



Partitioning of soil CO₂ efflux in un-manipulated and experimentally flooded plots of a temperate fen

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Abstract. Peatlands store large amounts of organic carbon, but the carbon stock is sensitive to changes in precipitation or water table manipulations. Restoration of drained peatlands by drain blocking and flooding is a common measure to conserve and augment the carbon stock of peatland soils. Here, we report to what extent flooding affected the contribution of heterotrophic and rhizosphere respiration to soil CO₂ efflux in a grass-dominated mountain fen in Germany. Soil CO₂ efflux was measured in three un-manipulated control plots and three flooded plots in two consecutive years. Flooding was achieved by permanent irrigation during the growing seasons. Radiocarbon signatures of CO₂ from different sources including soil CO₂ efflux, incubated peat cores and live grass roots were repeatedly analyzed for partitioning of soil CO₂ efflux. Additionally, heterotrophic respiration and its radiocarbon signature were determined by eliminating rhizosphere respiration in trenched subplots (only control). In the control plots, rhizosphere respiration determined by ¹⁴C signatures contributed between 47 and 61 % during the growing season, but was small (4 ± 8 %) immediately before budding. Trenching revealed a smaller rhizosphere contribution of 33 ± 8 % (2009) and 22 ± 9 % (2010) during growing seasons.

Flooding reduced annual soil CO₂ efflux of the fen by 42 % in 2009 and by 30 % in 2010. The reduction was smaller in 2010 mainly through naturally elevated water level in the control plots. A one-week interruption of irrigation caused a strong short-lived increase in soil CO₂ efflux, demonstrating the sensitivity of the fen to water table drawdown near the peat surface. The reduction in soil CO₂ efflux in the flooded plots diminished the relative proportion of rhizosphere respiration from 56 to 46 %, suggesting that rhizosphere respiration was slightly more sensitive to flooding than heterotrophic respiration.

1 Introduction

Northern peatlands play a significant role in the global carbon (C) cycle and store approximately one-third of the global soil C pool (Gorham, 1991; Turunen et al., 2002). This large organic C pool has accumulated since the retreat of the ice sheets over the past 5000–10 000 yr. Average peat accumulation of 24 g C m⁻² yr⁻¹ (Lavoie et al., 2005) to 40 g C m⁻² yr⁻¹ (Gorham, 1991) results from the difference of relatively large C fluxes, namely production and mineralization of plant detritus. According to Turunen et al. (2002), the variation in peat accumulation partly results from the ecosystem type where bogs have higher average accumulation rates than fens. The accumulation and stabilization of the organic C pool is attributed to reduced decomposition of peat and fresh plant detritus under anoxic conditions. Oxygen concentrations typically decline exponentially from the peat surface with increasing depth, and control thereby together with temperature the decomposition of organic C in most peat profiles. Fluctuations in the water table largely affect the gas transport and, thus, the concentration profile of oxygen in the peat body. Long-term changes in the water table by climate change or by direct anthropogenic encroachments have therefore the potential to alter the C balance of peatlands. Descending or ascending water table may turn peatlands into net C sources or even stronger net C sinks (Bridgman et al., 2008).

Significant increases of CO₂ effluxes have been achieved in several peatlands through water table drawdown under manipulative or natural conditions (e.g. Bridgman et al., 2008; Ellis et al., 2009; Laiho, 2006; Riutta et al., 2007). On average, CO₂ efflux increased by 9.5 g C m⁻² yr⁻¹ per 1 cm lowering of the water table and effective drainage by ditching

almost doubled the CO₂ efflux in various boreal mires (Silvola et al., 1996). Temporarily elevated soil CO₂ effluxes were also observed during dry and warm summers when the water table dropped (Alm et al., 1999; Moore et al., 2002). However, not all peatlands seem to respond to water table drawdown. Muhr et al. (2011) reported no increase of the soil CO₂ efflux in a minerotrophic fen, although the water table was permanently lowered during growing seasons. In the long run, peatlands may adapt to the new hydrological regime and constrain or compensate C losses by changing the vegetation community and plant productivity (Laiho, 2006; Strack and Waddington, 2007; Weltzin et al., 2000).

Flooding of peatlands generally reduces the aerobic decomposition of peat and often promotes growth of *Sphagnum* or graminoides depending on the peatland type (Chivers et al., 2009; Rochefort et al., 2002; Urbanová et al., 2011; Weltzin et al., 2000). The optimum water level for maximum plant productivity, however, varies among vegetation communities and peatlands (Bridgham et al., 2008). Restoration of previously drained peatlands is not always accompanied by a rise in CH₄ emissions, representing an additional gaseous C loss (Bortoluzzi et al., 2006). Similar to CO₂ effluxes, vegetation type largely controls the emissions of CH₄ from peatlands to the atmosphere (Nilsson et al., 2001; Wright et al., 2011). In particular, the abundance and species composition of vascular plants affect gas fluxes as their aerenchyma acts a gas conduit between subsurface peat and atmosphere (Ström et al., 2005).

Soil CO₂ effluxes originate from different resources, including peat and litter decomposition (heterotrophic respiration), root respiration and respiration of organisms relying on root exudates (hereafter summarized as “rhizosphere respiration”). The contribution of both components to soil CO₂ efflux may vary seasonally and spatially, and both components could respond differently to changes in water table. Different techniques have been applied to partition soil CO₂ effluxes under field conditions, but most techniques require a disturbance of the soil-plant system (Subke et al., 2006). Radiocarbon analyses of respired CO₂ provide a tool that allows the partitioning of soil CO₂ effluxes under field conditions without disturbances of the peat profile. This approach has been successfully applied in different ecosystems (Borken et al., 2006; Hardie et al., 2009; Schuur and Trumbore, 2006). Additionally, the radiocarbon signature provides information about the mean age of respired CO₂. Hardie et al. (2009) reported the release of old CO₂ from the catotelm, contributing up to 23 % to total ecosystem respiration of a bog ecosystem in the UK. Assessing the origin of soil CO₂ will improve our understanding of changes in the C cycle of flooded peatlands.

The aims of this study were (1) to quantify the effect of flooding on soil CO₂ efflux, (2) to partition the soil CO₂ efflux into heterotrophic and rhizosphere respiration and (3) to assess the CO₂ net turnover at different depth in peat profiles of a minerotrophic fen. In a field experiment, three plots of

the fen were flooded during two growing seasons and compared to three non-flooded control plots.

2 Material and methods

2.1 Study site

The fen Schlößnerbrunnen is located in the Lehstenbach catchment of the Fichtelgebirge (50°07′54″ N, 11°52′51″ E) in northeastern Bavaria, Germany, at an elevation of 700 m a.s.l. The site is characterized as a temperate minerotrophic fen covering an area of 0.8 ha. The soil is a histosol on granite bedrock covered mainly by *Molinia caerulea* (L. Moench), *Nardus stricta* (L.), *A. canina* (L.), *Carex rostrata* (Stokes), *Eriophorum vaginatum* (L.) and *Sphagnum fallax*. Mean annual temperature was 6.3 °C and mean annual precipitation was 1020 mm between 1995 and 2007. The site features a small slope from NNE to SSW, and groundwater flows slowly through the site parallel to this slope. A peat body with a thickness of 40–100 cm and an average C stock of 49 kg m⁻² has accumulated since the last deglaciation. The peat below 10–15 cm depth was strongly decomposed as indicated by an increase in bulk density from 0.11 to 0.29 g cm⁻³. Radiocarbon data of organic matter revealed a mean age of > 8000 yr at a depth of 41–81 cm (J. Muhr, personal communication, 2012). The peat formation was likely disturbed by natural events and by human activity in the past. A ditch of unknown age runs through the site parallel to the slope.

