Responses of CO$_2$ Exchange and Primary Production of the Ecosystem Components to Environmental Changes in a Mountain Peatland

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ABSTRACT

The complexity of natural ecological systems presents challenges for predicting the impact of global environmental changes on ecosystem structure and function. Grouping of plants into functional types, that is, groups of species sharing traits that govern their mechanisms of response to environmental perturbations, reduce the complexity of species diversity to a few key plant types for better understanding of ecosystem responses. Chambers were used to measure CO$_2$ exchange in grass and moss growing together in a mountain peatland in southern Germany to assess variations in their response to environmental changes and how they influence ecosystem CO$_2$ exchange. Parameter fits and comparison for net ecosystem exchange (NEE) in two ecosystem components were conducted using an empirical hyperbolic light response model. Annual green biomass production was 320 and 210 g dwt m^{-2}, whereas mean maximum NEE was –10.0 and –5.0 µmol m^{-2} s^{-1} for grass and moss, respectively. Grass exhibited higher light use efficiency (α) and maximum gross primary production [$(\beta+\gamma)_{2000}$]. Leaf area index explained 93% of light use and 83% of overall production by the grass. Peat temperature at 10-cm depth explained more than 80% of the fluctuations in ecosystem respiration (R_{eco}). Compared to grass, moss NEE was more sensitive to ground water level (GWL) draw-down and hence could be more vulnerable to changes in precipitation that result in GWL decline and may be potentially replaced by grass and other vegetation that are less sensitive.

Key words: Carbon dioxide exchange; environmental variables; ground water level; peatlands; primary production; respiration.

INTRODUCTION

Peatlands cover about 3.5% (or 5 × 10^6 km^2) of the Earth's land surface (Gorham 1991). More than 95% of total peatlands occur in cool, humid climates of the temperate belt in Northern Hemisphere. During the last millennium, northern

peatlands have acted as carbon (C) sinks, with an average annual C uptake of 20–35 g C m^{-2} y^{-1} (Gorham 1991; Turunen and others 2002). This has resulted in an enormous C pool in peatland soils, amounting to approximately one-third of the world's total soil C (4.5×1017 g) (Turunen and others 2002). As a result of this large stock of partially decomposed plant material, peatlands are potential CO_2 sources (Chapin and others 1992; Smith and others 2004).

Despite their significant role in terrestrial C cycle, the regulation of C flow in peatlands is still poorly understood (Fenner and others 2004; Riutta and others 2007). The integrated dynamics of ground water level (GWL) may determine the long-term ecological function of temperate peatlands as C sinks as in the case of arctic tundra (compare Ostendorf and others 1996). Lowering of the GWL could enhance decomposition over assimilation resulting in decreased net CO_2 uptake or even net CO_2 loss (Oechel and others 1995; Bubier and others 2003; Tuittila and others 2004; Riutta and others 2007). On the other hand, several studies consider the effect of the water table as minimal and emphasize the significant influence of microclimatic parameters such as temperature and light (see Lafleur and others 2005). Finally, rainfall and water table may indirectly influence C balance by modifying phenology, nutrient availability, and development of aboveground leaf area (LA) in a particular season (Shaver and others 1998; Hastings and others 1989).

Lack of consensus on how CO_2 exchange is controlled may arise from the wide range of methodologies that are employed to assess ecosystem responses (Oechel WC and others 1995; Ruimy and others 1995; Frolking and others 1998) and the ability to identify and describe the objects under study. Some of the methods (for example, eddy covariance) do not take into account the interspecific differences associated with inherent physiological adaptations that are bound to influence plant responses (Semikhatova and others 1992). Such adaptations may buffer plants from the impact of short-term habitat changes during the growing season and modify ecosystem response to environmental changes (Riutta and others 2007). Mosses for example, have shallow rhizoids and, therefore, are likely to be sensitive to shifts in GWL, with a significant influence on overall ecosystem CO_2 exchange. Moss photosynthesis and growth should, therefore, be directly influenced by the water table (Clymo and Hayward 1982; McNeil and Waddington 2003; Robroek and others 2007). This may not be the case with grass or sedge, which

have relatively deep rooting systems (Bortoluzzi and others 2006; Riutta and others 2007). Thus, characteristics of the vegetation mosaic reflect resource availability and correlate with aspects of C balance and net primary production (Ostendorf and others 1996; Leadley PW and Stocklin 1996).

Understanding of the biotic controls over functional groups and ecosystem CO_2 exchange processes and their interaction with the physical environment is crucial and provides a basis for predicting how functional groups and entire peatland ecosystems may respond to changes in the habitat. We used chamber methods to examine the variation in ecosystem CO_2 exchange response of two dominant functional groups (moss and grass) occurring in a mountain peatland of Germany. The peatland is gently sloping, homogeneous in terms of species presence, but characterized by a recurring mosaic in fine scale structure where the community is either dominated by grass and sedge tussocks with little moss, or relatively open troughs or inter-tussocks dominated by moss, with little graminoid biomass. Our objectives were; (1) to monitor annual biomass production of moss and grass in the peatland, (2) to monitor diurnal and seasonal CO_2 exchange in grass and moss-dominated plots and to determine how the individual growth forms are influenced by GWL, temperature, and light, and (3) to examine how grass and moss contribute to the overall net ecosystem CO_2 exchange of the plots and the peatland over the course of the season. Although each plot studied is structurally unique, the exact composition of vegetation included in each measurement was determined. The average behavior of the natural mosaic components, dominated either by moss or graminoid biomass, in gas exchange is compared, which will allow us to use abundance-weighted estimates of C exchange to model the mixed-functional-type community in subsequent steps.

