**Catchment-Wide Atmospheric Greenhouse Gas Exchange as Influenced by Land Use Diversity**

The turbulent fluxes of carbon dioxide between the land surface and the atmosphere were measured with the eddy covariance technique above three contrasting land use types in the Skjern River catchment in western Denmark, namely an agricultural area, a forest plantation, and a wet grassland. The measurements also included the turbulent fluxes of methane above the wet grassland and of nitrous oxide above the agricultural area and ran continuously throughout the year 2009. The highest CO$_2$ uptake rates (around 30 µmol m$^{-2}$ s$^{-1}$) were observed at the agricultural site; however, the site was a CO$_2$ sink only from April to June and a CO$_2$ source during the rest of the year. Over the whole year the forest plantation fixed about 1850 g CO$_2$ m$^{-2}$ compared to only 870 g m$^{-2}$ at the agricultural site, and it remained a CO$_2$ sink throughout all seasons. The wet grassland was a CO$_2$ sink from March to October, and its annual CO$_2$ fixation was only marginally higher than that of the agricultural site. The emission of CH$_4$ from the wet grassland showed large seasonal variations. Its annual total corresponded to 276 g CO$_2$ equivalents m$^{-2}$ (based on a 100-yr time horizon) and reduced the greenhouse gas sink strength of the site by one-third. At the agricultural site this sink strength was reduced by 9% through the N$_2$O emissions. Scaled up to the catchment, the observed net uptake of CO$_2$ by the land surface was reduced by roughly one-tenth, in terms of CO$_2$ equivalents, due to the emission of CH$_4$ and N$_2$O.

**Accurate regional carbon budgets** are essential for understanding and quantifying the sources and sinks for atmospheric greenhouse gases (GHG). Over the last 20 years a comprehensive measuring network has been developed, and continuous carbon flux measurements have been conducted over a broad range of ecosystems. This has resulted in considerable improvement in our understanding of the diversity in functioning among European ecosystems (Valentini et al., 2000; Gilmanov et al., 2007). Despite the growing number of flux stations measuring the exchange of greenhouse gases between the land surface and the atmosphere, there is still uncertainty in explaining the large variability of fluxes between sites, especially if the variability affects sites with similar land use types and similar climatic conditions (Jacobs et al., 2007). For example, Luyssaert et al. (2007) presented evidence that the net ecosystem production of forests depended on the history, management, disturbance, and successional stage of the sites more than on the climate. This emphasizes the need for more studies at the field scale in different ecosystems.

The assessment of catchment-wide GHG budgets requires three steps (Jacobs et al., 2007; Soussana et al., 2007) in terms of the components to be accounted for: (i) the CO$_2$ fluxes between the land surface and the atmosphere; (ii) the corresponding fluxes of other greenhouse gases (which require more advanced measurement techniques); and (iii) the import and export of carbon, having been fixed from CO$_2$, through land management. This study is a case study that comprises the first two steps for various vegetation types within one catchment.

With respect to step number two, only recently attention has been drawn to the fact that fluxes of CH$_4$ and N$_2$O can compensate for the carbon sequestration by terrestrial ecosystems in terms of their global warming potential (Friborg et al., 2003; Soussana et al., 2007; Schulze et al., 2009). This is based on the assumption that, in terms of radiative forcing, 1 g CH$_4$ is equivalent to 25 g CO$_2$, and 1 g N$_2$O is equivalent to 298 g CO$_2$ if a time horizon of 100 yr is considered (IPCC, 2007). A carbon sink can thus be a greenhouse gas source (Friborg et al., 2003). At present, the driving factors for the production,
The study was performed in the Skjern River catchment in western Denmark having a maritime climate with an annual mean temperature of 8°C and an annual precipitation of about 850 mm. The catchment covers about 1500 km² and slopes gently from 100 m in the east to sea level in the west. The geology is dominated by glacial and melt-water deposits, and therefore the soils consist mainly of coarse sand. The three measurement sites comprised the most typical land use types in the catchment. The site located furthest west in the catchment, Skjern Meadows, is a restored wetland covering 2200 ha with a variable water table height. During the summer most of the area is grazed by cattle, and the grass is cut once annually. The restoration project was completed in 2002, and the site is now classified as a “wetland of international importance” (Nielsen and Schierup, 2007).

Gludsted Plantage, located on the northeastern boundary of the catchment, is Denmark’s largest spruce plantation and covers about 35 km². The area around the investigation site consists of 50-m-wide stripes with 15- and 20-m-high Norway spruce [Picea abies (L.) H. Karst.] trees, respectively. Every 100 m the spruce canopy is interrupted by one row of about 25-m-high grand fir [Abies grandis (Douglas ex D. Don) Lindl.] trees. The basal area, measured in the northern part of the plantation, is 42 m² ha⁻¹ (Gundersen et al., 2009). The management practices are designed to maintain a relatively young stand with a high growth rate. Flux measurements above a forest stand with such a structure need to ensure spatial representativeness. Therefore the eddy flux sensors were placed more than 10 m above the highest tree tops. This ensured that the flux footprint was at least several hundred meters at any time. Thus, the scale of variation of the forest canopy was comfortably smaller than the footprint.