2.2 Experimental design

Three control plots (hereafter C1, C2, and C3; each 7 × 5 m²) were installed in the summer of 2005 to assess natural dynamics of biogeochemical processes at the site (Fig. 1). Three plots of identical size (hereafter D1, D2, and D3) were installed a few meters downstream in terms of groundwater flow to carry out water table manipulation experiments. All plots were accessible via wooden walkways. Each plot was equipped with soil temperature sensors at six depths (5, 10, 20, 30, 40, and 60 cm) and soil moisture sensors at 5, 10, 25, 40, and 60 cm depth. Piezometers (26PCBFA6D, IBA Sensorik GmbH, Seligenstadt, Germany) in the immediate vicinity of the installations allowed for continuous monitoring of the water table (for this work, the data of six piezometers per plot were used). Precipitation was measured at a climate station at a distance of about 1 km from the plots.

The D1–3 plots were drained by means of transparent roofs and an active drainage system that pumped out groundwater of the plots during the growing seasons in 2006, 2007 and 2008. Water level quickly recovered after ending the drainage in October of each year through lateral water inflow and natural precipitation (see Muhr et al., 2011 for more details). In a second experiment, reported here, the D1–3 plots were permanently flooded during the growing seasons

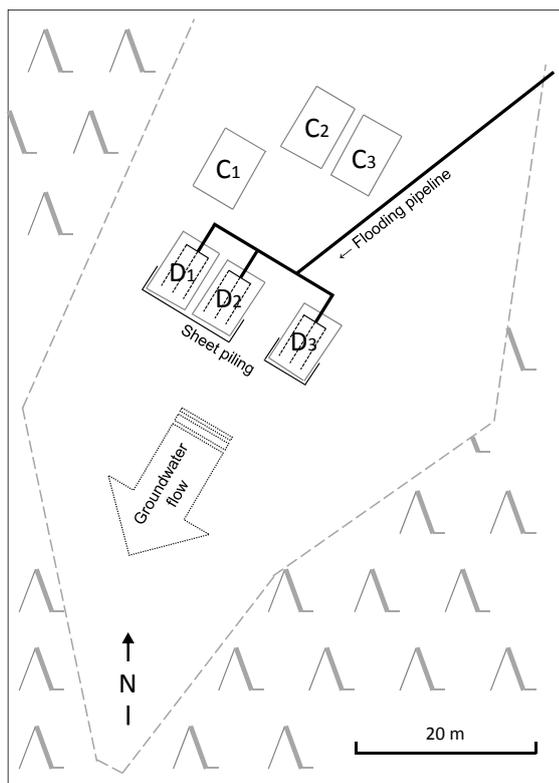


Fig. 1. Schematic illustration of the study site showing control (C1–C3) and flooded plots (D1–D3) and installations made for flooding.

of 2009 (14 May–30 October) and 2010 (10 May–9 November) using water from a creek directly beside the fen (Table 1). The water was channelled by a tube from the upper part of the creek and dammed up in the D1–3 plots by sheet pilings (Fig. 1). Daily applied water amount ranged between 50 and 70 m³ per plot, except for one week in 2010 (24–30 July) when flooding was completely interrupted after a storm event. Mean pH of applied water was 4.7, and mean element concentrations were in mg l⁻¹: 3.5 (Na⁺), 0.8 (K⁺), 2.4 (Ca²⁺), 0.7 (Mg²⁺), 0.6 (Feⁿ⁺), 0.6 (Alⁿ⁺), 3.8 (NO₃⁻-N), 3.5 (SO₄²⁻-S), 0.6 (PO₄³⁻-P), and 14.6 (DOC). Depending on the slope and position, mean water level was approximately 0–10 cm above the peat surface. The applied water discharged along the slope gradient over the sheet pilings.

2.3 Soil CO₂ efflux

In the middle of each plot, three collars (length: 45 cm, inner diameter 48 cm) were driven about 5 cm into the peat for measurements of soil CO₂ efflux in 2006. The size of collars allowed the integration of both hollows and hummocks in the collars, and thus the natural micro-topography of this fen. As insertion of collars may affect soil CO₂ efflux and the partitioning of soil CO₂ efflux due to partial abscission of roots (Heinemeyer et al., 2011) we perforated collars at

2–4 cm peat depth which allowed ingrowth of roots. The top peat layer of 0–5 cm depth contains about 30 % of the total root biomass (Otieno et al., 2012). Green leaves of grasses were clipped and removed from the collars before CO₂ measurements and returned as litter input after CO₂ measurements. Additionally, one collar (length: 90 cm, inner diameter 48 cm) was driven about 50 cm into the peat body in each of the three control plots in April of 2008. Trenching of roots and permanent covering of the peat surface with a non-transparent, gas-permeable foil prevented plant growth and plant respiration. For CO₂ measurements, collars were manually closed with a non-transparent plastic lid and then connected to a portable infrared gas analyzer (Li-820, LI-COR Environmental, Bad Homburg, Germany) by two tubes. A pump circulated the air between the chamber headspace and the gas analyzer at a constant flow rate of 0.5 l min⁻¹. CO₂ concentration was logged every 10 s for a period of 5–10 min. The increase in CO₂ concentration was usually less than 50 ppmv and was mostly strictly linear over the entire monitoring time, indicating that soil CO₂ effluxes were not over- or underestimated. CO₂ effluxes were calculated by performing a linear regression on the logged CO₂ concentration data (with a few exceptions: $r^2 > 0.95$). Data were corrected for atmospheric pressure and chamber air temperature. Measurements of soil CO₂ efflux were carried out in rotation on the C1–3 and the D1–3 plots between 08:30 a.m. and 12:00 p.m. (midday) on 42 sampling dates between 2009 and 2010. When snow completely covered the collars during winter time, three conical chambers (12 l) per plot were carefully inserted 5 cm into the snow cover for CO₂ measurements.

2.4 Radiocarbon measurements

Radiocarbon signatures of soil CO₂ efflux ($\Delta^{14}\text{C}_{\text{SR}}$), heterotrophic respiration ($\Delta^{14}\text{C}_{\text{HR}}$) and rhizosphere respiration ($\Delta^{14}\text{C}_{\text{RR}}$) were measured on five dates between May 2009 and May 2010. We installed two additional collars (length: 10 cm, inner diameter 30.8 cm) per plot for measuring $\Delta^{14}\text{C}_{\text{SR}}$ in April 2009, because the headspace volume of the regular chamber system (72 l) was too large. Green vegetation of grasses was clipped off and removed from the collars one day before sampling. Our goal was to maintain the natural rate of soil respiration and its ¹⁴C signature; however, we cannot exclude that both parameters were altered by clipping. Prior to sampling of soil CO₂ efflux, chambers (22 l volume) were placed on the collars and then flushed with CO₂-free synthetic air at least for 40 min at a moderate flow rate of 1.5 l min⁻¹. The amount of applied synthetic air represents three times the headspace volume and was sufficient for removal of atmospheric CO₂. Following flushing, the chambers were sealed and left until the CO₂ concentration inside the chambers reached at least 1500 ppmv. Incubation time depended on CO₂ flux rates on the sampling day. Evacuated stainless steel sampling cylinders (2 l) were connected to the chambers and slowly filled with gas from inside the chamber.

