

Original Research

# Comparison of Daytime and Nighttime Ecosystem Respiration Measured by the Closed Chamber Technique on a Temperate Mire in Poland

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## Abstract

Ecosystem respiration ( $R_{eco}$ ) plays an important role in estimating the global carbon balance of terrestrial ecosystems, and knowledge of respiration is required to correctly assess the gross primary ( $GPP$ ) production of such ecosystems. In our paper, daytime  $R_{eco}$  fluxes are compared with nighttime  $CO_2$  fluxes which were measured manually by the closed chamber technique on a wetland site in Poland. The  $CO_2$  fluxes measurements were performed between July 2008 and May 2009. Our study indicated that there are significant differences between modeled daytime and nighttime  $R_{eco}$  fluxes and that these differences are higher when the nighttime fluxes are restricted only to nights with stable atmospheric conditions. The nighttime sums of cumulative  $R_{eco}$  are much higher than the one estimated for daytime conditions, while there is nearly no difference between daytime and nighttime sums of cumulative  $R_{eco}$ , when the nighttime fluxes are restricted only for nights with turbulent atmospheric conditions. Consequently,  $R_{eco}$  models developed on the basis of nighttime data series can overestimate  $CO_2$  fluxes when they are used to estimate daytime respiration. In order to reduce uncertainties in estimation of daily  $R_{eco}$  fluxes on the basis of the nighttime chamber measurements, the nighttime  $R_{eco}$  models should be restricted only to the fluxes that were measured in turbulent atmospheric conditions. The biases in nighttime chamber measurements (especially when conducted in stable atmospheric conditions) as well as differences in estimated daytime and nighttime  $R_{eco}$  fluxes can have a significant effect on the assessment of global carbon balances of terrestrial ecosystems.

**Keywords:** nighttime ecosystem respiration, daytime ecosystem respiration, chamber measurements,  $CO_2$  fluxes, mire

## Introduction

Ecosystem respiration ( $R_{eco}$ ) plays an important role estimating global carbon balances of terrestrial ecosystems [e.g. 1, 2], and knowledge of respiration is required to correctly assess the gross primary ( $GPP$ ) production of such ecosys-

tems (as a sum of net ecosystem exchange ( $NEE$ ) and  $R_{eco}$ ). The net ecosystem exchange indicates the quite small difference between C uptake by plants in photosynthesis and C release through the respiration of plants and soil. Small errors in the estimation of  $R_{eco}$  can lead to large errors in the estimation of  $NEE$  [3]. The eddy covariance community has already proved that intersite and interannual variation in ecosystem respiration greatly influences variation in the

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net ecosystem exchange and terrestrial C sequestration [2, 4-6]. As a result, there is extensive discussion about how to measure and model ecosystem respiration and how to minimize errors and biases in the estimation of CO<sub>2</sub> fluxes. CO<sub>2</sub> fluxes are quantified most commonly by means of the eddy covariance method [7-9] and various types of chambers [10-12]. However, both techniques have different spatial and time resolutions, use different approaches, and have different disadvantages. For example, the eddy covariance method can only be used for CO<sub>2</sub> flux measurements when turbulence in the atmospheric boundary layer is well developed. Low-turbulence conditions, typical for stable atmospheric status, are insufficient for the eddy covariance measurements [8] and lead to the underestimation of CO<sub>2</sub> fluxes, especially in calm night conditions [8, 13, 14]. Due to this, the closed chamber technique was frequently applied to quantify CO<sub>2</sub> flux underestimation by the eddy covariance systems in stable conditions [15-17]. The problem, however, is that nighttime chamber measurements carried out in calm stable conditions also can be biased [18-20], and it is reported that nighttime CO<sub>2</sub> fluxes measured by chambers are overestimated when measured in stable atmospheric conditions in comparison to the fluxes measured in turbulent atmospheric conditions during the night [21]. On the other hand, chamber fluxes in most cases tend to be underestimated, both in static (non-steady state non-through flow) and dynamic chambers (non-steady state through flow), and the rate of the underestimation or sometimes overestimation is difficult to assess in field conditions [11, 22, 23].

