Sensitivity of carbon gas fluxes to weather variability on pristine, drained and rewetted temperate bogs

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SUMMARY

Climate change is considered to alter the functioning of boreal peatland ecosystems, but the vulnerability of pristine, rewetted and drained peatlands to climate change in temperate regions is unknown. We measured carbon (C) gas exchange during wet (2009) and dry (2010) growing periods in pristine, drained and rewetted sites in mountain bogs in the Bohemian Forest (Czech Republic). Wetter lawns with sedges and drier habitats dominated by ericaceous shrubs were distinguished and studied at each site.

Methane (CH_4) emissions, which decreased in the order pristine > rewetted > drained, were generally lower during the 2010 growing period than in 2009 as a consequence of a drought. During the drought in 2010, photosynthesis (P_G) in the drier habitats with shrub vegetation increased on pristine and rewetted sites, while total respiration (R_{ECO}) remained the same. Communities dominated by sedges maintained similar rates of P_G and R_{ECO} during both growing periods. Generally, this led to higher C accumulation during the drought on pristine and rewetted bogs. At the drained bog site, the decreased water table (WT) during the drought led to increased P_G and R_{ECO}, such that the net C accumulation was similar in the two years.

Drained peatlands may be more threatened by future climate change than pristine or rewetted peatlands because of their limited buffering capacity for decreased WT. In the case of further decreases in WT, they could lose the peatland vegetation and functions that have partly persisted through decades of drainage.

KEY WORDS: carbon dioxide; drainage; methane; photosynthesis; respiration; restoration; sedge

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INTRODUCTION

Northern peatlands, which comprise about half of the global wetland area, store approximately one third of the world's soil carbon (C) in the form of peat and act as a sink for atmospheric carbon dioxide (CO_2) and a source of methane (CH_4) (Gorham 1991, Turunen *et al.* 2002). The C sink function is driven by the long-term imbalance between photosynthetic uptake and respiratory loss (Tolonen *et al.* 1992). However, at an inter-annual scale, there can be considerable variability in net ecosystem exchange (NEE) caused by the different responses of respiration (R_{ECO}) and photosynthesis (P_G) to environmental controls. The structure and function of peatlands may be significantly affected by both human activities (especially drainage) and climate change (Gorham 1991, Frolking *et al.* 2011). Warmer and drier conditions predicted by climate models for peatland regions may result in the increased release of CO_2 to the atmosphere and induce a positive feedback to climate change (Updegraff *et al.* 2001, Weltzin *et al.* 2003). In the past, many peatlands in the Bohemian Forest (Czech Republic) were drained for forestry, leading to changes in the functioning of these ecosystems. Today, restoration work that is being implemented in this region aims to halt peatland degradation by repairing disturbed hydrology. Drainage is known to turn peatlands from long-term CO_2 sinks into sources of CO_2 (Ojanen *et al.* 2010) and cause significant changes in vegetation structure (Laiho *et al.* 2003). Moreover, climate scenarios for central Europe have predicted increased warming during winter and decreased precipitation in summer, especially during the first half of the growing period (IPCC 2007). If the climate changes as predicted, water table levels will decrease and this will be followed in peatlands by changes in vegetation (towards a drier successional stage) and C gas fluxes. Although the effect of climate change on pristine peatland has been addressed in case studies, it is still poorly understood (Bridgham 1995, Weltzin *et al.* 2003, Strack *et al.* 2006, Turetsky *et al.* 2008). As far as we know, the vulnerability of managed (drained, rewetted) peatlands to climate change has not been studied.

Although peatlands are long-term sinks of C (Gorham 1991), several studies have shown that they can change from annual sinks to annual sources of atmospheric C depending on hydroclimatic conditions (Shurpali *et al.* 1995, Alm *et al.* 1999b, Griffis *et al.* 2000). In most cases, lowering of the water table increases the rate of CO_2 loss (Shurpali *et al.* 1995, Alm *et al.* 1999b, Lafleur *et al.* 2003) through increased soil respiration. Griffis & Rouse (2001) demonstrated that changes in air temperature and the timing of precipitation events strongly influence NEE on subarctic fen, and suggested that P_G is a more important determinant of NEE than R_{ECO}. However, many other studies have indicated that changes in the water table level affect both plant production and decomposition (Alm *et al.* 1999b, Frolking *et al.* 2002, Whiting & Chanton 2001, Bubier *et al.* 2003b). Moreover, within a single peatland, under certain conditions some plant communities may act as sinks while others concurrently act as sources (Waddington & Roulet 1996, Bubier *et al.* 2003a). Some studies have also shown that evergreen shrubs are more resilient to drought than sedges (Weltzin *et al.* 2000, Weltzin *et al.* 2003, Bubier *et al.* 2003a). Different growth forms (evergreen and deciduous shrubs, sedges, *Sphagnum* mosses) are known to respond differently to drainage, when deciduous shrubs spread at the expense of other growth forms (Laiho *et al.* 2003, Riutta *et al.* 2007, Urbanová *et al.* 2012a). A similar trend in vegetation change is predicted by climate and ecosystem models (Kittel *et al.* 2000). Thus, an understanding of inter-annual NEE variability in the distinct plant community types of (wetter) lawns and hollows as opposed to (drier) hummocks in relation to environmental controls can deepen our knowledge about the response to climate change of the entire ecosystem.

We measured CO_2 and CH_4 fluxes using the closed-chamber method in pristine, drained and rewetted sites in a temperate mountainous bog over two growing periods. An exceptionally dry period occurred during midsummer in the second season. In this paper we aim to:

(1) compare the seasonal pattern of CO_2 fluxes and assess the impact of a drought period on different plant community groups (dominated by shrubs, grasses, or sedges); and

(2) estimate and compare P_G, R_{ECO} and NEE between different plant community groups in pristine, rewetted and drained sites over two different growing periods.

METHODS

Study sites

The study was carried out at three ombrotrophic bog sites (pristine, drained and rewetted) in the Šumava National Park (Bohemian Forest) in the southern part of the Czech Republic during the growing periods of 2009 and 2010. All study sites were part of the ongoing 'Peatland Restoration Programme in the Šumava National Park'.

Due to the high resolution of aerial photographs available in Google Maps, sites can be seen in detail; for example, location of drainage ditches and the surface structure of studied and surrounding peatlands. In general, the peatlands in this area were drained for forestry *ca.* 50 years ago but no trees were planted. Ditches are relatively large, being 2 m deep and as wide as 3.5 m, and their spacing ranges from 25 m to 40 m. From the point of view of forest production, the drainage was a failure because economically productive tree stands did not evolve. Rewetting of the bog was carried out in 2008 and included the blocking of ditches with timber dams and also the partial infilling of ditches with organic material such as branches and other tree remains.

