

# Seasonal and inter-annual variability of carbon dioxide exchange at a boreal peatland in north-east European Russia

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## SUMMARY

Although peatlands cover about 10 % of north-east European Russia, few publications report carbon dioxide (CO<sub>2</sub>) fluxes in the tundra and middle taiga peatlands of this region. In this study the CO<sub>2</sub> balance of a boreal peatland in the Komi Republic was determined using the eddy covariance method, for the summer periods (10 June to 10 September) of 2012 and 2013. Monthly totals of net ecosystem exchange (*NEE*) varied significantly over the two years. The total net CO<sub>2</sub> flux from the atmosphere to the peatland was 30 % greater in June 2013 than during the same month in 2012. The difference for July was smaller. In 2012 the total CO<sub>2</sub> flux in August was 29 % higher, and in September it was 2.4 times lower, than in 2013. Despite the differences in seasonal dynamics of *NEE* between 2012 and 2013, the mean monthly indicators of gas exchange in the peatland ecosystem were mostly similar. Maximum values of gross photosynthesis (*P<sub>gross</sub>*) and ecosystem respiration (*R<sub>eco</sub>*) were observed in July, which is the period of maximum development of the green biomass of plants. The CO<sub>2</sub> fluxes were constrained by the precipitation and temperature regimes. During the drought of 2013, *P<sub>gross</sub>* and *R<sub>eco</sub>* were mostly influenced by the incidence of precipitation. The peatland was a CO<sub>2</sub> sink during both growing seasons and, in June–September 2012, it sequestered 317.66 g m<sup>-2</sup> of CO<sub>2</sub>, which is 10.5 % more than during the same period in 2013. Our results are broadly comparable with measurements in similar peatland ecosystems across northern Europe and south-east Canada.

**KEY WORDS:** CO<sub>2</sub>, eddy covariance, *NEE*, *P<sub>gross</sub>*, *R<sub>eco</sub>*, seasonal dynamics, taiga, water table, weather

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## INTRODUCTION

Peatlands store more carbon than any other terrestrial ecosystem. Covering only about 3 % of Earth's land area, they hold the equivalent of half of the carbon that is in the atmosphere as CO<sub>2</sub> (Dise 2009). Northern peatlands are a globally important carbon sink, and annual carbon sequestration in boreal and subarctic peatlands amounts to 29 g m<sup>-2</sup> (Gorham 1991). The carbon sequestration ability of peatland ecosystems depends on microtopography, plant composition and hydrothermal regime during the snow-free period (Aurela *et al.* 2004, Korrensalo *et al.* 2017), and the inter-annual variability of total carbon dioxide (CO<sub>2</sub>) assimilation/emission is determined by weather conditions (Arneeth *et al.* 2006). Even small changes in environmental conditions can transform a peatland ecosystem from a sink to a source of carbon (Lund *et al.* 2015). The relationship between the carbon cycle in terrestrial ecosystems and climate warming was discussed by Gorham (1991) (see also Heimann & Reichstein

2008), who concluded that in boreal and temperate regions the photosynthetic uptake is stimulated by increasing CO<sub>2</sub> concentration in the atmosphere and by rising temperatures. On the other hand, an increase in CO<sub>2</sub> release through respiration will also occur as temperature rises, due to the intensification of physiological processes in plants and microbes.

The majority of previous research on carbon dioxide exchange in northern peatlands and tundra has been carried out in Alaska (Kwon *et al.* 2006), Canada (Lafleur *et al.* 2001, Frohling *et al.* 2002, Lafleur *et al.* 2003), Scandinavia (Heikkinen *et al.* 2002, Christensen *et al.* 2012, Gažovič *et al.* 2013), Greenland (Westergaard-Neilsen *et al.* 2013) and Siberia (Arneeth *et al.* 2002, Friberg *et al.* 2003, Kutzbach *et al.* 2007). Although peatlands cover about 10 % of north-east European Russia, investigations of carbon dioxide fluxes in this region are not numerous. Only a few publications report CO<sub>2</sub> fluxes in the tundra (Zamolodchikov *et al.* 1998, Marushchak *et al.* 2013) and peatlands of the middle taiga (Schneider *et al.* 2012, Mikhaylov *et al.* 2013,

Miglovets *et al.* 2014).

In this article we present data on net ecosystem exchange ( $NEE$ ), gross photosynthesis ( $P_{gross}$ ) and ecosystem respiration ( $R_{eco}$ ) from a peatland in the middle taiga subzone, obtained using the eddy-covariance method. The inter-annual variability of growing-season carbon dioxide exchange between the atmosphere and a peatland ecosystem in this region is described for the first time. The objectives of the study were to fill in a gap in many years of research at the site, to identify the conditions under which the ecological functioning of the peatland can change, and to discover how the inter-annual variability of weather conditions affects the cumulative value of CO<sub>2</sub> assimilation.

## METHODS

### Study site

The meso-oligotrophic peatland Medla-Pev-Nyur (Ust-Pojeg) is situated in the middle taiga subzone of north-east European Russia, 40 km north-west of Syktyvkar (Republic of Komi; 61° 56' N, 50° 13' E; Figure 1). The area of the peatland is 2790 ha and the mean peat thickness is 1.4 m. It belongs to the 'South-Western Plain' climatic region of the Komi Republic (GDGC 1964).

According to long-term measurements (1965–2012) made at the Ust-Vym meteorological station (34.5 km north of Medla-Pev-Nur; operated by the Centre for Hydrometeorology and Environmental

