

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

O.A. Mikhaylov, S.V. Zagirova and M.N. Miglovets

Institute of Biology, Komi Science Centre, Russian Academy of Sciences Ural Division, Syktyvkar, Russian Federation

---

## 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

---

## 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 (Arneth *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 (Arneth *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

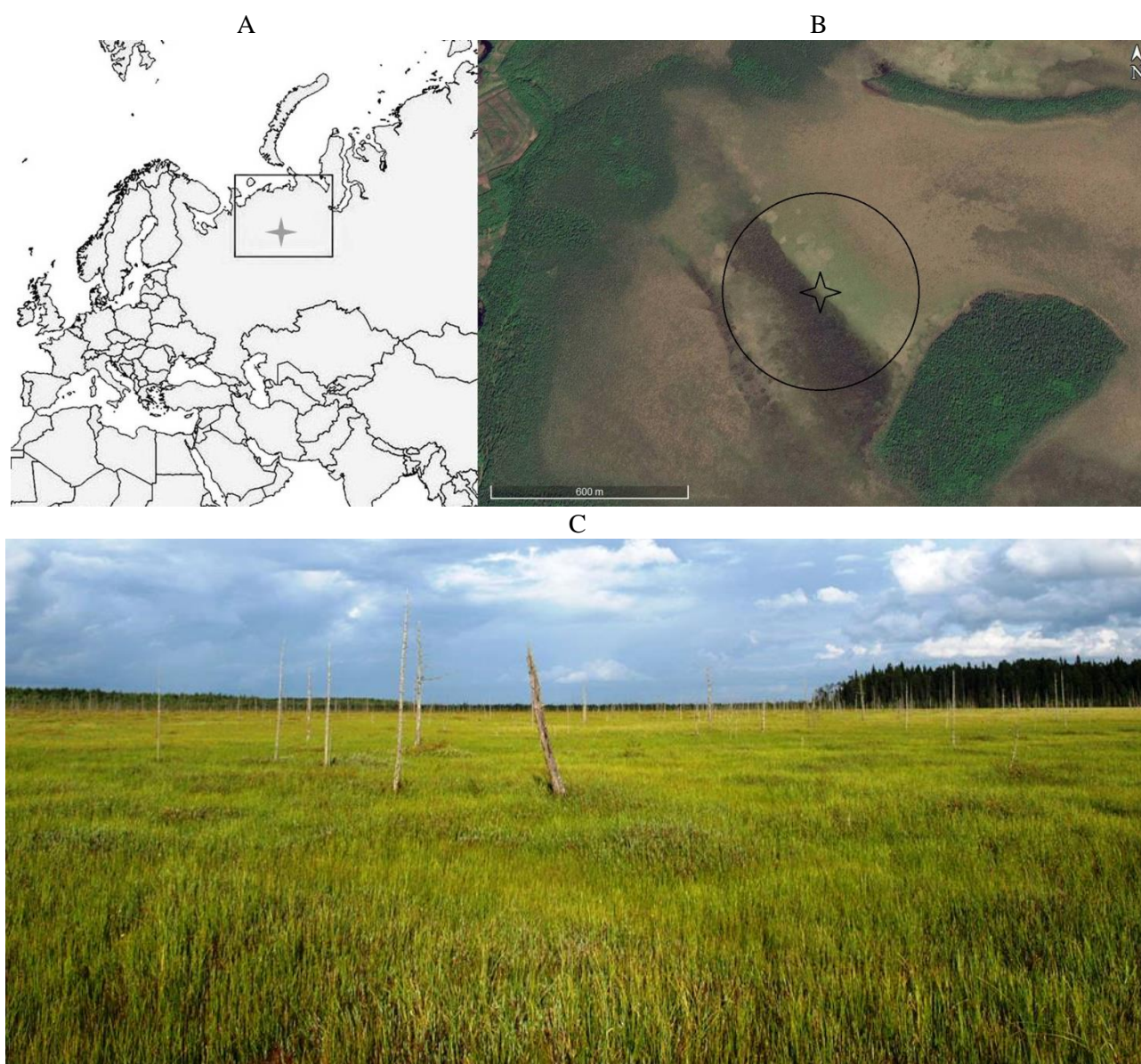


Figure 1. Study site (Medla-Pev-Nyur (Ust-Pojeg) peatland). A: map of Europe showing the location of the study site; B: location of the eddy covariance tower on the study site; C: typical landscape of the study site.









