Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

A multi-year study of ecosystem production and its relation to biophysical factors over a temperate peatland

Patryk Poczta [a,b,*], Marek Urbaniak [c], Torsten Sachs [d], Kamila M. Harenda [a], Agnieszka Klarzyńska [e], Radosław Juszczak [a], Dirk Schüttemeyer [f], Bartosz Czernecki [g], Anna Kryszak [e], Bogdan H. Chojnicki [a]

[a] *Laboratory of Bioclimatology, Department of Ecology and Environmental Protection, Faculty of Environmental and Mechanical Engineering, Poznan University of Life Sciences, Poznan 60-649, Poland*
[b] *Institute of Geophysics, Faculty of Physics, University of Warsaw, Warsaw 02-093, Poland*
[c] *Institute of Civil Engineering and Geoengineering, Faculty of Environmental and Mechanical Engineering, Poznan University of Life Sciences, Poznan 60-649, Poland*
[d] *GFZ German Research Centre for Geosciences, Telegrafenberg, Potsdam 14473, Germany*
[e] *Department of Grassland and Natural Landscape Sciences, Faculty of Agronomy, Horticulture and Bioengineering, Poznan University of Life Sciences, Poznan 60-632, Poland*
[f] *European Space Research and Technology Centre, European Space Agency (ESA), Noordwijk 2201, the Netherlands*
[g] *Department of Meteorology and Climatology, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznan 61-680, Poland*

ARTICLE INFO

ABSTRACT

Peatlands are among the largest stocks of soil carbon, which can be stored for thousands of years under well-wetted conditions. The main goals of the study were to assess annual and seasonal CO_2 balances of a temperate peatland and the main biophysical factors affecting these CO_2 fluxes. The studied peatland was usually a CO_2 sink with a mean annual net ecosystem production (NEP) of 110 ± 83 gCO_2-C·m^{-2}·yr^{-1} and extreme balances in 2006 (-17 gCO_2-C·m^{-2}·yr^{-1}) and 2011 (194 gCO_2-C·m^{-2}·yr^{-1}). Annual fluxes were not significantly correlated with biophysical variables, unlike seasonal data. Furthermore, the average air temperature in spring and summer was related to NEP at $r^2=0.65$ and $r^2=0.61$, respectively (warmer spring increased NEP while hot summer decreased NEP in these seasons). A decrease in daytime measured NEP during the summer period (June-August) was observed when TA exceeded 25 °C or VPD was above 15 hPa, respectively, due to the growing R_{eco} and possibly plant photorespiration. These findings suggest a negative impact of ongoing global warming on temperate peatland CO_2 balances.

1. Introduction

The global carbon budget is one of the most-discussed issues in the context of carbon dioxide emissions and global warming (IPCC, 2021; Friedlingstein et al., 2019). Peatlands, which cover only about 3% of the terrestrial area (mainly in the boreal and subarctic zones), store approximately 400–600 Gt of carbon in peat (Gorham, 1991; Frolking et al., 2011; Page et al., 2011), which is one-third of global soil carbon (Lappalainen, 1996; Page et al., 2011; Rydin and Jeglum, 2013).

Pristine and semi-natural peatlands are usually net carbon sinks (Turunen et al., 2002; Mäkilä and Saarnisto, 2008), but their degradation due to human activity (Hooijer et al., 2010; Page et al., 2011; Moore et al., 2013) and climate change (IPCC, 2021; Gallego-Sala et al., 2018; Harenda et al., 2018) may turn them into net sources of carbon. This feature makes these ecosystems an essential element of the biosphere that can substantially modify the atmospheric CO_2 concentration. Therefore, research on these vulnerable ecosystems is a vital issue in the context of ongoing global warming (Dise, 2009; de Jong et al., 2010).

The CO_2 balance of the ecosystem consists of three elements: net CO_2 uptake (net ecosystem production – NEP), which is the difference between the total CO_2 uptake (gross ecosystem production – GEP) and the sum of autotrophic and heterotrophic CO_2 emission (ecosystem respiration – R_{eco}). Positive values of NEP indicate net CO_2 uptake of the

Fig. 1. Picture of Rzecin peatland, the status of 2015, with marked EC tower location. Presented tower design was maintained between 2004 and 2011.

ecosystem. Currently, the eddy covariance (EC) technique is a measuring standard of CO_2 exchange between the vegetation and the atmosphere, and its continuous observations enable to determine of the seasonal and annual estimations of the CO_2 balance on the ecosystem scale (Baldocchi 2003; Aubinet et al., 2012; Baldocchi 2014, 2020).

There are two groups of factors that have an impact on the ecosystem carbon balance: an abiotic (precipitation, temperature, water table depth, humidity) and biotic one (vegetation communities, plant phenology; Law et al., 2002; van Dijk et al., 2005; Richardson et al., 2010; Yi et al., 2010; Acosta et al., 2017; Harenda et al., 2022). An increase in air/soil temperature and the frequency of droughts may decrease the net productivity of peatlands (Lafleur et al., 2003; Sonnentag et al., 2010; Fortuniak et al., 2017). In many studies of peatland productivity, the water table depth (WTD) impact on the NEP has been analyzed (Lafleur et al., 2003; Yurova et al., 2007; Aurela et al., 2007; Lund et al., 2012a; Peichl et al., 2014; Aslan-Sungur et al., 2016; Strachan et al., 2016). Generally speaking, the lowering of WTD reduces the net CO_2 sink. On the other hand, Hurkuck et al. (2016) found no correlation between the nighttime measured R_{eco} and WTD. The effect of WTD lowering on the well wetted floating peat carpet can be limited due to the fact that WTD is followed by this layer of vegetation, roots and plant debris (Juszczak et al., 2013). Manipulation experiments presented the significance of precipitation and air temperature for the photosynthetic capacity of plants on a peatland (Bragazza et al., 2016; Rastogi et al., 2019). Vapour pressure deficit (VPD) stimulates evapotranspiration, as well as the photosynthetic activity of plants (Farquhar and Sharkey, 1982). The leaf stomata are closed under high VPD (during warm conditions), and this mechanism protects plants from drying out (Massmann et al., 2019) but also substantially reduces photosynthesis intensity via the reduction of gas exchange at the leaf level (Oren et al., 1999). The evaluation of a general physiological status (phenological phase) of plant canopy is commonly made based on data sensed remotely, e.g., spectral Vegetation Indices (VIs) as Normalized Difference Vegetation Index (NDVI; Chojnicki, 2013) and Enhanced Vegetation Index (EVI; Matsushita et al., 2007). The VIs are most commonly obtained with Advanced Very High Resolution Radiometer (AVHRR; Goward and Prince, 1995), Moderate Resolution Imaging Spectroradiometer (MODIS; Friedl et al., 2002), Landsat (Escuin et al., 2008) and Sentinel (Drusch et al., 2012) sensors.

Research carried out on the study site in Rzecin peatland, Poland, was usually related to chamber measurements of GHG fluxes (Chojnicki et al., 2010; Juszczak et al., 2012, 2013; Juszczak and Agustin, 2013; Acosta et al., 2017;), spectral vegetation indices (Bandopadhyay et al.,

2019, 2021) and manipulation experiments (Rastogi et al., 2019, 2020; Basińska et al., 2020; Górecki et al., 2021). At the same time, EC-related studies concerned short-time data sets (Chojnicki, 2013; Kowalska et al., 2013; Harenda et al., 2021, 2022).

In this study, we present an 8-year long data set of EC-measured CO_2 fluxes from a peatland site in Poland since 2004. The aim of the study is to present the seasonal carbon dioxide flux patterns, the annual balances and its inter-annual variability at a pristine fen with a floating peat carpet in East-Central Europe. The flux data were compiled with meteorological observations and satellite-delivered VIs to determine the effect of biophysical factors on the CO_2 exchange of this ecosystem. The presented results contribute to expanding the knowledge of CO_2 balances of temperate zone peatlands, especially that the Rzecin peatland formed on the overgrowing lake, which makes them a unique ecosystem in this climatic zone, and their productivity has not been widely described in the literature so far.

2. Material and methods

2.1. Site description

The study area is located at the PolWET station in Rzecin (52°45′43″N, 16°18′35″E, 56 m a.s.l.; Fig. 1) in Puszcza Notecka forest (Western Poland). This ecosystem is protected within the Natura 2000 Network (PLH300019) Habitats Directive. Rzecin peatland is a result of the shallowing of the lake that remains in the eastern part of the ecosystem (Barabach, 2012) and is classified as a fen (Chojnicki et al., 2007) with about 260 years of carbon accumulation time (Milecka et al., 2016; Salmon et al., 2022). The total area covers 86 ha, including 15 ha of the lake (Basińska et al., 2020). Two main peatland phytocoenosis are present at the site footprint: *Phragmites australis* (Cav.) *Trin. ex Steud* and *Sphagnum spp.* covering the northern part, while the southern part is a floating peat carpet (70 cm thick). The latter is more biologically diverse and is dominated by *Sphagnum spp., Menyanthes trifoliata L., Carex nigra L., Carex limosa L.* and *Oxycoccus palustris L.* In addition, a small number of pine trees was also observed, which may indicate that the peatland had gone through drought periods in recent years. A more detailed description of the site's vegetation can be found in Chojnicki et al. (2007), Kowalska et al. (2013), Milecka et al. (2016), Acosta et al. (2017), Bandopadhyay et al. (2019) and Basińska et al. (2020). The site climate is typical for Central Europe and results from oceanic (more often) and continental air masses. The mean annual air temperature is found to be 8.6 °C, with January and July means of −0.9 °C and 18.9 °C,

respectively – the reference period of 1981–2010 (based on Szamotuły-Baborówko station meteorological data, 29 km SE of the PolWET station; IMGW-PIB, 2021). The average annual precipitation is 526 mm (Farat et al., 2004). The soil type of this peatland is classified as Limnic Hemic Floatic Ombric Rheic Histosol (Epidystric), according to the FAO 2006 classification. The surface water has a pH of 4.9 ± 0.4 and a conductivity of 53 ± 4 µS·cm^{-1} (Romanowska, 2015).

2.2. Eddy covariance measurements

The eddy covariance system at the PolWET station in Rzecin consists of a CO_2/H_2O infrared gas analyzer (IRGA) with an open path, model LI-7500 (LI-COR Biosciences Inc., Lincoln, NE, USA) and a three-dimensional sonic anemometer, model R3–100 (Gill Instruments Ltd., Lymington, Hampshire, UK), mounted at the height of 4.5 m above ground level (AGL; Fig. 1). The data obtained from these two instruments were saved with a 20 Hz sampling rate by an analogue-digital converter – datalogger KEST16 (Kest Electronic, Poznan, Greater Poland, Poland).

2.3. Auxiliary data

Meteorological measurements (METEO) were carried out along with EC observations with a measurement frequency of 1 Hz and 20 s aggregation time, which were further averaged into 30 min values. The HMP90Y sensor (Vaisala Inc., Helsinki, Uusimaa, Finland) with a ventilated radiation shield collected air temperature (TA) and relative humidity (RH) data. Short- and long-wave radiation measurements were made with a net radiometer, model CNR1 (Kipp & Zonen B.V., Delft, South Holland, The Netherlands). Photosynthetic photon flux density data were collected by the sensor SKP215 (Skye Instruments Ltd., Llandrindod Wells, Powys, UK) and BF3H (Delta-T Devices Ltd., Burwell, Cambridge, UK). All radiation and TA/RH instruments were mounted at a height of 2.5 m AGL. All METEO data were recorded by the KEST32 datalogger (Kest Electronic, Poznan, Greater Poland, Poland). The tipping-bucket rain gauge model HOBO RG2-M (Onset Computer Corporation, Bourne, MA, USA) was used for precipitation observations. The gaps in the precipitation time series were filled based on rain measurements carried out at the Miały station (located 10 km NW of the Rzecin peatland) owned by the Polish Institute of Meteorology and Water Management – National Research Institute (IMGW-PIB, 2021).

2.4. Flux data processing

The collected EC data have been initially processed within the EddyPro program (ver. 6.2.2). The 30 min integration time was applied (FLUXNET standard). We applied well-established correction methods, including despiking, angle-of-attack (Nakai and Shimoyama, 2012), double axis rotation (Kaimal and Finnigan, 1994), block average detrending, WPL (Webb et al., 1980) and spectral correction of flux attenuation (Moncrieff et al., 1997). The quality assessment of the flux data was based on stationarity (Mauder and Foken, 2006) and friction velocity (u*$_{th}$) tests, and the latter was determined using the breakpoint detection method (Reichstein et al., 2005; Barr et al., 2013; Wutzler et al., 2018). The daytime values were selected using the global short-wave radiation values threshold of 10 W·m^{-2}. Nocturnal data series were tested in terms of outliers detections using the *anomalize* package (Dancho and Vaughan, 2020) for the R program (R Core Team 2019). This package detects outliers in data series characterised by trends and seasonality. For this analysis, we applied a two-week window and a threshold of two standard deviations (±2σ), which resulted in a rejection of 1.8% of the flux data. Finally, only 47% of all analyzed flux data was of the highest quality (qc=0), according to Mauder and Foken (2004) and was used in this study.

