of NEE together with the accumulated NEE sum at Siikaneva in 2004–2005. The accumulative curve for 2004 and the corresponding annual balance presented in the legend are calculated using the data of 2005 for the January–May period.

air and high uptake rates were observed before that. These observations would suggest that the high VPD had a suppressing effect on the CO_2 uptake, and that the reduction in NEE is partly due to the decreased photosynthesis. However, when the VPD influence was tested by including it in the NEE model used for gap-filling (eq. 1), it was found out that VPD did not significantly improve the long-term performance of the model.

3.4. *The annual balances*

3.4.1. The monthly and annual CO_2 balances at Siikaneva. The Siikaneva fen acted as a net source of CO_2 for 6 months, with a mid-winter (January–February) efflux of about 20 $gCO_2\ m^{-2}$ $month^{-1}$ (Fig. 9). In March 2005, the fluxes were lower, probably due to a cold period freezing the peat. In June the net uptake was higher in 2005 than in 2004, resulting from the difference in the phenological state of the vegetation. In July the depression due to the drought period in 2005 was also seen clearly in the monthly balance. In August the sink term was higher in 2004, partly due to the low radiation conditions in 2005, while in September the opposite was the case (Figs. 1 and 9). The highest monthly net efflux was observed in November 2005, when most of the photosynthesis had ceased, but the air temperature was still high. It was actually markedly warmer then than in any November in the normal period 1971–2000. The accumulated NEE showed somewhat differing paths for the measurement years, revealing that autumn, too, has an important role to play in the annual CO_2 budget (Fig. 9). An annual balance of $-188 \pm 47\ gCO_2\ m^{-2}\ yr^{-1}$ was observed for the full measurement year 2005. Assuming that the first 5 months of 2004 were similar to those of 2005, an annual balance of $-219 \pm 55\ gCO_2\ m^{-2}\ yr^{-1}$ would be obtained for 2004. The calculation of the associated uncertainty estimates is described in Appendix.

3.4.2. Comparison with other studies. Continuous flux measurements on different wetland types have become more common during the last few years, but continuous round-the-year measurements on these ecosystems are still scarce. The closest comparison with Siikaneva is a poor sedge fen at Degerö in Sweden (64°11′N, 19°33′E), where Sagerfors et al. (2007) have observed highly comparable annual balances of -176 to $-225\ gCO_2\ m^{-2}\ yr^{-1}$ in 2001–2003. A 6-yr data set collected on a sub-Arctic fen at Kaamanen in Finland (69°08′N, 27°17′E) showed annual balances from -15 to $-192\ gCO_2\ m^{-2}\ yr^{-1}$, with an average of $-80\ gCO_2\ m^{-2}\ yr^{-1}$, during 1997–2002 (Aurela et al., 2004). Balances between -55 and $-279\ gCO_2\ m^{-2}\ yr^{-1}$ were obtained on a Storadalen mire in northern Sweden (68°21′N, 19°02′E) (Lindroth et al., 2007).

The uptake of bogs is generally considered to be higher than that of fens, but the results from the Siikaneva fen are quite close to the available balances for bogs. Lafleur et al. (2003) observed annual CO_2 balances in the range of -15 to -444 (mean $-248\ gCO_2\ m^{-2}\ yr^{-1}$) during six measurement years at the Mer Bleue bog in central Canada (45°40′N, 75°50′W). Sottocornola and Kiely (2005) reported on net fluxes of -180 and $-224\ gCO_2\ m^{-2}\ yr^{-1}$ during two measurement years on a blanket bog in Ireland (51°55′N, 9°55′W). Arneth et al. (2002) estimated annual balances from -80 to $-130\ gCO_2\ m^{-2}\ yr^{-1}$ for a boreal bog in central Siberia (60°45′N, 89°23′E).

The uptake rates in permafrost areas are typically somewhat lower than those observed in more southern sites. Nordstroem et al. (2001) estimated a small sink of $-20\ gCO_2\ m^{-2}\ yr^{-1}$ on a high Arctic fen in northeast Greenland (75°N, 8°E). A markedly higher uptake of $-139\ gCO_2\ m^{-2}\ yr^{-1}$ was observed by Corradi et al. (2005) on tussock tundra permafrost in Siberia (68°37′N, 161°20′E).