Considering the above-mentioned facts, several data screening methods were developed to discard fluxes measured in stable atmospheric conditions [13], which can be applied both in the case of the eddy covariance and the chamber measurements. A  $u^*$  friction velocity filter method is most commonly used to deal with stable stratified canopy flows [24]. However, various researchers use different  $u^*$  thresholds that seem to be site- or ecosystem-specific. For peatlands, the friction velocity threshold of 0.1 m·s<sup>-1</sup> [21, 25, 26] is used most commonly, but van der Molen et al. [27] applied quite a high threshold of 0.2 m·s<sup>-1</sup>, while Zamolodchikov et al. [17] used one of the smallest  $u^*$ -threshold <0.025 m·s<sup>-1</sup>, both applied for peatlands sites. Practically, the underestimated observed nighttime CO<sub>2</sub> fluxes measured by the eddy covariance systems in stable atmospheric conditions should be replaced by respiration fluxes predicted by empirical models with soil temperature as a predictor variable [10]. The simple first order exponential equations with temperature as the only determinant have been most commonly used to assess ecosystem respiration and these equations have been modified very little since their 19<sup>th</sup> century origin [28]. The application and correctness of such models are currently criticized as these models poorly reflect the complex nature of ecosystem respiration components and the drivers controlling these processes [3, 28, 29]. Most modifications of empirical approaches used to model  $R_{eco}$  reveal the influence of soil moisture and precipitation [28, 30, 31], water table depth [32-34] or the rate of photosynthesis [3]. Although most

studies found temperature to be an important control driver of ecosystem respiration on peatland sites, the influence of soil water content or water table depth on  $R_{eco}$  is much less clear and understood [35].

There is ample evidence confirming that the nighttime CO<sub>2</sub> fluxes measured by the eddy covariance systems in stable atmospheric conditions are underestimated. Other papers indicate that the nighttime chamber  $R_{eco}$  fluxes used for gap-filling of the eddy covariance fluxes when measured in stable conditions can be biased and overestimated in the same conditions with no turbulence in the atmosphere. However, there is no paper where daytime  $R_{eco}$  fluxes measured by chambers are compared to the  $R_{eco}$  fluxes measured in nighttime conditions. It can be assumed that these fluxes can be significantly different when measured under various conditions. There are many papers showing, for example, that autotrophic respiration of plants can be inhibited in light conditions. Most studies focusing on leaf respiration have reported that the rate of leaf respiration in the light is much smaller than the rate of respiration in the darkness [36-41], with the degree of inhibition ranging from 16% to even 77%, depending mostly on the plant species, age of leaves and N content in plants. Assuming that even 50% of the ecosystem respiration in peatlands consists of autotrophic respiration [42], then the processes described above should have significant impact on the measured daytime  $R_{eco}$  fluxes. What is more, the rate of respiration is supposed to be inhibited by elevated CO<sub>2</sub> concentrations, which is typical during stable atmospheric conditions [43-46]. However, the responses of plant respiration to elevated CO<sub>2</sub> remain uncertain [47-48].

Most of the manual chamber measurements are conducted in daytime conditions [12, 49, 50], and based on them, empirical equations are found for relationships of daytime  $R_{eco}$  to temperatures that are then used to estimate the whole 24-hour  $R_{eco}$  fluxes. The question is whether there are significant differences between the day and night  $R_{eco}$  fluxes or not, and in which direction are these differences? Is it correct to apply the above-mentioned equations to estimate the nighttime CO<sub>2</sub> fluxes? On the other hand, most of the automatic chamber systems operating 24 hours per day and used for CO<sub>2</sub> flux measurements consist only of transparent chambers for *NEE* estimations. For these systems, nighttime  $R_{eco}$  fluxes are used to generate equations that describe relationships of CO<sub>2</sub> fluxes to temperature that are applied then to calculate *GPP* values during the day. If there is a difference in response of the ecosystem respiration to temperature in day and nighttime conditions, then the modeled *GPP* values may also be biased.

In this paper, we compare daytime  $R_{eco}$  fluxes with nighttime CO<sub>2</sub> fluxes that are measured manually by the chamber closed technique on a peatland site in Poland. The CO<sub>2</sub> flux measurements were performed in the period between July 2008 and May 2009. Despite the weaknesses of such analyses, clear differences of such CO<sub>2</sub> fluxes have been found.

## Experimental Procedures

### Study Site

The study was carried out at Rzecin peatland site, Poland (52°45' N latitude, 16°18' E longitude, 54 m a.s.l.), 70 km northwest of Poznań – the main city of the region. The Rzecin site (POLWET) is owned by Poznań University of Life Sciences and is managed by the Meteorology Department. This is the first wetland site in Poland where continuous measurements of CO<sub>2</sub> and H<sub>2</sub>O fluxes by means of the eddy covariance method have been carried out since January 2004 (within the CARBOEUROPE-IP and then NITROEUROPE-IP) [51]. Additionally, the manual chamber techniques have been used for measurements of CH<sub>4</sub> fluxes since 2005 and CO<sub>2</sub> fluxes (both *NEP* and *R<sub>eco</sub>*) since 2007.