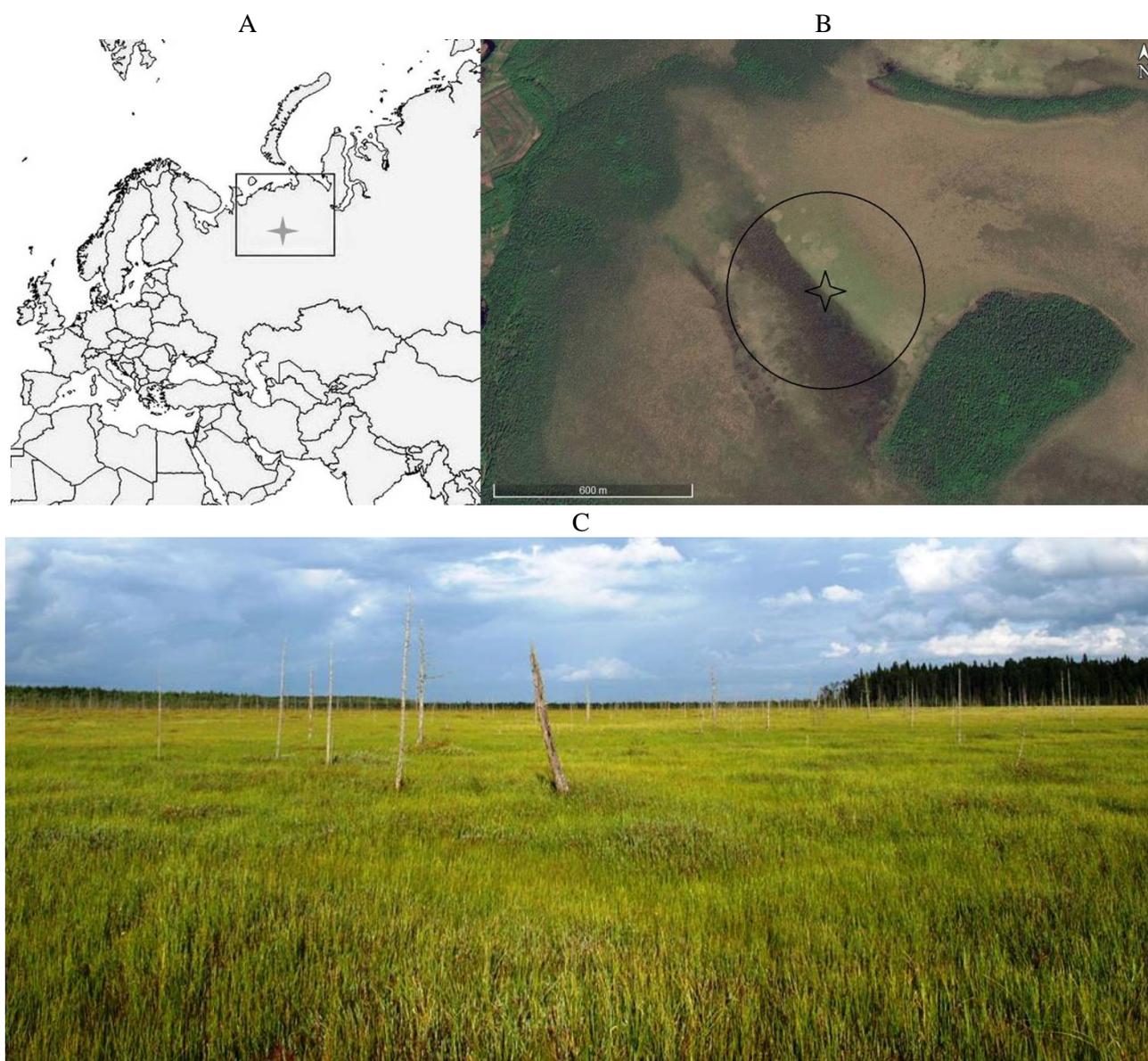


Figure 1. Study site (Medla-Pev-Nyur (Ust-Pojeg) peatland). A: map of Europe showing the location of the study site; B: location of the eddy covariance tower on the study site; C: typical landscape of the study site.

Monitoring of the Komi Republic), mean annual temperature in the study area is  $1.1 \pm 1.2$  °C and mean annual precipitation is  $586 \pm 94$  mm. Snow cover forms around 20 October, lasts for 165–175 days and melts on 05 May. The duration of the frost-free period is 90–105 days. The annual growing season (with mean temperature above +5 °C) lasts for 100–110 days and mean annual sunshine duration is 1600 hours. For the period 1965–2012, the mean annual temperature of the atmospheric surface layer was higher by 0.4 °C, and mean annual precipitation was greater by 89 mm, as compared with the first half of the twentieth century; the sum of effective temperatures and number of days with air temperature above 0 °C were also higher during the later of these periods (Zagirova & Schneider 2016).

Within the footprint of the eddy covariance tower at Medla-Pev-Nur, the dominant plant communities are: (1) *Carex rostrata* Stokes - *Oxycoccus palustris* Pers. - *Carex limosa* L. - *Sphagnum* sp. (5.9 %); and (2) *Andromeda polifolia* L. - *Oxycoccus palustris* - *Scheuchzeria palustris* L. - *Sphagnum* sp. (78.3 %). The oligotrophic plant community (*Chamaedaphne calyculata* (L.) Moench - *Oxycoccus palustris* - *Andromeda polifolia* - *Sphagnum* sp.) occupies 15.8 % of the area. A more detailed description of the land cover of the Medla-Pev-Nyur (Ust-Pojeg) peatland is available elsewhere (Zagirova & Schneider 2016).

### Microclimate measurements

Microclimate variables were recorded every 30 minutes by an automatic meteorological station using specialised sensors and a CR3000 micrologger (Campbell Scientific Inc., USA). Air temperature at a height of 2 m above the moss surface was measured using a HMP50 sensor; intensity of photosynthetically active radiation (PAR) was measured using a Li-190SB quantum sensor; and atmospheric pressure was measured with a CS106 barometric pressure sensor. Soil temperature at 0.3 m depth was measured using a TCAV-L probe (Campbell Scientific Inc., USA). Precipitation data were obtained from Ust-Vym meteorological station. Water table measurements were carried out in 2013 using Diver pressure sensors (Van Essen Instruments B.V., The Netherlands) installed in dipwells (with perforated walls) at three points near the eddy covariance measurement system. No water table data were recorded in 2012, for technical reasons.

### CO<sub>2</sub> flux measurements

The investigation of CO<sub>2</sub> gas exchange between the peatland and the atmosphere proceeded from 10 June to 10 September in 2012 and 2013. It was carried out

in the central part of the peatland using the eddy-covariance method, which determines the exchange rate of the gas across the interface between the atmosphere and the plant canopy by measuring the covariance between fluctuations in vertical wind velocity and the mixing ratio of the gas being studied (Baldocchi 2003). The measuring system included an ultrasonic anemometer to measure temperature and wind speed in three dimensions (CSAT3, Campbell Scientific Inc., USA) and an open-path infrared gas analyser (Li-7500A, Li-Cor Inc., USA). These devices were located at a height of 3.93 m above the moss surface. Data were recorded at a frequency of 10 Hz and processed using EddyPro software (Li-Cor Inc., USA). The analysis program included mathematical and statistical raw data processing at 30-minute time intervals.

At the first stage of processing, the raw data were filtered according to the flag system “0-1-2”, based on the steady state and integral turbulence characteristics tests (Mauder & Foken 2006). In this system “0” means high quality fluxes, “1” means fluxes are acceptable for budget analysis, and “2” that fluxes are discarded.

At the next stage, the quality of the selected data was evaluated according to the ratio of Monin-Obukhov surface-layer scaling parameter ( $z/L$ ) and footprint ( $d_{fetch70}$ ) to friction velocity ( $u^*$ ) at the moment of measurement, as is customary in investigations of vertical greenhouse gas fluxes in terrestrial ecosystems (Kutzbach *et al.* 2007, Lund *et al.* 2015). The atmospheric stability indicated by the surface layer scaling parameter ( $z/L$ ) as introduced by Monin & Obukhov (1954) was closely related to the friction velocity ( $u^*$ ). Since very stable ( $z/L > 1$ ) and very unstable ( $z/L < -5$ ) atmospheric conditions corresponded to low values of  $u^*$  ( $u^* < 0.1$  m s<sup>-1</sup>), we did not include the CO<sub>2</sub> gas flux measurements obtained at (30-minute mean)  $u^*$  below 0.1 m s<sup>-1</sup> in further calculations. These were often night-time measurements, when the turbulence of the atmospheric boundary layer is low.

At the final stage the data were checked visually, and outlier data points (exceeding the moving average by two standard deviations) that had not previously been detected were removed from the dataset. As a result, 2920 data points (65.4 % of the whole raw dataset) for the year 2012 and 3356 data points (75.2 % of the whole raw dataset) for the year 2013 were used in further processing.