We used the Marginal Distribution Sampling algorithm based on nighttime data (Reichstein et al., 2005) to fill the data gaps and partition net flux into GEP and R$_{eco}$. For this purpose, we applied the *REddyProc* package for the R (Wutzler et al., 2018, 2020) and its internal procedures along with u* filtering. An uncertainty analysis of NEP flux was completed using the *openeddy* package for R (function *agg_fsd()*; Šigut, 2022). The estimated uncertainty result was multiplied by 1.96 to obtain a 95% confidence interval, according to the *REddyProc* methodology. Within this study, we assumed EC-delivered Net Ecosystem Exchange (NEE) multiplied by −1 as NEP (NEP = −1*NEE) and Gross Primary Production (GPP) approximated as GEP. The same approach was applied to cited articles for consistency and discussion clarity.

2.5. Vegetation indices

The spectral vegetation indices Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) installed on board Terra (product MOD13Q1) and Aqua (product MYD13Q1) satellites. The processing of data sets with 250 m spatial resolution and 16-day intervals from two satellites by applying the MODISTools package (Tuck et al., 2014) dedicated to the R programming language (R Core Team, 2019) allowed us to obtain an average overpass of every eight days. We applied the quality control procedure for received pixels, i.e., "VI quality" with a range of 0–1 out of 0–2 and "VI usefulness" with a range of 0–5 out of 0–15. We used the linear interpolation for gaps within obtained 8-day interval NDVI/EVI data set to reach daily values of VIs.

2.6. Meteorological data processing and seasons determination

Small gaps in the radiation, air temperature and humidity times series, caused for example by a lack of electricity, were filled by the Marginal Distribution Sampling method (Reichstein et al., 2005). We used the TA and RH values for vapour pressure deficit calculation (Walter et al., 2005). The light use efficiency (LUE) was calculated as LUE=GEP/PPFD from daytime half-hourly values. In this paper, we defined spring as March-May, summer as June-August, autumn as September-November, winter as December-February (Ziemblińska et al., 2016) and the growing season as May-September.

2.7. Measured half-hour NEP fluxes in relation to TA and VPD

2.7.1. Seasonal nighttime net CO_2 emission and TA

Nocturnal half-hourly periods with measured values of R$_{eco}$ (nighttime measured NEP=R$_{eco}$) were divided into four seasons, as described in Section 2.6. We extrapolated the daily NDVI into half-hourly values assuming each half-hour value is the same as the daily one. Within each season, we excluded R$_{eco}$ values below the 1st percentile and air temperature values below the 1st and above 99th percentile from the analyzed dataset (to exclude outliers). The temperature range of 39 °C between the minimum winter temperature of −12.7 °C and the maximum summer temperature of 26.3 °C was split into 100 air temperature bins (0.39 °C each), and R$_{eco}$ and NDVI values were averaged within those TA bins separately for each season. For example, all values of spring R$_{eco}$ which correspond to TA of 0.0–0.39 °C, were averaged to one value, then for 0.39–0.78 °C etc. This approach sustains the same temperature scale and bins position, e.g., averaging bin for TA of 0.0–0.39 °C is the same for all seasons. However, the number of points for each season differs due to the other air temperature ranges.

2.7.2. Summer daytime net CO_2 uptake and TA/VPD

We used the daytime half-hourly data for June-August (summer) to estimate VPD and TA impact on measured NEP. We excluded NEP values above the 99th percentile and VPD below 1st and higher than the 99th percentile from the first analyzed dataset. From the second dataset, we excluded NEP values above the 99th percentile and TA below 1st and higher than the 99th percentile. The remaining datasets were filtered
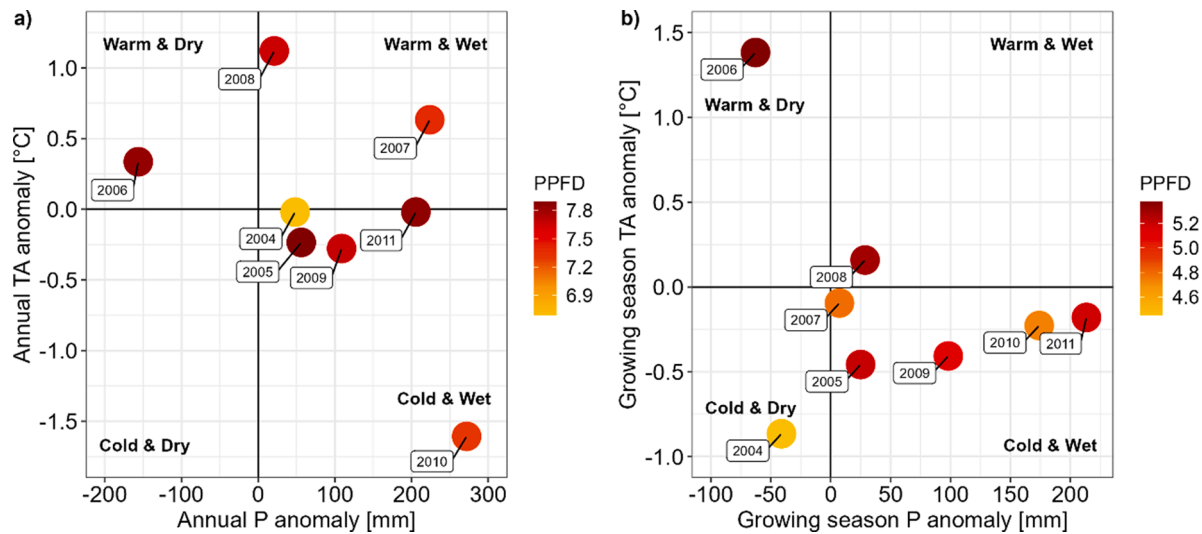
Fig. 2. Annual (a) and growing season (b) anomalies of air temperature (TA) and precipitation (P) during the study years 2004–2011 at the Rzecin peatland. The circle colour indicates the yearly (a) or growing season (b) sum of photosynthetic photon flux density (PPFD kmol·m^{-2}). The Y-axis represents the TA anomaly, and the X-axis represents the P anomaly concerning the reference period of 1981–2010 based on data from Szamotuły-Baborówko station (IMGW-PIB, 2021).

using the light use efficiency factor of NEP (LUE$_{NEP}$; calculated as LUE$_{NEP}$=NEP/PPFD) for LUE$_{NEP}$±2σ. The VPD- and TA-dependant datasets were split into 100 vapour pressure deficit and air temperature bins, respectively (0.367 hPa and 0.23 °C each). We also calculated the NEP values standard deviation within each bin. The remaining data processing was completed following that described in Section 2.7.1.

3. Results

3.1. Climate patterns of the analyzed period

The combination of both annual average air temperature and the total precipitation was used for the classification of each year (Fig. 2a). The precipitation and air temperature values of the reference period (512 mm and 8.63 °C, respectively) were calculated based on a dataset from Szamotuły-Baborówko station (IMGW-PIB, 2021). The annual TA and P deviations range from −1.6 °C to 1.1 °C and from −156 mm to 272 mm, respectively. Four of the analyzed years (2007, 2009–2011)
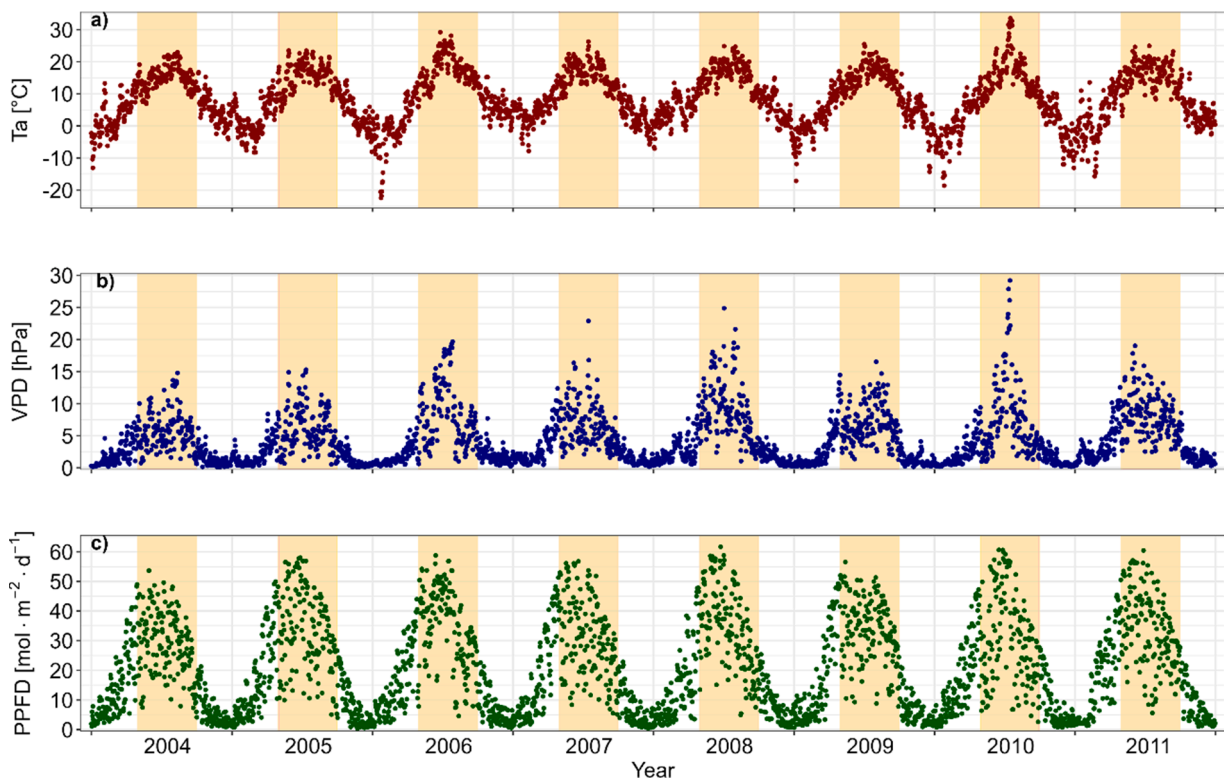
Fig. 3. The daily mean runs of the (a) air temperature (TA) and (b) vapour pressure deficit (VPD), and total (c) photosynthetic photon flux density (PPFD) at the Rzecin peatland for 2004–2011. The coloured background represents the growing season (May-September).
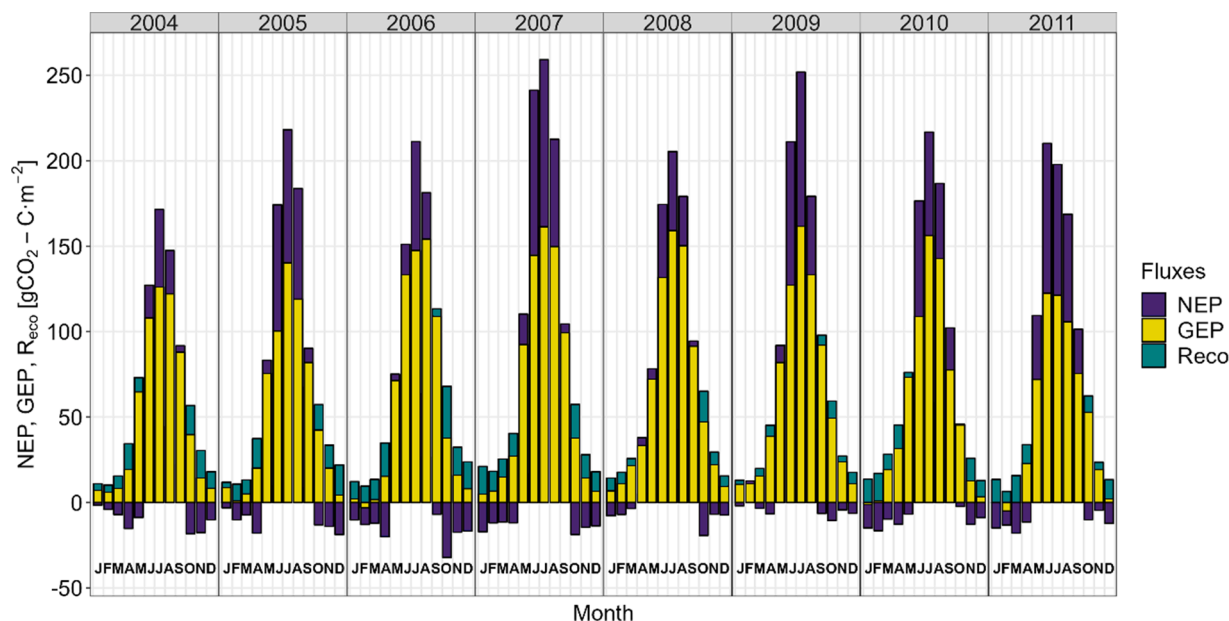
Fig. 4. Monthly sums of gross ecosystem production (GEP – yellow), ecosystem respiration (R_{eco} – green) and net ecosystem production (NEP – purple) in 2004–2011 at the Rzecin peatland (positive NEP – net sink of CO_2; negative NEP and positive R_{eco} – net source of CO_2; if there is no R_{eco}, then R_{eco}=GEP).

can be classified as wet (P anomaly > 100 mm), but it must be mentioned that an extraordinary daily total precipitation (20 July, 155 mm) was observed in 2011. Whereas 2006 was characterised by extremely low total precipitation (P anomaly < −150 mm), the rest of the years with precipitation was higher than the reference period (Fig. 2a). We found five of the analyzed years (2004–2006, 2009, 2011) to have an average TA close to the reference period (±0.5 °C), while 2008 and 2010 were the warmest and coldest years with an average temperature of 9.8 °C and 7.0 °C, respectively.