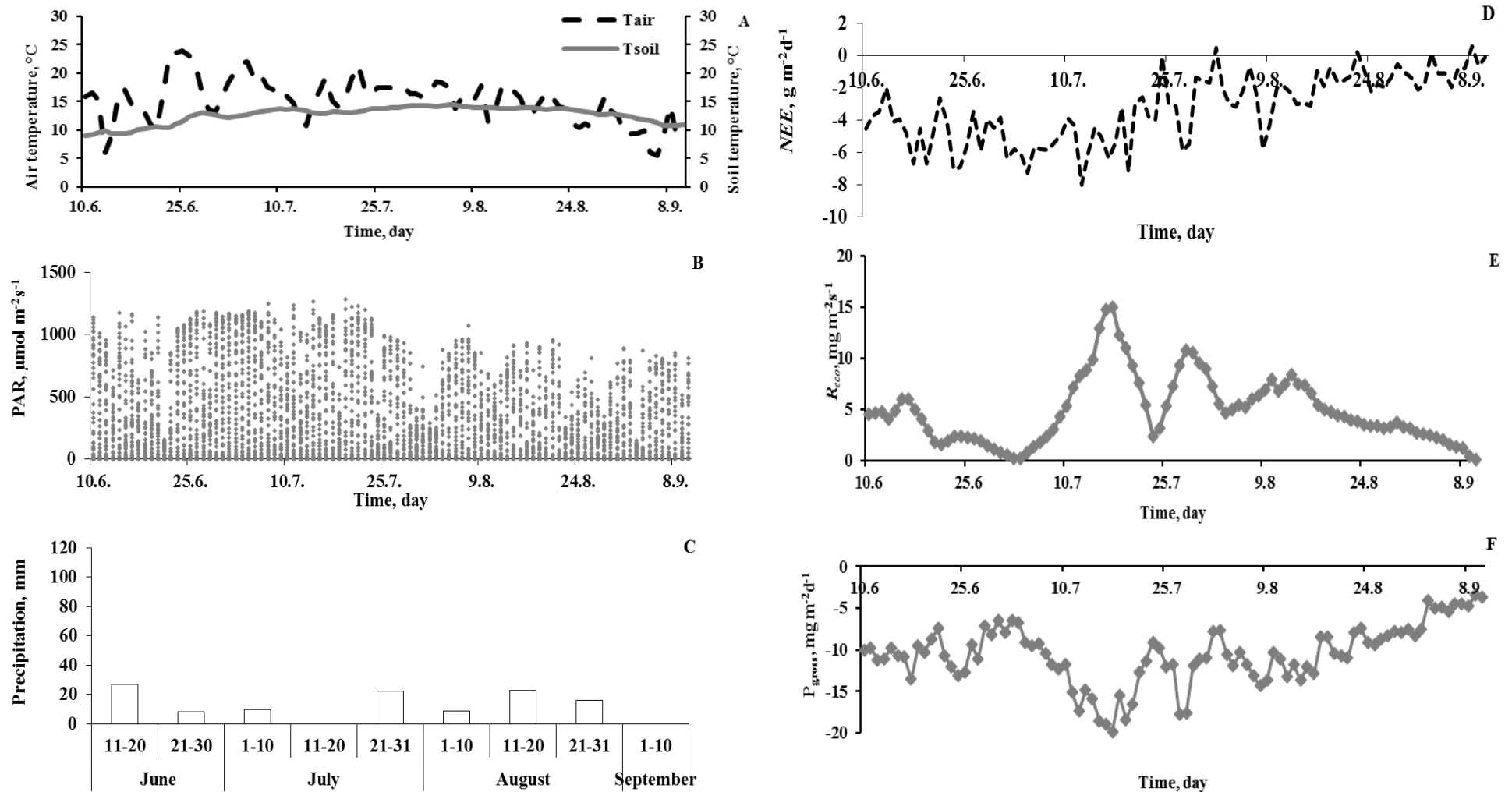


Figure 3. Meteorological conditions and CO<sub>2</sub> fluxes during the measurement period in 2013. A: air temperature (T<sub>air</sub>) and soil temperature at depth 0.3 m (T<sub>soil</sub>) (°C); B: PAR intensity (μmol m<sup>-2</sup> s<sup>-1</sup>); C: precipitation (mm; each column shows the cumulative 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