Table 1. Mean air temperature (*T*), sum of precipitation (*P*), mean water table and mean (\pm SD) cumulative soil CO₂ effluxes in the flooded and control plots and in the trenched subplots for different periods in 2009 and 2010. Growing season from 1 May–31 October. P-values indicate the statistical significance between cumulative soil CO₂ effluxes of the treatments for different time periods.

Year	Period	Duration (days)	<i>T</i> (°C)	<i>P</i> (mm)	Water table		Cumulative soil CO ₂ efflux			p-value
					(m)		(g C m ⁻²)			
					<i>Flooding</i>	<i>Control</i>	<i>Flooding</i>	<i>Control</i>	<i>Trenching</i>	
2009	Pre-treatment	133	1.7	323	-0.05	-0.03	61 ± 10	79 ± 13		0.137
	Treatment	170	12.5	445	0.10	-0.09	129 ± 21	271 ± 36		0.008
	Post-treatment	62	1.0	204	0.04	-0.01	21 ± 5	14 ± 3		0.099
	Total	365	6.6	972	0.04	-0.06	212 ± 9	365 ± 52		0.033
	Growing season	184	12.3	491				296 ± 40	198 ± 17	0.036
2010	Pre-treatment	129	-0.3	232	0.02	-0.01	41 ± 8	45 ± 5		0.683
	Treatment	184	11.5	664	0.11	-0.06	158 ± 47	251 ± 39		0.059
	Post-treatment	52	-3.4	188	0.06	0.01	16 ± 7	12 ± 1		0.364
	Total	365	5.2	1084	0.08	-0.05	216 ± 62	307 ± 35		0.107
	Growing season	184	11.6	653				255 ± 38	200 ± 19	0.113

For determination of $\Delta^{14}\text{C}_{\text{RR}}$, three peat cores (20 cm × 20 cm × 20 cm) with live grasses (*Molinia caerulea* (L. Moench), *Eriophorum vaginatum* (L.), *A. canina* (L.)) were taken between the control and treatment plots. Roots of the peat cores were washed out from the bulk peat, cleaned with tap water to remove dead organic matter and afterwards separated into live and dead root fractions. Live roots were transferred into airtight mesocosms (7 l) within 1 h, flushed with synthetic air and then incubated until a minimum CO₂ concentration of 1500 ppmv was reached. Gas samples were taken with the same evacuated stainless steel cylinders.

$\Delta^{14}\text{C}_{\text{HR}}$ was determined in two different ways. Firstly, one undisturbed peat core (10 cm diameter) was taken from 0–25 cm depth of each plot using PVC cylinders. After removal of green vegetation, peat cores were stored under weak artificial light at 15 °C for 12 weeks to reduce the pool of non-structural carbohydrates (NSC) in live roots. We assumed that NSC were reduced either by decomposition of roots or by budding of new leaves; the latter were removed before ¹⁴CO₂ sampling. Water level was adjusted to a few cm below the peat surface. Thereafter, peat cores were transferred into gas-tight mesocosms and processed for gas sampling as described above. Secondly, $\Delta^{14}\text{C}_{\text{HR}}$ was determined under natural conditions from the three trenched subplots within the control plots.

Via mass-flow controllers, the cylinders were connected to a high-vacuum extraction line in the Department of Soil Ecology at the University of Bayreuth. CO₂ was cryogenically purified and converted to graphite targets using the modified sealed tube zinc reduction method described by Xu et al. (2007). Graphite targets were analyzed by the Keck Carbon Cycle AMS facility at UC Irvine, USA with a precision of 2–3 ‰. Radiocarbon data are expressed as $\Delta^{14}\text{C}$, which is the per mil deviation from the ¹⁴C/¹²C ratio of ox-

alic acid standard in 1950. The sample ¹⁴C/¹²C ratio has been corrected to a $\delta^{13}\text{C}$ value of -25 ‰ to account for any mass-dependent fractionation effects (Stuiver and Polach, 1977).

We partitioned soil CO₂ efflux into heterotrophic and rhizosphere respiration using a two source mixing model (Borken et al., 2006) as follows:

$$F_{\text{CO}_2, \text{SR}} = F_{\text{CO}_2, \text{HR}} + F_{\text{CO}_2, \text{RR}} \quad (1)$$

$$F_{\text{CO}_2, \text{SR}} \times \Delta^{14}\text{C}_{\text{SR}} = F_{\text{CO}_2, \text{HR}} \times \Delta^{14}\text{C}_{\text{HR}} + F_{\text{CO}_2, \text{RR}} \times \Delta^{14}\text{C}_{\text{RR}} \quad (2)$$

where F_{CO_2} are CO₂ effluxes (mg C m⁻² h⁻¹) and $\Delta^{14}\text{C}$ radiocarbon signatures (‰) of soil respiration (SR), heterotrophic respiration (HR) and rhizosphere respiration (RR). Errors of soil CO₂ efflux partitioning arising from the variability in isotopic signatures of both the sources ($\Delta^{14}\text{C}_{\text{HR}}$, $\Delta^{14}\text{C}_{\text{RR}}$) and soil CO₂ efflux ($\Delta^{14}\text{C}_{\text{SR}}$) were calculated following Phillips and Gregg (2001).

2.5 Soil CO₂ profiles

One passive diffusion gas sampler was installed at each plot for analyzing the vertical CO₂ concentration profile at 10, 20, 30, 40, 50 and 60 cm depth of the peat body. A gas sampler consisted of a fragmented PVC cylinder (ID 70 mm, OD 79 mm, 70 cm height); each 10 cm fragment was equipped with a coiled 5 m silicon tube (ID 3 mm, OD 5 mm). Gas diffusion between the gas phase of the silicon tube and the aqueous or gas phase of the peat was enabled by perforation of each fragment at 10 cm intervals. Fragmentation of the PVC cylinder prevented gas exchange between the silicon tubes (Goldberg et al., 2008). Sampling was performed from the soil surface using gas impermeable polyurethane tubing (ID 1.8 mm, OD 3 mm) fitted with lock rings and thread style caps (Luer Lock, Value Plastics, Fort

Collins, CO, USA). Before sampling, a plastic syringe with a three-way stopcock was connected with the lock ring of the polyurethane tubing. After discarding the first 5 ml gas, a 20 ml gas sample was taken with a 20 ml syringe (OMNIFIX Solo, Braun, Melsungen, Germany) and then injected into an airtight 22 ml glass vial. The vials were filled with argon and equilibrated to atmospheric pressure and temperature before sample injection. The pressure of each vial was measured with a pressure sensor (TensioCheck TC 03S, Tensio-Technik, Geisenheim, Germany) before and after gas injection for calculation of sample dilution by argon. Gas profile sampling and soil CO₂ effluxes were simultaneously conducted on 42 dates between 2009 and 2010.

CO₂ concentration in the vials was analyzed within one day after sampling on a gaschromatograph (GC-14A, Shimadzu Corporation, Kyoto, Japan) equipped with an autosampler (HSS 1000, DANI Strumentazione Analitica S.p.A., Monza, Italy) and an electron capture detector (ECD). Seven certified standards (380, 600, 1000, 3000, 10 000, 20 000 and 30 000 μl l⁻¹ CO₂ in N₂) were measured for calibration of the gaschromatograph.