### Gap filling

After completion of the raw data processing stages, the gap-filling method of Falge *et al.* (2001) was applied, taking into account the covariation of gas

fluxes with meteorological variables and temporal autocorrelation of fluxes (Reichstein *et al.* 2005), using the online gap-filling tool (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/>) from the Max Planck Institute, Germany. The values of vertical CO<sub>2</sub> flux ( $F_{CO_2}$ ) obtained are equivalent to the net carbon dioxide exchange between the peatland ecosystem and the atmosphere ( $NEE$ ).  $NEE$  is the sum of gross photosynthesis ( $P_{gross}$ ), which in our study has a negative sign, and ecosystem respiration ( $R_{eco}$ ) which has a positive sign. If, during the 30-minute measurement period, CO<sub>2</sub> uptake was predominant as a result of photosynthesis,  $NEE$  would have a negative sign; and if respiration predominated,  $NEE$  would be positive. The Max Planck Institute's online tool was also used for flux partitioning.

Daily and monthly vertical fluxes of carbon dioxide between the peatland and the atmosphere were derived as cumulative sums of the CO<sub>2</sub> exchange rate averaged over 30-minute periods.

### Statistical tests

For comparison of independent samples, Student's *t*-test with a significance level of  $p < 0.01$  was used. The program STATISTICA 13 was used to identify correlation dependences and to construct regression equations between variables.

## RESULTS

### Meteorological conditions

The analysis of on-site data in conjunction with information from the Ust-Vym meteorological station showed that temperature and precipitation differed noticeably between the growing seasons (June–September) of 2012 and 2013 (Table 1, Figures 2 and 3).

June 2012 was dominated by warm and rainy weather; mean monthly air temperature was +15.1 °C, which is 1.4 °C higher than the long-term (1965–2012) mean value for this month, and the precipitation total was 233 % of the June long-term mean. July was also warm and wet. In this month mean monthly air temperature reached +17.3 °C (1.3 °C above long-term mean) and precipitation was 239 % of the long-term mean value. August 2012 had a mean monthly air temperature of +14.0 °C and abundant precipitation (24 % above long-term mean). Night frost was noted at the beginning of September despite the fact that mean monthly air temperature for that (calendar) month was 1.5 °C higher than the long-term mean. The total amount of precipitation during September was 216 % higher than the long-term mean.

The weather of June 2013 was unstable with rapid drops in air temperature. There was no rainfall during the first ten days of the month (data not shown); most of the precipitation fell between 11 and 20 June. The weather in July was hot and dry. Diurnal averages of air temperature ranged from +14 to +21 °C, and precipitation amounted to only half of the long-term mean. August was warm with mean monthly air temperature +15 °C and more rainy days than July. Cool weather with rain was established at the end of September. The sums of precipitation during the annual investigation periods (10 June to 10 September) were 432 mm in 2012 and 115 mm in 2013. Thus, the summer of 2013 was warmer and drier than the summer of 2012.

In both 2012 and 2013, soil temperature at 0.3 m depth followed the seasonal march of air temperature with a delay of four days, the diurnal average soil temperature increasing in June and July (+15 °C at the end of July) then decreasing gradually (+10 °C at the beginning of September) (Figures 1 and 2).

During the summer periods of both years, the wind directions in the study area were north-easterly (33–39 %) and south-easterly (24–27 %). The peak contribution to the total CO<sub>2</sub> flux originated from <70 m upwind of the eddy covariance tower in 95 % of all cases; and 60 m upwind in 41 % of cases in 2012 or 39 % of cases in 2013. More than 95 % of the CO<sub>2</sub> flux came from within 600 m upwind.

The average summer (June–September) wind velocity was 1.9 m s<sup>-1</sup> in 2012 and 2.2 m s<sup>-1</sup> in 2013 (maximum 7.3 m s<sup>-1</sup> in 2012, 7.4 m s<sup>-1</sup> in 2013). Atmospheric pressure varied between 98 and 102 kPa during the investigation periods of 2012 and 2013. The length of the growing season was 129 days in 2012 (07 May to 30 September) and 127 days in 2013 (05 May to 26 September).

During the 2013 investigation period the water table level relative to the moss surface (WT) was noticeably below the 2008–2014 mean (no data from 2012). In the middle of June WT was -8.0 cm and gradually decreased further throughout the investigation period. At the beginning of September it was -41.7 cm.

### Carbon dioxide fluxes

There were similarities in the seasonal course of carbon dioxide exchange during the two years of observations (Figures 2 and 3; see Appendix for daily data). The mean values of net ecosystem exchange ( $NEE$ ) for the first ten days of the measurement period were -3.08 g m<sup>-2</sup> d<sup>-1</sup> (2012) and -4.46 g m<sup>-2</sup> d<sup>-1</sup> (2013), and decreased gradually to -4.47 (2012) and -5.19 g m<sup>-2</sup> d<sup>-1</sup> (2013) for the ten days in the middle of July - the time of most favourable light and

Table 1. Weather conditions ( $\pm$  SD) recorded (mostly) at Medla-Pev-Nyur during the calendar months of June to September in the years 2012 and 2013. Soil temperature was measured at depth 0.3 m. Precipitation data were obtained from the Ust-Vym meteorological station (Centre for Hydrometeorology and Environmental Monitoring of the Komi Republic; 34.5 km north of Medla-Pev-Nur). LTM = long-term mean (1965–2012) value derived from data collected at Ust-Vym.

Year	Month	Mean monthly air temperature (°C)			Mean soil temperature (°C)	Precipitation (mm)		Mean wind speed (m s <sup>-1</sup> )
		LTM	this month	(this month - LTM)	this month	LTM	this month (% of LTM)	this month
2012	June	13.7	15.1 $\pm$ 4.4	+1.4	11.0 $\pm$ 1.1	67	156 (233)	2.0 $\pm$ 1.3
	July	16.0	17.3 $\pm$ 4.7	+1.3	14.0 $\pm$ 0.6	69	165 (239)	2.0 $\pm$ 1.2
	August	13.7	14.0 $\pm$ 5.8	+0.3	13.4 $\pm$ 1.5	67	83 (124)	1.9 $\pm$ 1.2
	September	7.5	9.0 $\pm$ 4.0	+1.5	10.3 $\pm$ 0.5	67	145 (216)	1.6 $\pm$ 1.0
2013	June	13.7	16.6 $\pm$ 6.2	+2.9	10.6 $\pm$ 0.7	67	35 (52)	2.0 $\pm$ 1.4
	July	16.0	19.0 $\pm$ 5.5	+3.0	13.3 $\pm$ 0.7	69	32 (46)	1.5 $\pm$ 1.1
	August	13.7	15.9 $\pm$ 4.4	+2.2	13.7 $\pm$ 0.5	67	48 (72)	1.8 $\pm$ 1.1
	September	7.5	8.5 $\pm$ 5.3	+1.0	11.5 $\pm$ 1.0	67	36 (54)	1.6 $\pm$ 1.0