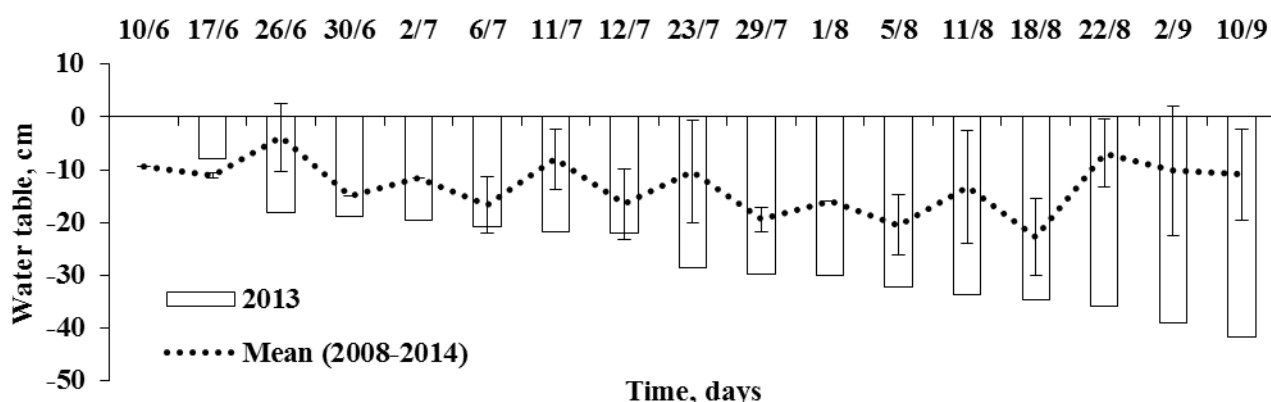


Figure 4. Seasonal course of water table level (WT) relative to ground surface level during the measurement period (10 June to 10 September) of 2013. The mean values are means of WT for six years (2008–2014 excluding 2012). The error bars show ± SD (standard deviation).

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).