MATERIALS AND METHODS

Site Description

Measurements were conducted in a fen ecosystem at Schlöppner Brunnen site (50°07′54″ N, 11°52′51″ E) at an elevation of 700 m a.s.l., where a clearing is surrounded by spruce trees (Figure 1). The fen is dominated by two main functional groups, which include moss (*Sphagnum fallax* and *Polytrichum commune*) and grass (*Agrostis canina, Agrostis stolonifera, Molinia caerulea*). A sedge (*Carex nigra*) is also found scattered within the vegetation, but it is overgrown quickly by the grasses and
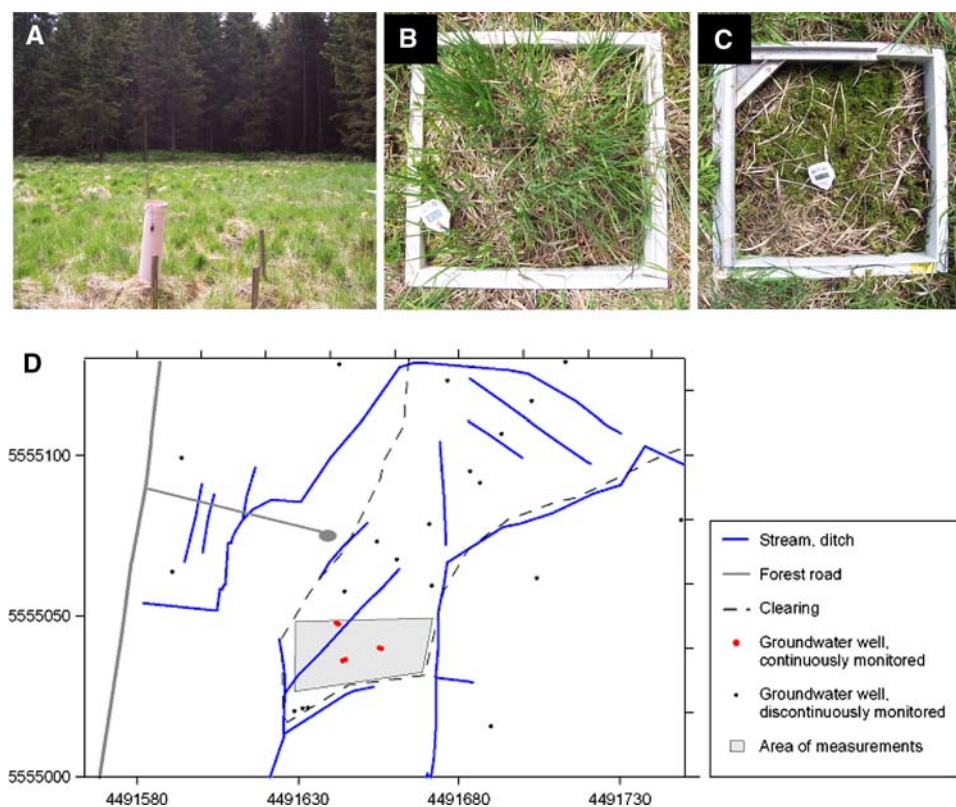
Figure 1. **A** Illustration of the vegetation at the Schlöppner Brunnen wetland. **B** Grass-dominated experimental plot as prepared for measurements, showing collars inserted into the organic soil. **C** Moss-dominated experimental plot as in **B** with a metal frame for mounting of cooling packs. **D** Map of the Schlöppner Brunnen site indicating drainage channels and groundwater wells. The axes are Gauss–Krüger coordinates in meters.

negligible in its contribution to biomass by early summer. The site structure is relatively flat but gently sloping, with a mosaic of grass-dominated tussocks and moss-dominated inter-tussock areas.

The soil at the site is classified as Fibric Histosol, moderately acidic (pH 3.5–5.5), with highly decomposed soils rich in sulfur (up to 4.6 mg kg^{-1}) and iron (up to >16 mg kg^{-1}). The fen has a slope of 3% and water flow direction is parallel to the slope from NNE to SSW (Figure 1). The annual precipitation in the catchment varies between 900 and 1160 mm y^{-1} and the mean annual air temperature is 5°C. The mean in situ water table level varies annually and was 0.13 ± 0.19 m (Paul and others 2006).

Measurements

Microclimate

Weather conditions were continuously recorded at a meteorological station set up at the field site. Precipitation (ARG100 rain gauge, EM Ltd., Sunderland, UK), global radiation, photosynthetic photon flux density (PPFD) (LI-190 Quantum sensor, Li-Cor, USA), air humidity and temperature (VAISALA HMP45A, Helsinki, Finland), and peat (0, −30, −100 cm) temperature profiles (Thermistor M841 Siemens, Germany) were recorded. Data

were measured every 5 min, averaged, and logged every 30 min by a data logger (DL2e, Delta-T Devices Ltd., Cambridge, UK). Water level was measured with pressure transducers (Piezometers 26PCBFA6D, IBA Sesorik GmbH, Seligenstadt, Germany) and data were recorded daily.

NEE Measurements with Chambers

Field measurements of ecosystem CO_2 exchange were conducted each month (1 week in a month, with 3 days of measurements) between May and October 2007, except for July when two sets of measurements were carried out. A set of six soil frames or collars, three on grass-dominated and three on moss-dominated vegetation were inserted into the soil a month before the measurements were conducted. Moss-dominated plots (hereafter called moss plots) were selected to have as few grass/sedges on them as possible (see Table 1 versus data in Figure 3). Also, the grass-dominated plots (hereafter called grass plots) had a combination of grass and sedge but the sedge (*C. nigra*) and moss biomass were very low. We avoided selective vegetation removal to maintain the natural conditions of the plots. Each soil frame constituted a measurement plot and, hence, during each measurement week, three grass and three moss plots were

Table 1. Green Biomass and LAI of Grass in So-Called Moss Plots, and Green Biomass of Moss Harvested in the 40 by 40 cm^2 Grass Plots (Expressed to unit m^2) for Each Measurement Campaign During the Measurement Period

DOY	Grass in moss plots		Moss in grass plots
	Green biomass (g m^{-2})	LAI (m^2 m^{-2})	Green biomass (g m^{-2})
131	20.75	0.02	20.01
171	17.28	0.05	0.00
198	23.08	0.33	12.00
206	53.27	0.61	24.92
227	32.83	0.13	19.45
263	22.56	0.03	41.44
297	8.08	0.01	9.13

Comparison with Figure 3 demonstrates that dominance by one or the other growth forms in the differently selected plots was almost complete.

monitored on day 1 and 2 to characterize CO$_2$ gas exchange. At the end of second measurement day (~18:00 h), all the aboveground biomass on each of the plots was harvested. CO$_2$ measurements were continued on day 3 (1 day after biomass removal) to determine the peat respiration. New plots were then established for the next cycle/round of monthly measurements and the soil frames re-installed. Non-destructive determination of biomass and leaf area index (LAI) within the studied plots was not possible; hence, biomass was harvested after every complete set of NEE measurements. The biomass estimates for each plot were used to normalize NEE per unit biomass; moss plots on the basis of total green moss biomass and grass plots based on green grass biomass.

During each monthly measurement series (three measurement days each month), net ecosystem exchange (NEE), and ecosystem respiration (R_{eco}) were sequentially observed with a systematic rotation over all plots using manually operated, closed gas exchange chambers, modified from the description given by Droesler (2005), Wohlfahrt and others (2005), and Li and others (2008b) as used in central European bogs and alpine grasslands. The 38 × 38 × 54 cm^3 chambers of our system were constructed of transparent plexiglass (3 mm XT type 20070; light transmission 95%). Dark chambers, for measuring ecosystem respiration, were constructed of opaque PVC and covered with an opaque insulation layer and with reflective aluminum foil. Using extension bases, chamber height was adjusted to the canopy height. Chambers were placed on the plastic frames/collars that were inserted 7 cm into the ground. They were sealed to the chamber with a flexible rubber gasket and the chamber firmly secured using elastic bands fastened onto the ground from two sides. Tests

indicated that leakage did not occur (see Droesler 2005 for details), however, this could not be examined regularly in the case of systematic field measurements and required that each set of data must be scrutinized for abnormalities.