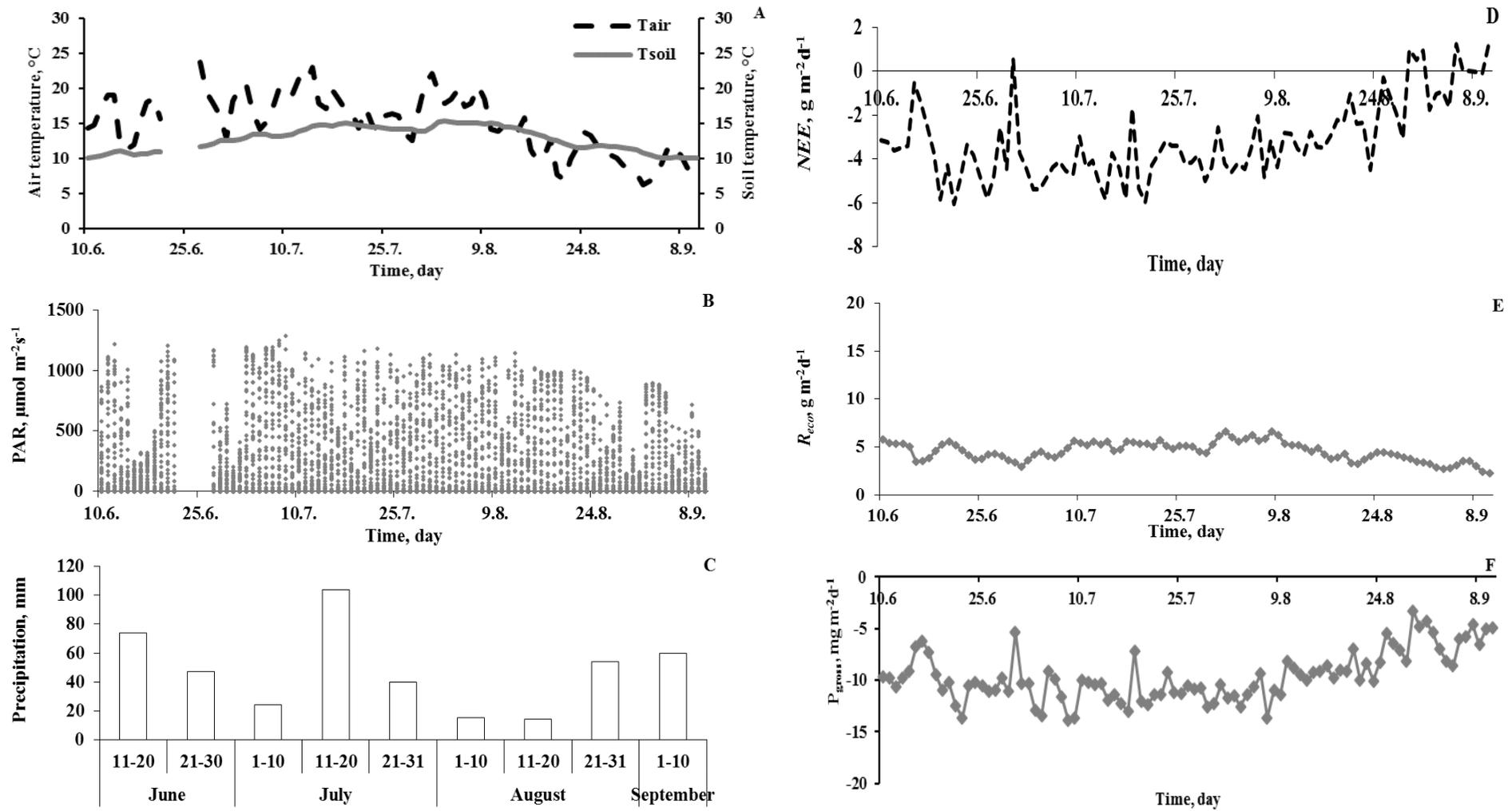


Figure 2. Meteorological conditions and CO<sub>2</sub> fluxes during the measurement period in 2012. A: air temperature (T<sub>air</sub>) and soil temperature at depth 0.3 m (T<sub>soil</sub>) (°C); B: PAR intensity (μmol m<sup>-2</sup> s<sup>-1</sup>); C: precipitation (mm; each column shows the cumulative rainfall in one-third of a month); D: NEE (g m<sup>-2</sup> d<sup>-1</sup>); E: R<sub>eco</sub> (g m<sup>-2</sup> d<sup>-1</sup>); F: P<sub>gross</sub> (g m<sup>-2</sup> d<sup>-1</sup>).

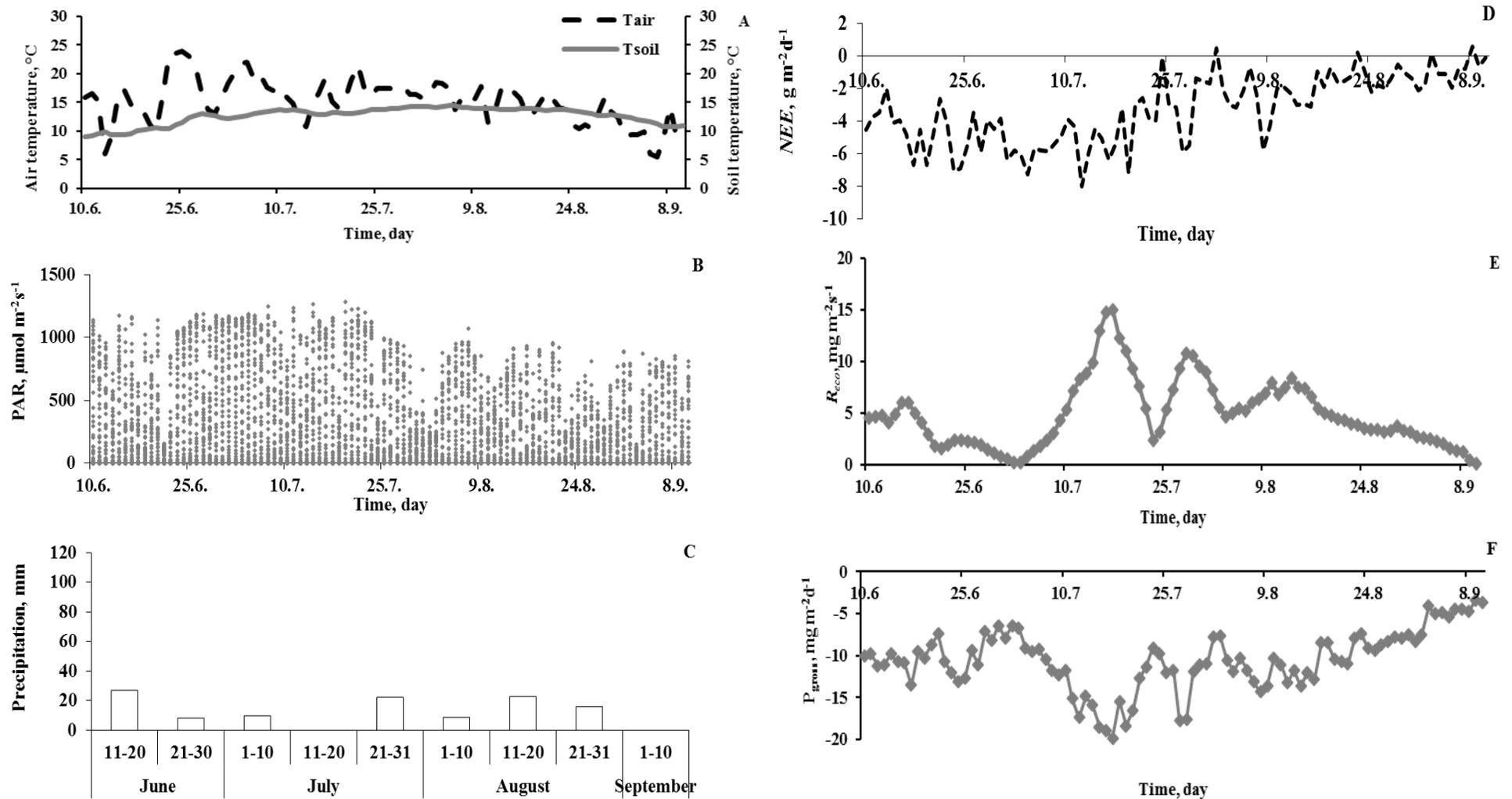


Figure 3. Meteorological conditions and CO<sub>2</sub> fluxes during the measurement period in 2013. A: air temperature (T<sub>air</sub>) and soil temperature at depth 0.3 m (T<sub>soil</sub>) (°C); B: PAR intensity (μmol m<sup>-2</sup> s<sup>-1</sup>); C: precipitation (mm; each column shows the cumulative rainfall in one-third of a month); D: NEE (g m<sup>-2</sup> d<sup>-1</sup>); E: R<sub>eco</sub> (g m<sup>-2</sup> d<sup>-1</sup>); F: P<sub>gross</sub> (g m<sup>-2</sup> d<sup>-1</sup>).