The pristine (BOG) and rewetted bog (BOGR) sites were located at an altitude of 1,200 m a.s.l. on the central upland plateau of the Bohemian Forest (48° 58' 34" N, 13° 27' 24" E and 49° 1' 42" N, 13° 24' 20" E, respectively). The climate of the upland plateau is cold and humid with mean annual temperature 3.2 °C and annual precipitation around 1,300 mm. The drained bog site (BOGD; 49° 10' 59" N, 13° 19' 6" E) was located at an altitude of 900 m a.s.l. in the Kremelna River Valley, which has a slightly milder climate with mean annual temperature 4 °C and mean annual rainfall 1,000 mm (long-term average 1961–1990, Czech Hydro-meteorological Institute).

The BOG site was a mountain slope bog with a well-developed surface structure consisting of wet hollows, drier hummocks and intermediate lawns in the open central part and *Pinus* × *pseudopumilio* (Willk.) Beck scrub on the steeper slopes. Sedges were the dominant plant group, with *Trichophorum cespitosum* most abundant on the lawns, *Eriophorum vaginatum* on the hummocks and *Carex limosa* in the hollows. Dwarf shrubs such as *Andromeda polifolia, Vaccinium uliginosum* and *Vaccinium oxycoccos* were characteristic of the hummocks. The moss layer consisted of *Sphagnum rubellum, Sphagnum capillifolium* and *Sphagnum magellanicum* on the hummocks, while the wetter hollow surface was covered by *Sphagnum cuspidatum*. The moss layer was virtually absent on the lawns.

On the BOGR site, lawns were restricted to the wettest areas away from ditches and mostly covered by *T. cespitosum*. Hollows were absent. The blocked ditches were surrounded by dwarf shrubs (*Vaccinium myrtillus*, *V. uliginosum*) and small *Picea abies* trees were scattered across the entire site. Dominant species of the moss layer were

S. magellanicum, *S. russowii*, *S. capillifolium*, *Polytrichum strictum* and *Pleurozium schreberi*.

The BOGD site was covered with hummock-type vegetation with *V. uliginosum*, *V. myrtillus* and *Molinia caerulea* the dominant species in the drier areas alongside the ditches while *Betula pubescens* covered the whole site. *P. strictum* and *S. russowii* comprised the field layer.

Six permanent sample plots (60 × 60 cm) for vegetation monitoring and C gas flux measurements were established at each site. On the BOGD and BOGR sites, three sample plots were placed along the margins of the ditches and three were placed in the wetter part farther away from the ditches. On the BOG site, three sample plots were located in wetter *T. cespitosum* lawns and three in drier shrubby areas.

Nomenclature follows Moore (1982) for vascular plants and Kučera & Váňa (2003) for bryophytes.

Vegetation monitoring

The vascular green area (VGA, $m^2\ m^{-2}$) according to Wilson *et al.* (2007) was measured in each sample plot at intervals of two or three weeks. Five sub-plots (8 × 8 cm) were established within each sample plot. Leaves and stems of each vascular plant species were counted in the sub-plots and the totals extrapolated to estimate the average number of leaves and stems of each species per square metre. The length and width of approximately 20 leaves of each species, collected outside the sub-plots, were measured manually in the field (sedges, grasses) or by a scanner in the laboratory (shrubs, herbs). In addition, we estimated the projected or top cover of mosses once during the growing period.

The species-specific VGAs were grouped into three different plant functional types (PFT): shrubs, forbs and grasses, and sedges (*E. vaginatum*, *T. cespitosum*). The seasonal development of VGA_{PFT} was modelled using unimodal response curves (Gaussian or log-normal function).

Sample plot classification

We classified the gas exchange sample plots according to vegetation and environmental variables (water table level (*WT*), pH, electrical conductivity (EC)) using cluster analysis with a complete linkage method, where the distance between groups was defined by the most distant members of the groups (STATISTICA 8, StatSoft Inc., USA) (for groups see Table 1). The classification confirmed *a priori* identified plant communities, which were used to select sample plots. Two groups; BOGD molinia (two sample plots) and BOGD high shrub (one sample plot) formed an exception as they were originally considered to represent one group (drier part of BOGD). In most of the statistical analyses, these two groups were combined as a single group BOGD molinia+high shrub. However, in CO_2 flux modelling it was not possible to analyse them together because of their very different responses to controlling factors (temperature, VGA, PAR, *WT*).

Environmental variables

The study sites were supported by two automatic meteorological stations (Fiedler-Mágr Electronics for Ecology, Czech Republic); one located on the upland area of BOGR (data used in the reconstruction of C fluxes for BOG and BOGR) and the other in the Kremelna River Valley in the vicinity of the BOGD site. Both meteorological stations measured air temperature at heights of 30 cm and 2 m above the soil surface, soil temperature at a depth of 5 cm, and precipitation (Fiedler-Mágr Electronics for Ecology). Radiation (PAR) was measured at the Churáňov Station of the Czech Hydro-meteorological Institute, located 15–25 km away from our study sites. Soil temperature (at depths of 5, 10 and 20 cm) was measured at each plot simultaneously with the CO_2 and CH_4 flux measurements. The level of the water table (*WT*) was measured in a perforated PVC dipwell (80 mm internal diameter) located next to each sample plot, manually at two-week intervals during the growing period, and as continuous time series using pressure sensors (Fiedler-Mágr Electronics for Ecology).

CO_2 and CH_4 flux measurement

Static closed chambers were used to measure CO_2 and CH_4 fluxes (e.g. Laine *et al.* 2009). Each permanent sample plot was defined by a plastic collar (60 × 60 cm) inserted into the soil to a depth of 15 cm one year prior to measurement. The collar was equipped with a water groove that ensured secure chamber placement and acted as an air-tight seal during gas exchange measurements. A boardwalk was constructed around the collar to avoid damage to the soil and plants during the measurements.

CO_2 exchange measurements were carried out at 2–3 week intervals during the 2009 and 2010 growing periods (from the end of April to the beginning of October). A set of measurements was obtained once a day, between 9 a.m. and 4 p.m., on all plots. NEE was measured using a transparent Plexiglas (Perspex) chamber equipped with a cooling water circuit, thermostat and two fans. Measurements were carried out at 15-second intervals over a period of 90–120 seconds in full light and under one or two lower levels of light intensity arranged by artificial shading. R_{ECO} was determined under darkened conditions, created by covering the chamber with an opaque hood. The

Table 1. Plant community groups based on cluster analysis. Dominant plant species and vascular green area (VGA) measured in the middle of the growing period (27 July 2009 and 08 July 2010) are shown for each group. VGA for three plant functional plant types (sedges, forbs and grasses, shrubs) and total VGA are shown. Moss cover was similar in both seasons. Mean seasonal water table level relative to ground surface and number of sampling plots (*n*) are shown for each group.