Increased air pressure in the chamber was avoided by a 12 mm opening at the top of the chamber, which was closed after the chamber had been placed onto the frame and before any records were taken. Circulation of air within the chamber was provided by three fans yielding a wind speed of 1.5 m s^{-1}. Change in chamber CO$_2$ concentration over time was assessed with a portable, battery operated IRGA (Li-Cor 820). Measurements were carried out in most cases within 3–5 min of placing the chamber on the frames. Once steady state was attained, data were logged every 15 s for 2 min and CO$_2$ fluxes were calculated from a linear regression describing the time dependent change in CO$_2$ concentration within the chamber. Influence of the CO$_2$ concentration change on plant physiological response was ignored. By mounting frozen ice packs inside and at the back of the chamber in the airflow, temperature during measurements could be maintained within 1°C relative to ambient. Air (at 20 cm above the ground surface) and peat (at –10 cm) temperatures inside and outside of the chambers were monitored during measurement and data were logged at the onset and end of every round of NEE measurement on each plot. Similarly, light levels within the chamber and above the vegetation (canopy) were monitored using a quantum sensor (LI-190, Li-Cor, USA) and data were logged every 15 s. Tests conducted in a controlled climate chamber showed that vapor pressure deficit (VPD) changes within our CO$_2$ measurement chambers were limited to 1 hPa during the period (~3 min) when the chambers

were placed on the vegetation. We, therefore, assumed that such small VPD changes should not affect CO_2 exchange via stomatal effects.

During each monthly measurement series, repeated light and dark chamber measurements were conducted from sunrise to sunset over single day comparing three moss and three grass plots. Eight to eleven measurement cycles were accomplished on individual days. To estimate gross primary production (GPP), ecosystem respiration was estimated for each NEE observation time by linearly extrapolating between dark chamber observations (R_{eco}), and then adding it to NEE (compare Li and others 2008a). As seen in Figure 5, the measurements of NEE and R_{eco} were closely associated in time; thus, the corrections made in R_{eco} were very small. Measurements were conducted from the beginning of May until October to develop a picture of the seasonal dynamics of CO_2 exchange. Limitation in manpower to carry out the labor intensive chamber measurements and the nature of our experimental site prevented continuation of the observations with chambers during night time periods.

Estimation of Model Parameters Describing Gas Exchange Response

Empirical description of the measured NEE fluxes was accomplished via a non-linear least squares fit of the data to a hyperbolic light response model, also known as the Michaelis–Menten or rectangular hyperbola model (compare Owen and others 2007):

$$\text{NEE} = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma \qquad (1)$$

where NEE is net ecosystem CO_2 exchange (μ mol CO_2 m^{-2} s^{-1}), α is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency (μ mol CO_2 m^{-2} s^{-1}/μ mol photon m^{-2} s^{-1}), β is the maximum NEE of the canopy (μ mol CO_2 m^{-2} s^{-1}), Q is the photosynthetic active radiation, PPFD (μmol photon m^{-2} s^{-1}), γ is an estimate of the average ecosystem respiration (R_{eco}) occurring during the observation period (μ mol CO_2 m^{-2} s^{-1}), (α/β) is the radiation required for half maximal uptake rate, and ($\beta + \gamma$) is the theoretical maximum uptake capacity. Because the rectangular hyperbola may saturate very slowly in terms of light, the term ($\alpha\beta Q$)/($\alpha Q + \beta$) evaluated at a reasonable level of high light ($Q = 2,000$ μmol photons m^{-2} s^{-1} is used in this study) approximates the potential maximum GPP and can be thought of as the average maximum canopy uptake capacity

during each observation period, noted here as ($\beta + \gamma$)$_{2000}$. The parameters ($\beta + \gamma$)$_{2000}$ (for example, NEE at PPFD(Q) = 2000) and γ were estimated for each functional group using NEE data from the three measurement plots per day. Data were pooled separately for grass and moss.

Biomass and LAI Measurements

After gas exchange measurements on the second day of each campaign, all the aboveground biomass within the 38 × 38 cm^2 area enclosed by the collars was harvested. The harvested moss and grass biomass was sorted into green and dead material. LA of the grass was measured using a leaf area meter (CI-202, CID, Camas, WA) before being oven dried at 80°C for 48 h and weighed. The rest of the biomass was oven dried at 80°C for 48 h and weighed to obtain the live and dead dry weight. Due to difficulties in determining the moss photosynthesizing surface area, the green biomass was simply dried and weighed. LAI of the grass was calculated by dividing the LA by plot area.

During the months of July, August, and September, root biomass was sampled with an 8-cm diameter soil corer. Sampling took place in the middle of the grass measurement plots after CO_2 measurements were finished. The 30-cm soil cores were divided into sections of 5 cm each, washed under running tap water using soil sieves (mesh 2 mm) and the collected roots were oven dried at 80°C before weighing them to obtain root dry weight in each of the soil profiles. Due to difficulty in separating dead and live biomass, the reported results include both dead and live root biomass. Moss rhizoid biomass was not quantified.

RESULTS

Meteorology

Weather conditions during the study period are shown in Figure 2. Light conditions inside and outside the chamber were not significantly different (Figure 2A). Temperature differences between the inside and outside of the chamber were maintained within ± 1°C. Mean annual VPD was around 5 kPa and VPD fluctuated on a daily basis (Figure 2B). Air and peat temperatures rose to a maximum in July, with peat temperature lagging behind. Maximum air temperature (daily mean) of 15°C was recorded in July. Peat temperature varied with depth and higher fluctuations occurred near the peat surface (Figure 2C). The shallow layers warmed up faster after the snow thaw, but also cooled down more rapidly in autumn, whereas temperatures at 1-m

depth lagged behind for several weeks. Compared to 1-m depth, peat temperatures at 30-cm depth were higher between April and August. Similarly, temperatures during the day measured at the peat surface were higher than at 30 cm, during the same period. Later in the year (autumn), the temperature profile inverted, with the warmest temperatures ($\sim$2°C warmer) at 1-m depth and the coldest near the surface, reflecting the decline in average daily air temperatures at that time.

Annual sum of precipitation was within the range of long-term average. The amount of rainfall received between April and December was 942 mm (Figure 2D). A dry spell occurred between March and May leading to a significant decrease (-0.4 m) in the GWL, the lowest water table being recorded in May. Afterward, GWL remained relatively high and did not decrease below -0.2 m.
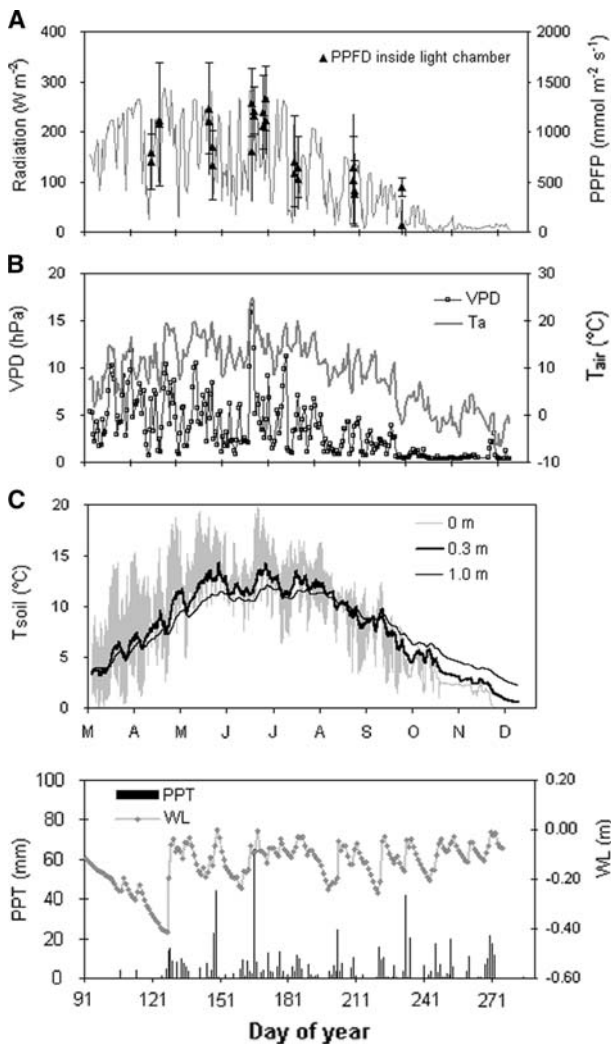