Concentration of dissolved CO₂ in pore water (μmol l⁻¹) was calculated from gas samples assuming equilibrium between the gas phase (silicon tube) and aqueous phase (pore water) using solubility coefficients for CO₂ (mol l⁻¹ atm⁻¹) for actual temperature (Weiss, 1974). We only considered physically dissolved CO₂, because the amount of chemically dissolved CO₂ (H₂CO₃, HCO₃⁻, CO₃²⁻) is small in water with low pH (Domenico and Schwartz, 1990). At pore water pH of 4.4–5.1 at our site, chemically dissolved CO₂ was < 6 % compared to physically dissolved CO₂.

Net turnover R_N of CO₂ (nmol cm⁻³ d⁻¹) in the individual layers was calculated from mass balance of diffusive fluxes according to the following equation:

$$R_N = \left[D_A \frac{\Delta c_{CO_2, upper}}{\Delta x} \right]_{upper} z^{-1} - \left[D_A \frac{\Delta c_{CO_2, lower}}{\Delta x} \right]_{lower} z^{-1} \quad (3)$$

The left-hand expression in parentheses represents the diffusive flux of CO₂ at the upper boundary, the right-hand expression at the lower boundary of a layer (D_A , apparent diffusion coefficient in soil corrected for porosity using $D = D_0\phi^2$ (Lerman, 1988); $\Delta c_{CO_2} / \Delta x$, concentration gradient at upper or lower end of segment; z , thickness of the layer). The diffusion coefficients D_A for CO₂ in the pore water of the fen were calculated for in situ temperature following Wilke and Chang (1955). The diffusion coefficients D_A for CO₂ in the unsaturated soil were calculated from the gaseous diffusion coefficient for CO₂ (Pritchard and Currie, 1982) corrected for temperature and a correction function $\alpha(a) = a^2\phi^{-2/3}$ (α , correction factor at air content a ; ϕ , soil porosity) (Jin and Jury, 1996). Volumetric gas content in the unsaturated soil was derived from total porosity and volumetric water contents (VWCs). For determination of total porosity, soil samples were fully saturated with water, weighed and then oven-dried. From a laboratory mesocosm study, a linear rela-

tionship of VWC and the respective distance from the water table with an r^2 of > 0.9 had been derived previously (K.-H. Knorr, personal communication, 2012). CO₂ net turnover rates of the uppermost peat layer have to be interpreted with caution, because there are inherent uncertainties in calculation of the respective diffusive CO₂ fluxes due to varying gas diffusivity in the unsaturated zone and steep and very likely non-linear CO₂ concentration gradients between the soil surface at 0 cm and –10 cm (Knorr et al., 2008).

2.6 Data analysis and statistics

For analysis of water table data, we formed corresponding pairs of D1–3 and C1–3 plots (D1–C1; D2–C2; D3–C3), because there is a natural gradient in peat body thickness from northwest to southeast affecting groundwater level. To test for statistically significant differences in soil CO₂ efflux between treatment and control plots on individual sampling dates, we used the two-sample t-test. Cumulative CO₂ effluxes were calculated on individual chamber basis and, thereafter, averaged plot by plot. We interpolated linearly between adjacent soil CO₂ efflux measurements and multiplied by time to calculate how much CO₂ was emitted in total between two measurements. Soil CO₂ effluxes were summed over treatment periods and years (total), respectively. In case of the trenched subplots, cumulative CO₂ effluxes were only calculated for the growing season from 1 May to 31 October in both years. For the flooded plots, cumulative CO₂ effluxes of 2010 exclude the peak in soil CO₂ efflux (28 July 2010) induced by the one-week interruption of flooding. For statistical analysis, cumulative soil CO₂ effluxes of the treatment and control plots were compared using the two-sample t-test.

3 Results

3.1 Soil temperature, precipitation and water table fluctuation

Mean soil temperature at 10 cm depth varied between 0.7 and 14.4 °C in the control plots throughout the experimental period (Fig. 2a). From mid-April to mid-May of 2010, mean soil temperature was 2.4 °C lower than in the respective time period of 2009. Considering air temperature, the year 2010 was 1.4 °C colder than the year 2009 (Table 1).

Soil temperature was reduced by 1.1 °C and 0.8 °C in the flooded plots during the growing seasons of 2009 and 2010, respectively. The differences in soil temperature between the control and flooded plots were greater at low water level in the control plots, indicating that soil temperature is sensitive to changes in water level. Overall, mean annual soil temperatures were 0.7 °C (2009) and 0.6 °C (2010) lower in the flooded plots.

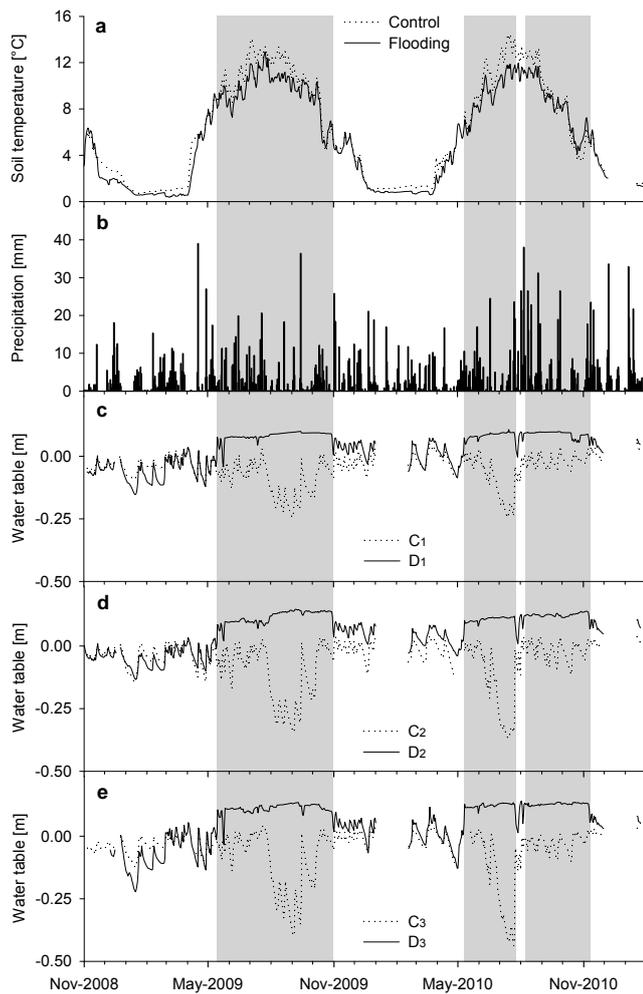


Fig. 2. Daily mean soil temperatures at 10 cm depth (a), precipitation (b) and water table levels (c–e) in the control (C) and flooded plots (D). Shaded areas mark the periods of experimental flooding with an interruption for technical reasons at the end of July 2010.

Mean water table fluctuated between 0.08 and -0.06 m during the pre- and post-treatment periods and was not statistically different between the control and flooded plots (Fig. 2c–e). In the control plots, mean water table varied along a gradient from the edge (C1) to the center (C3) of the peatland. Minimum water tables of -0.40 to -0.44 m were measured in the plot C3 during the growing seasons of both years, indicating that the topography of the peatland affected the water table on a small scale. The period of reduced water table below -0.10 m was longer in 2009 than in 2010 because of less precipitation in 2009. Heavy rain events caused rapid recovery in the water table of the control plots.