SITE	Group	Dominant species	VGA m^2 m^{-2}								Moss cover (m^2m^{-2})	Water table (cm)		*n*
			sedges		forb - grass		shrubs		total					
			2009	2010	2009	2010	2009	2010	2009	2010		2009	2010	
BOG	trich lawn	*Trichophorum cespitosum*	3.06	2.67	0.00	0.00	0.07	0.08	3.13	2.78	0.03	-2.9 ±2.4	-3.9 ±3.3	3
	low shrub	*Andromeda polifolia, Eriophorum vaginatum, Vaccinium uliginosum*	1.70	1.71	0.00	0.00	0.37	0.37	2.70	2.09	0.76	-10.6 ±7.7	-10.2 ±4.7	3
BOGR	trich lawn	*Trichophorum cespitosum*	2.28	2.38	0.00	0.00	0.16	0.14	2.44	2.52	0.02	-9.8 ±8.1	-11.0 ±7.9	3
	high shrub	*Vaccinium myrtillus, V. uliginosum, Sphagnum magellanicum, S. capillifolium*	0.36	0.06	0.14	0.01	1.77	2.63	2.27	2.70	0.82	-18.5 ±7.7	-17.6 ±5.0	3
BOGD	inter shrub	*V. uliginosum, E. vaginatum, Molinia caerulea, Calluna vulgaris*	0.75	1.13	0.42	1.07	0.77	1.05	1.94	3.25	0.77	-13.2 ±6.5	-16.9 ±10.3	3
	molinia	*Molinia caerulea*	0.09	1.46	7.12	7.28	0.01	0.03	7.22	8.77	0.00	-24.2 ±10.3	-25.6 ±10.3	2
	high shrub	*V. myrtillus, V. uliginosum, Polytrichum strictum, S. magellanicum*	0.00	0.00	0.01	0.14	2.27	2.63	2.28	2.77	0.25	-53.1 ±10.3	-57.1 ±7.4	1

concentration of CO_2 (ppmv) in the chamber headspace was measured using a portable infra-red gas analyser (EGM-4, PP System, UK) connected to the chamber. Simultaneously, photosynthetically active radiation (μmol m^{-2} s^{-1}) inside the chamber and chamber temperature were recorded using a temperature/PAR probe (TRP-2, PP System, UK). CO_2 flux rates (mg CO_2 m^{-2} hr^{-1}) were calculated from the linear change in CO_2 concentration in the chamber headspace over time, taking into account the chamber volume and temperature. Gross photosynthesis (P_G) was calculated from the equation:

$$\mathrm{NEE} = P_\mathrm{G} - \mathrm{R_{ECO}} \qquad [1]$$

so that positive values of NEE indicated CO_2 uptake by the ecosystem and negative values reflected release of CO_2 to the atmosphere.

CH_4 fluxes were measured on the same plots as CO_2 exchange using closed opaque chambers. Each of these chambers was equipped with a fan for air circulation and a gas-tight rubber septum for sampling (using a syringe). Gas samples (three replicates) were taken from the ambient air and chamber headspace, when the chamber was closed and 20 minutes later. The gas samples were injected into Labco Exetainer vials (Labco Limited, UK) and taken to the laboratory. CH_4 concentration (ppb) was then analysed within 48 hours on a HP 6890 gas chromatograph (Agilent, USA) equipped with a 0.53 mm × 30 m GS-Alumina column (Agilent, USA) and flame ionisation detector, using nitrogen as the carrier gas and Agilent Chemstation A.08.03 software (Agilent, USA). The CH_4 flux (mg CH_4 m^{-2} hr^{-1}) was calculated assuming a linear change in its concentration during closure of the chamber (Tuittila *et al.* 2000). The seasonal CH_4 flux was estimated by integrating daily emissions calculated using linear interpolation between the measured data. The relationships between measured R_{ECO} and *WT* and between measured CH_4 emissions and *WT* were tested by simple regression (STATISTICA 9, StatSoft Inc., USA).

CO_2 exchange models

Process-based non-linear regression models for CO_2 exchange were constructed and parameterised individually for each gas exchange sample plot, following Tuittila *et al.* (2004) and Laine *et al.* (2009), using the SPSS 15.0 statistical package (SPSS Inc., USA). The relationship between P_G (calculated as NEE+R_{ECO}) or R_{ECO} and environmental variables was determined and the combination of factors was tested to obtain an unbiased residual distribution, the highest possible coefficient of determination (R^2) and smallest standard error of the estimate.

The model construction for P_G was based on the Michaelis-Menten relationship for light dependence of the photosynthesis rate. PAR, VGA, air temperature (T_{air}) and *WT* were tested as explanatory variables in the P_G models. The amount of photosynthesising plant material (VGA) was added as an explanatory variable in Equation 2 and Equation 3, and *WT* was also added in Equation 4:

$$P_G = P_{\max}\frac{\mathrm{PAR}}{k+\mathrm{PAR}}\mathrm{VGA} \qquad [2]$$

$$P_G = P_{\max}\frac{\mathrm{PAR}}{k+\mathrm{PAR}}\left[1-\exp\left(-a\mathrm{VGA}\right)\right] \qquad [3]$$

$$P_G = P_{\max}\frac{\mathrm{PAR}}{k+\mathrm{PAR}}\mathrm{VGA}\times\exp\left[-0.5\left(\frac{WT-W_{\mathrm{opt}}}{W_{\mathrm{tol}}}\right)^2\right] \qquad [4]$$

where P_{max} denotes the maximum light-saturated photosynthesis rate and the parameter *k* is equal to the PAR value at which the photosynthesis rate is half its maximum. Parameter *a* denotes the initial slope of the saturation VGA response function. W_{opt} and W_{tol} are the water level optimum and tolerance for photosynthesis. Equation 2 was used for all plots in 2009 and Equation 3 for most of the plots in 2010. Equation 4 was used for three sample plots from the BOGR trich lawn group in 2010.