Figure 2. Prevailing weather conditions (**A**, **B**, **C**, **D**) and ground water level (**D**) at the study site during the measurement period.

Biomass Development

Biomass did not vary greatly among the selected moss and grass plots during any single monthly measurement campaign, but changes were large between monthly measurements (Figure 3A). Green biomass development in grass was recorded from May to July, when the grasses attained maturity. Maximum green biomass (dry weight) of grass was 320 g m^{-2}. After July, grass biomass declined significantly with the declining air and peat temperatures and by the end of October, when the first snowfall occurred, there was almost no green biomass remaining (Figure 3A). The pattern of LAI development in grass was similar to that of biomass development, because biomass is used as a scaling factor in the conversion from sub-samples to plot level. The highest LAI of 3.8 occurred in July (Figure 3A). Afterward, LAI declined significantly, reaching zero values in October. Root biomass of the grass decreased with depth, but extended well below 20 cm into the soil profile (Figure 3B). The highest root mass occurred within the top 5–10 cm layer, totaling 1.0 kg m^{-2}. The moss rhizoids were shallow and formed a thick mat within the first 1-cm top soil layer (data not shown). Moss green
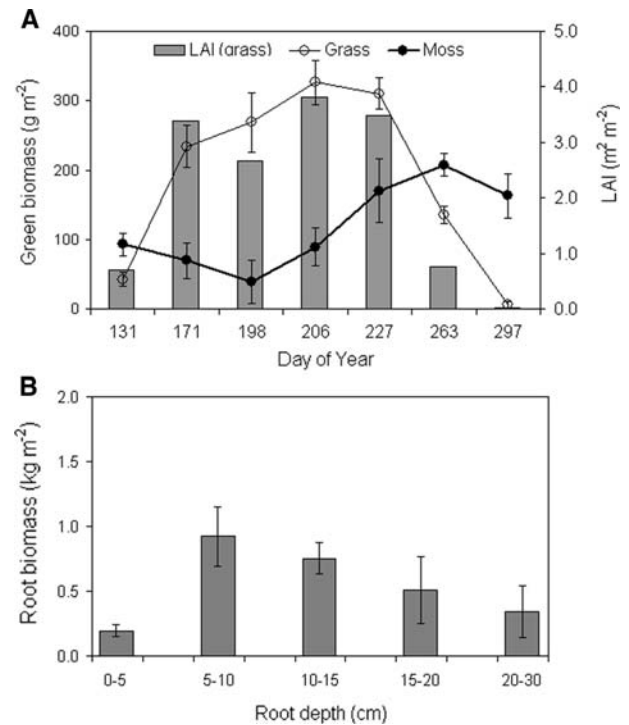

Figure 3. Seasonal variation in (**A**) green biomass (moss and grass) and LAI (grass only) development. (**B**) Root biomass of grasses in varying soil depths determined at selected periods during the season. Bars are SE.

biomass changed in a very different manner, declining between DOY 131 and 198. Maximum biomass of 210 g m^{-2} occurred in September.

Seasonal and Diurnal Patterns of CO_2 Fluxes

The maximum daily values for NEE, R_{eco} and GPP increased significantly between May (DOY 131) and July (DOY 206) in both moss and grass (Figure 4). The highest R_{eco} (30.0 and 22.0 μmol m^{-2} s^{-1} for grass and moss, respectively) occurred in mid July. R_{eco} declined to near zero at the end of the growing season. Similar patterns were observed for GPP and NEE. Compared to grass, maximum NEE attained during the day were lower in moss (close to zero) between May and June, whereas moss exhibited higher R_{eco} during the same period. Maximum NEE, however, occurred later in July. The highest GPP recorded during the season (37.0 μmol m^{-2} s^{-1}) occurred in the grass plots and was about 10 μmol m^{-2} s^{-1} more than in the moss plots. Parameters derived from the empirical light response model (equation (1)) are shown in
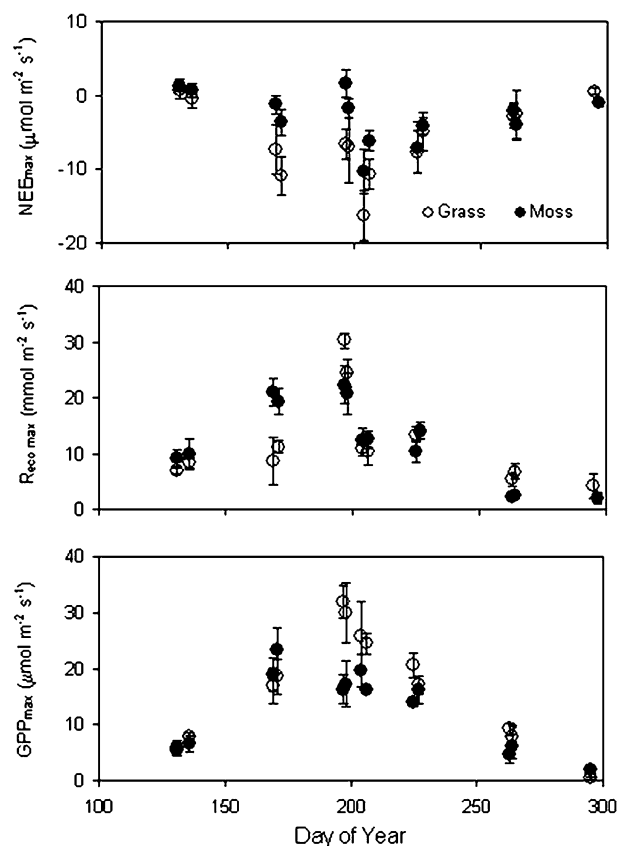
Figure 4. Seasonal variation of maximum NEE, R_{eco}, and GPP determined from diurnal course flux measurements conducted on specific days during the year. Bars are SE.