The growing seasons (Fig. 2b) were characterised by TA close to the reference period (±0.5 °C) for most of the seasons, with two exceptions for the coldest 2004 (15.3 °C) and warmest 2006 (17.5 °C), respectively. However, 6 of 8 analyzed growing seasons were colder than the reference (2004–2005, 2007, 2009–2011). Precipitation values classified three growing seasons as wet (2009–2011) and two as dry (2004 and 2006), with overall humid conditions for 6 out of 8 analyzed growing seasons (2005, 2007–2011).

The warmest (2008) and coldest (2010) years were characterised by the growing season mean air temperature close to the reference one. The opposite situation represents the temperature-average years 2004 (8.6 °C) and 2006 (9.0 °C), with the coldest and warmest growing season mean air temperature, respectively. The growing seasons classification

of climate conditions only partly corresponds with the annual classification (Fig. 2b). The strongest heat-waves periods occurred in the summers of 2006 and 2010 (Fig. 3a). They correspond with some of the highest VPD values (Fig. 3b). High VPD values were also observed in summer 2008 (Fig. 3b). Seasonal runs of PPFD are also variable with the highest values for the growing seasons of 2006 and 2008 (Figs. 2b, 3c), and noticeable reductions of the PPFD in 2004 in both, annual and growing season scales (Figs. 2a-b, 3c).

3.2. Monthly patterns of CO_2 exchange

The summer (June-August) is the period in which the Rzecin peatland has always been a net sink of CO_2 (Fig. 4). At the same time, in the growing season (May-September), approximately 86.9% and 75.1% of the annual GEP and R_{eco} were accumulated, respectively (Table A1). Meanwhile, the lowest NEP (highest net CO_2 emission) was usually observed in October (2004, 2006–2009) and remained negative for the next six months (with an exception for April 2008 and February 2009; Fig. 4). This net CO_2 emission for 7 out of 12 months of the year (October-April average NEP) is 89% compensated by the average net CO_2 uptake in July (Table A1). The second most productive month is June, both in the context of GEP and NEP, which underlines the

Table 1

Annual (A) and growing season (GS) sums of the net ecosystem production (NEP), gross ecosystem production (GEP), ecosystem respiration (R_{eco}), photosynthetic photon flux density (PPFD) and precipitation (P), average air temperature (TA) and vapour pressure deficit (VPD) in 2004–2011 at the Rzecin peatland; (*) denotes aggregated uncertainty of the net flux; SD = standard deviation; minor discrepancies are due to rounding values in the table.

Year	NEP [gCO2-C·m−2]		GEP [gCO2-C·m−2]		Reco [gCO2-C·m−2]		PPFD [kmol·m−2]		TA [°C]		P [mm]		VPD [hPa]	
	A(*)	GS(*)	A	GS	A	GS	A	GS	A	GS	A	GS	A	GS
2004	6(29)	79(41)	706	603	694	517	6.7	4.5	8.6	15.3	560	244	3.4	5.8
2005	163(37)	247(63)	851	749	703	517	7.9	5.2	8.4	15.7	568	310	3.5	6.0
2006	−17(29)	104(52)	805	727	814	620	7.8	5.4	9.0	17.5	355	222	4.5	8.3
2007	174(41)	272(73)	1040	927	856	648	7.4	4.8	9.3	16.0	736	292	4.2	6.8
2008	73(30)	119(46)	888	731	806	605	7.7	5.3	9.8	16.3	533	314	5.0	8.8
2009	184(47)	216(66)	988	826	795	602	7.7	5.1	8.4	15.7	621	383	4.1	7.0
2010	107(46)	184(67)	868	755	750	562	7.3	4.7	7.0	15.9	784	459	4.2	7.6
2011	194(37)	278(55)	880	787	666	497	7.9	5.2	9.0	16.0	718	498	5.0	8.1
Mean	110(37)	187(58)	878	763	760	571	7.5	5.0	8.6	16.0	609	340	4.2	7.3
SD	±83(7)	±78(11)	±103	±92	±68	±56	±0.4	±0.3	±0.8	±0.65	±138	±99	±0.6	±1.1

Table 2

The coefficients of determination r^2 between annual sums of the net ecosystem production (NEP), gross ecosystem production (GEP), ecosystem respiration (R_{eco}), photosynthetic photon flux density (PPFD) and precipitation (P), average air temperature (TA), vapour pressure deficit (VPD) and light use efficiency (LUE) in 2004–2011 at the Rzecin peatland; * denotes p-value < 0.1; ** denotes p-value < 0.05; if not marked = no statistical significance.

Annual	NEP [$gC \cdot m^{-2}$]	GEP	R_{eco}
NDVI [-]	0.02	0.25	0.25
EVI [-]	0.04	0.55**	0.66**
PPFD [$\mu mol \cdot m^{-2}$]	0.16	0.15	0.01
TA [°C]	0.02	0.02	0.16
VPD [hPa]	0.01	0.08	0.06
P [mm]	0.49*	0.23	0.03
LUE [-]	0.31	0.64**	0.31

importance of the early summer in the annual CO_2 balance of Rzecin peatland. The August GEP is similar to June on average, however, higher R_{eco} in the second part of the growing season resulted in slightly less NEP (Table A1). The high summer photosynthetic assimilation rates of Rzecin peatland correspond well to the period of the highest NDVI and EVI (Table A1).

We found the ecosystem to be more productive in September than in May, and monthly GEP values were equal to 98.2 ± 6.9 gCO_2-$C \cdot m^{-2} \cdot mth^{-1}$ and 85.8 ± 16.8 gCO_2-$C \cdot m^{-2} \cdot mth^{-1}$, respectively. Simultaneously, the higher GEP in September was accompanied by higher R_{eco} (90.6 ± 12.7 gCO_2-$C \cdot m^{-2} \cdot mth^{-1}$) than in May ($76.9 \pm 7.2$ gCO_2-

$C \cdot m^{-2} \cdot mth^{-1}$), which resulted in a nearly equal role in the annual balance of CO_2 of these months of 8.3 ± 14.2 and 6.5 ± 12.3 gCO_2-$C \cdot m^{-2} \cdot mth^{-1}$ for May and September, respectively. However, in 3/4 of the cases, the net CO_2 fluxes in May and September are relatively low in the range of approximately −9 to 10 gCO_2-$C \cdot m^{-2} \cdot mth^{-1}$ (Fig. 4).

3.3. Seasonal patterns of CO₂ exchange

The mean annual NEP value of Rzecin peatland ($\pm$ standard deviation) was equal to 110 ± 83 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$ with an average yearly uncertainty of 37 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$ (Table 1). The highest annual NEP was observed in 2011 (194 ± 37 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$) and 2009 ($184 \pm 47$ gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$), while lowest NEP in 2006 ($−17 \pm 29$ gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$) and 2004 ($6 \pm 29$ gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$). The highest interannual span of NEP of two consecutive years reached 191 gCO_2-$C \cdot m^{-2}$ between 2006 and 2007 (−17 against 174 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$, respectively). The NEP analysis of the growing seasons showed that the maximum NEP occurred in 2011 (278 ± 55 gCO_2-$C \cdot m^{-2} \cdot gs^{-1}$), while the lowest one was found in 2004 (79 ± 41 gCO_2-$C \cdot m^{-2} \cdot gs^{-1}$).

The linear regressions of annual CO_2 fluxes and environmental drivers showed very few significant relationships between the variables (Table 2). The only exception is precipitation, which explains about 49% of annual NEP variability. Additionally, LUE is correlated with GEP at $r^2 = 0.64$, and EVI is correlated with GEP and R_{eco} at $r^2 = 0.55$ and 0.66, respectively (Table 2).

In summer, the Rzecin peatland was a net CO_2 sink for all years in the study period with a prolonged net CO_2 uptake until early autumn in
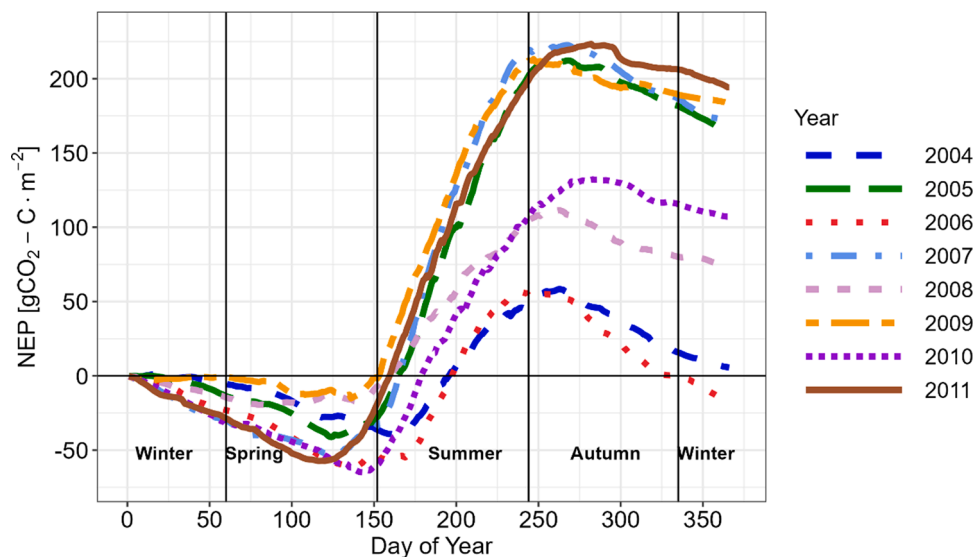

Fig. 5. Cumulative annual net ecosystem production (NEP) in 2004–2011 at the Rzecin peatland. Seasons discrimination according to Section 2.6.

Table 3

The coefficients of determination r^2 between seasonal sums of the net ecosystem production (NEP), gross ecosystem production (GEP), ecosystem respiration (R_{eco}), photosynthetic photon flux density (PPFD) and precipitation (P), average air temperature (TA), vapour pressure deficit (VPD) and light use efficiency (LUE) in 2004–2011 at the Rzecin peatland; * denotes p-value < 0.05; ** Summer regression with NEP does not including 2004; if not marked = p-value > 0.05; the results are based on the values in Table B1.

| Seasonal	NEP [$gC \cdot m^{-2}$]			GEP [$gC \cdot m^{-2}$]			R_{eco} [$gC \cdot m^{-2}$]		
	Spring	Summer**	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
NDVI [-]	0.52*	0.53	0.04	0.83*	0.86*	0.61*	0.37	0.15	0.25
EVI [-]	0.18	0.07	0.19	0.59*	0.78*	0.27	0.49	0.51*	0.40
PPFD [$kmol \cdot m^{-2}$]	0.57*	0.70*	0.06	0.35	0.01	0.23	0.02	0.11	0.0
TA [°C]	0.65*	0.62*	0.49	0.57*	0.0	0.0	0.09	0.29	0.60*
VPD [hPa]	0.85*	0.71*	0.01	0.50*	0.0	0.36	0.0	0.24	0.14
P [mm]	0.22	0.10	0.45	0.0	0.07	0.02	0.39	0.06	0.50
LUE [-]	0.09	0.46	0.0	0.48	0.77*	0.15	0.63*	0.23	0.04
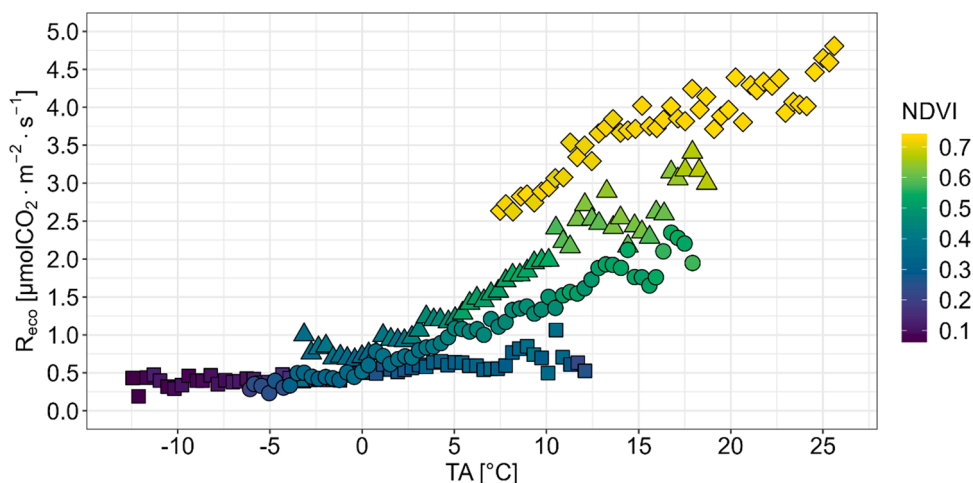
Fig. 6. Seasonal nocturnal bin-averaged from half-hourly measured ecosystem respiration (R_{eco}) against air temperature (TA) in 2004–2011 at the Rzecin peatland. Square = winter, circles = spring, diamonds = summer, triangles = autumn, point colour represents NDVI.

2010 and 2011 (Fig. 5). However, there is variability in summer net uptake, with summer 2007 taking up three times as much CO_2 as summer 2004 (Table B1). Outside the growing season, the Rzecin peatland is usually a net source of CO_2 (with different intensities).