In the R_{ECO} models (Equation 5), VGA, T_{air}, the soil temperature at a depth of 5 cm (T_{soil}) and *WT* were tested. In most (but not all) cases, T_{air} explained the variability better than T_{soil}.

$$\mathrm{R_{ECO}} = \exp\,(c\ \mathrm{T}) + v\ (\mathrm{VGA}) \qquad [5]$$

where T denotes the temperature of air or soil and the parameters *c* and *v* are multipliers for temperature and VGA, respectively.

To obtain cumulative growing period fluxes for each plant community, P_G and R_{ECO} were reconstructed separately for each sample plot using plot-specific environmental data (reconstructed VGA, continuously measured *WT*), continuously measured environmental variables from weather stations (PAR, T_{air}, T_{soil}), and sample-plot-specific models. We used a one-hour time step in reconstruction. Hourly NEE was calculated from estimated P_G + R_{ECO}. The seasonal estimates were calculated as a sum of the hourly P_G, R_{ECO} and NEE values from 01 May to 10 October for BOGD (162 days), and from 15 May to 10 October for BOG and BOGR (147 days), because the growing period started two weeks earlier on BOGD.

The relationship between estimated R_{ECO}, NEE, CH_4 and *WT* were tested by simple regression (STATISTICA 9, StatSoft Inc., USA). Estimated CO_2 fluxes were tested by repeated measures ANOVA to show the effects of study site, year and the combination of study site and year.

RESULTS

Environmental variables

The 2009 growing period was, on average, warmer than the 2010 growing period (12.15 °C and 11.55 °C, respectively). The first half of the 2009 growing period was wet with a cold and rainy period at the end of June and the beginning of July, and the rest of it was relatively dry. The first half of the growing period was drier in 2010 than in 2009 and included a very warm and exceptionally dry period in June and early July (Figure 1). Rainfall events were more frequent during the second half of the 2010 growing period. Mean air temperature for the growing period (01 May to 10 October) at upland and lowland sites (12.1 °C and 12.2 °C, respectively) was the same in 2009 and differed only slightly in 2010 (11.4 °C and 11.7 °C). The upland sites received 811 mm of precipitation in the 2009 growing period and 883 mm in the 2010 growing period; whereas the BOGD site received 614 and 587 mm in the 2009 and 2010 growing periods, respectively (Figure 1). The growing period started two weeks earlier on the lowland site in comparison to the upland sites due to the slower melting of snow at higher altitudes.

The water table was highest and most stable in the BOG site, whilst the lowest mean *WT* and highest *WT* fluctuations occurred in the most intensively drained parts of the BOGD site (molinia and high shrub groups; Table 1). Mean *WT* at the BOGR site was lower than at the BOG site. *WT* was relatively stable during the first half of the 2009 growing period and then slowly decreased at the beginning of autumn (Figure 2). In contrast, in 2010 *WT* fluctuated more in June and reached its lowest level at the beginning of July. For the rest of the 2010 growing period, *WT* was more stable.

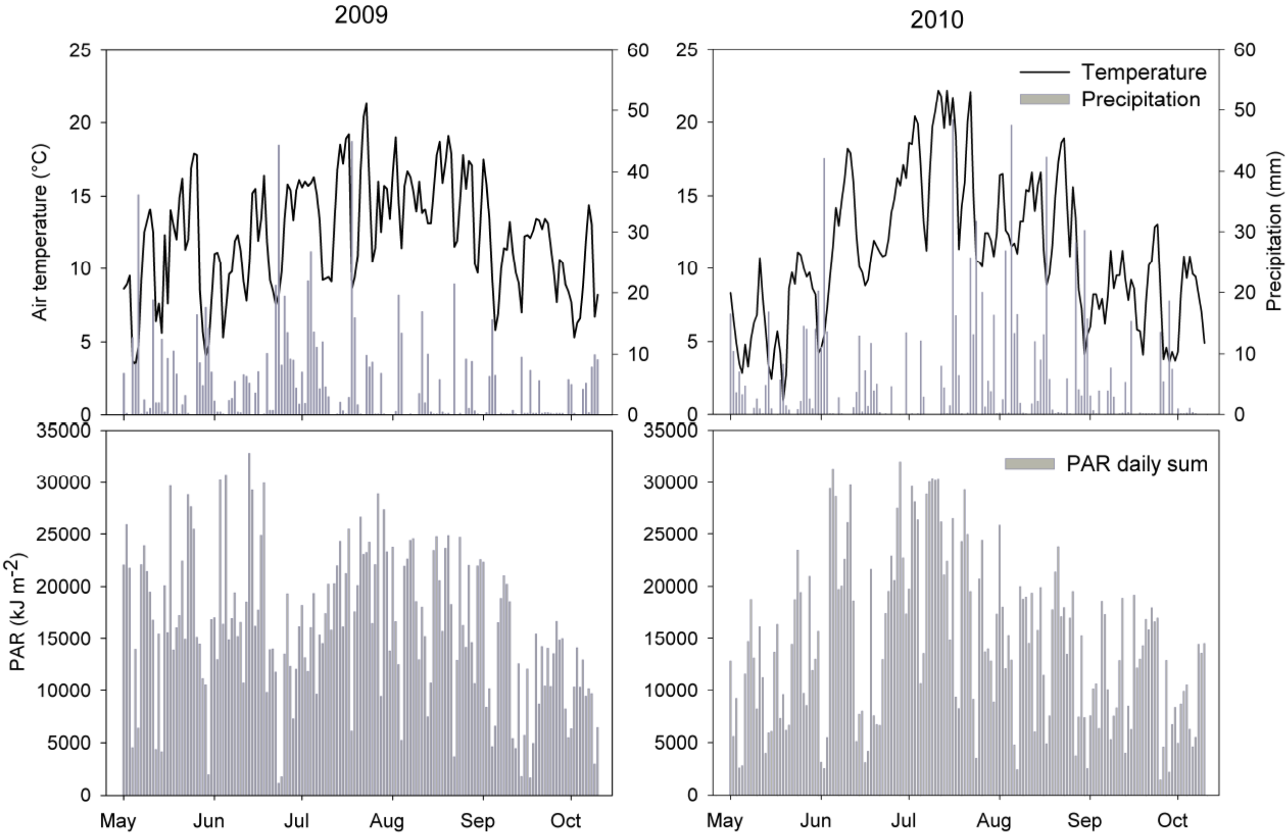

Figure 1. Above: daily average air temperature 30 cm above the soil surface and daily precipitation sums, measured during the 2009 and 2010 growing periods (01 May to 10 October). Below: daily sums of photosynthetically active radiation (PAR) during the 2009 and 2010 growing periods.