The water table increased to approximately 0.05 – 0.10 m above the peat surface following permanent irrigation (Fig. 2c–e). This level was relatively constant during the flooding periods, and it was never reached in the control plots. In the summer of 2010, however, irrigation was inter-

rupted for one week due to technical problems. Water table shortly dropped to about 0 m during the interruption. The daily amount of irrigation water (1400 – 2000 mm d^{-1}) exceeded by far the average amount of precipitation (2.6 and 3.6 mm d^{-1} in 2009 and 2010, respectively).

3.2 Soil CO₂ efflux

Soil CO₂ efflux was not significantly different in the control and treatment plots during the pre-treatment periods in 2009 and 2010 (Table 1). Flooding immediately reduced soil CO₂ efflux in May 2009 and prevented an increase during the following months despite an increase in soil temperature (Fig. 3a). In the control plots, soil CO₂ efflux reached a maximum in August 2009 at high soil temperature and low water table. A period of heavy rainfalls accompanied by an increase in water level and a decrease in soil temperature caused a strong decline in soil CO₂ efflux in mid-September of 2009. Thereafter, CO₂ effluxes were no longer different in the control and treatment plots. Flooding reduced cumulative soil CO₂ efflux by 142 g C m^{-2} in the treatment period of 2009, representing an annual reduction of 42 %.

The influence of flooding on soil CO₂ efflux was not statistically significant in 2010 (Table 1). On the one hand, cumulative CO₂ efflux of the control plots was smaller although the treatment period was prolonged by 14 days in 2010. The reduced CO₂ efflux in the control plots may be attributed to the lower temperature and shorter period of natural water table drawdown. On the other hand, cumulative soil CO₂ efflux in the treatment plots was slightly greater in 2010 (158 g C m^{-2}) than in 2009 (129 g C m^{-2}).

The short interruption of irrigation in July 2010 induced a short-lived pulse of soil CO₂ efflux which was slightly higher than the respective CO₂ efflux in the control plots, indicating the prompt response to changes in the water table near the peat surface. Again, soil CO₂ efflux declined below the control level after resumption of irrigation. A slight increase in soil CO₂ efflux was observed in October 2010 shortly after the irrigation was switched off.

3.3 Partitioning of soil CO₂ efflux

Exclusion of root respiration by trenching significantly reduced cumulative soil CO₂ efflux by 94 g C m^{-2} in the control plots during the growing season of 2009 (Table 1). The difference between the trenched subplots and the control was smaller (54 g C m^{-2}) and not significant in 2010. This resulted from a decrease in soil CO₂ efflux of the non-manipulated subplots in spring, whereas the cumulative CO₂ efflux of the trenched subplots was similar in both years. The small soil CO₂ efflux in the control plots coincided with relatively low temperatures from mid-April to mid-May which delayed and decelerated the growth of grasses and microbial activity in early spring of 2010.

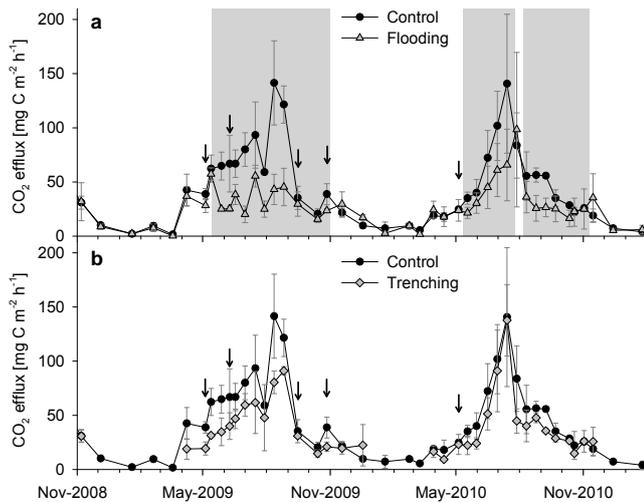


Fig. 3. Soil CO₂ effluxes in (a) control and flooded plots and (b) in control plots and trenched subplots. Error bars represent the standard deviation of the mean (SD). Shaded areas mark the periods of experimental flooding with an interruption for technical reasons at the end of July 2010. Arrows point to dates of radiocarbon sampling.

Heterotrophic ¹⁴CO₂ signatures of the control plots were determined by two different approaches on five occasions (Fig. 4a). The temporal course of Δ¹⁴CO₂ values (66.3–103.2‰) from incubated peat samples displayed a seasonal change in the mineralization of younger (May 2009, May 2010) towards older organic matter (June, September, October 2009). Radiocarbon signatures of heterotrophic CO₂ efflux in the trenched subplots (69.2–89.2‰) exhibited a less pronounced seasonal pattern. The Δ¹⁴CO₂ values of both methodological approaches corresponded in May 2009/2010 and October 2009, but were different in June and September 2009. Incubated peat samples mostly revealed variable Δ¹⁴CO₂ values at the same sampling date, whereas the respective Δ¹⁴CO₂ values of the trenched subplots were relatively homogenous.

Radiocarbon signatures of soil CO₂ efflux varied between 60.6 and 66.0‰ in the control plots during the growing season of 2009 (Fig. 4b). A smaller Δ¹⁴CO₂ value of 53.1‰ was measured in May 2010. In the pre-treatment period, Δ¹⁴CO₂ values of soil CO₂ efflux were not different between the control and flooded plots. Elevated Δ¹⁴C signatures (68.4–82.7‰) were determined in the flooded plots from September 2009 to May 2010. This shift in the isotopic signature corresponded to the shift in the heterotrophic Δ¹⁴CO₂ signature of incubated peat samples.

The ¹⁴CO₂ signatures of live grass roots ranged between 35.0 and 39.6‰ (Fig. 4b) and were slightly below the mean annual atmospheric CO₂ signature of 41.9‰ in 2009 measured at Schauinsland, Germany (I. Levin, personal communication, 2011).

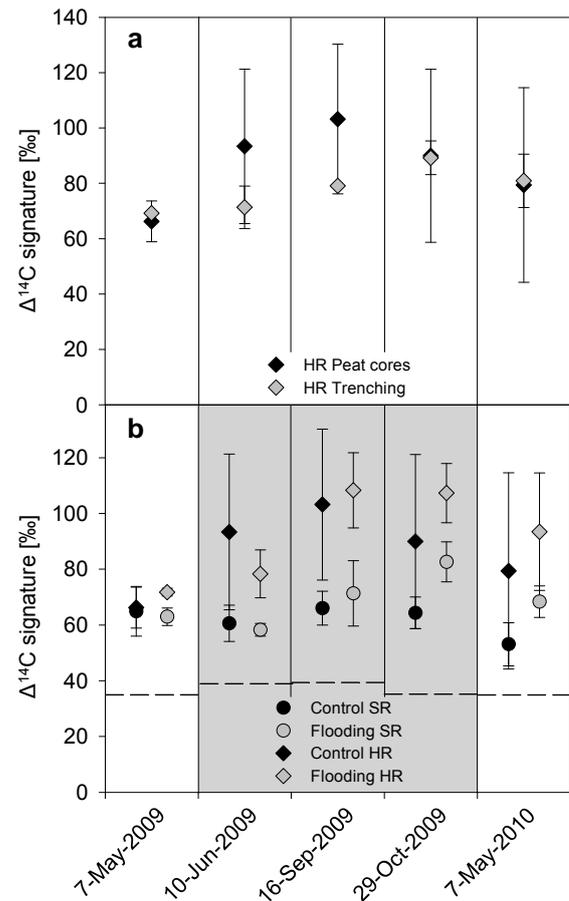


Fig. 4. (a) Mean Δ¹⁴C signatures of heterotrophic respiration (HR) determined by laboratory incubation of peat cores from control plots (black diamonds) and by field incubation in the trenched subplots (grey diamonds). (b) Mean Δ¹⁴C signatures of soil CO₂ efflux (SR, circles) and heterotrophic respiration (HR, diamonds) in control (black) and flooded plots (grey). Dashed lines represent the mean Δ¹⁴C signatures of rhizosphere respiration (RR). Sampling dates within the period of experimental flooding are shaded. Error bars represent the standard deviation of the mean (SD).