All years with above-average spring TA (2007–2009, 2011) resulted in above-average NEP this season. However, the second-highest spring
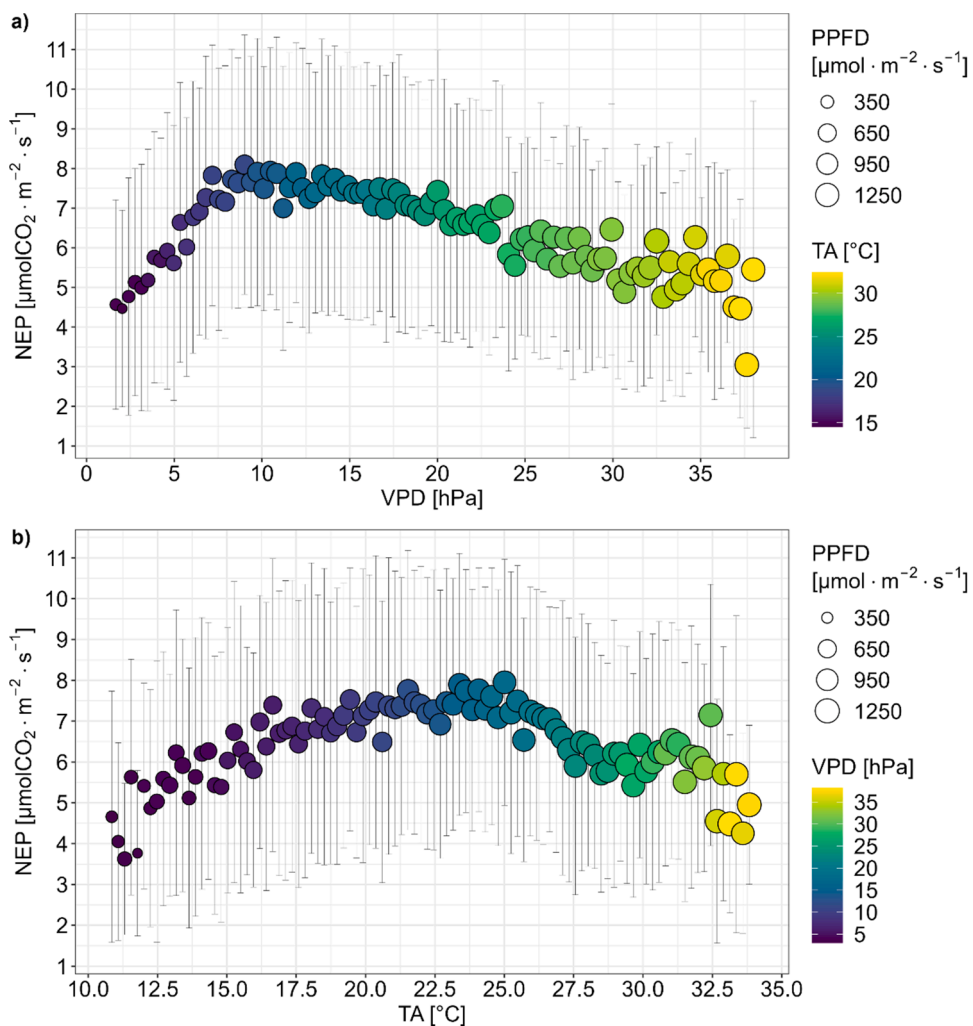
Fig. 7. Daytime bin-averaged from half-hourly vapour pressure deficit (VPD; panel a) and air temperature (TA; panel b) against measured net ecosystem production (NEP) in June-August period 2004–2011 at the Rzecin peatland. Where circle size is photosynthetic photon flux density (PPFD), circle colour is TA and VPD at (a) and (b) panel, respectively. Error bars indicate the standard deviation of the data averaged in each bin.

TA in 2011 resulted in the second-lowest R_{eco}, while second-lowest TA in 2010 occurred with second-highest R_{eco} (Table B1), which are unexpected results taking into account the known relation between temperature and ecosystem respiration. On the other hand, years with low spring NDVI (2004–2006) resulted in low GEP, while higher GEP was observed in 2007–2011 when NDVI was also higher (Table B1). The fourth low-NEP season (2004) was affected by low PPFD in both spring and summertime and characterised by the lowest NDVI and EVI (Table B1). Additionally, in 2004 the latest start of continuous CO_2 uptake was observed (~165 DOY Fig. 5). Three years of low summer NEP (2006, 2008 and 2010) were observed under high VPD and TA conditions. On the other hand, years with the highest summer sums of NEP (2005, 2007, 2009, 2011) overlapped with below-average TA. The highest summer NEP (2007) occurred with the highest mean values of NDVI and EVI (Table B1). The highest 2006 and lowest 2010 TA during autumn resulted in the highest and lowest R_{eco} from the study years, respectively (Table B1). The Rzecin peatland is a net CO_2 source for ¾ of the year, with a high CO_2 sink during the summer period, which usually exceeds the emission annually (Fig. 5, Table B1).

PPFD and TA can explain 57% and 65% of the spring NEP variability, respectively (Table 3). The high correlation between spring NEP and VPD ($r^2 = 0.85$) was considered an artefact due to the relationship between VPD and TA/PPFD, and the low VPD values did not likely have an impact on plant photosynthesis during this period. On the other hand, the variance of the spring GEP was explained by TA, EVI and NDVI at 57%, 59% and 83%, respectively (Table 3). Summer NDVI and EVI values explained 86% and 78% of the GEP variability, respectively, while LUE correlated with GEP at $r^2 = 0.77$ during the summer season. Summer correlations with NEP appeared only in the case of excluding the non-typical 2004 year (affected by insufficient plant development represented by lowest NDVI and EVI and consequently late start of net CO_2 sequestration) - then NEP variability is explained in 61%, 70% and 71% by variability in summer TA, PPFD and VPD (Table 3). In spring, R_{eco} is correlated with LUE at $r^2 = 0.64$, while in autumn, the correlation between R_{eco} and air temperature is visible, where TA explains 60% of the R_{eco} variability. Additionally, only GEP correlation with NDVI remains during an autumn period ($r^2 = 0.6$). Winter values presented in Table B1 were calculated according to the scheme: December of the previous year and January-February of the current year - for this reason, in 2004, the sums/averages were prepared only based on data from January and February (except for precipitation). Winter periods were found as a continuous source of CO_2 into the atmosphere with no clear patterns between CO_2 fluxes and biophysical factors, except for LUE, which correlates with GEP and NEP at $r^2=0.79$ and 0.53, respectively.

3.4. Air temperature and nocturnal NEP

Ecosystem respiration is an effect of the sum of heterotrophic and autotrophic respiration. Both are correlated with the temperature (higher air/soil temperature increases respiration). However, autotrophic respiration is also directly connected to the plant development stage, i.e., the amount of biomass involved in the respiration process. That is why the analysis of R_{eco} has been performed for different seasons. The EC system can measure R_{eco} fluxes only during nighttime periods (when NEP=R_{eco}); hence, only those NEP data were used to build the R_{eco} versus temperature relationship (Fig. 6).

During the winter season, the CO_2 emission is relatively constant in the range of about 0.25 to 0.75 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$, while the lowest emission corresponds to TA<0 °C and the higher emission to TA>0 °C. Spring and autumn CO_2 emission ranges have a minimum of about 0.25 and 0.7 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$, respectively, while maximum CO_2 release reached about 2.3 and 3.4 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ in spring and autumn, respectively. The average standard deviation of the averaged R_{eco} values in each bin in Fig. 6 was 0.62, 1.1, 0.76 and 0.34 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ for spring, summer, autumn, and winter, respectively. The NDVI values were higher during autumn than spring for TA>5°C, probably due to

dead biomass at the beginning of the growing season. Meanwhile, the season with the highest plant development stage (summer) was characterised by the highest nocturnal R_{eco} in the range of about 2.6 to 4.8 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ for 8°C and 26°°C, respectively (Fig. 6).

3.5. Vapour pressure deficit and air temperature

Two commonly observed factors influencing photosynthesis are the air temperature and vapour pressure deficit. We compared both factors with the summer daytime NEP measurements (Fig. 7).

The VPD is highly correlated with both TA and PPFD. Thus, the increase of net CO_2 uptake under low VPD (up to 9 hPa; Fig. 7a) is most likely related to the morning/evening conditions when the photosynthetic activity of plants is starting or ending. NEP remains stable until VPD reaches 15 hPa, and over this threshold, the value of net CO_2 uptake noticeably decreases and this trend is maintained until the maximum values analyzed VPD. The highest NEP values (7.63 ± 0.27 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) were observed at the range of VPD 8–15 hPa, which corresponds to TA and PPFD values range of 20.87 ± 1.29 °C and 863 ± 71 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively (Fig. 7a). The cited values are representative of data from Fig. 7 (i.e., already bin-averaged).

On the other hand, net CO_2 uptake increases up to 25 °C (Fig. 7b). After crossing the threshold of 25 °C, the NEP rapidly decreases to about 29.5 °C and stabilises to about 32.5 °C. Then the NEP value declines again until the maximum values of analyzed TA. The highest NEP values (7.40±0.33 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$) were observed at the range of TA 20–25 °C, which corresponds to VPD and PPFD values range of 13.83 ±2.42 hPa and 992±81 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively (Fig. 7b). The decreasing of NEP value above 23 and 25 °C thresholds (for Fig. 7a and 7b, respectively) can correspond with increasing of R_{eco} together with higher temperatures (confirmed by summertime R_{eco} in Fig. 6), which exceeded CO_2 uptake growth or CO_2 uptake stabilization (taking into consideration that ecosystem production has limitations) in such temperature conditions. Despite these connections with TA and R_{eco}, an unexpected peak of NEP for TA between 29.5 °C and 32.5 °C occurred (Fig. 7b). The NEP standard deviation (error bars of Fig. 7) remains stable throughout the entire scale, and the mean value is equal to ±3.0 and ±3.1 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ for Fig. 7a and 7b, respectively.

4. Discussion

Despite the initial character of the Rzecin peatland (the result of the lake overgrowing), the ecosystem is characterized by a large variability of annual and seasonal CO_2 balances, which makes the peatland a net CO_2 source under drought and heat stress (2006), CO_2 neutral in seasons with limited irradiance and plant canopy development (2004), or a robust net CO_2 sink in periods with mild temperatures (2005, 2009). At the same time, the Rzecin peatland is represented by optimal net CO_2 uptake in air temperature conditions of about 22.5–25 °C and VPD not exceeding 15 hPa.

4.1. Net CO_2 emission in 2006

Despite well-wetted conditions (floating peat carpet on an overgrowing lake), the peatland was a net carbon dioxide source in the summer and autumn of 2006, coinciding with the highest TA of 1.9 °C and 1.8 °C above average and the lowest P (42% and 56% less than average). Low CO_2 uptake in 2006 was also observed by Peichl et al. (2014) for a boreal fen, where 2006 was characterised as extremely dry (with WTD dropping in the late summer) with the lowest annual NEP across 12 study years. Moreover, droughts in 2018 observed across Europe (Ramonet et al., 2020; Thompson et al., 2020) affected 3 out of 5 Scandinavian peatlands located at lower latitudes to be net CO_2 sources, as presented by Rinne et al. (2020). Additionally, Fenner and Freeman (2011) manipulation experiment and field observations showed that drought conditions cause peatland ecosystems to release CO_2. Generally

speaking, bacterial growth in aerobic conditions accelerated the decomposition of organic matter (Fenner and Freeman 2011). This is in line with another manipulation experiment (over the same peatland as in this study; Górecki et al., 2021), where researchers found that although the litter decomposition rates depend on temperature, the WTD and its fluctuations were the main controlling factors of decomposition rates. Increased decomposition and respiration rates with lower WTD and its fluctuations were also reported by Barel et al. (2021). Our study did not present the WTD time series (due to the lack of WTD data for a representative period). However, we assumed that periods with less precipitation represent droughts with lower WTD. This assumption is based on many studies where a direct correlation between precipitation and WTD was reported for peatlands (Dyukarev et al., 2019; Ahmad et al., 2021; Miao et al., 2017). The floating carpet lowering and reduced precipitation favour drier and more aerobic conditions on the peatland surface. These conditions, along with high TA, accelerated the R_{eco}.

4.2. Neutral CO_2 balance in 2004

The neutral CO_2 balance indicated in this study in 2004 is most probably a combined effect of low irradiance and NDVI/EVI (as a proxy of plant phenology and biomass) values, which delayed the starting point of the growing season. The direct relation between NEP and PPFD on peatland is well known (Frolking et al., 1998), with NEP/GEP saturation over high radiation values (Stoy et al., 2014). GEP is commonly modeled as a function of incoming radiation (Dyukarev, 2017), and NDVI is related to plant phenology (Soudani et al., 2012). Light response curves analysis (Flanagan et al., 2002) based on Michaelis-Menten kinetics for daytime conditions in July each year presented a significant difference between 2004 and the remaining years. The GEP increase of up to 10 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ was reached for PPFD at about 595 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in 2004, while the average PPFD value for the rest of the years was about 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which indicates lower light response dynamics in 2004 compared to other years. Considering both can be supposed that low PPFD during the summer of 2004 (Table B1) limited the plant development (visible in low NDVI/EVI), which resulted in less ecosystem-scale photosynthetic capacity (lowest summer/annual GEP across the study) and consequently low annual net CO_2 uptake of the ecosystem.

4.3. Carbon dioxide environmental control

Despite statistically significant correlations between CO_2 fluxes and biophysical factors, there is no single factor that plays a dominant role in controlling the CO_2 balance in the Rzecin peatland. However, the air temperature can promote R_{eco} ($r^2 = 0.6$ in the autumn) and contribute to a higher NEP ($r^2 = 0.65$ in the spring). Most likely, factors such as higher surface moisture after winter and spring growth or autumn decomposition of plant biomass play a role here.