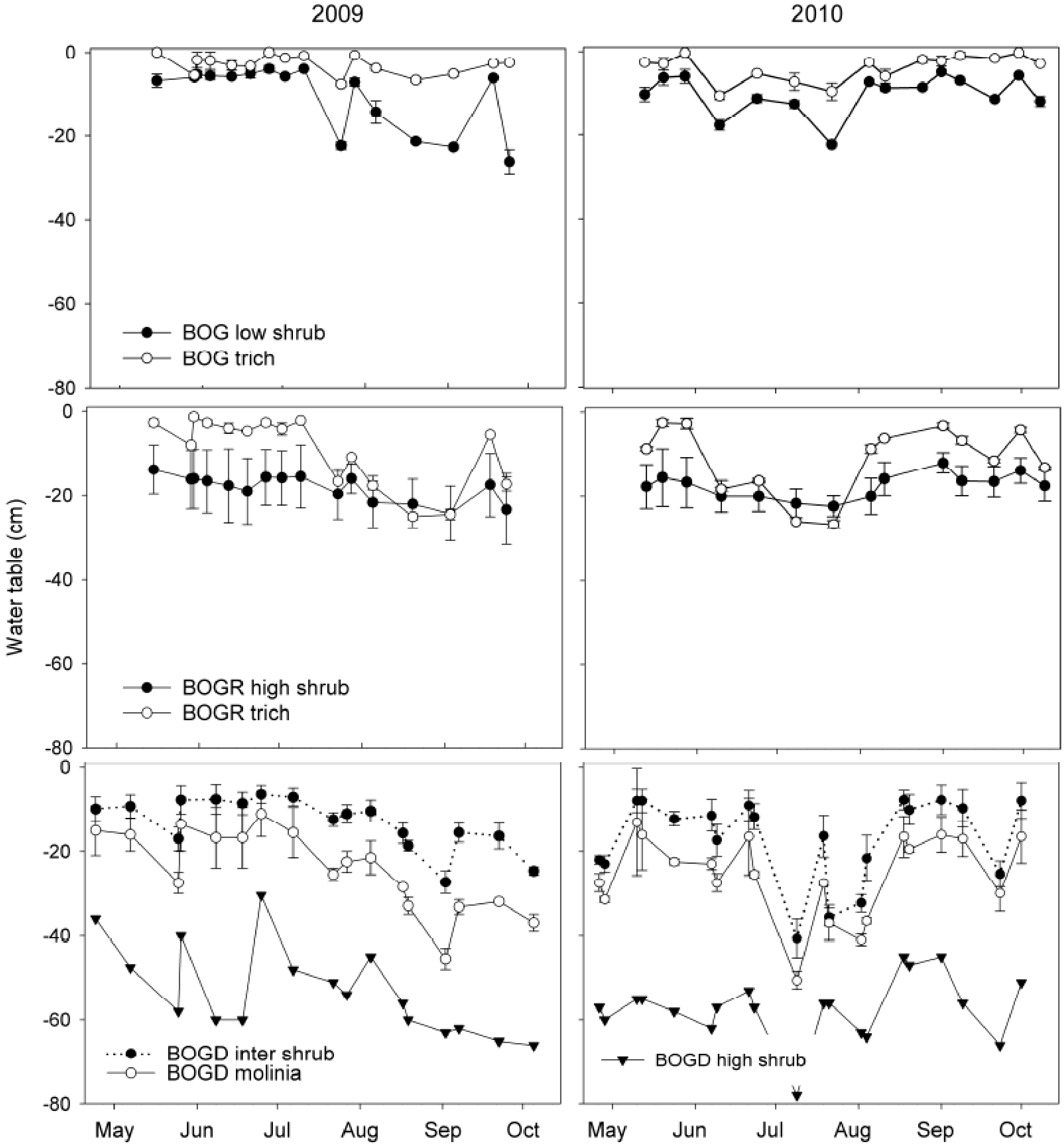

Figure 2. Mean measured water table level ± standard deviation in each plant community group at all study sites (n = 1–3) during the 2009 and 2010 growing periods.

Vegetation

No changes in plant composition were observed within the sampling plots at the BOG and BOGD sites. Although the majority of the BOGR vegetation did not change during the first two growing periods after rewetting, noticeable changes were observed in the vicinity of the blocked drainage channels, where *Sphagnum* and *E. vaginatum* were spreading and dwarf shrubs (*V. myrtillus*, *V. uliginosum*) were decreasing

The vegetation was separated into seven plant community groups (Table 1) on the basis of vegetation composition and selected environmental variables (*WT*, EC, pH). These groups effectively reflected the spatial variation observed in the bogs. The differences in vegetation between the groups were coupled with the differences in *WT*.

The highest vascular green area (VGA) was measured in the dry BOGD molinia group, whereas VGA in the BOGD inter shrub and high shrub groups was similar to that on the BOGR and BOG sites (Table 1). The seasonal development of VGA was clearly reflected in photosynthesis and respiration (Figure 3). The seasonal maximum of