Table 2. Light use efficiency (α) increased between May and June and was significantly ($P < 0.05$) higher in the grass compared to the moss. The highest α recorded for grass (0.08 ± 0.01) was in mid summer (DOY 198–204), whereas the highest for moss (0.04 ± 0.01) occurred much earlier (DOY 171). These values coincide with the highest assimilation capacities (β) of −18.70 ± 2.48 and −10.31 ± 4.59 for grass and moss, respectively. Both α and β declined later during the growing season. Similar responses were observed for γ and $(β + γ)_{2000}$. Model results showed the maximum value of average GPP $[(β + γ)_{2000}]$ occurring in July both in moss and grass and both the model-derived results and the direct GPP estimates were comparable.

Observed diurnal courses of NEE and R_{eco} on selected measurement days of the year along with the prevailing weather conditions on the respective days are shown in Figure 5. On sunny days, CO_2 assimilation increased from its lowest rates in the morning to maximum around midday, but declined to near zero values later in the day. The daily peaks of C assimilation changed during the season depending on the prevailing air temperature (T_{air}) and light (PPFD) conditions. CO_2 uptake in grass plots occurred only around midday in May, whereas moss plots were net CO_2 sources throughout the day during May and only became CO_2 sinks from June onward. July and August were characterized by CO_2 uptake by both moss and grass during most of the day. Ecosystem respiration (R_{eco}) was relatively constant during the day but changed seasonally. Very low CO_2 exchange rates occurred later in the year (see DOY 263 Figure 5).

Biotic Influence Ion Ecosystem CO_2 Exchange

Both the biomass and CO_2 changed simultaneously during the season. To separate the influence of biomass changes on seasonal ecosystem CO_2 fluxes, NEE and R_{eco} were normalized with biomass in each of the plots (Figure 6). Until July, grass exhibited higher NEE per unit biomass than moss. After this period, both vegetation types had similar NEE per unit biomass. An abnormally high R_{eco} per unit biomass occurred in the moss on DOY 198. There was a strong correlation between LAI and model-derived physiological parameters α ($R^2 = 0.93$) and maximum GPP $(β + γ)_{2000}$ ($R^2 = 0.83$) in the grasses (Figure 7), but this was lacking in the mosses. Peat, which includes soil and roots, contributed a significant proportion (∼50%) of the total CO_2 output

Table 2. Best-Fit Parameters of the Empirical Hyperbolic Light Response Model for (A) Grass NEE and Their Statistics and (B) Moss NEE and Their Statistics

DOY	α	β	γ	(β+γ)$_{2000}$	S. E.$_{\cdot\alpha}$	S. E.$_{\cdot\beta}$	S. E.$_{\cdot\gamma}$	R^2
(A) Grass NEE								
131	0.02	−5.58	6.50	11.51	0.001	0.75	0.38	0.77
135	0.01	−11.98	5.17	10.75	0.001	2.13	1.08	0.39
169	0.07	−15.31	8.17	21.91	0.004	2.92	2.35	0.50
171	0.08	−16.70	11.94	26.98	0.002	5.40	1.84	0.79
197	0.08	−19.60	20.81	32.25	0.002	2.31	0.85	0.96
198	0.05	−20.05	16.78	34.77	0.006	2.48	1.52	0.92
204	0.08	−17.30	8.98	24.57	0.010	1.60	1.06	0.98
206	0.07	−20.92	7.48	25.67	0.002	1.63	1.08	0.85
225	0.06	−17.64	8.30	23.57	0.003	4.01	1.90	0.57
227	0.05	−16.69	7.10	25.23	0.001	8.00	1.22	0.68
263	0.02	−8.34	4.50	12.26	0.005	0.02	0.89	0.62
294	0.03	−6.26	7.26	13.32	0.007	1.55	0.88	0.61
(B) Moss NEE								
131	0.01	−8.97	7.05	14.28	0.002	1.89	2.26	0.51
135	0.01	−12.72	9.30	18.30	0.001	3.72	0.96	0.60
169	0.04	−13.83	16.04	22.04	0.003	7.34	2.99	0.43
171	0.04	−15.31	17.79	30.80	0.005	4.59	2.50	0.69
197	0.02	−14.98	17.24	31.27	0.001	4.65	1.20	0.80
198	0.03	−12.67	19.36	32.32	0.002	3.81	1.27	0.88
204	0.01	−10.49	17.71	28.96	0.001	3.98	2.47	0.46
206	0.03	−10.98	10.21	24.65	0.002	3.33	1.68	0.58
225	0.02	−8.05	6.24	17.74	0.001	2.89	0.93	0.78
227	0.02	−7.17	4.87	17.07	0.001	4.45	0.82	0.74
263	0.01	−6.60	1.43	6.85	0.005	1.07	0.34	0.79
294	0.02	−4.14	1.61	5.58	0.003	0.72	0.48	0.65

(R_{eco}). Contribution of the peat to the overall R_{eco} became dominant later in the season (Table 3).

Abiotic Influence on Ecosystem CO$_2$ Exchange

Figure 8 shows the relationship between NEE and PPFD (Q) in the grass and moss on specific periods of the year when measurements were conducted. The growing season was divided into three phases: May, July, and September, which represented early, mature, and late stages of growth to demonstrate the influence of light on NEE. During May, soon after the snow thaw, increasing light intensity was accompanied by increasing CO$_2$ uptake, both in grass and moss. For grass, light compensation point was reached at a proximately 1,200 μmol m^{-2} s^{-1}, above which there was net ecosystem C gain. This was not the case with moss, where despite increased CO$_2$ uptake, stimulated by increasing light intensities, there was still an overall net CO$_2$ production from the moss plots. In July, the vegetation showed rapid response to increasing light intensities and both grass and moss plots had relatively low light compensation points

(<500 μmol m^{-2} s^{-1}). Thus, the ecosystem was an active CO$_2$ sink during most of the day. Compared to moss, higher NEE rates were observed in grass at similar light intensities during this period. Later in the season (September), although NEE rates were low, both moss and grass showed net CO$_2$ uptake, with low light compensation points. The results reveal that apart from light, other factors were also responsible for the regulation of CO$_2$ uptake in both moss and grass.