temperature conditions for photosynthesis. In June 2012 there were two short periods when *NEE* was close to or even exceeded zero. The same phenomenon was observed during the periods of short-term drops in air temperature and notable precipitation shortage in the second part of July 2013. Subsequently, the mean diurnal CO<sub>2</sub> exchange decreased gradually, in 2012 from -2.65 g m<sup>-2</sup> d<sup>-1</sup> in August to -0.30 g m<sup>-2</sup> d<sup>-1</sup> at the beginning of September and in 2013 from -1.93 g m<sup>-2</sup> d<sup>-1</sup> in August to -0.78 g m<sup>-2</sup> d<sup>-1</sup> at the beginning of September. For the entire season of measurements the mean value of *NEE* was  $-3.15 \pm 1.81$  g m<sup>-2</sup> d<sup>-1</sup> in 2012 and  $-3.31 \pm 2.12$  g m<sup>-2</sup> d<sup>-1</sup> in 2013; whereas maximum daily uptake was -6.06 g m<sup>-2</sup> d<sup>-1</sup> in 2012 and -8.01 g m<sup>-2</sup> d<sup>-1</sup> in 2013. Thus, during the June–September observation periods of both years the peatland ecosystem functioned as a sink of atmospheric CO<sub>2</sub>.

In contrast, there were significant differences in the seasonal course of *R<sub>eco</sub>* between 2012 and 2013 (Figures 2E and 3E). In 2012 the seasonal variation in mean diurnal ecosystem respiration followed the mean air temperature, with ecosystem respiration intensifying as air temperature increased. Conversely, ecosystem respiration was characterised by high variability in June–August 2013. Low ecosystem respiration followed the extreme period of much higher (3 °C above the long-term value) mean monthly air temperature without rainfall in June (Table 1). An increase in ecosystem respiration occurred at the beginning of July 2013, following rainfall. Even a short period of lower air temperature did not affect the trend of increasing ecosystem respiration during this period. In the middle of July ecosystem respiration of 14.95 g m<sup>-2</sup> d<sup>-1</sup> was observed

when the air temperature reached +21 °C. Respiration peaks were also observed when rainy weather occurred at the end of July and in mid-August. Thus, the rate of ecosystem respiration appeared to be influenced more by the occurrence of rainfall than by the ambient temperature in 2013. Despite the differences in dynamics of *R<sub>eco</sub>* during July–August, the mean monthly values of this indicator were comparable between the two years of observations, except in July (Table 2).

In 2012 the mean diurnal ecosystem respiration followed the mean air temperature and a close correlation between them was established ( $r=0.78$ ,  $p<0.05$ ,  $N=88$ ); but in 2013 mean diurnal air temperature and ecosystem respiration rate were not closely correlated ( $r=0.11$ ,  $N=93$ ,  $p>0.05$  i.e. not significant). Total growing-season precipitation in 2013 was 3.8 times less than in 2012, and the water table level was up to 5 times lower than the 2008–2014 mean (Figure 4). Analysis of the seasonal course of water table level in 2013 showed a close correlation between it and the mean diurnal ecosystem respiration ( $r=0.70$ ,  $p<0.05$ ,  $N=64$ ) from mid-July to early September.

The seasonal dynamics of gross photosynthesis (*P<sub>gross</sub>*) mostly followed the changes in PAR intensity in both years (Figures 2B,F and 3B,F). There was one deviation from this pattern, during a period at the end of June / beginning of July 2013. The reason for the decline in *P<sub>gross</sub>* observed during this period was probably the extreme drought that occurred at that time (Shi *et al.* 2014). In 2013, June–July gross photosynthesis was more variable than in 2012 (Figure 3F) and was probably affected by lack of precipitation in the same way as ecosystem

Table 2. Total *NEE* (g m<sup>-2</sup>) and mean CO<sub>2</sub> exchange fluxes (g m<sup>-2</sup> d<sup>-1</sup>) during each month of the 2012 and 2013 measurement periods.

Period	<i>NEE</i>				<i>P<sub>gross</sub></i>		<i>R<sub>eco</sub></i>	
	total (g m <sup>-2</sup> )		mean flux (g m <sup>-2</sup> d <sup>-1</sup> )		mean flux (g m <sup>-2</sup> d <sup>-1</sup> )		mean flux (g m <sup>-2</sup> d <sup>-1</sup> )	
	2012	2013	2012	2013	2012	2013	2012	2013
10–30 Jun	-80.90	-89.97	$-3.56 \pm 1.66$	$-4.65 \pm 1.39$	$-9.77 \pm 1.99$	$-10.19 \pm 1.90$	$4.48 \pm 0.79$	$3.14 \pm 1.65$
01–31 Jul	-144.09	-127.96	$-4.28 \pm 0.97$	$-4.61 \pm 1.91$	$-11.24 \pm 1.46$	$-12.97 \pm 3.82$	$4.91 \pm 0.69$	$6.74 \pm 4.41$
01–31 Aug	-89.31	-58.51	$-2.65 \pm 1.59$	$-1.93 \pm 1.25$	$-8.96 \pm 2.39$	$-10.23 \pm 2.16$	$4.73 \pm 1.03$	$5.22 \pm 1.62$
01–10 Sep	-3.36	-7.92	$-0.30 \pm 1.05$	$-0.78 \pm 0.80$	$-6.20 \pm 1.37$	$-4.76 \pm 1.14$	$2.94 \pm 0.43$	$1.65 \pm 0.91$

respiration. The maximum rate of CO<sub>2</sub> assimilation (-19.83 g m<sup>-2</sup> d<sup>-1</sup>) was observed in mid-July. Short-term declines in gross photosynthesis were observed in the latter parts of both June and July, when rainfall occurred in the study area. After the early August maximum of -10.98 to -14.77 g m<sup>-2</sup> d<sup>-1</sup>, gross photosynthesis decreased gradually for the rest of that month. In early September PAR was one-third of the July value (Figure 3B) and  $P_{gross}$  reached its lowest rate during the measurement period (-4.43 to -5.94 g m<sup>-2</sup> d<sup>-1</sup>) (Figure 3F). Gross photosynthesis is strongly influenced by air temperature, PAR and water stress (Reichstein *et al.* 2013). In our investigation the relationship between gross photosynthesis, PAR and air temperature during the 2012 investigation period was described by the equation:

$$P_{gross} = 0.01 \text{ PAR} + 0.40 T_{air} \quad [1]$$

( $R^2 = 0.98$ ,  $F = 1741.70$ ,  $p \leq 0.01$ );

and for 2013, when data for WT were also available, we obtained the equation:

$$P_{gross} = 0.01 \text{ PAR} + 0.09 \text{ WT} + 0.66 T_{air} \quad [2]$$

( $R^2 = 0.94$ ,  $F = 300.58$ ,  $p \leq 0.01$ ).