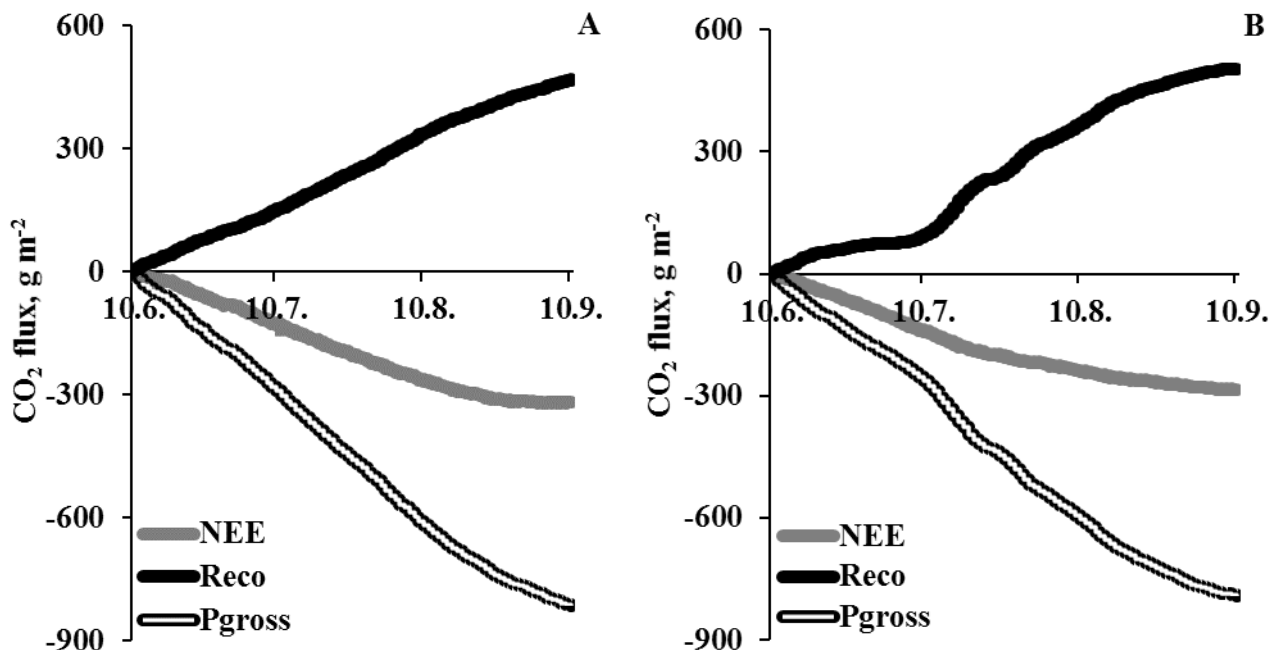


Figure 5. Cumulative sums of carbon dioxide exchange ( $\text{g m}^{-2}$ ) for the growing seasons (10 June to 10 September) of (A) 2012 and (B) 2013.

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.

## ACKNOWLEDGEMENTS

The investigations were financially supported by the UNDP-GEF programme within Project № 00059042 “Strengthening Protected Areas System of the Komi Republic to Conserve Virgin Forests Biodiversity in the Pechora River Headwaters Region” and the programme of the Ural Branch of the Russian Academy of Sciences “Living Nature and Climate” (Project № 18-4-4-17). We thank the editors and Dr Gareth Clay for their critical comments, which helped to improve the article.

## REFERENCES

- Arneth, A., Kurbatova, J., Kolle, O., Shibistova, O.B., Lloyd, J., Vygodskaya, N.N. & Schulze, E.-D. (2002) Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian peatland II. Interseasonal and interannual variability of CO<sub>2</sub> fluxes. *Tellus*, 54B, 514–530.
- Arneth, A., Lloyd, J., Shibistova, O., Sogachev, A. & Kolle, O. (2006) Spring in the boreal environment: observations on pre- and post-melt energy and CO<sub>2</sub> - fluxes in two central Siberian ecosystems. *Boreal Environment Research*, 11, 311–328.
- Aurela, M., Laurila, T. & Tuovinen, J.-P. (2001) Seasonal CO<sub>2</sub> balances of a subarctic mire. *Journal of Geophysical Research*, 106(D2), 1623–1637.
- Aurela, M., Laurila, T. & Tuovinen, J.-P. (2004) The timing of snow melt controls the annual CO<sub>2</sub> balance in a subarctic fen. *Geophysical Research Letters*, 31(16), L16119, doi:10.1029/2004GL020315.
- Aurela, M., Riutta, T., Laurila, T., Tuovinen, J.-P., Vesala, T., Tuittila, E.-S., Rinne, J., Haapanala, S. & Laine, J. (2007) CO<sub>2</sub> exchange of a sedge fen in southern Finland - the impact of a drought period. *Tellus*, 59B, 826–837.
- Baldocchi, D.D. (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, 9, 479–492.
- Christensen, T.R., Jackowicz-Korczynski, M., Aurela, M., Crill, P., Heliasz, M., Mastepanov, M. & Friborg, T. (2012) Monitoring the multi-year carbon balance of a subarctic palsa mire with micrometeorological techniques. *Ambio*, 41, 207–217.