To reveal the underlying physiological mechanisms, data from the respective measurement days were fitted with a light response function (equation (1)). Physiological parameters derived from the function are summarized in Table 2. Strong positive correlation (R^2 between 0.50 and 0.98) between NEE and PPFD for most of the measurements and best fits occurred between June and August, particularly on days when minimum fluctuations in light intensities during the day occurred. In most cases, NEE saturated at relatively lower light intensities (900 μmol m^{-2} s^{-1}) in moss compared to grass (1,200 μmol m^{-2} s^{-1}) and grass exhibited higher NEE, GPP, α, and β values. Differences that occurred between moss and grass on any single
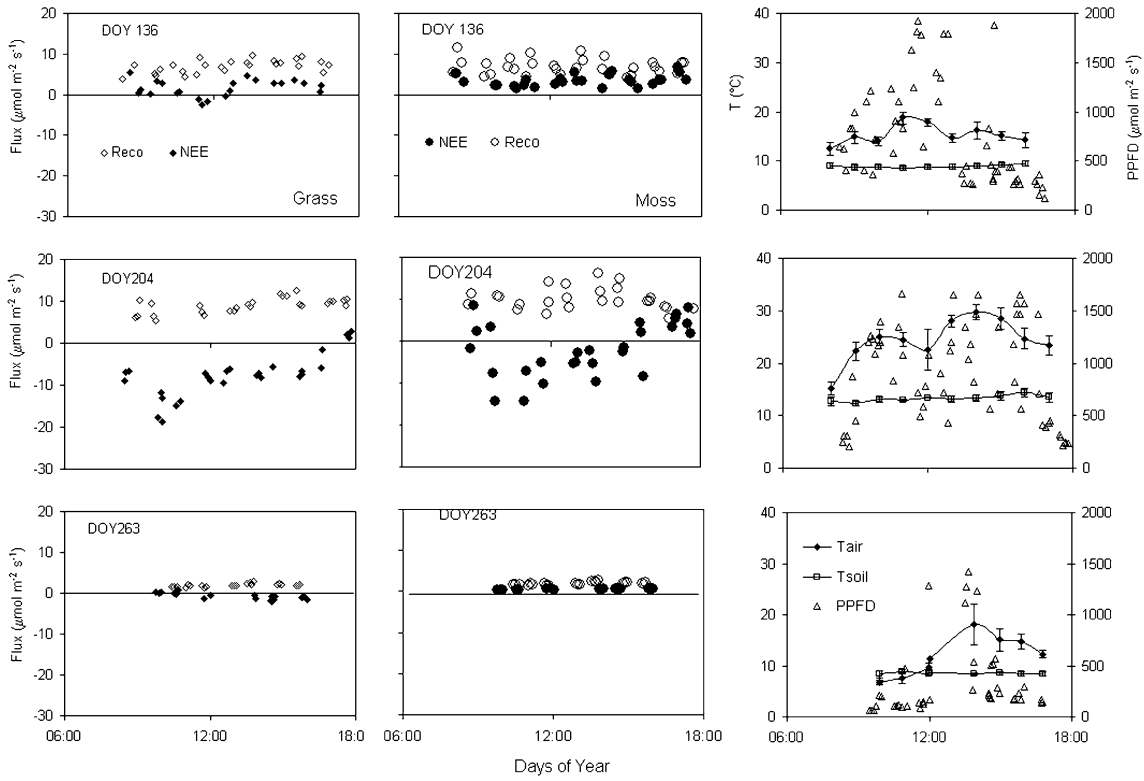
Figure 5. Diurnal variation of measured NEE and R_{eco} for selected periods during the growing season. Parallel air temperature (T_{air}) at 20 cm above the vegetation, peat temperature (T_{soil}) at –10 cm depth and light conditions (PPFD) inside the chamber are also shown. Bars are SE.
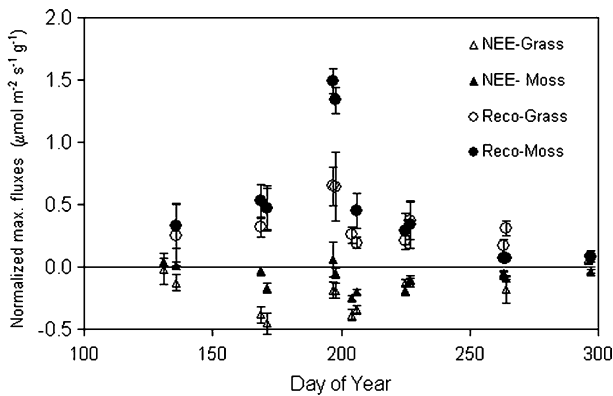

Figure 6. Seasonal courses of NEE and R_{eco} for both moss and grass/sedge normalized for green biomass. Bars are SE.

Figure 7. Relationship between LAI and **A** light use efficiency (α) and **B** potential maximum GPP $(\beta+\gamma)_{2000}$ of the grass component of the ecosystem.

measurement campaign were likely associated with differences in photosynthesizing surface (LAI), α, and β, whereas seasonal differences between campaigns (Figure 7) were due to changing LAI, α, β, and air temperatures. When similar fits were conducted on all the data, grouped toge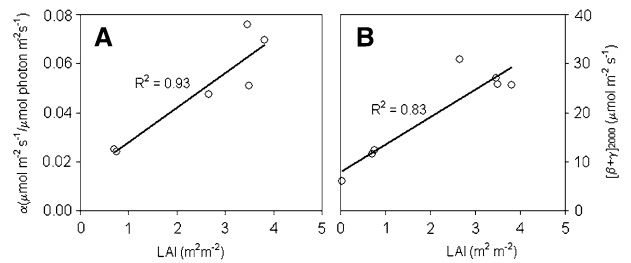ther for the entire measurement period, the relationship was weaker, however, it was better for moss compared to grass ($R^2 = 0.68$ in moss vs. $R^2 = 0.60$ in grass).

There was no correlation between air temperature and NEE. Using boundary analysis, however, it was evident that net CO_2 uptake (more negative NEE) increased until an air temperature of 25°C (not shown). Further increase in air temperature above 25°C was accompanied by decline in net uptake. Although NEE declined during the time when lowest GWL (−20 cm during measurements) was experienced, the relationship between GWL and NEE was not consistent. Peat temperature at

Table 3. Mean Soil and Total Ecosystem Respiration (µmol m^{-2} s^{-1}) in Grass and Moss Plots During Respective Months When Measurements Were Conducted