The last measurement site, Voulund, is located a few kilometers to the southwest in the midst of an intensively managed agricultural area. During the first part of the investigation period, the largest part of the source area around the flux mast consisted of winter barley (Hordeum vulgare L.) crops that were regularly irrigated and fertilized. Nitrogen fertilizer was applied on 27 February (153 kg ha⁻¹) and on 11 April (225 kg ha⁻¹). The possible influence of a spring barley crop located further west and a sparse pine forest located further north on the flux measurements is discussed in the companion papers by Ringgaard et al. (2011) and Schelde et al. (2011) in this issue. Immediately after the harvest in July 2009 a spring barley crop located further west and a sparse pine forest was sown, which developed into a crop with only sparse ground cover.

**Materials and Methods**

**Measurement Sites**

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**Instrumentation**

The exchange of greenhouse gases between the land surface and the atmosphere was measured with the eddy covariance technique. At each of the three sites, a sonic anemometer [R3–50, Gill Instruments Ltd., Lymington, UK] was installed on a boom mounted at the top of an instrument mast. The measurement heights were 38 m at Gludsted, 12 m at Voulund, and 7 m at Skjern Meadows. Open-path infrared gas analyzers (LI-7500, LI-COR, Lincoln, NE) were installed at the respective heights at Gludsted and Skjern Meadows to measure the CO₂ concentration in the air. At Voulund, a closed-path infrared gas analyzer (LI-7000, LI-COR, placed in a hut on the ground, in connection with a membrane pump (N 89 KNDC, KNF Neuberger, Freiburg, Germany) was used instead, which was replaced by an open-path sensor in October 2009. The tube length was 20 m, and the flow rate was 6 L min⁻¹. Additional tube inlets were mounted close to the sonic anemometers at Skjern Meadows and Voulund and connected to closed-path CH₄ and N₂O gas analyzers, respectively. At Skjern Meadows the mole fraction of CH₄ was determined by means of an analyzer of type DLT-100 (Los Gatos Inc., Mountain View, CA) based on off-axis integrated cavity output spectroscopy. A vacuum pump (TriScroll 300, Varian Inc., Palo Alto, CA) sucked the air at a nominal pumping speed of 250 L min⁻¹ through the 10.65-m-long tubing into the analyzer, which was placed in a small hut near the mast and operated with a cell pressure of about 16 kPa. In this setup the average delay time was 0.5 s, and the average Reynolds number was 8200. This gas analyzer required monthly maintenance work comprising the change of two air filters (5-μm pore size outside and 2-μm pore size inside the instrument) and the cleaning of the mirrors in the measurement cell. At Voulund, the N₂O concentration was measured by means of a quantum cascade laser (QC-TILDAS-76, Aerodyne Inc., Boston, MA) connected to a vacuum pump similar to the one used at Skjern Meadows but...
with a nominal flow rate of 500 L min\(^{-1}\). The laser frequency was 1271 cm\(^{-1}\), and the cell pressure was kept at 8 kPa. All measurements were taken at a nominal sampling frequency of 10 Hz. The actual response times of the closed-path gas analyzers in the complete field setup were 0.12 s for the LI-7000, 0.14 s for the DLT-100, and 0.17 s for the QC-TILDAS-76. The corresponding cut-off frequencies were 1.4, 1.1, and 0.9 Hz, respectively.

At both Skjern Meadows and Voulund, the leaf area index (LAI) was measured with an optical sensor (LAI-2000, LI-COR Inc.) about once a month. Each data point presented in this study is the average LAI calculated from 6 above-canopy and 60 below-canopy readings at the wetland site and from 12 above- and 48 below-canopy readings at the agricultural site. Immediately after the grass cut at Skjern Meadows the vegetation was too low to be measured with the LAI-2000, and based on the still continuous vegetation cover a value of 1 was assumed. At Gludsted, logistical problems with obtaining “above canopy” readings prevented the use of the LAI-2000, and instead the LAI was calculated from routine measurements of net radiation above and below the canopy by inverting the Lambert–Beer formula and assuming an attenuation coefficient of 0.52 being typical for coniferous forests (Pierce and Running, 1988).

Ancillary meteorological data were taken as 30-min averages at each site and included in- and outgoing short- and long-wave radiation, net radiation, soil heat flux, air and soil temperatures, and air humidity. Details about the equipment used are given by Ringgaard et al. (2011).