Partitioning of soil CO₂ effluxes using Eqs. (1) and (2) revealed large seasonal differences in the origin of CO₂ at the control plots (Fig. 5a). Heterotrophic respiration peaked in May 2009 with 37 mg C m⁻² h⁻¹ and decreased afterwards to 10 mg C m⁻² h⁻¹ in May 2010. Maximum rhizosphere respiration of 41 mg C m⁻² h⁻¹ was measured in June 2009. Afterwards, rhizosphere respiration dropped to 15 mg C m⁻² h⁻¹ in May 2010. Minimum rhizosphere respiration of 2 mg C m⁻² h⁻¹ occurred in May 2009, although temperature was higher than in 2010.

The relative contribution of rhizosphere respiration to soil CO₂ efflux amounted to 47–61% at the control plots from June 2009 to May 2010, but rhizosphere respiration (4 ± 8%) was very small in May 2009 (Fig. 5b). Rhizosphere respiration of 24 ± 13% in the flooded plots displayed

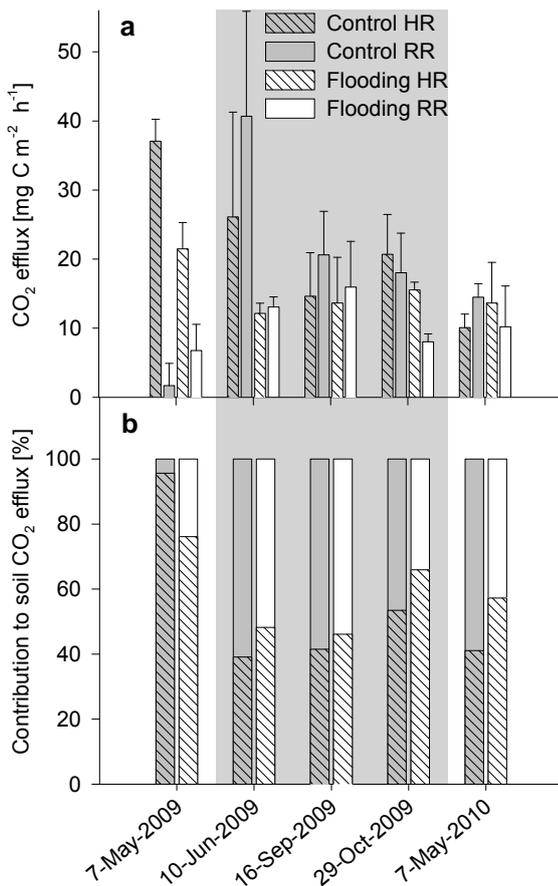


Fig. 5. (a) Soil CO₂ effluxes (mean ± SE) originating from heterotrophic (HR) and rhizosphere respiration (RR), and (b) their relative contributions to soil CO₂ effluxes in the control and flooded plots.

the differences in metabolic active vegetation during the pre-treatment period in May 2009. An intermediate contribution of rhizosphere respiration ($13 \pm 8\%$) was calculated using the heterotrophic ¹⁴C signature (69.2‰) from the trenched subplots (not shown). Both approaches illustrated the dominance of heterotrophic respiration as the main source of soil CO₂ efflux in May 2009.

In the flooded plots, rhizosphere and heterotrophic respiration were similar ($12\text{--}16 \text{ mg C m}^{-2} \text{ h}^{-1}$) in June and September, whereas rhizosphere respiration decreased to $8 \text{ mg C m}^{-2} \text{ h}^{-1}$ in October 2009. Except for the pre-treatment period, the percentage of rhizosphere respiration was always smaller in the flooded than in the control plots (Fig. 5b).

3.4 Pattern of CO₂ concentrations and CO₂ net turnover in peat profiles

The CO₂ concentration profiles exhibited large differences among individual control and flooded plots, reflecting the spatial heterogeneity of the peatland (Fig. 6). In the control

plots, elevated CO₂ concentrations of $> 4000 \mu\text{mol CO}_2 \text{ l}^{-1}$ were found during the treatment period in 2009. Except for the 50–60 cm depth at plot C2 from January to February of 2009, CO₂ concentrations were always $< 4000 \mu\text{mol CO}_2 \text{ l}^{-1}$ during the dormant seasons. In the treatment period of 2010, CO₂ concentration profiles were similar at plot C1 and C2 whereas C3 had on average smaller CO₂ concentrations than in 2009. Flooding significantly reduced the CO₂ concentrations in the peat profiles down to 60 cm depth in both years (Fig. 6). A strong increase in CO₂ concentrations occurred below 30 cm depth immediately after termination of the flooding treatment in 2009. Compared to 2009, the flooding was less effective in 2010 as mean CO₂ concentrations were higher at most depths.

CO₂ net turnover rates varied between -30 and $> 300 \text{ nmol cm}^{-3} \text{ d}^{-1}$ from -10 to -50 cm depth in the control plots (Fig. 7). Negative CO₂ net turnover rates were calculated for specific layers when the diffusive CO₂ flux at the upper layer boundary was smaller than that at the lower layer boundary causing a net CO₂ influx into that layer, regardless of its vertical direction. Such patterns result either from spatial variability of CO₂ concentrations in the peat body or from increased CO₂ production within individual peat layers. Positive turnover rates of $> 30 \text{ nmol cm}^{-3} \text{ d}^{-1}$ occurred only in the control plots during short periods of the growing seasons. By contrast, the turnover rates of the flooded plots remained below $30 \text{ nmol cm}^{-3} \text{ d}^{-1}$ and exhibited no seasonal differences in both years.

4 Discussion

The large amount of added irrigation water as well as the unevenly water level along the slope likely influenced the spatial pattern of C turnover in the flooded plots. Permanent input of oxygen by irrigation water could have promoted both autotrophic and heterotrophic respiration in the top cm of the peat surface. Moreover, DOC input by irrigation water represented an additional and continuous C source for heterotrophic respiration. However, the conditions within the collars, installed for CO₂ measurements, were different due to minor water exchange and, thus, small inputs of oxygen and DOC. Hence, the conditions within the collars correspond to conditions in flooded fens with standing water.