The highest correlations were found between CO_2 fluxes and NDVI/ EVI. The NDVI variability was responsible for 83% and 86% of the GEP variance in spring and summer, respectively (Table 3). Moreover, during the summer months, when the peatland presented its highest photosynthetic efficiency, LUE explained 77% of the variability in GEP. The net CO_2 flux, which results from two opposing processes, is more challenging to parameterise. Therefore, it is usually represented by a lower coefficient of determination than GEP, which was also seen in Armstrong et al. (2015).

Other peatland-related studies also evaluated different controlling factors of seasonal/yearly CO_2 fluxes. Studies by Aurela et al. (2004) and Lund et al. (2012b) found a clear positive correlation between snow melt time and annual CO_2 balance, while Humphreys and Lafleur (2011) did not notice this kind of correlation. Moreover, researchers noticed a positive correlation between the length of the growing season and the CO_2 accumulated for this period (Christensen et al., 2012) or the inter-annual variability of net CO_2 uptake (Helfter et al., 2015). On the other hand, many studies indicate that the CO_2 balance in a peatland is mainly controlled by WTD (Fortuniak et al., 2021; Strachan et al., 2016).

Defining the impact of the most significant meteorological factors (TA, WTD/precipitation and radiation) on CO_2 fluxes can allow determining whether they affect NEP by controlling GEP (Sonnentag et al., 2010; Niu et al., 2011) or R_{eco} (Aurela et al., 2007; Cai et al., 2010). Our observations contain periods with the predominant impact of GEP or R_{eco} on the overall CO_2 balance. For example, the difference in annual net CO_2 flux between 2004 and 2005 was caused by the difference in GEP while R_{eco} remained the same. Between 2008 and 2009, we observed a similar situation; however, GEP and R_{eco} were much higher than in 2004–2005. On the other hand, differences in annual NEP between 2005 and 2006 and also 2010 and 2011 seem to be linked with R_{eco} variability. It suggests that this study contains seasons with completely diverse meteorological conditions that affect CO_2 fluxes differently.

In our particular study, we found that LUE in winter correlates with GEP and NEP. However, the lack of any correlation between other meteorological factors and CO_2 fluxes in winter, nor any correlation with other seasons, does not allow for defining winter conditions as a determinant of the CO_2 balance. In contrast, Helfter et al. (2015) noticed that the winter average air temperature is responsible for the inter-annual variability of CO_2 absorption in the following summer.

4.4. NEP response to daytime TA and VPD

Based on summer data sets of measured NEP, we considered that the TA between 22.5 and 25 °C represents the highest values of net CO_2 uptake (Fig. 7b). Huang et al. (2019) found similar outcomes, where 24.5 °C was established as the optimal temperature for vegetation productivity of the Rzecin peatland (site ID: PL-wet; these results were derived from daily Gross Primary Productivity). Taking into account decreasing daytime NEP for TA>25 °C (Fig. 7b), it can be assumed that average daily summer TA in 2006, 2008, and 2010 (22.71 °C, 21.24 °C and 22.31 °C, respectively; the highest values across the study) were one of the main reasons of small NEP in these seasons. Moreover, summer TA explained 61% of NEP variability from 2005 to 2011 (higher TA decreased NEP).

A process that may significantly reduce the summertime daytime NEP under hot conditions is the increase of R_{eco} due to the correlation between temperature and ecosystem respiration (Loyd and Taylor, 1994). This study observed an interaction between TA and nighttime R_{eco} which in the summer reached a mean increase of R_{eco} of about 0.71 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ for every 5 °C (Fig. 6; considered summer R_{eco} for 18 °C>TA>9 °C to maximise respiration flux), while the mean decline of daytime NEP for TA>25 °C reached about of 1.13 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$ per 5 °C (Fig. 7b). Thus, the decrease in the daytime NEP is not only due to the increase in R_{eco}. Additionally, the inhibition of dark leaf respiration (mitochondrial respiration) under sunlight conditions (Keenan et al., 2019) suggests that summertime R_{eco} fluxes could be lower during the daytime than at nighttime.

In addition to the increased R_{eco} at higher temperatures, a daytime NEP reduction was noticed when a VPD>15 hPa threshold was exceeded. A decrease in daytime NEP under higher VPD values was also observed by Aurela et al. (2007). This net CO_2 flux reduction may be related to the stomatal closure influenced by higher VPD and the plant photorespiration process (releasing CO_2 molecules instead of assimilating them; Foyer et al., 2009). Photorespiration is a process that always coexists with photosynthesis and, for example, leads to the energy dissipation reaction (protection of photosynthesis from photoinhibition) and metabolic repair (Kozaki and Takeba, 1996; Voss et al., 2013; Eisenhut et al., 2017). However, higher temperature, as well as lower CO_2 and higher O_2 concentration in leaves (e.g., when plant stomata are closed to prevent dehydration under high VPD conditions; Otieno et al., 2012), promotes Rubisco enzyme to increase oxygenation of Ribulose 1, 5-bisphosphate (RuBP; fixing the RuBP with O_2 instead of CO_2) and

Table 4
Mean annual NEP from multi-year studies in northern peatlands.

Site and location	Type of ecosystem	Years of measurements	Mean annual NEP (gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$)	Refs.
PolWET site in Rzecin, north-western Poland	fen peatland	2004–2011 (8)	110±83	this study
Degerö Stormyr in northern Sweden	oligotrophic minerogenic mire	2001–2012 (12)	58±21	Peichl et al. (2014)
Lac Le Caron site in north-western Quebec, Canada	ombrotrophic bog	2008–2012 (5)	76±40	Strachan et al. (2016)
Bog Lake Fen site in northcentral Minnesota, USA	transitional poor fen	2009–2011 (3)	35.3 ± 6.6	Olson et al. (2013)
Kopytkowo site in northeastern Poland	Biebrza mire	2013–2018 (6)	49±95	Fortuniak et al. (2021)
Mer Bleue, east of Ottawa, Canada	ombrotrophic peatland	Nov.1998-Oct.2004 (6)	40.2 ± 40.5	Roulet et al. (2007)
Mer Bleue, east of Ottawa, Canada	freshwater marsh	2005–2009 (5)	224±54	Strachan et al. (2015)
Kaamanen, northern Finland	mesotrophic fen within the aapa mire region	1997–2002 (6)	22±20	Aurela et al. (2004)
Northeast of Athabasca, central Alberta, Canada	moderately rich treed fen	2004–2009 (6)	189±47	Flanagan and Syed (2011)
Near Glencar, southwestern Ireland	atlantic blanket bog	Sep.2002-Aug.2012 (10)	55.7 ± 18.9	McVeigh et al. (2014)
Auchencorth Moss site, south of Edinburgh, Scotland	low-lying ombrotrophic peatland	2003–2013 excluded 2011 (10)	64.1 ± 33.6	Helfter et al. (2015)
Stordalen Mire site, subarctic Sweden	palsa mire	2001–2008 (8)	66±29.1	Christensen et al. (2012)
7 northern peatlands	24 site years (incl. 2 years data set from PolWET site)		103±103	Lund et al. (2010)
Mean ±SD			84±60.1	

consequently lower photosynthesis to photorespiration ratio. Thus, the gap between increasing R_{eco} and decreasing NEP rates during summer may indicate that photorespiration negatively affects the daytime NEP fluxes under high VPD/TA conditions at Rzecin peatland. Furthermore, ecosystem respiration and photorespiration possibly explain the higher CO_2 balance during colder summer seasons. Although cooler summers may be associated with more frequent cloud presence, and diffused radiation can increase ecosystem productivity (Harenda et al., 2021; Zhou et al., 2021), this study did not find a clear correlation between summer PPFD diffusion index and NEP.

The calculation method shown in Fig. 7 has one major characteristic: each bin has a different number of values averaged within the bin. This is not an issue for commonly observed values; however, extreme values may contain greater standard deviation due to the (usually) higher number of outliers. Nevertheless, based on the error bars in Fig. 7, this study has no such situation. Therefore, this calculation method and presentation were found appropriate for the general presentation of a broad set of measured data (non-gap-filled NEP) containing data from different, often contrasting, seasons and years.

4.5. Productivity of Rzecin peatlands compared to northern peatlands

The mean annual CO_2 balance (NEP±SD) at Rzecin was 110 ± 83 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$, making this peatland a robust sink of carbon dioxide. The average uncertainty of the annual flux reached 34% of NEP. However, the share of uncertainty in the total flux is higher in years with a small annual balance (e.g. 2004) and could indicate a change in a Rzecin peatland CO_2 balance from a minimal sink to a significant source of CO_2. Other multi-year studies over northern peatlands found mean annual NEPs ranging from 22 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$ in sub-arctic fen to 224 gCO_2-$C \cdot m^{-2} \cdot yr^{-1}$ in a temperate freshwater marsh (Table 4).

These studies were characterised by different mean annual CO_2 uptake and standard deviations, which place the PolWET site among the most productive peatlands. The high standard deviation of the annual NEP over Rzecin peatland suggests sensitivity to biophysical factors in various combinations and intensities. Moreover, the high inter-annual variability of NEP (e.g., from source to strong sink of CO_2 year-by-year) also suggests the photosynthetic capacity of the ecosystem, which can be "released" under optimal conditions and result in a high annual NEP value.

5. Conclusions

This study of the CO_2 balance over a young temperate fen peatland with a floating peat carpet adds a multi-year perspective to the knowledge about annual CO_2 balances of peatlands in East-Central Europe. Our peatland site was generally a robust net CO_2 sink, also compared to other northern peatlands. However, the CO_2 dynamics observed at the Rzecin peatland site do not provide a complete picture of the carbon balance of the studied ecosystem. In future research, it is crucial to ensure continuous measurements of CH_4 exchange rates to fill the knowledge gap on the carbon balance of the peatland on the overgrowing lake. Additionally, regular observations of CH_4 fluxes should be carried out at the site to estimate the global warming potential of this interesting ecosystem. Despite the relatively young age of the fen (formed approximately 260 years ago), the presence of a ~70 cm peat carpet suggests that the Rzecin peatland has very good carbon accumulation and storage capabilities, which are key functions of peatlands in the context of the global carbon cycle. However, this high CO_2 uptake capacity may be disrupted by unfavourable weather conditions, both shown in this study. The observed net CO_2 emission in 2006 contrasts with the assumption that peatlands with floating peat carpets should be drought-resistant by their ability to lower the peat mat together with WTD. The monitoring of WTD with the accurate estimation of the moisture profile of floating carpet could be an interesting research issue, as well as an absolute measurement of the rise and drop of the peat carpet.

Warmer springs favour higher NEP during this period, while higher air temperature and vapour pressure deficit over the summer significantly reduce the net CO_2 uptake of the peatland. In other words, mild temperatures ensure optimal conditions for high net CO_2 uptake (2005, 2009). However, reduced radiation and consequently diminished vegetation development may be the NEP limiting factor (2004). Vegetation indices can serve as reliable predictors of spring and summer GEP, still, they are not suitable for assessing the net CO_2 balance. The nighttime R_{eco} revealed different values at the same temperature depending on the season, indicating plants' explicit participation in creating the total ecosystem respiration. The estimated optimal ranges of air temperature (22.5–25 °C) and vapour pressure deficit (8–15 hPa) for summertime net CO_2 uptake raise concerns regarding the carbon dioxide balance of this ecosystem, in the context of ongoing global warming. Nevertheless, the studied peatland retains daytime uptake capacity even for years with extreme TA and VPD values. Thus, the statement that Rzecin-like peatlands do not pose a potential climate

Table A1
Monthly mean values of sums of gross ecosystem production (GEP), ecosystem respiration (R_{eco}), net ecosystem production (NEP), air temperature (TA), photosynthetic photon flux density (PPFD), normalised difference vegetation index (NDVI), and enhanced vegetation index (EVI) in 2004–2011 at the Rzecin peatland (AVG – mean, SD – standard deviation, share – share in yearly total value, mth – month).

Month	GEP AVG [gCO_2-C·m^{-2}·mth^{-1}]	GEP SD	GEP share [%]	R_{eco} AVG [gCO_2-C·m^{-2}·mth^{-1}]	R_{eco} SD	R_{eco} share [%]	NEP AVG [gCO_2-C·m^{-2}·mth^{-1}]	NEP SD	TA AVG [°C]	TA SD	PPFD [mol·m^{-2}·mth^{-1}]	PPFD SD	NDVI AVG [-]	NDVI SD	EVI AVG [-]	EVI SD
1	4.9	4.2	0.6%	13.8	3.1	1.8%	−8.9	6.3	−1.7	4.0	142	33	0.19	0.13	0.12	0.06
2	3.7	6.4	0.4%	12.6	4.4	1.7%	−9.3	5.7	−0.2	2.7	227	36	0.20	0.14	0.12	0.06
3	10.8	8.1	1.2%	19.7	6.0	2.6%	−9.0	4.8	3.2	1.9	558	84	0.36	0.05	0.18	0.03
4	26.7	8.7	3.0%	38.1	5.0	5.0%	−11.3	7.8	9.1	1.4	936	143	0.45	0.05	0.22	0.03
5	85.8	16.8	9.8%	76.9	7.2	10.1%	8.3	14.2	13.0	1.2	1082	166	0.57	0.06	0.31	0.04
6	183.2	36.3	20.9%	122.1	15.1	16.1%	60.3	31.7	16.8	1.4	1184	140	0.71	0.04	0.42	0.04
7	216.4	28.3	24.6%	146.7	16.0	19.3%	68.9	19.7	19.5	2.5	1125	165	0.74	0.02	0.47	0.02
8	179.8	18.1	20.5%	134.6	17.6	17.7%	43.5	17.2	17.5	0.7	935	124	0.74	0.02	0.43	0.03
9	98.2	6.9	11.2%	90.6	12.7	11.9%	6.5	12.3	13.3	1.3	695	79	0.66	0.03	0.37	0.03
10	44.2	5.6	5.0%	58.9	6.8	7.8%	−15.5	8.8	8.1	1.4	397	66	0.55	0.02	0.28	0.02
11	17.9	4.1	2.0%	28.8	3.3	3.8%	−11.4	5.5	3.9	1.5	166	43	0.40	0.10	0.20	0.03
12	6.7	3.1	0.8%	17.6	3.8	2.3%	−11.7	4.4	0.4	3.1	90	16	0.24	0.14	0.14	0.06

threat in the context of CO_2 emission-related feedback is justified to some extent.