### Data Analysis

The turbulent fluxes of CO\(_2\), CH\(_4\), and N\(_2\)O were calculated as 30-min averages from the covariances of the vertical wind component and the respective gas concentrations by means of the Alteddy software, version 3.5 (Alterra, University of Wageningen, The Netherlands), which includes a dilution correction (Webb et al., 1980) for all greenhouse gas fluxes. Additionally, the fluxes were corrected for errors due to surface heating of the LI-7500 sensor head (Burba et al., 2008) and for errors caused by the tilt of the anemometer relative to the mean streamline coordinate system (“planar fit” method after Wilczak et al., 2001). A quality control of the flux data was performed using the quality classes proposed by Foken et al. (2004), and only data having one of the three best quality flags were accepted for further analysis. The original data from the remaining half-hourly intervals, along with a few spikes undetected by Foken’s method, were replaced with values estimated by the standard gap-filling method used by both CarboEurope and FLUXNET and available online at http://gaia.agraria.unitus.it/database/eddyproc/ (Moffat et al., 2007) to estimate annual totals of the atmospheric GHG fluxes.

For the regressions of the CO\(_2\) fluxes \(F_{\text{CO2}}\) with meteorological variables a further filtering was performed, and only data from periods with a friction velocity \(u^*\) higher than 0.2 m s\(^{-1}\) were used to make the results better comparable with other studies. The remaining half-hourly data were corrected for storage of CO\(_2\) \(S\) in the air column between the measurement height and the soil surface to obtain the net ecosystem exchange (NEE) according to Eq. [1].

\[
\text{NEE} = F_{\text{CO2}} + S \tag{1}
\]

At the wetland and agricultural sites \(S\) was calculated from the change in the CO\(_2\) partial pressure \(\Delta_{\text{CO2}}\) at the measurement height \(b\) over the half-hourly time interval \(t\) as

\[
S = \Delta_{\text{CO2}} \frac{b}{nt} \tag{2}
\]

where \(n\) is the molar volume of an ideal gas \((0.0224 \text{ m}^3 \text{ mol}^{-1})\). At the forest site the CO\(_2\) concentration was measured at four additional heights \((2, 8, 15, \text{and } 30 \text{ m above the ground})\) by use of a LI-8100 gas analyzer which was connected to four gas inlets through a LI-8100 multiplexer (LI-COR Inc.).

The air column was thus divided into four parts, assuming that each measurement height was representative for the part of the column extending halfway up to the next measurement height. Equation [2] was then applied separately to the four heights and the total storage calculated as the sum of the four values.

The resulting NEE rates were separated into day- and nighttime data and related to incoming solar radiation \(R_C\) and air temperature \(T\) in °C, respectively. The nonlinear regressions used were

\[
\text{NEE}_{\text{night}} = R_{10} 308.6 e^{ \frac{1}{56} - \frac{1}{T+46} } \tag{3}
\]

for the nighttime data (Lloyd and Taylor, 1994, henceforth LT equation) and

\[
\text{NEE}_{\text{day}} = \frac{abr_G}{aR_G + b} + c \tag{4}
\]

for the data-time data. This equation was originally suggested by Falge et al. (2001) to relate gross primary production to irradiance. The parameter \(a\) corresponds to the initial slope of the curve, \(b\) is the maximum CO\(_2\) uptake rate, and \(c\) is the CO\(_2\) emission when the radiation is zero.

The curve fits for these regressions were performed with the SigmaPlot 9.0 software (SSI, San Jose, CA). Its fitting routine is based on the Marquardt-Levenberg algorithm (Marquardt, 1963), which uses least squares analysis.
Results

Site Characteristics

The sum of irradiance was statistically not different among the three sites, although in the summer it tended to be slightly higher at Skjern Meadows due to a larger number of sunshine hours close to the coast (data not shown). The average diurnal courses of the air temperature at the three sites are shown in Fig. 1 for different times of the year. Since each half-hourly value is an average calculated over more than 90 d, the standard error for any time of the day, calculated as the standard deviation divided by the square root of the number of observations, was low and usually ranged between 0.3 and 0.4 (data not shown). Thus, it was concluded that the difference between the nighttime temperatures at the wetland site and the agricultural site were significant, but that the three sites otherwise experienced a statistically identical temperature regime, despite the apparent tendency toward milder winter and cooler summer temperatures during daytime at the wetland site. Whether these small differences could have affected the comparability of the average fluxes will be discussed in “Universality of CO2 Response Functions” section below. Rainfall was not measured during the whole year, but between mid February and late September it was lower at the inland sites (348 mm at Gludsted) than at the coast (446 mm at Skjern Meadows). However, the agricultural site was irrigated six times between mid April and mid June, with about 22 to 25 mm water being deployed on each occasion.

The LAI at Skjern Meadows varied between 3 and 4 during the summer and recovered quickly after the grass cut in late June (Fig. 2). The barley field at Voulund had a higher LAI than the wetland in the spring, but the LAI of the radish crop succeeding the barley in the late summer never exceeded one. In the spruce forest the LAI was slightly above 4 all year round and thus remained always higher than at the wetland site. It was not significantly different from the highest values measured on the barley field in the late spring, as can be seen from the error bars in Fig. 2. They represent the standard error of the LAI-2000 measurements for the agricultural and wetland sites and the typical uncertainty for the estimated data from the forest site, assuming a 10% uncertainty both in the net radiation measurements (mainly due to spatial variability, unaccounted for by the point measurements) and in the extinction coefficient taken from the literature.