4.1 Response of soil CO₂ effluxes to flooding

Flooding reduced annual soil CO₂ efflux of the fen Schlöppnerbrunnen by 42 % in 2009 and by 30 % in 2010. We assume that the reduction in soil CO₂ efflux was not triggered by a decrease in peat temperature. Within the collars, peat temperature was probably elevated due to standing water compared to the decrease in peat temperature outside the collars. More likely, flooding limited the aeration of the peat body at our site (Estop-Aragonés et al., 2012)

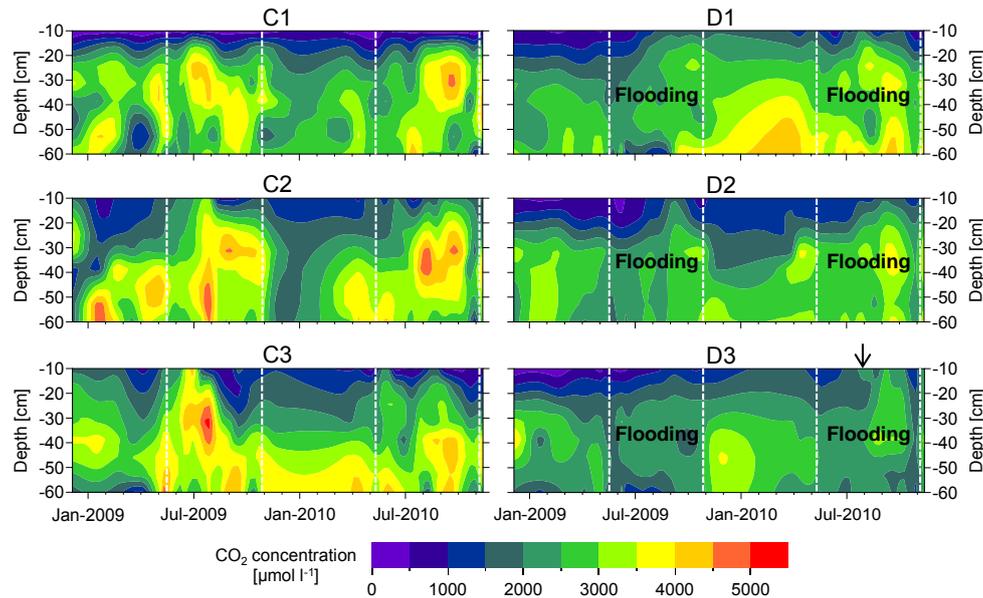


Fig. 6. Concentrations of dissolved CO₂ in pore water along soil profiles on control and flooded plots. Dashed white lines indicate start and end of the flooding periods during the growing seasons in 2009 and 2010. The arrow in D3 points to the date with an exceptional high soil CO₂ efflux due to interrupted flooding.

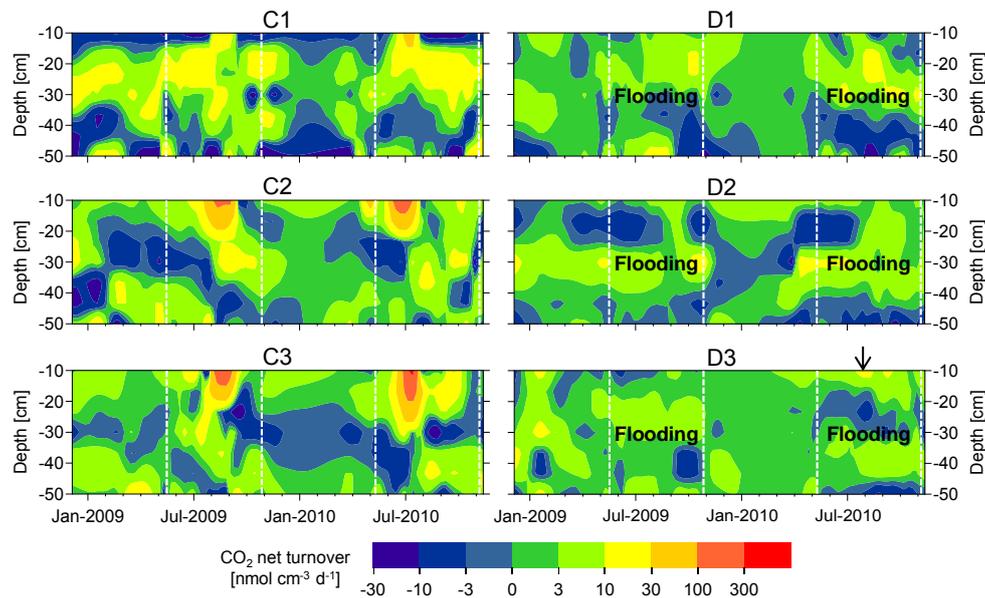


Fig. 7. Net turnover of CO₂ along soil profiles in the control and flooded plots. Dashed white lines indicate start and end of the flooding periods during the growing seasons in 2009 and 2010. The arrow in D3 points to the date with an exceptional high soil CO₂ efflux due to interrupted flooding.

which is a prerequisite for suppression of peat decomposition. The weaker response to flooding in 2010 emerged from changes in soil CO₂ efflux in the control and treatment plots. Temporarily elevated water level following intensive precipitation likely diminished soil CO₂ efflux in the control plots in 2010. Surprisingly, cumulative CO₂ efflux

slightly increased in the flooded plots at the same time. We have no well-founded explanation for this increase; perhaps it resulted from a slow change in vegetation (see below).

Our results underpin the impact of water fluctuations in the uppermost peat layer on soil CO₂ efflux in this fen ecosystem. However, the few existing studies on the response of

CO₂ effluxes to flooding revealed varying findings. Chimner and Cooper (2003) adjusted different water tables in a sub-alpine fen and measured a 35 % decrease in soil respiration at a water table of 6 to 10 cm above the soil surface. In their study, water table of the ambient control was on average 2–3 cm above the soil surface whereas average water table in our control plots was –9 cm (2009) and –6 cm (2010) below the soil surface. A decrease of the water table in the range of –6 to –10 cm more than tripled the CO₂ efflux relative to the raised water table of 6 to 10 cm (Chimner and Cooper, 2003). The response was possibly weaker at our partly drained fen because of the advanced loss of the easily degradable C pool in the uppermost peat layer.

Other studies reported no or minor effects of flooding on soil CO₂ efflux or ecosystem respiration. Chivers et al. (2009) raised the water table of a boreal fen by 9 to 11 cm above the control, though the water table was still below the soil surface. They found no change in ecosystem respiration, but the sink strength of the fen for atmospheric CO₂ was reinforced by an increase in gross primary production primarily through mosses. In view of differences in vegetation, peat decomposability and water table history, it is comprehensible that the C cycle of fen ecosystems responds inconsistently to flooding.

Surprisingly, water table drawdown together with exclusion of rainwater during the growing season had absolutely no effect on soil CO₂ efflux at Schlöppnerbrunnen (Muhr et al., 2011), although oxygen penetrated large parts of the unsaturated zone (Reiche et al., 2009; Estop-Aragonés et al., 2012). Muhr et al. (2011) attributed the missing drought effect to the low water level in the adjacent control plots and the insignificant C mineralization below 10–15 cm depth. It was concluded that the degraded peat below this depth was hardly vulnerable to elevated oxygen concentration (Knorr et al., 2008). This finding was supported by the small CO₂ net turnover rates in the peat profile (–10 to –50 cm) of the control plots which barely contributed to soil CO₂ efflux. Hence, almost all CO₂ was produced in the uppermost peat layer that was usually not water saturated in the control plots during the growing seasons. Turnover rates of 16–54 yr derived from radiocarbon signatures of peat highlighted the dominance of peat decomposition in the top 15 cm of this fen (J. Muhr, personal communication, 2012). In another study at this site, Estop-Aragonés et al. (2012) found ash contents of > 20 % in peat samples below 10–15 cm depth, indicating a strongly humified organic matter. Leaf litter and root litter input continuously replenish the organic matter pool in the uppermost peat layer and provide a pool of relatively easily decomposable C.