- Dise, N.B. (2009) Peatland response to global change. *Science*, 326, 810–811.
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.-O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.W., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S. & Vesala, T. (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology*, 107(1), 43–69.
- Friborg, T., Soegard, H., Christensen, T.R., Lloyd, C.R. & Panikov, N.S. (2003) Siberian wetlands: Where a sink is a source. *Geophysical Research Letters*, 30(21), 2129, doi:10.1029/2003GL017797.
- Frolking, S., Roulet, N.T., Moore, T.R., Lafleur, P.M., Bubier, J.L. & Crill, P.M. (2002) Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. *Global Biogeochemical Cycles*, 16(3), 1030, doi:10.1029/2001GB001457.
- Gažovič, M., Forbrich, I., Jäger, D.F., Kutzbach, L., Wille, C. & Wilmking, M. (2013) Hydrology-driven ecosystem respiration determines the carbon balance of a boreal peatland. *Science of The Total Environment*, 463–464, 675–682.
- GDGC (1964) Атлас Коми АССР (*Atlas of Komi ASSR*). Главное управление геодезии и картографии (General Directorate of Geodesy and Cartography), Moscow, 112 pp. (in Russian).
- Golovatskaya, E.A. (2009) Головацкая, Е.А. (2009) Биологическая продуктивность олиготрофных и эвтрофных болот южнотаежной подзоны Западной Сибири (Biological productivity of oligotrophic and eutrophic mires in the Southern Taiga of Western Siberia). *Журнал СВУ. Биология*, (*Journal of Siberian University, Biology*), 2(1), 38–53 (in Russian).
- Gorham, E. (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, 1(2), 182–195.
- Heikkinen, J.E.P., Maljanen, M., Aurela, M., Hargreaves, K.J. & Martikainen, P.J. (2002) Carbon dioxide and methane dynamics in a sub-Arctic peatland in northern Finland. *Polar Research*, 21(1), 49–62.
- Heimann, M. & Reichstein, M. (2008) Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, 451, 289–292.
- Humphreys, E.R., Charron, C. & Brown, M.J.R. (2014) Two bogs in the Canadian Hudson Bay Lowlands and a temperate peatland reveal similar annual net ecosystem exchange of CO<sub>2</sub>. *Arctic, Antarctic, and Alpine Research*, 46, 103–113.
- Korrensalo, A., Alekseychik, P., Hájek, T., Rinne, J., Vesala, T., Mehtätalo, L., Mammarella, I. & Tuittila, E.-S. (2017) Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration. *Biogeosciences*, 14, 257–269.
- Kutzbach, L., Wille, C. & Pfeiffer, E.-M. (2007) The exchange of carbon dioxide between wet arctic tundra and the atmosphere at the Lena River Delta, Northern Siberia. *Biogeosciences*, 4(5), 869–890.
- Kwon, H.-J., Oechel, W.C., Zulueta, R.C. & Hastings, S.J. (2006) Effects of climate variability on carbon sequestration among adjacent wet sedge tundra and moist tussock tundra ecosystems. *Journal of Geophysical Research - Biogeosciences*, 111, G03014, doi:10.1029/2005JG000036.
- Lafleur, P.M., Roulet, N.T. & Admiral, S.W. (2001) Annual cycle of CO<sub>2</sub> exchange at a bog peatland. *Journal of Geophysical Research - Atmospheres*, 106, 3071–3081.
- Lafleur, P.M., Roulet, N.T., Bubier, J.L., Frolking, S. & Moore, T.R. (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, 17(2), 1036, doi:10.1029/2002GB001983.
- Lund, M., Bjerke, J.W., Drake, B.G., Engelsen, O., Hansen, G.H., Parmentier, F.J.W., Powell, T.L., Silvennoinen, H., Sottocornola, M., Tømmervik, H., Weldon, S. & Rasse, D.P. (2015) Low impact of dry conditions on the CO<sub>2</sub> exchange of a Northern-Norwegian blanket peatland. *Environmental Research Letters*, 10, 025004, doi:10.1088/1748-9326/10/2/025004.
- Marushchak, M.E., Kiepe, I., Biasi, C., Elsakov, V., Friborg, T., Johansson, T., Soegaard, H., Virtanen, T. & Martikainen, P.J. (2013) Carbon dioxide balance of subarctic tundra from plot to regional scales. *Biogeosciences*, 10, 437–452.
- Mauder, M. & Foken, T. (2006) Impact of post-field data processing on eddy covariance flux estimates and energy balance closure. *Meteorologische Zeitschrift*, 15, 597–609.
- McVeigh, P., Sottocornola, M., Foley, N., Leahy, P. & Kiely, G. (2014) Meteorological and functional response partitioning to explain interannual variability of CO<sub>2</sub> exchange at an Irish Atlantic blanket peatland. *Agricultural and Forest Meteorology*, 194, 8–19.
- Meir, P., Metcalfe, D., Costa, A. & Fisher, R. (2008) The fate of assimilated carbon during drought:

- Impacts on respiration in Amazon rainforests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 1849–1855.
- Miglovets, M.N., Mikhaylov, O.A. & Zagirova, S.V. (2014) Мигловец, М.Н., Михайлов, О.А., Загирова С.В. (2014) Вертикальные потоки CH<sub>4</sub> и CO<sub>2</sub> в растительных сообществах мезоолиготрофного болота средней тайги (Vertical CH<sub>4</sub> and CO<sub>2</sub> fluxes in plant communities of mesooligotrophic peatland of middle taiga). *Известия Самарского научного центра Российской академии наук (Proceedings of the Samara Scientific Centre of the Russian Academy of Sciences)*, 16(1), 193–197 (in Russian).
- Mikhaylov, O.A., Zagirova, S.V., Miglovets, M.N. & Wille, C. (2013) Carbon dioxide fluxes in the ecosystem of meso-oligotrophic peatland during the period of transition from autumn to winter. *Contemporary Problems of Ecology*, 6(2), 143–148, doi:10.1134/S1995425513020108.
- Monin, A.S. & Obukhov, A.M. (1954) Basic laws of turbulent mixing in the atmosphere near the ground. *Труды Академии Наук СССР Геофизический Институт (Proceedings of the USSR Academy of Sciences Geophysical Institute)*, 24(151), 163–187.
- Nordstroem, C., Soegaard, H., Christensen, T.R., Friberg, T. & Hansen, B.U. (2001) Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in NE-Greenland. *Theoretical and Applied Climatology*, 70, 149–166.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havrankova, K., Iivesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D. & Valentini, R. (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, 11, 1424–1439.
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A. & Wattenbach, M. (2013) Climate extremes and the carbon cycle. *Nature*, 500, 287–295, <https://doi.org/10.1038/nature12350>.
- Sagerfors, J., Lindroth, A., Grelle, A., Klemetsson, L., Weslien, P. & Nilsson, M. (2008) Annual CO<sub>2</sub> exchange between a nutrient poor, minerotrophic, boreal mire and the atmosphere. *Journal of Geophysical Research - Biogeosciences*, 113, G01001 doi:10.1029/2006JG000306.
- Schneider, J., Kutzbach, L. & Wilmking, M. (2012) Carbon dioxide exchange fluxes of a boreal peatland over a complete growing season, Komi Republic, NW Russia. *Biogeochemistry*, doi:10.1007/s10533-011-9684-x.
- Shi, Z., Thomey, M.L., Mowll, W., Litvak, M., Brunsell, N.A., Collins, S.L., Pockman, W.T., Smith, M.D., Knapp, A.K. & Luo, Y. (2014) Differential effects of extreme drought on production and respiration: synthesis and modeling analysis. *Biogeosciences*, 11, 621–633.
- van der Molen, M.K., van Huissteden, J.C., Parmentier, F.J., Petrescu, A.M.R., Dolman, A.J., Maximov, T.C., Kononov, A.V., Karsanaev, S.V. & Suzdalov, D.A. (2007) The growing season greenhouse gas balance of a continental tundra site in the Indigirka lowlands, NE Siberia. *Biogeosciences*, 4(6), 985–1003.
- von Buttlar, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Arain, M.A., Buchmann, N., Cescatti, A., Geinelle, D., Kiely, G., Law, B.E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., Montagnani, L., Oechel, W., Pavelka, M., Peichl, M., Rambal, S., Raschi, A., Scott, R.L., Vaccari, F.P., van Gorsel, E., Varlagin, A., Wohlfahrt, G. & Mahecha, M.D. (2018) Impacts of droughts and extreme temperature events on gross primary production and ecosystem respiration: a systematic assessment across ecosystems and climate zones. *Biogeosciences*, 15, 1293–1318.
- Welp, L.R., Randerson, J.T. & Liu, H.P. (2007) The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems. *Agricultural and Forest Meteorology*, 147, 172–185.
- Westergaard-Nielsen, A., Lund, M., Hansen, B.U. & Tamstorf, M.P. (2013) Camera derived vegetation greenness index as proxy for gross primary production in a low Arctic wetland area. *ISPRS Journal of Photogrammetry and Remote Sensing*, 5, 89–99.
- Wolf, S., Eugster, W., Ammann, C., Häni, M., Zielis, S., Hiller, R., Stieger, J., Imer, D., Merbold, L. & Buchmann, N. (2013) Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland. *Environmental Research Letters*, 8, 035007, doi:10.1088/1748-9326/8/3/035007.