Data statement

Funding

Table B1
Seasonal sums of the net ecosystem production (NEP gCO_2-C·m^{-2}), gross ecosystem production (GEP gCO_2-C·m^{-2}), ecosystem respiration (R_{eco} gCO_2-C·m^{-2}), photosynthetic photon flux density (PPFD kmol·m^{-2}) and precipitation (P mm), average air temperature (TA°C), vapour pressure deficit (VPD hPa), normalised difference vegetation index (NDVI), enhanced vegetation index (EVI) and light use efficiency (LUE multiplied by 1000) during spring, summer, autumn and winter in 2004–2011 at the Rzecin peatland; SD = standard deviation.

Season	Variable	2004	2005	2006	2007	2008	2009	2010	2011	Mean±SD
Spring	NEP	−30.9	−15.2	−29	−6.1	7.5	−0.2	−29.1	7.1	−12±16.3
	GEP	92.3	108.4	92.3	152.3	137.7	146.2	124.4	132.7	123.3 ± 23.3
	R_{eco}	123	126.2	119.8	158.4	131.2	147	149.6	121.6	134.6 ± 14.9
	PPFD	2.27	2.66	2.52	2.83	2.55	2.75	2.21	2.83	2.58±0.24
	TA	8.21	7.45	7.01	9.96	9.38	8.83	7.12	9.48	8.43±1.15
	P	69	123	111	125	58	119	157	52	102±38
	VPD	3.75	3.85	3.92	5.37	5.35	5.03	3.36	6.06	4.59±0.98
	NDVI	0.41	0.42	0.4	0.49	0.51	0.48	0.48	0.48	0.46±0.04
	EVI	0.2	0.21	0.21	0.25	0.27	0.25	0.27	0.23	0.24±0.03
	LUE	5.6	6.6	3.9	8.5	6.9	6.1	7.1	5.5	6.3 ± 1.4
Summer	NEP	83.2	228.4	107.6	254.3	112	212.1	165.8	218.3	172.7 ± 64.8
	GEP	446.1	576	543.4	712.8	558.8	641.9	579.8	576.6	579.4 ± 76.7
	R_{eco}	356.3	359.7	435	455.8	441.0	422.2	407.8	349.6	403.4 ± 42.3
	PPFD	2.85	3.37	3.45	3.04	3.45	3.26	3.36	3.18	3.25±0.21
	TA	17.05	17.04	19.81	17.66	18.2	17.36	19.07	17.36	17.94±1.01
	P	182	200	142	243	264	245	281	399	245±77
	VPD	6.49	6.55	9.7	7.55	10.34	7.78	10.26	8.57	8.41±1.56
	NDVI	0.69	0.72	0.71	0.77	0.72	0.76	0.73	0.74	0.73±0.03
	EVI	0.39	0.42	0.44	0.48	0.44	0.47	0.46	0.44	0.44±0.03
	LUE	16.7	23.1	20.8	34.4	18.6	22.6	20.5	20.6	22.2 ± 5.7
Autumn	NEP	−31.1	−18	−56.3	−32.1	−24.9	−21.2	10.5	9.1	−20.5 ± 22
	GEP	146	152.8	162.6	156.5	164	165.5	161	173.5	160.2 ± 8.4
	R_{eco}	175.1	172.8	213.6	184.6	186	184.5	148.9	161.4	178.4 ± 19.2
	PPFD	1.12	1.41	1.32	1.12	1.24	1.25	1.22	1.4	1.26±0.11
	TA	8.75	8.86	10.18	7.23	8.86	8.73	6.57	8.14	8.42±1.11
	P	127	75	55	115	112	166	227	120	125±53
	VPD	2.52	2.86	3.44	2.41	2.73	2.84	2.35	3.51	2.83±0.44
	NDVI	0.49	0.5	0.59	0.53	0.55	0.55	0.49	0.59	0.54±0.04
	EVI	0.26	0.25	0.31	0.3	0.28	0.3	0.27	0.28	0.28±0.02
	LUE	14.6	15.0	13.9	17.1	13.6	15.4	16.1	13.3	14.9 ± 1.3
Winter	NEP	−5.5	−23.2	−41.6	−45.5	−28.2	−8.1	−37.5	−36.8	−28.3 ± 15.1
	GEP	12.9	18.1	3.6	19.8	24.7	32.8	10.7	−1.6	15.1 ± 11.2
	R_{eco}	21.2	40.7	43.7	63.2	49.9	39.7	48.3	32.8	42.4 ± 12.4
	PPFD	0.38	0.46	0.5	0.45	0.4	0.44	0.5	0.46	0.45±0.04
	TA	−0.44	0.58	−2.73	3.08	2.68	−1.1	−3.14	−3.74	−0.6 ± 2.59
	P	181	111	118	239	154	54	93	140	136±57
	VPD	0.88	0.91	0.68	1.33	1.45	0.67	0.72	1.31	0.99±0.32
	NDVI	0.26	0.25	0.07	0.32	0.39	0.19	0.13	0.06	0.21±0.12
	EVI	0.13	0.12	0.06	0.19	0.19	0.14	0.1	0.06	0.12±0.05
	LUE	6.4	8.3	3.0	4.0	8.5	10.2	4.9	1.9	5.9 ± 3.0

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Monthly values of CO_2 fluxes and biophysical variables

A summary of CO_2 fluxes and key biophysical parameters for individual months was prepared to evaluate the variability of the fluxes and their share in the annual carbon dioxide balance (Table A1).

Appendix B. Seasonal values of CO_2 fluxes and biophysical variables

Correlations between the annual values of variables are usually challenging to identify. Therefore, a list of all variables used in this work, divided into individual seasons, has been prepared. The data presented in Table B1 were the basis for obtaining the coefficient of determination r^2 illustrated in Table 3.

References

Acosta, M., Juszczak, R., Chojnicki, B.H., Pavelka, M., Havránková, K., Lesny, J., Krupková, L., Urbaniak, M., Machačová, K., Olejnik, J., 2017. Co_2 fluxes from different vegetation communities on a peatland ecosystem. Wetlands 37, 423–435. https://doi.org/10.1007/s13157-017-0878-4.

Ahmad, S., Liu, H., Alam, S., Günther, A., Jurasinski, G., Lennartz, B., 2021. Meteorological controls on water table dynamics in fen peatlands depend on management regimes. Front. Earth Sci. 9, 1–13. https://doi.org/10.3389/feart.2021.630469.

Armstrong, A., Waldron, S., Ostle, N.J., Richardson, H., Whitaker, J., 2015. Biotic and abiotic factors interact to regulate northern peatland carbon cycling. Ecosystems 18 (8), 1395–1409. https://doi.org/10.1007/s10021-015-9907-4.

Aslan-Sungur, G., Lee, X., Evrendilek, F., Karakaya, N., 2016. Large interannual variability in net ecosystem carbon dioxide exchange of a disturbed temperate peatland. Sci. Total Environ. 554–555, 192–202. https://doi.org/10.1016/j.scitotenv.2016.02.153.

Aubinet, M., Vesala, T., Papale, D., 2012. Eddy covariance—a practical guide to measurement and data analysis. 10.1007/978-94-007-2351-1_15.

Aurela, M., Laurila, T., Tuovinen, J.P., 2004. The timing of snow melt controls the annual co_2 balance in a subarctic fen. Geophys. Res. Lett. 31, 3–6. https://doi.org/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_2 exchange of a sedge fen in southern finland–the impact of a drought period. Tellus B Chem. Phys. Meteorol. 59, 826–837. https://doi.org/10.1111/j.1600-0889.2007.00309.x.

Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Glob. Chang. Biol. 9, 479–492. https://doi.org/10.1046/j.1365-2486.2003.00629.x.

Baldocchi, D.D., 2014. Measuring fluxes of trace gases and energy between ecosystems and the atmosphere - the state and future of the eddy covariance method. Glob. Chang. Biol. 20, 3600–3609. https://doi.org/10.1111/gcb.12649.

Baldocchi, D.D., 2020. How eddy covariance flux measurements have contributed to our understanding of global change biology. Glob. Chang. Biol. 26, 242–260. https://doi.org/10.1111/gcb.14807.

Bandopadhyay, S., Rastogi, A., Rascher, U., Rademske, P., Schickling, A., Cogliati, S., Julitta, T., Mac Arthur, A., Hueni, A., Tomelleri, E., Celesti, M., Burkart, A., Stróżecki, M., Sakowska, K., Gąbka, M., Rosadziński, S., Sojka, M., Iordache, M.D., Reusen, I., Van Der Tol, C., Damm, A., Schuettemeyer, D., Juszczak, R., 2019. Hyplant-derived sun-induced fluorescence—a new opportunity to disentangle complex vegetation signals from diverse vegetation types. Remote Sens. 11, 1691. https://doi.org/10.3390/rs11141691.

Bandopadhyay, S., Rastogi, A., Cogliati, S., Rascher, U., Gąbka, M., Juszczak, R., 2021. Can vegetation indices serve as proxies for potential sun-induced fluorescence (sif)? a fuzzy simulation approach on airborne imaging spectroscopy data. Remote Sens. 13, 2545. https://doi.org/10.3390/rs13132545.

Barabach, J., 2012. the history of lake rzecin and its surroundings drawn on maps as a background to palaeoecological reconstruction. Limnol. Rev. 12, 103–114. https://doi.org/10.2478/v10194-011-0050-0.

Barel, J.M., Moulia, V., Hamard, S., Sytiuk, A., Jassey, V.E.J., 2021. Come rain, come shine: peatland carbon dynamics shift under extreme precipitation. Front. Environ. Sci. 9, 659953 https://doi.org/10.3389/fenvs.2021.659953.

Barr, A.G., Richardson, A.D., Hollinger, D.Y., Papale, D., Arain, M.A., Black, T.A., Bohrer, G., Dragoni, D., Fischer, M.L., Gu, L., Law, B.E., Margolis, H.A., McCaughey, J.H., Munger, J.W., Oechel, W., Schaeffer, K., 2013. Use of change-point detection for friction–velocity threshold evaluation in eddy-covariance studies. Agric. For. Meteorol. 171–172, 31–45. https://doi.org/10.1016/j.agrformet.2012.11.023.

Basińska, A.M., Reczuga, M.K., Gąbka, M., Stróżecki, M., Łuców, D., Samson, M., Urbaniak, M., Leśny, J., Chojnicki, B.H., Gilbert, D., Sobczyński, T., Olejnik, J., Silvennoinen, H., Juszczak, R., Lamentowicz, M., 2020. Experimental warming and precipitation reduction affect the biomass of microbial communities in a sphagnum peatland. Ecol. Indic. 112, 106059 https://doi.org/10.1016/j.ecolind.2019.106059.

Bragazza, L., Buttler, A., Robroek, B.J.M., Albrecht, R., Zaccone, C., Jassey, V.E.J., Signarbieux, C., 2016. Persistent high temperature and low precipitation reduce peat carbon accumulation. Glob. Chang. Biol. 22, 4114–4123. https://doi.org/10.1111/gcb.13319.

Cai, T., Flanagan, L.B., Syed, K.H., 2010. Warmer and drier conditions stimulate respiration more than photosynthesis in a boreal peatland ecosystem: analysis of automatic chambers and eddy covariance measurements. Plant Cell Environ. 33, 394–407. https://doi.org/10.1111/j.1365-3040.2009.02089.x.

Chojnicki, B.H., Urbaniak, M., Józefczyk, D., Augustin, J., Olejnik, J., 2007. Measurements of gas and heat fluxes at rzecin wetland. Monitoring, Modeling and Management. Taylor & Francis Group, London, pp. 125–131 eds T. Okruszko, E. Maltby, J. Szatylowicz, D. Światek, and W. Kotowski.

Chojnicki, B.H., Michalak, M., Acosta, M., Juszczak, R., Augustin, J., Drösler, M., Olejnik, J., 2010. Measurements of carbon dioxide fluxes by chamber method at the rzecin wetland ecosystem, Poland. Pol. J. Environ. Stud. 19 (2), 283–291.

Chojnicki, B.H., 2013. Spectral estimation of wetland carbon dioxide exchange. Int. Agrophys. 27, 1–79. https://doi.org/10.2478/v10247-012-0061-3.

Christensen, T.R., Jackowicz-Korczyński, 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 (3), 207–217. https://doi.org/10.1007/s13280-012-0302-5.