Comparison of monthly mean carbon dioxide exchange values for the June–September growing season using a Student's t-test did not identify any statistically significant differences between 2012 and 2013. Despite this, period and monthly totals of *NEE* varied noticeably between the years. During a 20-day period of measurements in June 2013 the flux of CO<sub>2</sub> from the atmosphere to the peatland was 30 % more than during the same period in 2012. The differences

were smaller in July. Total *NEE* for August was 29 % higher in 2012 than in 2013, and for September it was 2.4 times lower in 2012 than in 2013. For the full 92 days of observations in June–September 2012, the cumulative total of *NEE* of the peatland ecosystem (-317.66 g m<sup>-2</sup>) was 10.5 % higher than for the same period in 2013 (-284.36 g m<sup>-2</sup>) (Table 2, Figure 5).

## DISCUSSION

The seasonal growth of plants influences the intensity of vertical carbon dioxide fluxes (Arneth *et al.* 2006). The formation of above-ground biomass in the peatlands of the middle taiga subzone is usually complete in July (Golovatskaya 2009), with maximum accumulation of pigments in the leaves of herbaceous plants (Yatsco *et al.* 2009). This could be a major reason for the intensification of carbon dioxide exchange with the atmospheric boundary layer in July. At a peatland ecosystem in southern Finland, Korrensalo *et al.* (2017) observed maximum gross photosynthesis in June due to maximum vascular plant leaf area index (LAI).

The highest negative daily CO<sub>2</sub> fluxes we observed (-6 to -8 g m<sup>-2</sup> d<sup>-1</sup>) were similar to those recorded at Kaamanen Fen, northern Finland (-6 to -7 g m<sup>-2</sup> d<sup>-1</sup>; Aurela *et al.* 2001), a bog in south-east Canada (-6.8 to -7.6 g m<sup>-2</sup> d<sup>-1</sup>; Lafleur *et al.* 2003) and on Zotino and Fyodorovskoye bogs in Siberia (-5.28 to -8.36 g m<sup>-2</sup> d<sup>-1</sup>; Arneth *et al.* 2002). Daily mean uptake over the growing season at the Degerö Stormyr mire complex in Sweden (-2.26 ± 0.32 g m<sup>-2</sup> d<sup>-1</sup>; Sagerfors *et al.* 2008), on blanket bog in northern Norway (-2.66 ± 0.38 g m<sup>-2</sup> d<sup>-1</sup>; Lund *et al.* 2015) and the Kobbefjord wetland in Greenland (-2.83 g m<sup>-2</sup> d<sup>-1</sup>; Westergaard-Neilsen *et al.* 2013) was 1.2–1.4 times

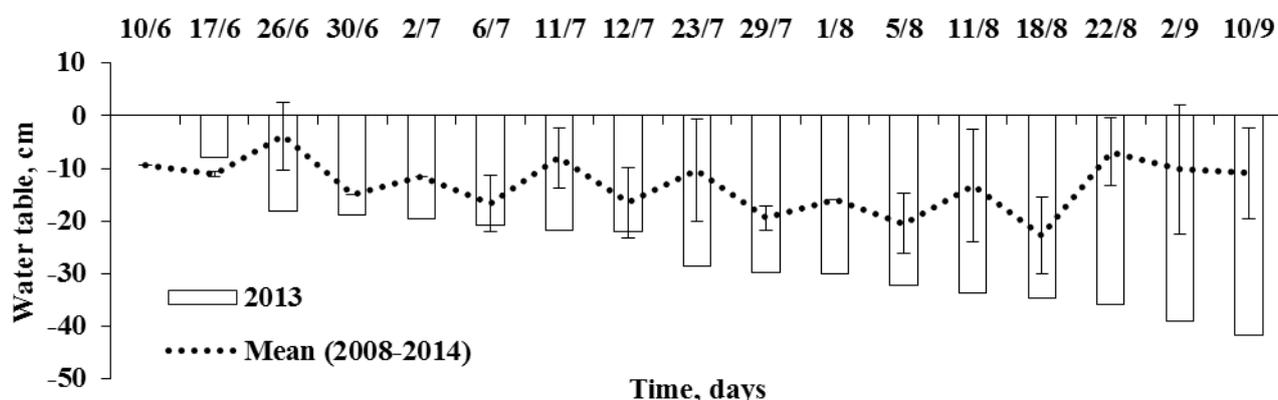


Figure 4. Seasonal course of water table level (WT) relative to ground surface level during the measurement period (10 June to 10 September) of 2013. The mean values are means of WT for six years (2008–2014 excluding 2012). The error bars show ± SD (standard deviation).

less than in Medla-Pev-Nyur. At Stordalen Mire in Swedish Lapland mean July fluxes of CO<sub>2</sub> were 12–24 % higher than our results ( $-3.71 \text{ g m}^{-2} \text{ d}^{-1}$ ; Christensen *et al.* 2012). Nevertheless, CO<sub>2</sub> fluxes from all these sites are comparable, and their similarity is probably explained by the fact that the above mires are more or less typical of the Northern Hemisphere. The small differences between them probably arise from differences in weather conditions during the measurement periods.

Our measurements of ecosystem respiration in summer ( $4.54\text{--}4.87 \text{ g m}^{-2} \text{ d}^{-1}$ ) are close to results obtained for peatland ecosystems in northern Finland (up to  $3.46 \text{ g m}^{-2} \text{ d}^{-1}$ ; Aurela *et al.* 2001), South Greenland ( $4.81 \text{ g m}^{-2} \text{ d}^{-1}$ ; Westergaard-Nielsen *et al.* 2013), south-east Canada ( $3.35 \pm 0.02 \text{ g m}^{-2} \text{ d}^{-1}$ ; Humphreys *et al.* 2014) and Sweden ( $4.18 \pm 1.44 \text{ g m}^{-2} \text{ d}^{-1}$ ; Sagerfors *et al.* 2008). At the same time, our values are two times higher than those reported from some peatlands in northern Norway ( $2.23 \pm 0.30 \text{ g m}^{-2} \text{ d}^{-1}$ ; Lund *et al.* 2015) and Ireland ( $1.84 \pm 0.11 \text{ g m}^{-2} \text{ d}^{-1}$ ; McVeigh *et al.* 2014).

As shown in previous research, ecosystem respiration could be largely regulated by high summer temperature (Shi *et al.* 2014). Van der Molen *et al.* (2007) attribute the enhancement of ecosystem respiration with increasing air temperature to heating of the upper layers of the soil. Alternatively, in studies of boreal forest ecosystems, drier surface soils can result in reduced  $R_{eco}$  because of the effect on the

heterotrophic microbial community (Welp *et al.* 2007). As showed in some investigations (Meir *et al.* 2008, von Buttlar *et al.* 2018), drought conditions directly reduce soil respiration. In our case, from July 2013, ecosystem respiration appeared to be regulated more strongly by soil water availability than by air temperature. Even a slight increase of water table level led to a rapid increase of ecosystem respiration in July and August. The reason could be the inhibition of soil microbial processes due to moisture limitation (von Buttlar *et al.* 2018). Thus, under the drought conditions of 2013, soil water availability appeared to be a more limiting factor for ecosystem respiration than air temperature. Conversely, under conditions of precipitation excess, air temperature became a limiting factor, as in 2012.