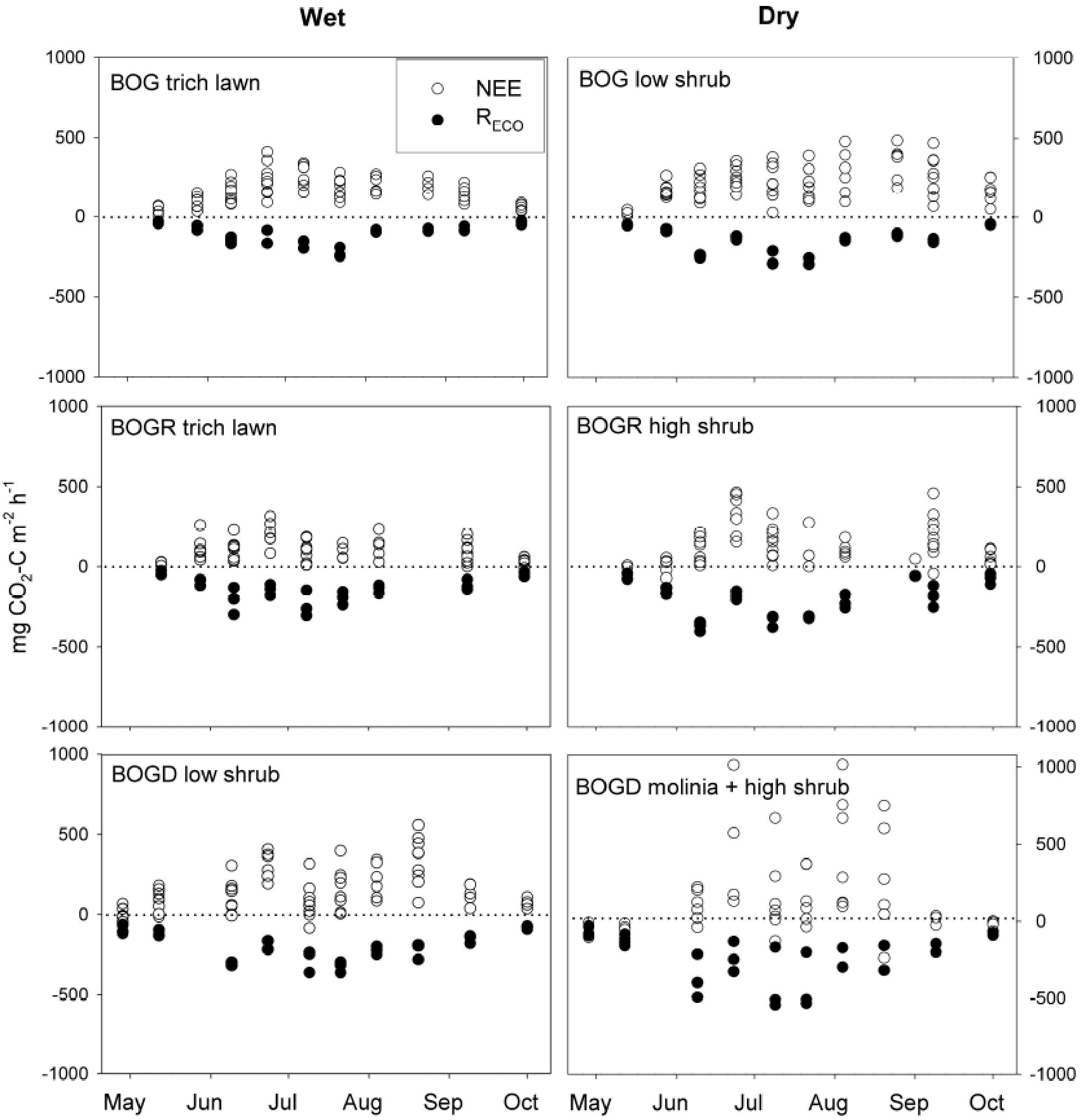

Figure 3. Measured instantaneous net CO_2 exchange (NEE, R_{ECO}) of studied plant community groups in the 2010 growing period (for comparison with the 2009 growing period, see Urbanová *et al.* 2012a).

VGA for selected plant groups did not vary much between the two growing periods, but it occurred two weeks earlier in 2010 because June and July were warmer and wetter that year in comparison to 2009.

The seasonal VGA development varied between the plant groups. The groups dominated by *T. cespitosum* (BOG trich lawn, BOGR trich lawn), by grasses (BOGD molinia) and deciduous shrubs (BOGD high shrub) were characterised by rapid growth in the spring and a rapid decrease in VGA during the second half of the growing period. Especially, after the maximum VGA was attained, the VGA of *Trichophorum* lawns and *Molinia* decreased faster than that of shrubby groups, and the trich lawn and molinia groups also exhibited decreased rates of photosynthesis. In contrast, the VGA development of low shrub and inter shrub groups was distinguished by a slow decrease in VGA during the autumn caused by the presence of evergreen shrub species (*V. oxyccocos*, *A. polifolia, Calluna vulgaris*) and *E. vaginatum*, which all remained photosynthetically active until the late autumn.

Measured CO_2 exchange

The measured CO_2 exchange (NEE, R_{ECO}) mostly varied between -400 and 600 mg CO_2-C m^{-2} h^{-1} in the growing periods of both years (see Figure 3 for 2010 and Figure 2 in Urbanová *et al.* 2012a for 2009). However, much larger CO_2 fluxes (between -600 and 1100 mg CO_2-C m^{-2} h^{-1}) were measured in the BOGD molinia plots. The differences in CO_2 fluxes between the groups were related to differences in VGA (Table 1).

The seasonal dynamics of CO_2 fluxes followed those of temperature, precipitation and PAR (Figure 3). Especially in the second halves of the two growing periods, the CO_2 fluxes at the BOG and BOGR sites were larger in the shrub plots than in the trich lawn plots, where the VGA decreased faster. In 2009, a short decline in NEE values occurred because of the cold and rainy period at the beginning of July. In July 2010, NEE decreased noticeably due to the hot and dry period, which led to a decrease in plant photosynthesis. After this, NEE in the wetter habitats (trich lawn groups) on the BOG and BOGR sites did not increase to the pre-drought level. In contrast, shrub groups on the BOG and BOGR sites and all plant community groups on the BOGD site reacted to the dry period only slightly and their NEE even increased in the second half of the 2010 growing period. R_{ECO} did not show much seasonal variation.

A significant correlation ($p < 0.05$) between the measured R_{ECO} and *WT* was found for all the plant community groups except the BOGD molinia+high shrub group.

CH_4 emissions

The level of CH_4 emissions decreased in the order BOG > BOGR > BOGD, but the differences between the sites were not statistically significant. During both growing periods, a clear seasonal maximum for the CH_4 fluxes was observed in the middle of August and the highest CH_4 emissions were measured in the BOG trich lawn (90 mg CH_4-C m^{-2} day^{-1}). However, almost no CH_4 emissions were measured for the BOGD high shrub group during either of the growing periods. Although the CH_4 emissions measured in the wetter parts of the sites (BOG trich lawn, BOGR trich lawn and BOGD inter shrub) were higher than those measured in the drier areas (BOG low shrub, BOGR high shrub and BOGD molinia+high srub), the differences were not significant and no correlation was found between the measured CH_4 emissions and *WT*. However, there was a significant correlation between seasonal CH_4 emissions and seasonal mean *WT* for both growing periods ($p < 0.05$; $r = 0.68$). In general, seasonal CH_4 emissions were higher during the 2009 growing period compared to the 2010 growing period (Table 2).