Greenhouse Gas Exchange

Annual Course of Original Data

Figure 3 shows those original half-hourly flux data that had quality flags from one to three after the criteria given by Foken et al. (2004). Upward fluxes are defined as positive.

Fig. 1. Average diurnal courses of air temperature for three sites and four periods. Each half-hourly temperature is an average over 3 mo.

Fig. 2. Leaf area index (LAI) as measured on the wetland and on the agricultural field between April and December 2009 and in the spruce forest during summer 2009. The grass at the wetland site was cut on 29 June. The barley at the agricultural site was harvested on 21 July and the radish was sown the following day.
In terms of CO₂ fluxes, the agricultural site reached the highest uptake rates (around 30 μmol m⁻² s⁻¹) among all sites, but a substantial uptake was confined to a period of 3 mo. The CO₂ exchange of the other two sites was distributed more evenly throughout the year. The gaps at Voulund occurred due to the collapse of the first instrument mast (mid July to mid August) and due to a failure of the LI-7000 analyzer in early September, which was replaced by a LI-7500 in late October.

The CH₄ fluxes at Skjern Meadows were highest in the late summer and autumn when they regularly exceeded 100 nmol m⁻² s⁻¹. The very high rates up to 500 nmol m⁻² s⁻¹ observed occasionally between late May and early July and again, more consistently, between mid September and early October coincided with the presence of cattle on the area east (June) and west (September) of the instrument mast. West was the main wind direction at all measurement sites. The details of this observation are subject of a separate study (Herbst et al., 2011).

The N₂O exchange at Voulund could only be measured during some parts of the year due to technical difficulties with the gas analyzer. While an average emission of N₂O into the atmosphere around 1 nmol m⁻² s⁻¹ was observed in the spring (fertilized and watered barley crop), the net exchange between the surface and the atmosphere was close to zero in the autumn (radish crop).

Figure 4 shows the relative frequency with which CH₄ and N₂O fluxes of different size classes occurred. The highest emissions visible in Fig. 3, >5 nmol m⁻² s⁻¹ N₂O and >100 nmol m⁻² s⁻¹ CH₄, respectively, were only observed during about 2% of the investigation period. It also becomes evident from Fig. 4 that during more than 90% of the time there was an emission of CH₄ from the wetland site. The N₂O emissions from the agricultural site were much more difficult to detect, since during almost 80% of the investigation period the N₂O fluxes remained within the two smallest size classes (between −1 and 1 nmol m⁻² s⁻¹).
**Diurnal Courses of CO₂ exchange**

Figure 5 shows that nighttime CO₂ exchange rates were similar for all three sites throughout the year with typical rates between 1 and 2 μmol m⁻² s⁻¹ during the winter months and around 4 μmol m⁻² s⁻¹ during the summer months. This similarity indicates a strong influence of the temperature and a lack of effects caused by the surface or vegetation type. The only exception from this observation was the data from the forest obtained in the late summer showing a higher nighttime efflux (often around 6 μmol m⁻² s⁻¹) in comparison to the other sites. In contrast, large differences during the daytime were observed between the different vegetation types. The agricultural site had higher CO₂ uptake rates than the other two sites in the spring with average rates around 15 μmol m⁻² s⁻¹ at noon, but much lower rates during the rest of the year, with the average CO₂ uptake never exceeding 2 μmol m⁻² s⁻¹. The uptake rates of the forest and the wetland were similar during the wetland’s growing season with average daily peak rates between 10 and 12 μmol m⁻² s⁻¹, but different in the winter when only the forest had substantial CO₂ fixation rates.

**Relating CO₂ Fluxes to Temperature and Irradiance**

The response of the nighttime ecosystem CO₂ emission to soil temperature at 10 cm depth was fairly similar between the three sites (Fig. 6) as long as they were vegetated. While the small difference in $R_{10}$ between the wet grassland and the other two sites was significant, there was no statistical difference in $R_{10}$ between the agricultural and forest sites (Table 1). In contrast, the nonvegetated field (and this includes the period with the sparse radish crop) had an $R_{10}$ that was lower than 2 μmol m⁻² s⁻¹, which indicates that the vegetation contributes substantially to the total CO₂ emission. Using air temperature instead of soil temperature resulted in lower $R^2$ values for the curve fits (data not shown). Soil temperature was measured at 5 and 20 cm, too; however, the temperature at the 10-cm depth gave the best correlation with nighttime NEE.