The maximum mean monthly values of  $P_{gross}$  obtained in July ( $-11.24 \pm 1.46$  to  $-12.97 \pm 3.82 \text{ g m}^{-2} \text{ d}^{-1}$ ) were 2–3 times higher than measurements on peatland in northern Norway ( $-4.85 \text{ g m}^{-2} \text{ d}^{-1}$ ; Lund *et al.* 2015) and on fen peatland in southern Greenland ( $-7.6 \text{ g m}^{-2} \text{ d}^{-1}$ ; Westergaard-Nielsen *et al.* 2013), and comparable with data from mixed tundra in the north-eastern part of European Russia ( $-9.8 \text{ g m}^{-2} \text{ d}^{-1}$ ; Marushchak *et al.* 2013). The cumulative sum of gross photosynthesis (as CO<sub>2</sub>) at Medla-Pev-Nyur during the 2012 growing season ( $-815 \text{ g m}^{-2}$ ) was comparable with the cumulative gross primary production ( $GPP$ ) of  $(-843 \text{ g m}^{-2})$  observed on peatland in southern Finland by Korrensalo *et al.* (2017).

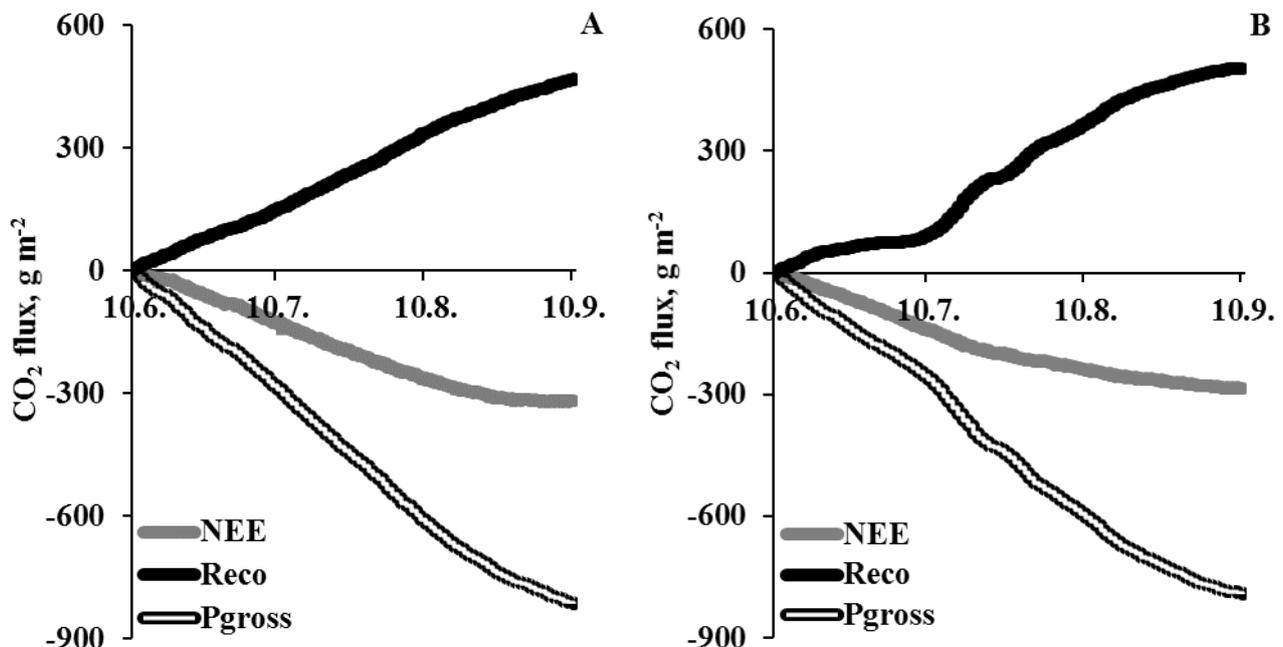


Figure 5. Cumulative sums of carbon dioxide exchange ( $\text{g m}^{-2}$ ) for the growing seasons (10 June to 10 September) of (A) 2012 and (B) 2013.

It has been shown in previous studies that low water availability coincident with heat can lead to a very strong reduction in  $P_{gross}$  (von Buttlar *et al.* 2018). In our investigation the warm and dry summer of 2013 can be clearly divided into periods when air temperature was the dominant influence on  $P_{gross}$  (up to 10 July and 03–10 September) and a drought period (11 July–02 September) when PAR and water table level were limiting factors. Other studies have shown that drought in combination with soil water shortage reduces  $P_{gross}$  (Aurela *et al.* 2007, Zhao & Running 2010, Wolf *et al.* 2013). Water stress directly forces plants to close their stomata to limit transpiration, reducing photosynthesis (von Buttlar *et al.* 2018).

The total cumulative net exchange of carbon dioxide on Medla-Pev-Nyur during the 2012 and 2013 growing seasons is comparable with results obtained on a fen in Greenland (-310 to -372 g m<sup>-2</sup>; Nordstroem *et al.* 2001), 1.5 times higher than on a mesotrophic fen in northern Finland (-186 to -217 g m<sup>-2</sup>; Aurela *et al.* 2001) and 2.1–2.4 times higher than on the ombrotrophic Zotino peatland in Western Siberia (-132.44 to -133.32 g m<sup>-2</sup>; Arneth *et al.* 2002). On the Fedorovskoye ombrotrophic peatland (European Russia) in July 1999 a negative balance of vertical CO<sub>2</sub> fluxes was observed (39.16 g m<sup>-2</sup>; Arneth *et al.* 2002), whereas on an oligotrophic peatland in south-eastern Canada (Lafleur *et al.* 2001) and an oligotrophic mire complex in Sweden (Sagerfors *et al.* 2008), total *NEE* during the growing season was -87 to -146 g m<sup>-2</sup> and -81 to -97 g m<sup>-2</sup>, respectively; these results are 1.9 to 3.9 times smaller than ours.

Overall, growing season (June–September) CO<sub>2</sub> assimilation at the Medla-Pev-Nyur peatland exceeded emissions in both 2012 and 2013. Despite differences between these years in the seasonal dynamics of *NEE*, mean monthly values of gas exchange in 2012–2013 were similar, with maximum values of  $P_{gross}$  and  $R_{eco}$  occurring when green plant biomass reached its maximum development in July. Although further monitoring is required for a long-term understanding of CO<sub>2</sub> dynamics at this site, on the basis of this two-year study it appears that soil water availability may be more limiting than air temperature for ecosystem respiration under conditions of precipitation shortage and, conversely, that air temperature becomes the limiting factor under conditions of precipitation excess. During drought, gross photosynthesis is influenced more by PAR intensity and water table level than by air temperature. Further data analyses, along with further data collection, will be needed to clarify these relationships.

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## Appendix

Table A1. Daily CO<sub>2</sub> exchange fluxes (g m<sup>-2</sup> d<sup>-1</sup>) for the 2012 and 2013 measurement periods.