Dancho, M., Vaughan, D., 2020. Anomalize: tidy anomaly detection. R package version 0.2.2, https://CRAN.R-project.org/package=anomalize.

de Jong, R., Blaauw, M., Chambers, F.M., Christensen, T.R., De Vleeschouwer, F., Finsinger, W., Fronzek, S., Johansson, M., Kokfelt, U., Lamentowicz, M., LeRoux, G., Mitchell, E.A.D., Mauquoy, D., Nichols, J.E., Samaritani, E., van Geel, B., 2010. Climate and peatlands. Dodson, J. (ed.). Changing Climates, Earth Systems and Society. International Year of Planet Earth Series. Springer, Heidelberg, pp. 85–121. https://doi.org/10.1007/978-90-481-8716-4_5.

Dise, N.B., 2009. Peatland response to global change. Science 326, 810–811. https://doi.org/10.1126/science.1174268.

Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., Martimort, P., Meygret, A., Spoto, F., Sy, O., Marchese, F., Bargellini, P., 2012. Sentinel-2: esa's optical high-resolution mission for gmes operational services. Remote Sens. Environ. 120, 25–36. https://doi.org/10.1016/j.rse.2011.11.026.

Dyukarev, E.A., 2017. Partitioning of net ecosystem exchange using chamber measurements data from bare soil and vegetated sites. Agric. For. Meteorol. 239, 236–248. https://doi.org/10.1016/j.agrformet.2017.03.011.

Dyukarev, E.A., Godovnikov, E.A., Karpov, D.V., Kurakov, S.A., Lapshina, E.D., Filippov, I.V., Filippova, N.V., Zarov, E.A., 2019. Net ecosystem exchange, gross primary production and ecosystem respiration in ridge-hollow complex at mukhrino bog. Geogr. Environ. Sustain. 12, 227–244. https://doi.org/10.24057/2071-9388-2018-77.

Eisenhut, M., Brautigam, A., Timm, S., Florian, A., Tohge, T., Fernie, A.R., Bauwe, H., Weber, A.P.M, 2017. Photorespiration is crucial for dynamic response of photosynthetic metabolism and stomatal movement to altered co_2 availability. Mol. Plant. 10, 47–61. https://doi.org/10.1016/j.molp.2016.09.011.

Escuin, S., Navarro, R., Fernández, P., 2008. Fire severity assessment by using nbr (normalised burn ratio) and ndvi (normalised difference vegetation index) derived from landsat tm/etm images. Int. J. Remote Sens. 29, 1053–1073. https://doi.org/10.1080/01431160701281072.

Farat, R., Mager, P., Pijewska, I., 2004. Climate Atlas of the Wielkopolska Region. Poznan: Institute of Meteorology and Water Management, Poznan Branch, Poland.

Farquhar, G.D., Sharkey, T.D., 1982. Stomatal conductance and photosynthesis. Annu. Rev. Plant Physiol. 33, 317–345. https://doi.org/10.1146/annurev. pp.33.060182.001533.

Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. Nat. Geosci. 4, 895–900. https://doi.org/10.1038/ngeo1323.

Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Glob. Chang. Biol. 8, 599–615. https://doi.org/10.1046/j.1365-2486.2002.00491.x.

Flanagan, L.B., Syed, K.H., 2011. Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. Glob. Chang. Biol. 17, 2271–2287. https://doi.org/10.1111/j.1365-2486.2010.02378.x.

Friedl, M.A., McIver, D.K., Hodges, J.C.F., Zhang, X.Y., Muchoney, D., Strahler, A.H., Woodcock, C.E., Gopal, S., Schneider, A., Cooper, A., Baccini, A., Gao, F., Schaaf, C., 2002. Global land cover mapping from modis: algorithms and early results. Remote Sens. Environ. 83 (1–2), 287–302. https://doi.org/10.1016/S0034-4257(02)00078-0.

Fortuniak, K., Pawlak, W., Bednorz, L., Grygoruk, M., 2017. Methane and carbon dioxide fluxes of a temperate mire in central europe. Agric. For. Meteorol. 232, 306–318. https://doi.org/10.1016/j.agrformet.2016.08.023.

Fortuniak, K., Pawlak, W., Siedlecki, M., Chambers, S., Bednorz, L., 2021. Temperate mire fluctuations from carbon sink to carbon source following changes in water table. Sci. Total Environ. 756, 144071 https://doi.org/10.1016/j. scitotenv.2020.144071.

Foyer, C.H., Bloom, A.J., Queval, G., Noctor, G., 2009. Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. Annu. Rev. Plant Biol. 60, 455–484. https://doi.org/10.1146/annurev.arplant.043008.091948.

Friedlingstein, P, Jones, M.W., O'Sullivan, M., Andrew, R.M., Hauck, J., et al., 2019. Global carbon budget 2019. Earth Syst. Sci. Data 11, 1783–1838. https://doi.org/10.5194/essd-11-1783-2019.

Frolking, S.E., Bubier, J.L., Moore, T.R., Ball, T., Bellisario, L.M., Bhardwaj, A., Carroll, P., Crill, P.M., Lafleur, P.M., McCaughey, J.H., Roulet, N.T., Suyker, A.E., Verma, S.B., Waddington, J.M., Whiting, G.J., 1998. Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. Glob. Biogeochem. Cycles 12, 115–126. https://doi.org/10.1029/97gb03367.

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.S., Roulet, N., 2011. Peatlands in the earth's 21st century climate system. Environ. Rev. 19, 371–396. https://doi.org/10.1139/a11-014.

Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., et al., 2018. The peatland carbon sink with warming. Nat. Clim. Chang. 8, 907–914. https://doi.org/10.1038/s41558-018-0271-1.

Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1, 182–195. https://doi.org/10.2307/1941811.

Goward, S., Prince, S., 1995. Transient effects of climate on vegetation dynamics: satellite observations. J. Biogeogr. 22, 549–564. https://doi.org/10.2307/2845953.

Górecki, K., Rastogi, A., Stróżecki, M., Gąbka, M., Lamentowicz, M., Łuców, D., Kayzer, D., Juszczak, R., 2021. Water table depth, experimental warming, and reduced precipitation impact on litter decomposition in a temperate sphagnum-peatland. Sci. Total Environ. 771, 145452 https://doi.org/10.1016/j. scitotenv.2021.145452.

Harenda, K.M., Lamentowicz, M., Samson, M., Chojnicki, B.H., 2018. The role of peatlands and their carbon storage function in the context of climate change. Interdisciplinary Approaches for Sustainable Development Goals. Springer, Cham, pp. 169–187. https://doi.org/10.1007/978-3-319-71788-3_12 eds. T. Zielinski, I. Sagan, W. SuroszGeoPlanet: Earth and Planetary Sciences.

Harenda, K.M., Samson, M., Juszczak, R., Markowicz, K.M., Stachlewska, I.S., Kleniewska, M., MacArthur, A., Schüttemeyer, D., Chojnicki, B.H., 2021. impact of atmospheric optical properties on net ecosystem productivity of peatland in poland. Remote Sens. 13, 2124. https://doi.org/10.3390/rs13112124.

Harenda, K.M., Markowicz, K.M., Poczta, P., Stachlewska, I.S., Bojanowski, J.S., Czernecki, B., McArthur, A., Schütemeyer, D., Chojnicki, B.H., 2022. Estimation of the effects of aerosol optical properties on peatland production in rzecin, Poland. Agric. For. Meteorol. 316, 108861 https://doi.org/10.1016/j. agrformet.2022.108861.

Helfter, C., Campbell, C., Dinsmore, K.J., Drewer, J., Coyle, M., Anderson, M., Skiba, U., Nemitz, E., Billett, M.F., Sutton, M.A., 2015. Drivers of long-term variability in co2 net ecosystem exchange in a temperate peatland. Biogeosciences 12, 1799–1811. https://doi.org/10.5194/bg-12-1799-2015.

Hooijer, A., Page, S., Canadell, J.G., Silvius, M., Kwadijk, J., Wösten, H., Jauhiainen, J., 2010. Current and future co2 emissions from drained peatlands in southeast asia. Biogeosciences 7, 1505–1514. https://doi.org/10.5194/bg-7-1505-2010.

Huang, M., Piao, S., Ciais, P., Peñuelas, J., Wang, X., Keenan, T.F., Peng, S., Berry, J.A., Wang, K., Mao, J., Alkama, R., Cescatti, A., Cuntz, M., De Deurwaerder, H., Gao, M., He, Y., Liu, Y., Luo, Y., Myneni, R.B., Niu, S., Shi, X., Yuan, W., Verbeeck, H., Wang, T., Wu, J., Janssens, I.A., 2019. Air temperature optima of vegetation productivity across global biomes. Nat. Ecol. Evol. 3, 772–779. https://doi.org/10.1038/s41559-019-0838-x.

Humphreys, E.R., Lafleur, P.M., 2011. Does earlier snowmelt lead to greater co2 sequestration in two low arctic tundra ecosystems? Geophys. Res. Lett. 38, L09703. https://doi.org/10.1029/2011GL047339.

Hurkuck, M., Brümmer, C., Kutsch, W.L., 2016. Near-neutral carbon dioxide balance at a seminatural, temperate bog ecosystem. J. Geophys. Res. Biogeosci. 121, 370–384. https://doi.org/10.1002/2015JG003195.

IMGW-PIB, 2021. Polish institute of meteorology and water management - national research institute. the source of the data is the institute of meteorology and water management - National Research Institute https://dane.imgw.pl/data/dane_pomia rowo_obserwacyjne/. Data from Szamotuły-Baborówko (no. 3203) and Miały (no. 93247) stations of the Institute of Meteorology and Water Management - National Research Institute have been processed.

IPCC, 2021: Climate change 2021: The physical science basis. contribution of working Group I to the sixth assessment report of the intergovernmental panel on climate change Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.). Cambridge University Press. InPress.

Juszczak, R., Acosta, M., Olejnik, J., 2012. Comparison of daytime and nighttime ecosystem respiration measured by the closed chamber technique on a temperate mire in poland. Pol. J. Environ. Stud. 21, 643–658.

Juszczak, R., Augustin, J., 2013. Exchange of the greenhouse gases methane and nitrous oxide between the atmosphere and a temperate peatland in central europe. Wetlands 33, 895–907. https://doi.org/10.1007/s13157-013-0448-3.

Juszczak, R., Humphreys, E., Acosta, M., Michalak-Galczewska, M., Kayzer, D., Olejnik, J., 2013. Ecosystem respiration in a heterogeneous temperate peatland and its sensitivity to peat temperature and water table depth. Plant Soil 366, 505–520. https://doi.org/10.1007/s11104-012-1441-y.

Kaimal, J.C., Finnigan, J.J., 1994. Atmospheric Boundary Layer Flows. Their Structure and Measurement. Oxford University Press, New York.

Keenan, T.F., Migliavacca, M., Papale, D., Baldocchi, D., Reichstein, M., Torn, M., Wutzler, T., 2019. Widespread inhibition of daytime ecosystem respiration. Nat. Ecol. Evol. 3, 407–415. https://doi.org/10.1038/s41559-019-0809-2.

Kowalska, N., Chojnicki, B.H., Rinne, J., Haapanala, S., Siedlecki, P., Urbaniak, M., Juszczak, R., Olejnik, J., 2013. Measurements of methane emission from a temperate wetland by the eddy covariance method. Int. Agrophys. 27, 283–290. https://doi.org/10.2478/v10247-012-0096-5.

Kozaki, A., Takeba, G., 1996. Photorespiration protects c3 plants from photooxidation. Nature 384, 557–560. https://doi.org/10.1038/384557a0.

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 Biogeochem. Cycles 17. https://doi.org/10.1029/2002 gb001983.

Lappalainen, E. 1996. General review on world peatland and peat resources. In Glob. Peat Resour.

Law, B., Falge, E., Gu, L., Baldocchi, D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A., Falk, M., Fuentes, J., et al., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agric. For. Meteorol. 113, 97–120.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. https://doi.org/10.2307/2389824.

Lund, M., Lafleur, P.M., Roulet, N.T., Lindroth, A., Christensen, T.R., Aurela, M., Chojnicki, B.H., Flanagan, L.B., Humphreys, E.R., Laurila, T., Oechel, W.C., Olejnik, J., Rinne, J., Schubert, P., Nilsson, M.B., 2010. Variability in exchange of co2 across 12 northern peatland and tundra sites. Glob. Chang. Biol. 16, 2436–2448. https://doi.org/10.1111/j.1365-2486.2009.02104.x.

Lund, M., Christensen, T.R., Lindroth, A., Schubert, P., 2012a. Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. Environ. Res. Lett. 7, 045704 https://doi.org/10.1088/1748-9326/7/4/045704.

Lund, M., Falk, J.M., Friborg, T., Mbufong, H.N., Sigsgaard, C., Soegaard, H., Tamstorf, M.P., 2012b. Trends in co2 exchange in a high arctic tundra heath, 2000–2010. J. Geophys. Res. 117, G02001. https://doi.org/10.1029/2011JG001901.

Mäkilä, M., Saarnisto, M., 2008. Carbon accumulation in boreal peatlands during the holocene— impacts of climate variations. Peatlands and Climate Change. International Peat Society, Finland edited by M Strack.

Massmann, A., Gentine, P., Lin, Ch., 2019. When does vapor pressure deficit drive or reduce evapotranspiration? J. Adv. Model. Earth Syst. 11, 3305–3320. https://doi.org/10.1029/2019MS001790.