The annual balances of -219 and $-188\ gCO_2\ m^{-2}\ yr^{-1}$ derived in this study are in accordance with the results of earlier studies, showing a lower uptake than the more southerly Mer Bleue bog, a higher uptake than the sub-Arctic fen at Kaamanen and similar values to those observed at a similar poor sedge fen in Degerö.

3.4.3. The carbon balance. In addition to the CO_2 flux between the atmosphere and the ecosystem (averaging $-56\ gC\ m^{-2}\ yr^{-1}$), the total carbon balance of the fen includes other carbon fluxes as well. The most important additional components are the methane flux from the ecosystem to the atmosphere and the leaching of total organic carbon (TOC) by lateral water flow. An annual methane efflux of 12.6 $gCH_4\ m^{-2}\ yr^{-1}$ (9.4 $gC\ m^{-2}\ yr^{-1}$) was observed at Siikaneva in 2005 by continuous eddy covariance measurements (Rinne et al., 2007). The leaching of carbon has not been measured at the Siikaneva fen, but at the nearby Lakkasuo fen the leaching of TOC has been estimated to be about 10 $gC\ m^{-2}\ yr^{-1}$ (Sallantaus, 1994). Some carbon also escapes from the fen in the form of volatile organic compound (VOC) emissions. Haapanala et al. (2006) observed the majority of the VOC emission at Siikaneva to be isoprene, and estimated the yearly emission to be of the order of 0.1 gC m^{-2}. Even though the compounds not detected by Haapanala et al. (2006), such as oxygenated VOCs, may contribute another 0.1 gC m^{-2} yr^{-1}, the carbon emitted as VOCs is unlikely to have any significant effect on the carbon balance of the fen. When taking these carbon losses into account, the net carbon balance for the Siikaneva fen was -36 gC m^{-2} yr^{-1} during the measurement years. This balance is somewhat higher than the long-term carbon accumulation rate of 18.5 gC m^{-2} yr^{-1} estimated for fens in southern Finland using peat core analysis (Turunen et al., 2002).

3.4.4. The global warming potential. While CO_2 is globally the most important greenhouse gas (GHG), the influence of CH_4 on the GHG budget of wetlands is highly relevant. The Global Warming Potential (GWP) describes the ability of different GHGs to trap heat in the atmosphere relative to CO_2. GWP depends on the time horizon adopted, and for a 100-yr time horizon the GWP of CH_4 is 23 (IPCC, 2001). Using this factor, the annual balance obtained for methane (299 gCO_2-eq m^{-2}) exceeds the annual CO_2 balance (-204 gCO_2 m^{-2}). Thus, even if the fen is at present a net sink of CO_2, its GHG balance has a warming influence on the atmospheric on a 100-yr time horizon. This is typical for northern fens, whereas more southern wetlands often have a net cooling effect on the atmosphere (Whiting and Chanton, 2001).

4. Conclusions

The CO_2 exchange between the atmosphere and a poor oligotrophic fen was measured at Siikaneva in southern Finland. The 1.5-yr measurement period included two summers with differing hydrometeorological conditions. A drought period in 2005 was observed to markedly suppress the net uptake of CO_2, with a clear response to various hydrometeorological quantities like temperature, VPD and WTL. As these parameters are all correlated with each other, it is difficult to distinguish their effects on the CO_2 exchange. By comparing the influence of temperature on the daytime uptake and on the night-time respiration, it was concluded that temperature was the single most important factor explaining the depression in net uptake. However, some evidence was also found concerning the effect of a high VPD on the daytime uptake, and thus on the photosynthesis.

Chamber measurements were utilized together with the EC data to partition the NEE into photosynthesis and respiration components. Both data suggested that the NEE responses to WTL and air temperature were not monotonic. The optimum WTL was found to be about -10 cm, while the optimum temperature was about 20 °C.