Unlike soil CO₂ effluxes, the CO₂ profiles of the peat body were permanently influenced by overflowing water. Nonetheless, flooding effectively reduced the biological CO₂ production at least at 10 cm depth and below as the CO₂ concentration did not build up in pore water. There are some hints that O₂ penetration was low in the top peat layer of the flooded

plots. The strong decline of electron acceptors like sulfate and nitrate, as well as methane production at 5 cm soil depth, suggests minor mixing of pore water and overflowing irrigation water (C. Estop-Aragonés, personal communication, 2012). Despite apparently minor O₂ penetration, we assume that irrigation water continued heterotrophic and rhizosphere respiration to some extent in the top peat layer compared to flooded fens with standing water.

How rapid and sensitive the uppermost peat layer responded to water table fluctuation, and consequently oxygen supply, was demonstrated by the interruption of flooding for one week in July 2010. Shortly after the interruption, the treatment plots had higher CO₂ effluxes than the control plots. Then, after re-initialization of flooding, CO₂ effluxes immediately declined again below the control level. A mesocosm experiment with peat cores from our study site supported the rapid response of soil CO₂ efflux, i.e. within one day, to water table drawdown and flooding (Chen et al., 2012). However, the response of CO₂ net turnover at –10 cm to the interrupted flooding was insignificant. A partly different response was observed in the control plots after water level rapidly increased due to intensive precipitation in August 2010. Here, both CO₂ net turnover at –10 to –20 cm and soil CO₂ efflux strongly declined at raised water level. The preconditions, however, were different, considering the preceding long period of lowered water table in the control plots.

4.2 Partitioning of soil CO₂ effluxes

We used two approaches to assess the contributions of rhizosphere respiration and heterotrophic respiration to soil CO₂ efflux in the control plots. According to trenching, rhizosphere respiration made an average contribution of 33 % whereas the radiocarbon method revealed 43 % in 2009. The difference between the two approaches resulted primarily from the measurements during the photosynthetic active months in June and September. Conservative estimates were obtained by the difference method (SR control – SR trenching) as leaf and root litter input was reduced in the collars of the control plots due to partial removal of green vegetation. Given the high CO₂ net turnover in the uppermost peat layer, litter input represents a main source of heterotrophic respiration in this peatland. Moreover, we cannot exclude that rhizosphere respiration was still reduced in the control plots three years after collar insertion. The relative disturbance of the root system through collar insertion, however, was constrained by the large area of collars (0.18 m²) and by the fact that grass-dominated hummocks were entirely included in the collars. Roots in the hummocks with a height of up to 30 cm above the hollows were barely affected by collar insertion. In a similar trenching experiment in various peatlands, the proportion of rhizosphere respiration varied between 10 and 40 % depending on the vegetation type (Silvola et al., 1996). They found that the proportion of rhizosphere

respiration increases with the amount of vascular plants and that rhizosphere respiration follows the typical phenology of the vegetation with a maximum around midsummer.

An overestimation of rhizosphere respiration was perhaps made with the radiocarbon method during the active growing season. Clipping of grass shoots shortly before sampling could have initiated a pulse of root respiration or of the root-shoot interface by mobilization of non-structural carbohydrates. Such a disturbance is unlikely for the other sampling dates in May and October as no or almost no green vegetation existed. The application of the radiocarbon method for partitioning of CO₂ fluxes has been challenged, because some peatland grasses have deep roots that act as conduits for gas exchange between the atmosphere and deep peat layers (Hardie et al., 2009). Release of CO₂ from decomposition of “old peat” by root aerenchyma would bias the mass balance approach. Depending on the CO₂ flux and its ¹⁴C signature, the “old peat” could potentially alter the contribution of rhizosphere respiration in two directions. In other words, the ¹⁴C signature of soil respiration could shift towards the heterotrophic or rhizospheric ¹⁴C signature. We cannot exclude such a mechanism at our study site, but CO₂ net turnover below 15 cm depth was negligible and the portion of aerenchyma roots is small. At our site, two-thirds of root biomass existed in the top 15 cm of the peat body (Otieno et al., 2012). The production of grass roots below this depth is apparently small.

Crow and Wieder (2005) reported a rhizosphere contribution of 19–32 % to soil CO₂ efflux in peat cores from an ombrotrophic bog following ¹⁴C pulse labelling. Mineralization of root exudates alone contributed up to 24 % to soil CO₂ efflux in their study, underpinning the role of root exudates for the C cycle in grass-dominated peatlands. The mineralization of peat, and thus the heterotrophic component, was underestimated in the 30-cm-long peat cores as the peat body had a natural depth of 3 m (Crow and Wieder, 2005).

In other field studies, not soil respiration but ecosystem respiration was partitioned which includes aboveground plant respiration as an additional component. In a previous study at our site, soil CO₂ efflux contributed on average 61 % to ecosystem respiration during June to October (Otieno et al., 2009). Considering the ¹⁴C-based estimates of heterotrophic respiration from June to October 2009 (Fig. 5), heterotrophic respiration would account for 27 % of ecosystem respiration in the control plots. This value is small compared to a study by Riutta et al. (2007) who stated that heterotrophic peat respiration was the largest component (i.e. 54–69 %) of ecosystem respiration in a boreal fen ecosystem. The difference to our study site can be attributed to the strong degradation of the peat and the relatively small peat stock.

Surprisingly, the percentage of rhizosphere respiration was slightly reduced from 56 % in the control plots to 46 % in the flooded plots. As this reduction still existed in the post-treatment period (May 2010), flooding had possibly a pro-

longed effect on the relative contribution of rhizosphere respiration. Provided that grasses maintain, at least in part, the oxygen supply of roots under flooded conditions, one would expect a relative increase in rhizosphere respiration. It seems that some grass species are not well adapted to rising water level of up to 10 cm above the peat surface. In fact, we made the observation that flooding promoted the growth of *Sphagnum* in some patches during the second treatment year. In agreement with our observation, Silvola et al. (1996) found a small percentage of rhizosphere respiration in a *Sphagnum*-dominated bog. If some grasses struggled under flooding conditions, elevated root litter input could have triggered a relative increase in heterotrophic respiration. Overall, the effect of flooding was small compared to the seasonal variation of rhizosphere and heterotrophic respiration.

5 Conclusions

The radiocarbon approach provided reasonable fluxes for heterotrophic and rhizosphere respiration under field conditions in this peatland. Seasonal flooding had an immediate effect on the soil C balance of the degraded fen despite small changes in the contribution of heterotrophic and rhizosphere respiration. CO₂ effluxes dominated the soil C balance while CH₄ fluxes were small and hardly affected by flooding (J. Köpp, personal communication, 2012). Rhizosphere respiration represents an important component of the C cycle in the grass-dominated fen ecosystem. However, partitioning of rhizosphere respiration and the role of root exudates require further efforts. The small heterotrophic respiration reflects the small stock of easily decomposable peat and the degradation of the fen. Our results cover the initial changes in the fen, while the long-term response of the C cycle to flooding, possibly due to a gradual shift of the plant community, remains unknown.

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