Month	Peat respiration		R_{eco}	
	Grass	Moss	Grass	Moss
June	4.9 ± 1.1	2.5 ± 5.3	9.9 ± 2.6	20.2 ± 2.4
July	13.0 ± 4.5	7.8 ± 3.3	24.5 ± 2.5	20.8 ± 3.7
August	10.5 ± 3.6	6.3 ± 2.0	14.1 ± 1.6	13.7 ± 1.1
October	3.8 ± 2.3	2.02 ± 0.9	4.15 ± 2.2	2.02 ± 0.9
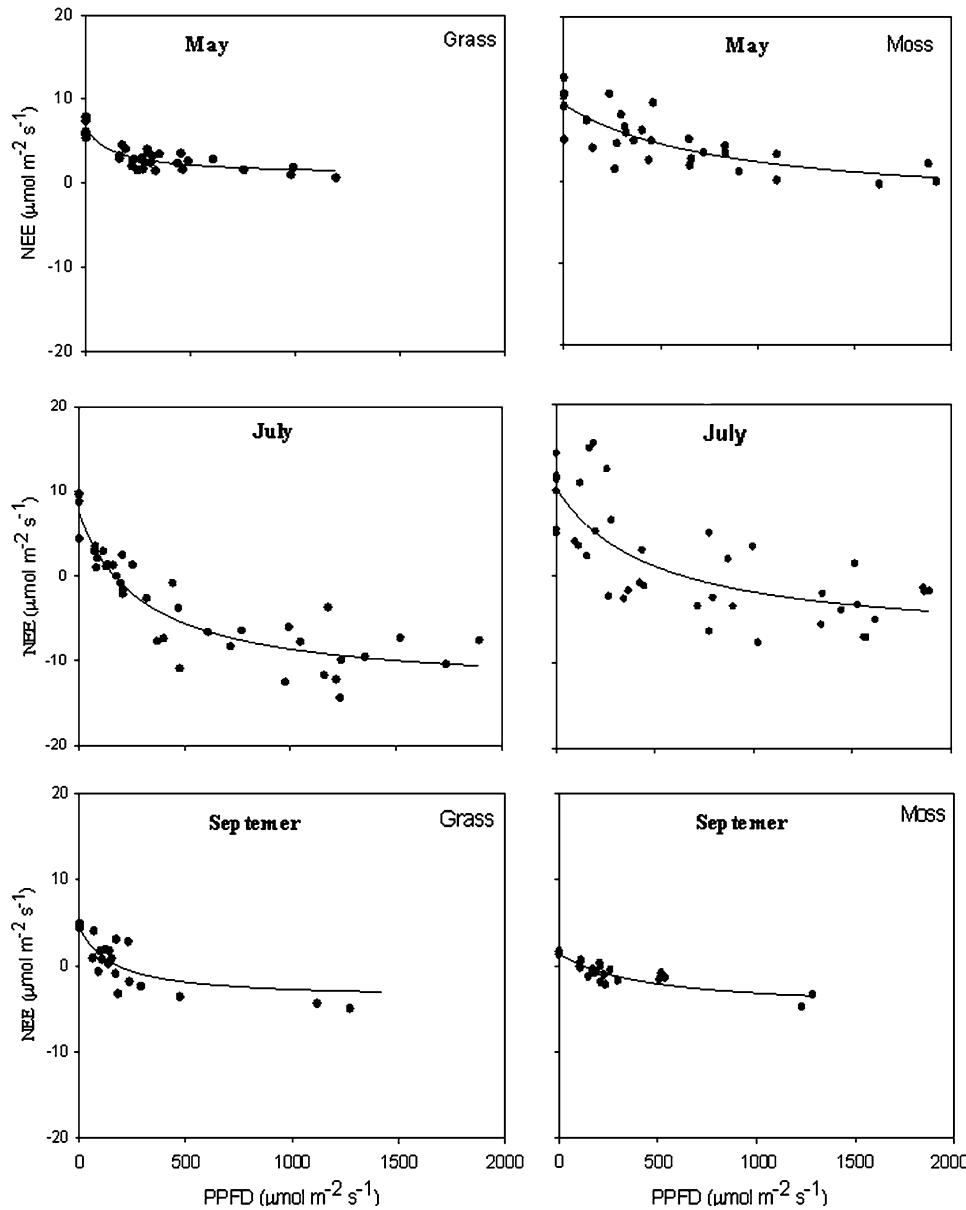
Figure 8. NEE-light response curves for grass (*left panel*) and moss (*right panel*) during early (May), mature (July), and late (September) stages of vegetation development. Regression analysis for light response curves were done with filtered data using Sigma plot 8.0 (residuals > 5 eliminated). Results are integrated data from the three measured plots for each plant type.

10°C, however, explained most (>80%) of the changes in R_{eco} and similar response patterns were observed in both moss and grass (Figure 9A). There was an increase in R_{eco} with declining GWL (R^2 = 85 and R^2 = 39 for grass and moss, respectively, Figure 9B), but shifts in GWL were also characterized by changes in peat temperature, making it difficult to discern the effects of GWL
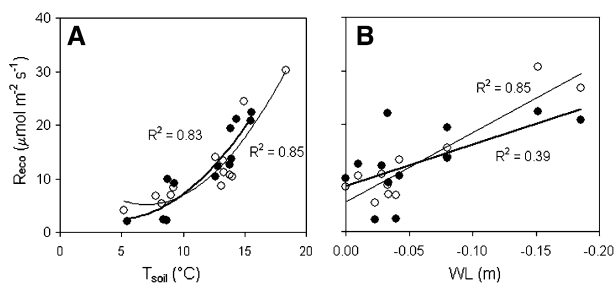
Figure 9. Relationships between daily averages of maximum R_{eco} of grass (*open circles*) and moss (*closed circles*) and **A** peat temperature (T_{soil}) measured at 10 cm depth within the collars and **B** mean ground water level (GWL), *thick regression lines* represent moss, whereas the *thin lines* are for grass.

from peat temperature changes. Changes in peat temperature and GWL were, however, not correlated and the influence of GWL on R_{eco} cannot be assumed.

DISCUSSION

Aboveground biomass production occurred between May and October with an annual green biomass production of 320 and 210 g m^{-2} for grass and moss, respectively. These values are within the range reported for most cool temperate peatlands of North America and Europe as summarized by Moore and others (2002). Dyck and Shay (1999) reported moss capitulum biomass of 278 g m^{-2} in a peatland of central Canada based on sampling to depth of green color. Annual biomass production of the moss capitulum in southern mires of Finland ranged between 260 and 400 g m^{-2} (Lindholm and Vasander 1990). Values obtained for eastern Canada for both vascular plant leaves and moss capitulum range between 114 and 672 g m^{-2} (Bubier and others 2006). Thus, in terms of biomass production, the studied peatland ecosystem is not very different from other peatlands occurring within the same latitudinal range. The results show that mosses are an important component of this community, representing ~30% of the total aboveground biomass during the growing period. Our findings are in agreement with those reported elsewhere (Shaver and Chapin 1991; Gordon and others 2001; Douma and others 2007), showing the significant contribution of moss to the overall community biomass as well as ecosystem function.

A combination of senescence of the grass, low radiation, and rapidly dropping temperatures could be the reasons for the decline in green biomass after August. This was not the case with moss where

green biomass development appeared to be more supported by low light intensities and air temperatures. The drop in moss green biomass between May (DOY 131) and June (DOY 198) may be due to the early spring drought that led to the drop in GWL down to –40 cm with possible reduction in soil moisture within the top soil layers. Recovery of moss, however, was a slow process, and it took almost a month before moss tissues were green and recovered. This may explain the observed 1.5 months' lag between GWL recovery and growth resumption. GWL, however, did not have any impact on biomass development in grass. Reasons for this could be due to: (1) unlike moss, green biomass development in grass started after April when there was rainfall and soil moisture conditions were already favorable and (2) grasses have deep rooting patterns, which could buffer them from low GWL compared to the moss (Limpens and others 2008). We observed grass roots growing down to −30 cm, indicating that even if the GWL drops down to this depth, grass will still have access to ground water. Moore and others (2002) reported fine root biomass accumulation of between 0.4 and 1 kg m^{-2} growing down –50 cm, making the grass vegetation less responsive to changes in GWL. Rooting depths below –50 cm have also been reported in Tundra, with mean biomass of 1.5 kg m^{-2} (Jackson and others 1996; Canadell and others 1996).