Matsushita, B., Yang, W., Chen, J., Onda, Y., Qiu, G., 2007. Sensitivity of the enhanced vegetation index (evi) and normalized difference vegetation index (ndvi) to topographic effects: a case study in high-density cypress forest. Sensors 7, 2636–2651. https://doi.org/10.3390/s7112636.

Mauder, M., Foken, T., 2004. Documentation and instruction manual of the eddy-covariance software package tk2. Arbeitsergebnisse, ISSN 1614-8924. 10.5281/zenodo.20349.

Mauder, M., Foken, T., 2006. Impact of post-field data processing on eddy covariance flux estimates and energy balance closure. Meteorol. Z. https://doi.org/10.1127/0941-2948/2006/0167.

McVeigh, P., Sottocornola, M., Foley, N., Leahy, P., Kiely, G., 2014. Meteorological and functional response partitioning to explain interannual variability of co2 exchange at an irish atlantic blanket bog. Agric. For. Meteorol. 194, 8–19. https://doi.org/10.1016/j.agrformet.2014.01.017.

Miao, G., Noormets, A., Domec, J.C., Fuentes, M., Trettin, C.C., Sun, G., McNulty, S.G., King, J., 2017. Hydrology and microtopography control carbon dynamics in wetlands: implications in partitioning ecosystem respiration in a coastal plain forested wetland. Agric. For. Meteorol. 247, 343–355. https://doi.org/10.1016/j.agrformet.2017.08.022.

Milecka, K., Kowalewski, G., Fiałkiewicz-Kozieł, B., Gałka, M., Lamentowicz, M., Chojnicki, B.H., Goslar, T., Barabach, J., 2016. Hydrological changes in the rzecin peatland (puszcza notecka, poland) induced by anthropogenic factors: implications for mire development and carbon sequestration. Holocene 1–14. https://doi.org/10.1177/0959683616670468.

Moncrieff, J.B., Massheder, J.M., de Bruin, H., Ebers, J., Friborg, T., Heusinkveld, B., Kabat, P., Scott, S., Soegaard, H., Verhoef, A., 1997. A system to measure surface fluxes of momentum, sensible heat, water vapor and carbon dioxide. J. Hydrol. 188-189, 589–611. https://doi.org/10.1016/S0022-1694(96)03194-0.

Moore, S., Eavns, Ch.D., Page, S.E., Garnett, M.H., Jones, T.G., Freeman, C., Hooijer, A., Wiltshire, A.J., Limin, S.H., Gauci, V., 2013. Deep instability of deforested tropical peatlands revealed by fluvial organic carbon fluxes. Nature 493, 660–663. https://doi.org/10.1038/nature11818.

Nakai, T., Shimoyama, K., 2012. Ultrasonic anemometer angle of attack errors under turbulent conditions. Agric. For. Meteorol. 162–163, 14–26. https://doi.org/10.1016/j.agrformet.2012.04.004.

Niu, S.L., Luo, Y.Q., Fei, S.F., Montagnani, L., Bohrer, G., Janssens, I.A., Gielen, B., Rambal, S., Moors, E., Matteucci, G., 2011. Seasonal hysteresis of net ecosystem exchange in response to temperature change: patterns and causes. Glob. Chang. Biol. 17, 3102e3114. https://doi.org/10.1111/j.1365-2486.2011.02459.x.

Olson, D., Griffis, T.J., Noormets, A., Kolka, R., Chen, J., 2013. Interannual, seasonal, and retrospective analysis of the methane and carbon dioxide budgets of a temperate peatland. J. Geophys. Res. Biogeosci. 118, 226–238. https://doi.org/10.1002/jgrg.20031.

Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant Cell Environ. 22, 1515–1526. https://doi.org/10.1046/j.1365-3040.1999.00513.x.

Otieno, D., Lindner, S., Muhr, J., Borken, W., 2012. Sensitivity of peatland herbaceous vegetation to vapor pressure deficit influences net ecosystem co2 exchange. Wetlands 32, 895–905. https://doi.org/10.1007/s13157-012-0322-8.

Page, S.E., Rieley, J.O., Banks, Ch.J., 2011. Global and regional importance of the tropical peatland carbon pool. Glob. Chang. Biol. 17, 798–818. https://doi.org/10.1111/j.1365-2486.2010.02279.x.

Peichl, M., Öquist, M., Löfvenius, M.O., Ilstedt, U., Sagerfors, J., Grelle, A., Lindroth, A., Nilsson, M.B., 2014. A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen. Environ. Res. Lett. 9, 055006 https://doi.org/10.1088/1748-9326/9/5/055006.

R Core Team, 2019. R: a language and environment for statistical computing. Vienna Austria. https://www.r-project.org/.

Ramonet, M., Ciais, P., et al., 2020. The fingerprint of the summer 2018 drought in europe on ground-based tmospheric co2 measurements. Philos. Trans. R. Soc. B 375, 20190513. https://doi.org/10.1098/rstb.2019.0513.

Rastogi, A., Stróżecki, M., Kalaji, H.M., Łucόw, D., Lamentowicz, M., Juszczak, R., 2019. Impact of warming and reduced precipitation on photosynthetic and remote sensing properties of peatland vegetation. Environ. Exp. Bot. 160, 71–80. https://doi.org/10.1016/j.envexpbot.2019.01.005.

Rastogi, A., Antala, M., Gąbka, M., Rosadziński, S., Stróżecki, M., Brestic, M., Juszczak, R., 2020. Impact of warming and reduced precipitation on morphology and chlorophyll concentration in peat mosses (sphagnum angustifolium and s. fallax). Sci. Rep. 10, 8592. https://doi.org/10.1038/s41598-020-65032-x.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, 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. Glob. Chang. Biol. 11, 1424–1439. https://doi.org/10.1111/j.1365-2486.2005.001002.x.

Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., Hollinger, D.Y., Kutsch, W.L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L., William, M.J., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., Varlagin, A., 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. Philos. Trans. R. Soc. B Biol. Sci. 365, 3227–3246. https://doi.org/10.1098/rstb.2010.0102.

Rinne, J., Tuovinen, J.P., Klemedtsson, L., Aurela, M., Holst, J., Lohila, A., Weslien, P., Vestin, P., Łakomiec, P., Peichl, M., Tuittila, E.S., Heiskanen, L., Laurila, T., Li, X., Alekseychik, P., Mammarella, I., Ström, L., Crill, P., Nilsson, M.B., 2020. Effect of the 2018 european drought on methane and carbon dioxide exchange of northern mire ecosystems. Philos. Trans. R. Soc. B 375, 20190517. https://doi.org/10.1098/rstb.2019.0517.

Romanowska, J., 2015. Analysis of the spatial variability of ph on the peatland in rzecin. poznan university of life sciences. MSc thesis (in Polish).

Roulet, N.T., Lafleur, P.M., Richard, P.J.H., Moore, T.R., Humphreys, E.R., Bubier, J., 2007. Contemporary carbon balance and late holocene carbon accumulation in a northern peatland. Glob. Chang. Biol. https://doi.org/10.1111/j.1365-2486.2006.01292.x.

Rydin, H., Jeglum, J.K., 2013. The Biology of Peatlands. Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199602995.001.0001. Biol. Peatlands.

Salmon, E., Jégou, F., Guenet, B., Jourdain, L., Qiu, C., Bastrikov, V., Guimbaud, C., Zhu, D., Ciais, P., Peylin, P., Gogo, S., Laggoun-Défarge, F., Aurela, M., Bret-Harte, M.S., Chen, J., Chojnicki, B.H., Chu, H., Edgar, C.W., Euskirchen, E.S., Flanagan, L.B., Fortuniak, K., Holl, D., Klatt, J., Kolle, O., Kowalska, N., Kutzbach, L., Lohila, A., Merbold, L., Pawlak, W., Sachs, T., Ziemblińska, K., 2022. Assessing methane emissions for northern peatlands in orchidee-peat revision 7020. Geosci. Model Dev. 15, 2813–2838. https://doi.org/10.5194/gmd-15-2813-2022.

Šigut, L., 2022. Openeddy: post-process eddy covariance data with ease. R package version 0.0.0.9006. https://github.com/lsigut/openeddy.

Sonnentag, O., Van Der Kamp, G., Barr, A.G., Chen, J.M., 2010. On the relationship between water table depth and water vapor and carbon dioxide fluxes in a minerotrophic fen. Glob. Change Biol. 16, 1762–1776. https://doi.org/10.1111/j.1365-2486.2009.02032.x.

Soudani, K., Hmimina, G., Delpierre, N., Pontailler, J.Y., Aubinet, M., Bonal, D., Caquet, B., de Grandcourt, A., Burban, B., Flechard, C., Guyon, D., Granier, A., Gross, P., Heinesh, B., Longdoz, B., Loustau, D., Moureaux, C., Ourcival, J.M., Rambal, S., Saint André, L., Dufrêne, E., 2012. Ground-based network of ndvi measurements for tracking temporal dynamics of canopy structure and vegetation phenology in different biomes. Remote Sens. Environ. 123, 234–245. https://doi.org/10.1016/j.rse.2012.03.012.

Stoy, P.C., Trowbridge, A.M., Bauerle, W.L., 2014. Controls on seasonal patterns of maximum ecosystem carbon uptake and canopy-scale photosynthetic light response: contributions from both temperature and photoperiod. Photosynth. Res. 119, 49–64. https://doi.org/10.1007/s11120-013-9799-0.

Strachan, I.B., Nugent, K.A., Crombie, S., Bonneville, M.C., 2015. Carbon dioxide and methane exchange at a cool-temperate freshwater marsh. Environ. Res. Lett. 10, 065006 https://doi.org/10.1088/1748-9326/10/6/065006.

Strachan, I.B., Pelletier, L., Bonneville, M.C., 2016. Inter-annual variability in water table depth controls net ecosystem carbon dioxide exchange in a boreal bog. Biogeochemistry 127, 99–111. https://doi.org/10.1007/s10533-015-0170-8.

Thompson, R.L., Broquet, G., Gerbig, C., Koch, T., Lang, M., Monteil, G., Munassar, S., Nickless, A., Scholze, M., Ramonet, M., Karstens, U., van Schaik, E., Wu, Z., Rodenbeck, C., 2020. Changes in net ecosystem exchange over europe during the 2018 drought based on atmospheric observations. Philos. Trans. R. Soc. Lond. B Biol. Sci. 375, 20190512 https://doi.org/10.1098/rstb.2019.0512.

Tuck, S.L., Phillips, H.R.P., Hintzen, R.E., Scharlemann, J.P.W., Purvis, A., Hudson, L.N., 2014. Modistools - downloading and processing modis remotely sensed data in r. Ecol. Evol. 4, 4658–4668. https://doi.org/10.1002/ece3.1273.

Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A., 2002. Estimating carbon accumulation rates of undrained mires in finland - application to boreal and subarctic regions. Holocene 12, 69–80. https://doi.org/10.1191/0959683602hl522rp.

van Dijk, A.I.J.M., Dolman, A.J., Schulze, E.D., 2005. Radiation, temperature, and leaf area explain ecosystem carbon fluxes in boreal and temperate european forests. Glob. Biogeochem. Cycles 19, 1–15. https://doi.org/10.1029/2004GB002417.

Voss, I., Sunil, B., Scheibe, R., Raghavendra, A.S., 2013. Emerging concept for the role of photorespiration as an important part of abiotic stress response. Plant Biol. J. 15, 713–722. https://doi.org/10.1111/j.1438-8677.2012.00710.x.

Walter, I.A., Allen, R.G., Elliott, R., Itenfisu, D., Brown, P., Jensen, M.E., Mecham, B., Howell, T.A., Snyder, R., Eching, S., Spofford, T., Hattendorf, M., Martin, D., Cuenca, R.H., Wright, J.L., 2005. The asce standardized reference evapotranspiration equation. ASCE-EWRI Task Committee Report.

Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. Q. J. R. Meteorol. Soc. 106, 85–100. https://doi.org/10.1002/qj.49710644707.

Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Šigut, L., Menzer, O., Reichstein, M., 2018. Basic and extensible post-processing of eddy covariance flux data with REddyProc, 15, 5015–30.

Wutzler, T., Reichstein, M., Moffat, A.M., Migliavacca, M., 2020. REddyProc: post processing of (half-)hourly eddy-covariance measurements. R package version 1.2.2, https://CRAN.R-project.org/package=REddyProc.

Yi, Ch., Li, R., Wolbeck, J., Xu, X., Nilsson, M., et al., 2010. Climate control of terrestrial carbon exchange across biomes and continents. Environ. Res. Lett. 5 https://doi.org/10.1088/1748-9326/5/3/034007.

Yurova, A., Wolf, A., Sagerfors, J., Nilsson, M., 2007. Variations in net ecosystem exchange of carbon dioxide in a boreal mire: modeling mechanisms linked to water table position. J. Geophys. Res. Biogeosci. 112, 1–13. https://doi.org/10.1029/2006JG000342.

Zhou, H., Yue, X., Lei, Y., Zhang, T., Tian, C., Ma, Y., Cao, Y., 2021. Responses of gross primary productivity to diffuse radiation at global fluxnet sites. Atmos. Environ. 244, 117905 https://doi.org/10.1016/j.atmosenv.2020.117905.

Ziemblińska, K., Urbaniak, M., Chojnicki, B.H., Black, T.A., Niu, S., Olejnik, J., 2016. Net ecosystem productivity and its environmental controls in a mature scots pine stand in North-Western Poland. Agric. For. Meteorol. 228–229, 60–72. https://doi.org/10.1016/j.agrformet.2016.05.022.