The uptake of CO₂ during daytime through photosynthesis responded to the incoming solar radiation (Fig. 7). In accordance with the observations of the diurnal variations, it is evident that the forest and the wetland reacted similarly during the growing season. In contrast, during the winter season the evergreen forest responded much more strongly than the wetland to increasing irradiance. At the agricultural site the influence of solar radiation on CO₂ uptake

<table>
<thead>
<tr>
<th>Surface type</th>
<th>$R_{10}$ ± SE (μmol m⁻² s⁻¹)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Restored wetland</td>
<td>2.44 ± 0.03</td>
<td>0.39</td>
</tr>
<tr>
<td>Forest plantation</td>
<td>3.33 ± 0.04</td>
<td>0.46</td>
</tr>
<tr>
<td>Agricultural field, LAI &gt; 1 (April–June)</td>
<td>3.40 ± 0.04</td>
<td>0.23</td>
</tr>
<tr>
<td>Agricultural field, LAI &lt; 1 (rest of the year)</td>
<td>1.94 ± 0.04</td>
<td>0.48</td>
</tr>
</tbody>
</table>

† Leaf area index.
was higher than at the other two sites from April to June but lower than at the other two sites during the rest of the year. The parameters for the curve fits using Eq. [4] are given in Table 2.

### Table 2. Parameters fitted to the half-hourly daytime net ecosystem exchange (NEE) data for three sites and four periods using the equation by Falge et al. (2001) referred to in the text. $R^2$ of the curve fit and standard errors for the individual parameters are also given.

<table>
<thead>
<tr>
<th>Period</th>
<th>Restored wetland</th>
<th>Spruce forest</th>
<th>Agricultural field</th>
</tr>
</thead>
<tbody>
<tr>
<td>January–March</td>
<td>$R^2 = 0.22$</td>
<td>$R^2 = 0.36$</td>
<td>$R^2 = 0.32$</td>
</tr>
<tr>
<td>$a$ (μmol J$^{-1}$)</td>
<td>$-0.048 \pm 0.012$</td>
<td>$-0.073 \pm 0.014$</td>
<td>$-0.034 \pm 0.008$</td>
</tr>
<tr>
<td>$b$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$-6.22 \pm 0.55$</td>
<td>$-10.44 \pm 0.69$</td>
<td>$-2.55 \pm 0.19$</td>
</tr>
<tr>
<td>$c$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$0.74 \pm 0.27$</td>
<td>$0.00 \pm 0.34$</td>
<td>$0.69 \pm 0.11$</td>
</tr>
<tr>
<td>April–June</td>
<td>$R^2 = 0.44$</td>
<td>$R^2 = 0.48$</td>
<td>$R^2 = 0.54$</td>
</tr>
<tr>
<td>$a$ (μmol J$^{-1}$)</td>
<td>$-0.063 \pm 0.007$</td>
<td>$-0.099 \pm 0.010$</td>
<td>$-0.098 \pm 0.069$</td>
</tr>
<tr>
<td>$b$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$-19.05 \pm 0.66$</td>
<td>$-20.18 \pm 0.54$</td>
<td>$-26.50 \pm 0.77$</td>
</tr>
<tr>
<td>$c$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$3.14 \pm 0.42$</td>
<td>$4.77 \pm 0.45$</td>
<td>$4.04 \pm 0.44$</td>
</tr>
<tr>
<td>July–September</td>
<td>$R^2 = 0.56$</td>
<td>$R^2 = 0.53$</td>
<td>$R^2 = 0.46$</td>
</tr>
<tr>
<td>$a$ (μmol J$^{-1}$)</td>
<td>$-0.075 \pm 0.008$</td>
<td>$-0.141 \pm 0.016$</td>
<td>$-0.054 \pm 0.014$</td>
</tr>
<tr>
<td>$b$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$-20.94 \pm 0.76$</td>
<td>$-20.82 \pm 0.57$</td>
<td>$-6.37 \pm 0.35$</td>
</tr>
<tr>
<td>$c$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$4.54 \pm 0.36$</td>
<td>$6.60 \pm 0.48$</td>
<td>$4.51 \pm 0.34$</td>
</tr>
<tr>
<td>October–December</td>
<td>$R^2 = 0.38$</td>
<td>$R^2 = 0.40$</td>
<td>$R^2 = 0.35$</td>
</tr>
<tr>
<td>$a$ (μmol J$^{-1}$)</td>
<td>$-0.051 \pm 0.010$</td>
<td>$-0.049 \pm 0.010$</td>
<td>$-0.016 \pm 0.003$</td>
</tr>
<tr>
<td>$b$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$-10.35 \pm 1.16$</td>
<td>$-19.52 \pm 3.68$</td>
<td>$-39 \pm 90$</td>
</tr>
<tr>
<td>$c$ (μmol m$^{-2}$ s$^{-1}$)</td>
<td>$1.18 \pm 0.25$</td>
<td>$0.00 \pm 0.34$</td>
<td>$0.42 \pm 0.11$</td>
</tr>
</tbody>
</table>