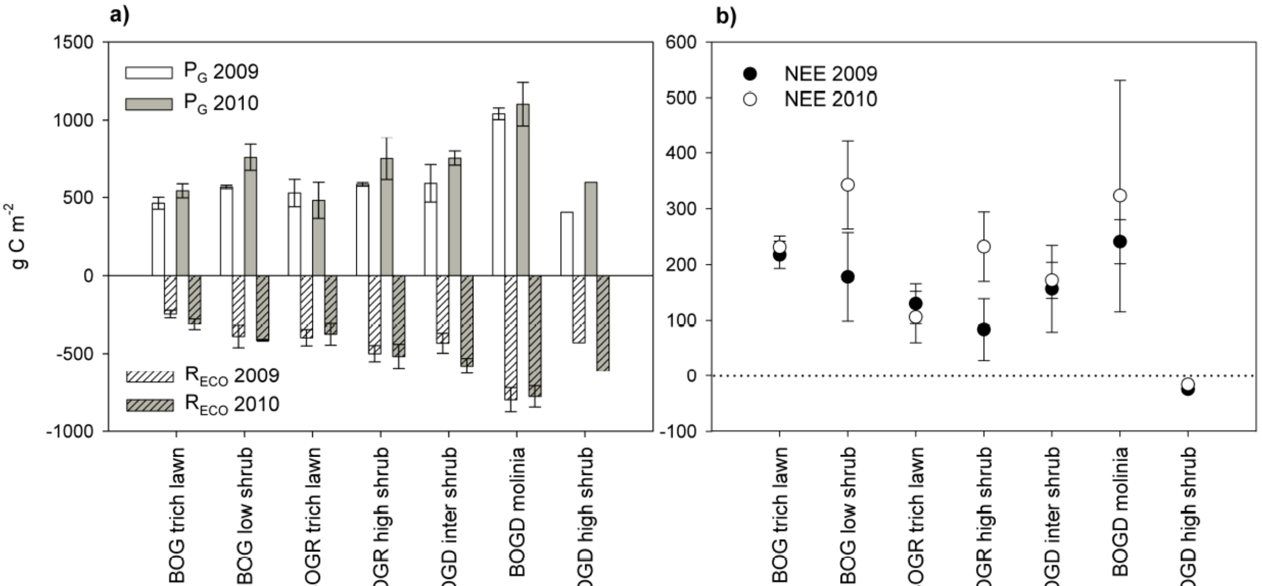

Figure 4. Growing period carbon fluxes (g C m^{-2}, 01 May / 15 May to 10 October) for 2009 and 2010. a) Estimated seasonal photosynthesis (P_G) and total respiration (R_{ECO}) ± standard deviation. b) Estimated net CO_2 exchange (NEE) ± standard deviation for plant community groups at the different study sites during both growing periods. Positive values denote influx to the ecosystem and negative values denote efflux from the ecosystem into the atmosphere.

Table 2. Estimated total fluxes of C (g m^{-2} per growing period) through gross photosynthesis (P_G), total respiration (R_{ECO}), net ecosystem exchange (NEE) and methane emissions (CH_4) for all plant community groups during the 2009 and 2010 growing periods (from 01 / 15 May to 10 October). Positive values denote influx into the ecosystem and negative values denote efflux from the ecosystem. C balance is the net result of the CO_2-C and CH_4-C fluxes (C balance = NEE + CH_4).

Plant community group	P_G		R_{ECO}		NEE		CH_4		C balance	
	2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
BOG trich lawn	462.6	542.3	-245.2	-311.2	217.4	231.1	-9.4	-8.2	208.0	222.9
BOG low shrub	567.0	756.1	-388.9	-413.6	178.1	342.5	-7.6	-7.9	170.5	334.6
BOGR trich lawn	527.8	481.2	-397.8	-375.0	130.1	106.2	-6.5	-3.8	123.6	102.4
BOGR high shrub	583.1	749.4	-499.5	-517.3	83.6	232.1	-1.0	-1.0	82.6	231.1
BOGD inter shrub	604.1	751.1	-444.1	-579.1	160.0	172.0	-5.7	-1.2	154.3	170.8
BOGD molinia	1047.1	1101.3	-808.1	-778.0	239.0	323.4	-1.1	-1.8	237.9	321.6
BOGD high shrub	415.4	596.4	-442.6	-612.6	-27.2	-16.3	0.0	-0.3	-27.2	16.6

Modelled CO_2 exchange

PAR and VGA were the main controlling factors of P_G in all plots (Equations 2 and 3). Adding *WT* into the equation (Equation 4) resulted in a better fit for the BOGR trich lawn group only. R_{ECO} was controlled by VGA and temperature, and T_{air} described the variation in R_{ECO} more accurately than T_{soil}. Despite a significant correlation between *WT* and R_{ECO}, the inclusion of *WT* in the R_{ECO} model did not increase its explanatory power, except for the BOGR trich lawn group.

The CO_2 balance of the growing period

The modelled seasonal NEE was positive for all the plant community groups, except for the BOGD high shrub group in both growing periods (Table 2, Figure 4). In general, as for CH_4 emissions, the seasonal NEE decreased in the order pristine > rewetted > drained; however, the differences between the study sites were not significant (Table 3). NEE was significantly higher in the 2010 growing period compared to the 2009 growing period (p = 0.04; n = 18). The pattern was similar for all of the sites.

The result of repeated measures ANOVA showed a non-significant difference of the combined effect of the site and year (Table 3). The NEE of the plant community groups on the BOGD site varied only slightly between 2009 and 2010 and the NEE values of BOG trich lawn and BOGR trich lawn were almost the same in both years (Figure 4, Table 2). In contrast, NEE in the drier shrub groups (BOG low shrub and BOGR high shrub; respectively) was 92 % and 178 % higher in 2010 than in 2009. This change was caused by increased P_G in these plant community groups. R_{ECO} also increased significantly between 2009 and 2010, but by less than the increase in P_G (Tables 2 and 3).

A negative relationship was identified for seasonal R_{ECO} fluxes and mean growing-period *WT* in both 2009 and 2010 (r = -0.64 and -0.66, respectively; p < 0.01, n = 18). However, weak or no correlation was identified between NEE and mean *WT* for both growing periods.

For all of the sites studied, CH_4 fluxes were relatively low and, therefore, of minor importance for the net C balance (Table 2).

Table 3. Results of repeated measures ANOVA test shown as p values (in **bold** type if statistically significant at 5 % risk level, n = 18). The effects of site, year and the interaction of these factors on CO_2 fluxes were tested.

	P_G	R_{ECO}	NEE
site	0.125	**0.005**	0.168
time	**0.009**	**0.043**	**0.037**
site*time	0.660	0.215	0.733

DISCUSSION

The seasonal balance

All the studied bogs acted as C sinks during both growing periods, with the exception of the driest area of the drained bog. The seasonal CO_2-C balances of between -27 and 342 g m^{-2} derived in this study are consistent with the results of earlier studies in temperate parts of Europe and Canada (Lafleur *et al.* 2003, Schrier-Uijl *et al.* 2010, Couwenberg *et al.* 2011) but show higher C uptake rates than reported for more northerly bogs (Alm *et al.* 1999b, Griffis *et al.* 2000, Waddington & Roulet 2000, Aurela *et al.* 2007). The high C sink function of the mountainous sites, which are thermo-climatically defined as boreal, appeared to be more related to the latitude and the associated level of light environment than to temperature.