- Yatsco, Ya.N., Dymova, O.V. & Golovko, T.K. (2009) Яцко, Я.Н., Дымова, О.В., Головки Т.К. (2009) Пигментный комплекс зимнее- и вечнозеленых растений в подзоне средней тайги Европейского Северо-Востока (Pigment complex of ever- and wintergreen plants in the middle taiga subzone of the European North-East). *Ботанический журнал (Botanical Journal)*, 94(12), 1812–1820 (in Russian).
- Zagirova, S. & Schneider, J. (eds.) (2016) *Ecosystem of a Mesooligotrophic Peatland in Northwestern Russia: Development, Structure, and Function*. Komi Scientific Centre of the Ural Branch of the Russian Academy of Science, Syktyvkar, 172 pp. ISBN: 978-5-89606-562-3.
- Zamolodchikov, D.G., Karelin, D.V. & Ivashchenko, A.I. (1998) Замолодчиков, Д.Г., Карелин, Д.В., Иващенко, А.И. (1998) Пороговая температура углеродного баланса южных тундр (The threshold temperature of the carbon balance of the Southern Tundra). *Доклады Академии наук (Reports of the Academy of Sciences)*, 358(5), 708–709 (in Russian).
- Zhao, M. & Running, S.W. (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, 329, 940–943.

*Submitted 22 Aug 2017, final revision 20 Nov 2019*  
*Editors: Stephan Glatzel and Olivia Bragg*

---

Author for correspondence:

Dr Oleg A. Mikhaylov, Institute of Biology, Komi Science Centre, Ural Division Russian Academy of Sciences, 167000 Syktyvkar, Kommunisticheskaya str. 28, Russian Federation.  
Tel. +7(8212)24-11-68; E-mail: mikhaylov@ib.komisc.ru

## 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