### Annual GHG Budgets after Gap Filling

Over the entire year 2009 the uptake of CO$_2$ through the forest amounted to 1846 ($\pm$277) g CO$_2$ m$^{-2}$ (Fig. 8). This was roughly twice as high as the CO$_2$ uptake of the wetland (979 $\pm$ 147 g CO$_2$ m$^{-2}$) and the agricultural site (869 $\pm$ 130 g CO$_2$ m$^{-2}$). The difference between these two sites was in the same order of magnitude as the uncertainty of the method used (see “Reliability of Catchment-Wide Fluxes” section below). The methane emission from the wetland was equivalent to an amount of 276 ($\pm$41) g CO$_2$ m$^{-2}$, reducing the overall annual greenhouse gas sink to 703 ($\pm$105) g CO$_2$ equivalents m$^{-2}$. The N$_2$O emission from the agricultural site equaled 81 ($\pm$12) g CO$_2$ equivalents m$^{-2}$, reducing the total atmospheric greenhouse gas budget to 788 ($\pm$118) g CO$_2$ equivalents m$^{-2}$. However, due to the lack of data, the entire year could not be gap-filled reliably, and thus the number given for N$_2$O refers to only about 7 mo in total, which makes it likely that the annual N$_2$O effect was underestimated.

From a catchment-wide perspective, the results mean that, under given climatic conditions, the forest plantation functions as a GHG sink more than twice as strong as the other two surface types that are typical for the Skjern River catchment. The restored wetland was the weakest GHG sink because of its significant methane emission.
Temporal Variations in the Fluxes

The temporal variations in the GHG fluxes did not always follow a gradual seasonal pattern (Fig. 3). Management activities and specific weather patterns had a visible influence on the fluxes. The downward CO$_2$ flux at the wetland site was reduced following the grass cut in late June, while the upward CH$_4$ flux, both in terms of average and peak rates, increased strongly in September, when the top soil was rewetted again following a drop in the water table during the summer and when cattle were grazing in the source area over a period of 3 wk (Herbst et al., 2011). Also on the farmland the CO$_2$ uptake decreased sharply in mid June when the barley crop matured and the irrigation was stopped. The N$_2$O measurements began a few days after the second fertilization of the barley field, and it can easily be seen that the peak emission rates decreased from this time. However, specific irrigation events are not clearly visible in the flux data because the irrigation systems operated only locally and were moved around to cover the whole area. This means that the source area of the flux measurements and the area where the irrigation took place were not always identical. A small, but distinct reduction in the CO$_2$ uptake at the forest site in late June and early July corresponded to the period with the lowest soil moisture content and a reduction in stomatal conductance (Ringgaard et al., 2011).

Annual CO$_2$ Budgets

The annual carbon budgets for the three land use types in the Skjern catchment fall within the range of other observations made in temperate regions. The annual uptake of 1846 g CO$_2$ equaling 503 g C m$^{-2}$ ground area in the spruce plantation exceeds the average value of 426 g C given by Luysaert et al. (2007) for temperate coniferous forests (derived from their Fig. 9) by about 12%. However, taking the uncertainty margin of the measurements into account (see “Reliability of Catchment-Wide Fluxes” section below), this difference was not significant. Lindroth et al. (2008) documented that, in coniferous forest plantations, a high LAI favors high photosynthesis rates, whereas a young stand age favors a low ecosystem respiration rate. A combination of these two factors would result in a comparatively high NEE, which agrees with the findings of this study. The maximum age of the trees in the source area of the flux measurements was about 50 yr, and one-half of this area consisted of an even younger stand, whereas the stands surveyed by Luysaert et al. (2007) had an average age of about 90 yr. The LAI at Gludsted Plantage, despite being lower than the average of 6.8 used by Luysaert et al. (2007), is still higher than in most other coniferous forests in the Scandinavian region, where it rarely exceeds 4 (Lindroth et al., 2008).

For agricultural crops, Soegaard et al. (2003) reported an average cumulative carbon uptake of 274 g C (or 1005 g CO$_2$) m$^{-2}$ during the summer period (April–September), which was similar to the findings in this study (CO$_2$ uptake of 1040 g m$^{-2}$ from 1 April to 30 September, see Fig. 8). However, in Soegaard et al. (2003) most of this amount was emitted again into the atmosphere during the rest of the year, and this could be attributed to the lack of vegetation on the fields during winter and to anthropogenic sources originating from a nearby town. In the present study, both the absence of settlements in the footprint of the measurements and the planting of radish as a catch crop after the harvest of the barley reduced the CO$_2$ release during winter, since there always was a small CO$_2$ uptake during daytime hours. The annual budget thus benefitted from the local conditions and management practices.

The carbon balance of grasslands in Europe is highly variable. In an analysis of carbon flux data from 20 European grassland sites, Gilmanov et al. (2007) found annual CO$_2$ budgets between 2400 g m$^{-2}$ uptake and 600 g m$^{-2}$ release. This means that the data from Skjern Meadows (uptake of 979 g CO$_2$ or 267 g C) fall into the middle of the reported span. They are also close to average values published by Jacobs et al. (2007) for eight Dutch grasslands (with 220 g annual carbon uptake for grass- and wetlands on organic soils and 90 g carbon emission for grasslands on mineral soils) and by Soussana et al. (2007) for nine European grasslands having an average annual uptake of 240 g carbon per square meter ground area. Gilmanov et al. (2007) identified both climatic and management effects that caused the large variability in grassland NEE. This underlines the fact that the ranking between grasslands and other land use forms, with respect to their annual carbon budgets, can vary substantially between regions and catchments.