The results from the second year of measurements agreed with the first year's results (Urbanová *et al.* 2012a), showing that drainage significantly changed the vegetation structure towards a drier successional stage but that the C sink function was disrupted only in the most intensively drained areas where the original peatland species were missing. *Molinia caerulea* represented an exception to this trend because it had the highest estimated C accumulation in both seasons. In contrast, the plant communities in the wetter parts of the drained bog site had positive C balance despite a changed vegetation structure, and were functionally similar to those in the pristine site. In both years, the rewetted bog had a slightly lower C balance compared to the pristine bog and the response of both these sites to the inter-annual variability in weather conditions was very similar. The effect of restoration on this bog can hardly be distinguished, because neither changes of vegetation structure in the sampling plots nor dramatic changes in CO_2 and CH_4 fluxes were observed during the first two years after restoration (Urbanová *et al.* in press). However, we can assume on the basis of previous studies (Tuittila *et al.* 1999, Waddington & Price 2000) that an increased and more stable water table level could reduce soil respiration. R_{ECO} was still slightly higher in the rewetted bog site compared to the pristine bog site but lower than in the drained site. The highest P_G and R_{ECO} values measured in the drained bog site were most likely related to the increased VGA of grasses and deciduous shrubs.

Seasonal CH_4 efflux ranged from zero in the drained bog site to 9.4 g CH_4-C m^{-2} in the pristine bog site and was lower in the second growing period (which included the drought). CH_4 efflux represented only a negligible portion (maximum 5 %) of the total C balance and did not switch the ecosystem from a sink to a source of C. However, the winter fluxes and C leached *via* subsurface water are also important components of the annual peatland C budget. Winter fluxes can represent more than 20 % of the total annual release of CO_2 (Alm *et al.* 1999a) and losses of C in the form of DOC, POC and gases transported by subsurface water can represent up to 30 % of the ecosystem uptake of C (Lafleur *et al.* 2003, Dinsmore *et al.* 2010, Koehler *et al.* 2011). However, these fluxes were not measured at our study sites.

Interannual variability and the response of different growth forms to drought

Peatlands can switch from C sinks to C sources under drought conditions due to enhanced rates of respiration and reduced photosynthesis (Alm *et al.* 1999b, Griffis *et al.* 2000, Bubier *et al.* 2003a, Lafleur *et al.* 2003, Aurela *et al.* 2007). During our study, there were only small differences in mean air temperature and total precipitation between the two growing periods. Although the 2010 growing period was, in general, slightly colder and wetter than that of 2009, there was a dry period at the peak of the growing period (June–July 2010) that influenced the rates of P_G and R_{ECO}. This suggests that the distributions and magnitudes of temperature and precipitation variation during the growing period are important for seasonal C fluxes, as also noted by Griffis & Rouse (2001).

Generally, wet conditions favour CO_2 accumulation and drier years lead to higher CO_2 release to the atmosphere due to increased respiration/decomposition (Alm *et al.* 1999b, Frolking *et al.* 2002, Lafleur *et al.* 2003). Different growth forms of plants can vary in their responses to changed hydrology and, therefore, make the response of the ecosystem complex. We observed enhanced shrub P_G and decreased sedge P_G during the drought period. The enhanced CO_2 uptake of the evergreen (BOG low shrub) and deciduous (BOGR high shrub) shrubs on the pristine and rewetted bog sites during the drought, with only slightly increased R_{ECO}, resulted in much higher NEE in the growing period of 2010 than in 2009. Although there were heavy rain events in the second half of July and August that resulted in a higher total summer precipitation than the long-term average (1961–1990; Czech Hydro-meteorological Institute), sedges had already started to senesce by this time and P_G values did not increase. Sedge-dominated peatlands usually have lower CO_2 uptake during dry years and can switch from sinks to sources of C due to the reduced photosynthesis of the sedges (Griffis *et al.* 2000). Similarly, Bubier *et al.* (2003b) observed lower net C uptake under drier conditions, which they attributed primarily to increased rates of respiration in all plant communities and reduced photosynthesis in the sedge communities. In contrast, a bog with shrubs did not show a decline in photosynthesis under the dry conditions (Bubier *et al.* 2003a). Evergreen shrubs have a competitive advantage over sedges under stressed conditions (Aerts 1995). Over the long term, it can lead to an increase in cover of shrubs and a decrease in cover of sedges/graminoids in peatlands due to the drier and warmer climate (Bubier *et al.* 2003b). In our study, the drought period did not lead to increased NEE on the drained site despite a similar deciduous shrub species composition to that of the rewetted bog site. The mean water table level at the drained site was on average 15 cm lower than at the pristine and rewetted sites, and a further decrease in the water table level may have led to enhancement of both shrub productivity and R_{ECO}. It is likely that there is a water table threshold value below which respiration starts to increase rapidly and the ecosystem can switch from sink to source. From this point of view, the drained peatland could be more sensitive to a further decrease in the water table level, which may cause wetter areas which still acted as C sinks to change into sources of C. Thus, peatlands that have partly preserved their original vegetation and functions even after decades of drainage might be more threatened by future climate change than pristine or restored peatlands, which can be considered as self-sustaining ecosystems (Belyea & Baird 2006, Teklemariam *et al.* 2010).

CONCLUSIONS

Our results showed different vulnerability to drought between the pristine, rewetted and drained peatlands. Plant communities on pristine and rewetted sites that were dominated by shrubs profited from drought, whereas further decrease of the water table level did not stimulate C accumulation in similar shrub plant communities on the drained site during the drought period. Sedge-dominated plant communities on the pristine and rewetted sites had similar C fluxes in both growing periods. Based on the results of this study, we can assume that future climate change could lead to changes in the production, abundance and distribution of different plant species and thus in functioning of the ecosystem. More frequent and longer-lasting drought events could lead to further lowering of the water table, which carries a higher risk for the functioning of drained peatland ecosystems than for pristine and rewetted ones. The original peatland vegetation preserved on wetter parts of drained sites could be replaced by forest and meadow plant species and thus the original peatland function can be lost. However, pristine and rewetted peatlands seem to preserve their functions under drier conditions in spite of the fact that the vegetation composition can change towards drier successional stages.

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