Month	Day	Year						
		2012			2013			
		<i>NEE</i>	<i>P<sub>gross</sub></i>	<i>R<sub>eco</sub></i>	<i>NEE</i>	<i>P<sub>gross</sub></i>	<i>R<sub>eco</sub></i>	
June	10	-3.16	-9.67	5.78	-4.56	-10.09	4.46	
	11	-3.25	-9.77	5.40	-3.73	-9.81	4.57	
	12	-3.61	-10.68	5.35	-3.49	-11.20	4.77	
	13	-3.47	-9.80	5.33	-2.00	-11.15	4.08	
	14	-3.38	-9.13	5.04	-4.10	-9.78	4.84	
	15	-0.54	-6.78	3.47	-3.96	-10.74	5.99	
	16	-1.43	-6.23	3.55	-4.82	-10.87	6.03	
	17	-2.50	-7.25	3.81	-6.72	-13.55	4.97	
	18	-3.68	-9.43	4.57	-4.53	-9.53	4.07	
	19	-5.83	-10.93	5.25	-6.69	-10.27	2.86	
	20	-4.29	-10.20	5.59	-4.81	-8.77	1.81	
	21	-6.06	-12.51	5.21	-2.62	-7.45	1.51	
	22	-4.86	-13.61	4.63	-4.19	-10.72	1.87	
	23	-3.36	-10.56	4.11	-7.07	-12.07	2.29	
	24	-3.83	-10.17	3.69	-6.90	-13.15	2.32	
	25	-4.78	-10.51	3.75	-5.62	-12.69	2.26	
	26	-5.79	-11.10	4.21	-3.51	-9.41	2.09	
	27	-4.82	-11.01	4.30	-5.93	-11.05	1.84	
	28	-2.57	-9.78	4.08	-3.96	-7.07	1.44	
	29	-4.45	-11.07	3.63	-4.50	-8.22	1.07	
	30	0.54	-5.32	3.36	-3.87	-6.44	0.76	
	July	01	-3.73	-10.35	2.93	-6.39	-7.91	0.51
		02	-4.41	-10.36	3.58	-5.81	-6.52	0.21
		03	-5.37	-12.88	4.19	-6.12	-6.69	0.23
		04	-5.36	-13.48	4.49	-7.28	-9.17	0.79
		05	-4.87	-9.13	4.07	-5.70	-9.51	1.36
		06	-4.38	-9.93	3.89	-5.78	-9.25	1.75
		07	-4.10	-11.62	4.28	-5.83	-10.50	2.34
		08	-4.53	-13.87	4.90	-5.36	-11.72	2.99
		09	-4.71	-13.64	5.60	-4.90	-12.35	4.22
10		-2.98	-9.95	5.44	-3.92	-11.76	5.28	
11		-4.36	-10.25	5.22	-4.34	-15.11	7.08	
12		-4.08	-10.42	5.52	-8.01	-17.35	8.29	
13		-5.10	-10.32	5.27	-6.00	-14.86	8.86	
14		-5.84	-11.97	5.54	-4.50	-15.92	9.88	
15		-3.72	-11.43	4.60	-5.08	-18.48	12.92	
16		-4.41	-12.22	4.74	-6.41	-18.96	14.78	
17		-5.78	-13.04	5.54	-5.45	-19.83	14.95	
18		-1.65	-7.15	5.46	-3.21	-15.47	12.20	
19		-5.31	-12.08	5.34	-7.21	-18.36	10.93	
20		-5.96	-12.34	5.34	-3.01	-16.50	9.24	
21		-4.28	-11.44	5.00	-2.60	-12.65	7.53	
22		-3.72	-11.41	5.72	-3.87	-11.33	5.38	
23		-3.20	-9.26	5.09	-3.97	-9.10	2.38	

		Year					
		2012			2013		
Month	Day	<i>NEE</i>	<i>P<sub>gross</sub></i>	<i>R<sub>eco</sub></i>	<i>NEE</i>	<i>P<sub>gross</sub></i>	<i>R<sub>eco</sub></i>
July	24	-3.38	-11.17	4.82	-0.07	-9.77	3.15
	25	-3.39	-11.25	5.12	-2.94	-11.96	5.30
	26	-4.20	-10.54	5.11	-3.19	-11.74	7.21
	27	-4.16	-10.88	5.06	-5.91	-17.76	9.29
	28	-3.83	-10.78	4.53	-5.47	-17.62	10.81
	29	-5.01	-12.61	4.35	-1.37	-11.88	10.49
	30	-4.38	-12.30	5.28	-1.56	-11.12	9.55
	31	-2.57	-10.44	6.13	-1.69	-10.99	8.90
August	01	-4.20	-11.66	6.58	0.46	-7.77	7.18
	02	-4.64	-11.49	6.00	-2.06	-7.59	5.52
	03	-4.20	-12.54	5.57	-3.02	-10.52	4.57
	04	-4.46	-11.38	5.84	-3.18	-11.87	4.96
	05	-3.48	-10.67	6.21	-2.14	-10.34	5.38
	06	-2.04	-9.35	5.64	-0.71	-11.76	5.18
	07	-4.84	-13.61	5.84	-2.36	-13.14	5.94
	08	-3.17	-10.99	6.58	-5.79	-14.29	6.30
	09	-4.37	-11.44	6.24	-4.36	-13.59	6.90
	10	-2.80	-8.10	5.34	-2.04	-10.28	7.87
	11	-2.85	-8.84	5.20	-1.93	-11.06	6.73
	12	-3.53	-9.46	5.15	-2.27	-13.26	7.44
	13	-3.82	-10.01	4.86	-3.02	-11.74	8.37
	14	-2.75	-9.26	4.50	-2.94	-13.68	7.49
	15	-3.43	-9.15	4.89	-3.13	-11.97	7.33
	16	-3.49	-8.61	4.17	-0.99	-12.89	6.54
	17	-2.94	-9.82	3.75	-1.94	-8.48	5.42
	18	-2.20	-9.06	3.91	-0.76	-8.48	4.94
	19	-2.31	-9.10	4.32	-1.64	-10.42	4.73
	20	-1.05	-6.98	3.29	-1.56	-10.76	4.44
	21	-2.38	-10.04	3.21	-1.29	-11.02	4.27
	22	-2.36	-8.34	3.65	0.21	-7.87	3.94
	23	-4.50	-10.08	4.05	-0.85	-7.33	3.84
	24	-2.36	-8.23	4.44	-2.22	-9.05	3.50
	25	-0.30	-5.41	4.42	-1.81	-9.36	3.34
	26	-1.13	-6.46	4.26	-1.99	-8.72	3.34
	27	-1.94	-7.05	4.15	-1.41	-8.32	3.13
	28	-3.07	-8.17	3.94	-0.56	-7.76	3.29
	29	0.98	-3.26	3.72	-1.07	-7.97	3.65
	30	0.51	-4.86	3.46	-1.39	-7.52	3.27
	31	0.94	-4.32	3.38	-2.14	-8.25	3.12
September	01	-1.77	-5.39	3.20	-1.82	-7.50	2.68
	02	-1.06	-6.97	2.86	0.14	-4.11	2.58
	03	-0.91	-8.13	2.73	-1.13	-5.03	2.49
	04	-1.64	-8.63	2.79	-1.13	-4.89	2.25
	05	1.25	-6.02	3.11	-1.97	-5.40	1.95
	06	0.04	-5.81	3.56	-0.82	-4.53	1.58
	07	0.03	-4.61	3.54	-0.80	-4.49	1.33
	08	-0.03	-6.58	2.99	0.54	-4.68	1.17
	09	-0.11	-5.03	2.37	-0.63	-3.41	0.42
	10	1.24	-4.87	2.27	-0.14	-3.61	0.07