Universality of CO$_2$ Response Functions

The functions chosen to describe the responses of nighttime NEE to temperature and daytime NEE to irradiance are well established and have been used in numerous studies. Their advantage is that they require a minimum number of empirical parameters, which correspond to meaningful physiological quantities. For intercomparisons with other studies one has to bear in mind that the problem of quality control and filtering of nighttime eddy flux data still is a matter of debate. The derived $R_{10}$ values depend strongly on the filtering procedure chosen; for example, the numbers given in this study would have been higher if the filtering method proposed by Van Gorsel et al. (2007) had been used instead of the $u^*$ filtering technique (Nordstroem et al., 2001).

To be able to attribute the observed differences in CO$_2$ fluxes among the three sites to the surface type alone, we had to determine whether the small temperature variations across the catchment (see above) could have contributed significantly to those differences too. This was achieved by taking the measured temperature from a different site and applying Eq. [3] to calculate the theoretical flux for a given site, in comparison to the flux resulting from the original temperature. The largest change in flux among all six possible combinations was observed when applying the wetland temperatures to the agricultural site, but even then the modest increase of 4.6% in CO$_2$ emissions was lower than the observed
There have been discussions about whether the parameters for the CO₂ response functions could be generalized in the sense that their variation could be attributed to other factors. According to Lindroth et al. (2008) the LAI could play a crucial role in this because the correlation between the daytime NEE and nighttime respiration parameters across different sites and seasons as observed by these authors could only be explained by the LAI, which correlated with all these parameters. While this applies to coniferous forest, Davis et al. (2010) made similar observations for an agricultural site in Ireland and found a strong dependence of barley NEE on LAI. Due to the lack of intercropping at this site, the corresponding cumulative NEE was slightly lower than in our study, with rates between approximately 350 and 750 g CO₂ m⁻² yr⁻¹ for three consecutive years. Also this temporal variability could be attributed to a corresponding variance in LAI. Besides LAI, latitude and, in terms of forest plantations, stand age have been identified as factors influencing the parameters of the respiration function (Valentini et al., 2000; Lindroth et al., 2008); besides this, species composition can be important for the daytime NEE response as well (Soegaard et al., 2003; Kutsch et al., 2005).

**Role of Greenhouse Gases other than CO₂**

In this study it was not considered necessary to measure methane or nitrous oxide fluxes at the forest site. It can reasonably be assumed that the N₂O flux at Gludsted Plantage was negligible because of the low position of the water table and relatively large C/N ratio in the sandy, aerobic forest soil (Jungkunst et al., 2004; Ambus et al., 2006). Despite that aerobic forest soils, especially soils with coarse texture, have been identified as the largest CH₄ sink among all ecosystems in the temperate zone, the reported flux rates are still small (Dutaur and Verchot, 2007), with an average CH₄ uptake of 4 kg per hectare and year which equals about 10 g CO₂ equivalents per square meter ground area and year. Schulze et al. (2009) estimated the CH₄ sink in forest soils to be even one order of magnitude lower. A forthcoming measurement campaign will include quantification of the potential CH₄ uptake at Gludsted Plantage. If this uptake equals the rates given by Dutaur and Verchot (2007), then about 28 ha of forest would be necessary to offset the CH₄ emissions of 1 ha of wetland.

The fluxes of CH₄ and N₂O measured at the wet grassland and agricultural sites, respectively, were of a more episodic nature than the CO₂ fluxes because different control factors are involved in the regulation of these GHG fluxes. The CH₄ emission from vegetated land surfaces is known to be strongly influenced by the water table height and the soil temperature (Waddington and Roulet, 2000; Christensen et al., 2003; Hendriks et al., 2007), by management practices such as grazing by cows (Ellis et al., 2010; Herbst et al., 2011), and by changes in species composition following drainage or restoration of wet grasslands (Waddington and Day, 2007), especially if aerenchymateous vegetation is involved. For the sum of the N₂O fluxes as caused by microbial nitrification and denitrification, Nefel et al. (2010) reported that their temporal pattern often consists of a close-to-zero or slightly negative background flux interrupted by short emission peaks due to rain events or fertilizer application, and also thawing of frozen soils can cause high N₂O emissions from agricultural sites (Johnson et al., 2010). The measurements made in this study confirm the fact that short-term ecosystem disturbances can play the largest role in determining the annual budget of non-CO₂ GHGs. For example, a grazing period of several months instead of just 3 wk at the wetland site or an additional input of fertilizer at the agricultural site could easily have doubled the CH₄ and N₂O emissions, respectively, according to their observed annual courses (Fig. 8).