Green biomass influences NEE and GPP because it determines the photosynthetic surface area (Street and others 2007; Shaver and others 2007; Limpens and others 2008). Mean seasonal maximum NEE were around –10.0 and −5 µmol m^{-2} s^{-1} for grass and moss, respectively, whereas the respective GPP were 23 and 12 µmol m^{-2} s^{-1}. These are within the range of 8–20 µmol m^{-2} s^{-1} for NEE (Tuittila and others 2004; Douma and others 2007; Riutta and others 2007; Lindroth and others 2007; Shaver and others 2007) and 10–40 µmol m^{-2} s^{-1} for GPP (Bubier and others 1998; Lindroth and others 2007) reported for most temperate peatlands of Northern Hemisphere. The moss plots, in some instances, comprised a few grass populations that could raise the CO$_2$ fluxes because they are more active and efficient (Douma and others 2007; Limpens and others 2008). Although NEE data of moss were corrected for contribution by the grass using aboveground biomass of the grass harvested in the moss plots, our values still remain at the extreme end of the scale for moss fluxes (Tuittila and others 2004; Riutta and others 2007; Douma and others 2007). This could be explained by the high light intensity levels reaching the moss vegetation at our

study site compared to those reported for the Northern Hemisphere. Our results show that moss contributes ∼30% of the overall ecosystem CO$_2$ uptake in this peatland. Douma and others (2007) reported that mosses contributed between 14 and 96% of the total CO$_2$ assimilated in an arctic ecosystem, depending on the proportion of vascular plants (shading) growing together with the moss.

When NEE was normalized with biomass, we still observed higher NEE for grass during the active growth phase. These differences result from higher CO$_2$ fixation capacity due to higher light use efficiency (α) and higher maximum light intensity at which saturation occurs in grass compared to moss (Street and others 2007). Our analysis showed that light alone explains more than 70% of NEE during the active phase of development in both moss and grass and that grass could increase light use efficiency by increasing LAI, with an overall increase in potential production. At ecosystem level, increased LAI in grass may affect moss production by reducing the light levels reaching moss, because moss biomass is short and grows under the grass canopy, with a possible impact on the overall ecosystem production. Similar conclusions have been arrived at in studies conducted on moss communities in northern peatlands (Shaver and Chapin 1991; Douma and others 2007).

A ground water level of around –10 cm is regarded as the optimum water level for most physiological responses in peatland species (Tenhunen and others 1992; Semikhatova and others 1992; Tuittila and others 2004). The ground water level declined to –40 cm in April and later to –20 cm in June, with significant influence on moss NEE. Despite resumption of rainfall in May, NEE by moss remained low and moss plots were net CO$_2$ sources during most of the day until June. This was not the case with grass that was a CO$_2$ sink during this period. Differences that occur between moss and grass in response to changing GWL may be due to differences in their physiological and morphological structures (Schipperges and Rydin 1998). Mosses, unlike grasses, lack roots and only possess rhizoids that do not penetrate into deeper soil layers and they show more sensitivity to tissue water changes (Schipperges and Rydin 1998), with a narrow tolerance to a small draw-down in GWL (Riutta and others 2007). Grasses, however, are deep rooted and are less sensitive to short-term changes in GWL (Lafleur and others 2005) because they have access to water in a large soil volume. Grass also possess adaptive strategies such as leaf rolling, as shown by a declining LAI (with no change in biomass) in early June, and stomatal

control ability (Busch and Lösch 1999) that minimize transpiration water loss. Combined with high light use efficiency, these adaptations could enhance CO$_2$ assimilation during GWL decline and rapid recovery after drought in grass compared to moss.

Except for the months of June and July, R$_\mathrm{eco}$ was similar (mean = 10 μmol m^{-2} s^{-1}) in moss and grass. Our values are higher compared to those reported for peatlands of Scandinavian and North American countries (Bubier and others 1998; Tuittila and others 2004; Lafleur and others 2005; Lindroth and others 2007), but are within the range of 12–20 μmol m^{-2} s^{-1} reported by Riutta and others (2007). Higher R$_\mathrm{eco}$ from our study site could be due to; (1) its southern location, that is, less continental climate with higher temperatures given that there was an exponential increase in R$_\mathrm{eco}$ with increasing temperatures, (2) relatively longer growing season/extended decomposition period, and (3) a large drop in GWL that occurred in early spring and resulting into the death of moss. Bortoluzzi and others (2006) reported R$_\mathrm{eco}$ of 8.0 μmol m^{-2} s^{-1} in a mountain bog at an altitude of 867 m.a.s.l. in France with LAI of 1.1 and mean maximum temperatures of 30°C. The exact contribution of the vegetation to the total ecosystem respiration at this site is not known, however, measurement of peat respiration (plus roots) indicated that at least half of the R$_\mathrm{eco}$ originates from the peat. Compared to moss, a significantly large proportion of R$_\mathrm{eco}$ originated from the peat under the grass. Although no analysis of peat characteristics under the two vegetation types was conducted, we anticipated similar peat characteristics. Thus, differences in R$_\mathrm{eco}$ that were observed between the two plots could only be attributed to the large root biomass in the grass plots compared to moss.

Past studies indicate that peat respiration increases with decreasing GWL (McNeil and Waddington 2003; Bortoluzzi and others 2006; Riutta and others 2007). We observed an increase in R$_\mathrm{eco}$ with declining GWL, and even though the effects of GWL on R$_\mathrm{eco}$ might be confounded by changes in peat temperature, the behavior response suggested that the two vegetation types were affected differently (R^2 = 0.85 and 0.39 in grass and moss, respectively). This was not the case with peat temperature, which had similar effects on both moss and grass. The poor correlation in moss suggests that its respiration could be influenced by GWL changes in a very narrow uppermost portion of the peat profile. This was different in grass because the extensive rooting system tracks the

changing soil moisture conditions (lagging behind GWL) as aeration of the soil profiles allows for aerobic respiration of the roots and soil micro-organisms (Basiliko and others 2006), whereas CO_2 assimilation remained unchanged. Influence of water table fluctuation on ecosystem respiration is well documented for other ecosystems (Alm and others 1999), whereas Lafleur and others (2005) explained the anomalies in such relationships.

Our results emphasize the significant role of temperature in determining ecosystem CO_2 exchange processes in this peatland. At high light intensities, temperature sets the upper boundary of NEE, which increases steadily with increasing temperature to an optimum of 25°C. Because there was an exponential increase in R_{eco} with increasing temperature, a rapid decline in NEE above 25°C could be the result of an increasing R_{eco} over CO_2 assimilation, an indication that at higher temperatures the peatland is likely to become a net CO_2 source.

CONCLUSION

Green biomass and LAI are important determinants of CO_2 assimilation by mosses and grasses. Apart from LAI, higher NEE in grasses compared to mosses was also attributed to more efficient light use. Mosses were more sensitive to GWL draw-down, which had significant influence on their CO_2 assimilation and biomass development. Grasses, however, showed less sensitivity to GWL changes, as a result of their extensive and deep rooting systems. Increasing peat temperatures at −10 cm depth resulted in an increase in R_{eco}. Because future climate scenarios in Europe indicate reduced precipitation amounts and increased air temperatures, lower GWL, and increased peat temperatures may turn this peatland into a net CO_2 source during most of the year. Other possible consequences are increased death of mosses and their replacement with grasses and other vascular plant species that are more resilient. Mosses, however, make significant contributions to the current total community biomass as well as eco-system CO_2 uptake in this peatland and their decline may disrupt the ecosystem CO_2 budget.

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