Keeping in mind the differences in spatial and temporal resolution of the EC and chamber techniques, the monthly mean flux components obtained with these methods were highly consistent, especially concerning the month-to-month and year-to-year variations. Chamber measurements confirmed the EC results of the importance of the respiration component during the drought period. In addition, the chamber measurements on bare peat implied that the drought influenced soil respiration more than plant dark respiration. The bare peat respiration was about 50% of the total respiration in a normal situation.

An annual CO_2 balance of -188 ± 47 gCO_2 m^{-2} yr^{-1} between the atmosphere and the fen ecosystem was obtained for the full measurement year, 2005. Assuming that the balances of the first 5 months were the same during both measurement years, the annual balance for 2004 was -219 ± 55 gCO_2 m^{-2} yr^{-1}. The drought period observed in July 2005 had a significant impact on the CO_2 balance of that particular month, but in the annual balance there were also other important phenomena of the same magnitude such as the lengthened growing season (September) and enhanced respiration (November) due to the warm autumn in 2005. The annual total carbon balance was estimated by taking into account the carbon lost as DOC and CH_4, and an averaged balance of -36 gC m^{-2} yr^{-1} was estimated. Taking into account the higher global warming potential of CH_4, a total greenhouse gas balance of $+95$ gCO_2-eq m^{-2} yr^{-1} was obtained for a 100-yr horizon, suggesting that the fen has a net warming effect on the atmosphere.

5. Appendix: error analysis

The long-term CO_2 balance obtained by the EC method has various potential error sources because of the statistical, methodological and instrumental uncertainties. The errors are here divided into random and systematic errors, and are analysed similarly to Aurela et al. (2002). The systematic biases are typically more severe for the long-term balances, as they do not decrease with a longer data set as the random error does (Moncrieff et al., 1996).

The random error in the annual balance was estimated according to Aurela et al. (2002) by comparing the observed fluxes to the modelled values. Random errors of 1.4 and 1.6% of the annual balance were obtained for 2004 and 2005, respectively.

Following Aurela et al. (2002), we considered the main sources of systematic errors. One of these is the well-known instrumental problem of an inadequate frequency response, which was taken into account by spectral corrections with a mean magnitude of 5% during the measurement period. However, there are uncertainties inherent in the correction procedure. Assuming an uncertainty of 30% in the frequency response correction, we obtain an uncertainty of 1.5% in the annual balance.

The night-time measurements are problematic in many ways. The u_*-correction is a standard way of dealing with the problem of low turbulent fluxes at night (Aubinet et al., 2000). However, the determination of the required u_*-limit is not trivial, and the annual balance has been found to be rather sensitive to the selected value. In this study we used a u_*-limit of 0.1 m s^{-1} for the data screening. In order to test the sensitivity of the annual balance to that value, we also modelled the fluxes using a higher u_*-limit of 0.2 m s^{-1}. This decreased the annual net uptake by 14% on average.

The limited set of night-time data due to calm periods may lead to problems in the fitting of the respiration model. The uncertainties related to the respiration parametrization were estimated by comparing the models based on air temperature and soil temperature observations. When using the soil temperature instead of the air temperature, the annual balances were 20% higher, on average.

It is not possible to evaluate every detail of the method, but as an example, we estimated the influence of the averaging method on the flux measurements. In this work we used block averaging, but the fluxes were also calculated using running-mean averaging. This resulted in a difference of 3% in the annual balance between the methods.

By adding these uncertainties together using the error accumulation principle, a total error of $\sqrt{0.015^2 + 0.015^2 + 0.14^2 + 0.20^2 + 0.03^2} = 25\%$ was obtained. It is evident that this error estimate does not cover all the uncertainties associated with the annual CO_2 balances, but it should be considered as indicative.

6. Acknowledgments

This work was supported by the Nordic Council of Ministers through the NECC project (Nordic Centre for Studies of Ecosystem Carbon Exchange and its Interactions with the Climate System) and the University of Helsinki through the Rebecca project of the Helsinki Environmental Research Centre (HERC). The authors would like to thank Jouni Meronen for technical assistance preceding and during the measurements.

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