If their total annual budgets are compared with other studies, then it turns out that the CH₄ emission from the wet grassland at Skjern Meadows was much higher (by a factor of about seven) than the European average “grassland” CH₄ emission after Schulze et al. (2009). In contrast, it fitted well within the range of CH₄ emissions from other restored wet grasslands (Waddington and Day, 2007; Hendriks et al., 2007) and thus behaved as a “wetland” rather than a “grassland” in the sense of Schulze et al. (2009). The annual N₂O emission from the agricultural site at Voulund (equaling 81 g CO₂ equivalents m⁻² yr⁻¹) agreed with observations made at a managed grassland site (Flechard et al., 2005) where 4.7 kg N₂O-N ha⁻¹ were emitted from the soil over a 2.5-yr period. This equals 88 g CO₂ equivalents per m² and year.

At the catchment scale, the total GHG balance was clearly influenced by the fluxes of CH₄ and N₂O. If buildings and roads are not considered, then roughly 60% of the Skjern River catchment is covered by agricultural fields, 25% by grasslands of various types (including both extensively managed wet grasslands and fertilized hay meadows) and 15% by mostly coniferous forest plantations. According to the data shown in Fig. 8, the catchment-wide weighted average for the annual CO₂ flux between the land surface and the atmosphere amounted to an uptake of 1043 g CO₂ m⁻². The emission of N₂O and CH₄ from agricultural sites and wet grasslands, respectively, would be equivalent to a release of 118 g CO₂ equivalents m⁻². These numbers are based on the assumption that all grasslands in the catchment behaved like the restored wet grassland. If we would instead assume that most of the grassland consists of fertilized hay meadows that function like agricultural land and that only 5% of the catchment area shows the wetland response observed in this study, then the CO₂ uptake would be 1021 g m⁻², which is statistically not different from the original value, and the emission of CH₄ plus N₂O would be 79 g CO₂ equivalents m⁻². A potential CH₄ uptake by all the forest soils in the catchment could reduce this further to 77 g m⁻².
Despite some uncertainty in these figures, especially with respect to N₂O (see above), it can be concluded on the basis of the measurements presented in this study that the CO₂ sink strength of the Skjern River catchment was reduced by about one-tenth through the release of CH₄ and N₂O from the soils into the atmosphere. This statement does not include any accounts of the import and export of carbon through management practices and is therefore not comparable to Schulze et al. (2009), who found that the full GHG budget of Europe’s land surface was near neutral.

**Reliability of Catchment-Wide Fluxes**

Despite the recent progress in modeling and scaling procedures, which resulted in the publication of Europe-wide GHG balances (Schulze et al., 2009), it is still not possible to account fully for the high spatial and regional variability of atmospheric GHG fluxes caused by site-specific factors such as species composition or management practices like, for instance, drainage, irrigation, fertilization, and grazing. The variability in GHG fluxes from one land use type within a small region facing the same climatic conditions can be as large as the overall variability in the respective fluxes across Europe (Jacobs et al., 2007).

This means that the uncertainty in the eddy covariance measurements due to systematic instrumental errors such as sensor calibration errors, frequency losses or density fluctuations is not the largest source of uncertainty for the estimation of catchment-wide GHG fluxes. Thanks to the use of the latest sensor technology and data processing algorithms it may reasonably be assumed that this error did not exceed 10%, according to the specifications provided by the manufacturers and to sensitivity tests for the flux corrections. Adding an additional error margin of 5% for the gap filling would result in an overall uncertainty of 15% for each of the annual totals presented in Fig. 8. However, given that the same instrumentation and the same calculation methods were applied at all sites, it seems likely that the accuracy of the comparison between the three sites is much better, since all data would have been affected by similar systematic errors. An additional source of uncertainty was the replacement of the closed-path with an open-path CO₂ gas analyzer at the agricultural site, since the two different sensor types are prone to different types of errors, most importantly radiative sensor heating of the open-path sensor and low pass filtering of the closed-path sensor. However, many papers have shown that the agreement between the two sensor types can be excellent if the specific errors are accounted for in the flux calculations (e.g., Ibm et al., 2007; Burbà et al., 2008; Haslwanter et al., 2009). Since all those latest correction protocols were performed in this study, it can reasonably be assumed that errors resulting from the use of two different sensor types were negligible.

More important for the accuracy of catchment-scale data is the representativeness of the selected sites, especially with respect to the occurrence of those activities and disturbances that were identified earlier as decisive factors for the annual GHG budgets. This affects the transferability of flux data to other sites and makes predictions of future changes in the GHG balance for specific catchments highly uncertain and more regional studies desirable. For example, in some catchments the ranking in the GHG balance between forest, grasslands and croplands will differ from the European average. Given that management practices play a crucial role in the GHG budget and that such practices are linked to decisions made regionally, it is important to monitor GHG fluxes for different land use forms at the regional or catchment scale. This should happen over a sufficiently long time period that allows the detection of interannual variability in the fluxes. Future research should also take into account import and export of GHG through land use activities such as biomass harvest and manure application.

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