The area of the studied peatland is about 86 ha. This is an mesotrophic, geogenous mire surrounded by the pine Notecka Primeval Forest. On the edge of the wetland (close to the forest), individual farms/buildings of Rzecin village are located, but the anthropogenic pressure exerted on the wetland ecosystem is relatively small. In the middle of the peatland there is a 70-cm thick floating carpet of peat-substrate overgrown mostly by moss. The vegetation is dominated by the following plant species: *Sphagnum* sp., *Dicranum* sp., *Carex* sp., *Phragmites communis* Trin., *Typha latifolia* L., *Oxycoccus palustris* Pers. *Drosera rotundifolia* L., *Potentilla palustris* L., *Ranunculus acris*, *Menyanthes trifoliata* L. [52]. The soil substrate is a Limnic Hemic Floatic Ombric Rheic Histosol (Epidystric), according to FAO 2006 classification. The average annual air temperature and the sum of precipitation are 8.5°C and 526 mm, respectively.

### Experimental Setup

Nighttime CO<sub>2</sub> fluxes were measured once a month, from July 2008 to the end of May 2009, by means of the closed dynamic chamber system. During each campaign, the measurements started late in the evening (close to sunset)



Fig. 1. Location of the investigated area of Rzecin wetland.

and continued until sunrise the following day. Daytime chamber measurements were carried out each year since 2008, starting in January/February and finishing in November/December. Daytime chamber campaigns were organized every 2-4 weeks and were carried out from before sunrise until late afternoon. In this study, only several daytime campaigns, conducted within the same period as nighttime chamber measurements, were taken into consideration for analyses.

Four different microsite types were established in 2007. The first microsite (S1) is dominated by *Caricetum elatae* plant communities, the second (S2) by *Calamagrostietum neglectae*, the third (S3) by *Menyantho-Sphagnetum teretis*, and the fourth (S4) by *Sphagno apiculati-Caricetum rostratae* [52]. Each microsite consists of three plots. Permanent collars made from PVC (75 cm × 75 cm) were installed in 2007 on each measurement plot. The insertion depth of the collar was about 20 cm. Elevated boardwalks were constructed on each microsite to prevent the disturbance of plant cover and peat during the measurements.

Soil temperature was measured on each microsite during chamber campaigns at the depths of 2, 5, and 10 cm with the sampling frequency of 5 seconds (T-109, Campbell Sci., USA). Soil thermometers were installed close to the middle plot of each microsite. Additionally, air temperature was measured with the same frequency at the height of 30 cm. Air thermometers (T-107, Campbell Sci., USA) were installed on the chamber wall in order to measure temperature, both inside and outside of the chamber. All sensors were connected to a data-logger (CR 1000, Campbell Scientific, USA) that recorded values at 5-second intervals. Moreover, air temperature at the height of 2 m and soil temperature profile at different depths (2, 4, 6, 10, 20, 30, and 50 cm) were continuously measured (together with other meteorological variables) at the eddy covariance tower during the whole year.

### CO<sub>2</sub> Flux Measurements

A dynamic chamber system (a non-steady-state through-flow chamber system according to [10]) was applied to measure nighttime and daytime CO<sub>2</sub> fluxes. The chamber (77 cm × 77 cm × 50 cm) was made from white PVC with wall thickness of 3 mm and volume of 0.3 m<sup>3</sup>. The dark chamber system applied was originally proposed and devised by Drösler [12]. The chamber was equipped with two fans (Sunon, MagLev, Taiwan), with flow of about 1 m·s<sup>-1</sup>, in order to mix the air during measurements. Also, two thermometers (T-107, Campbell Scientific, USA) were installed in order to measure air temperature inside and outside the chamber. Pressure changes during measurements were minimized by a vent tube (Ø6 mm and 40 cm long) that was inserted downward into one of the chamber walls. During measurements, the chamber was put on the preinstalled collars and fixed to them by two elastic belts connecting the top of the chamber and the base of the frame. The tightness of the chamber during measurements was assured by a rubber gasket installed on the chamber's lower edge (according to the system developed by Drösler [12]).

CO<sub>2</sub> concentration changes were measured by means of a CO<sub>2</sub> infrared gas analyzer (LI-820, Licor, USA) with a flow rate of 600 ml·min<sup>-1</sup>. The readings were recorded at 5-second intervals, for over 150 seconds in summer and for up to 240 seconds in winter. The data were recorded by a data logger (CR-1000, Campbell Sci., USA) installed in a portable control box. The logger was connected to a palm-top so that all measured parameters and system performance were easily checked during measurements. Additionally, in order to identify each measurement plot, the chamber was equipped with a bar code scanner. The bar code label on a metal stick was preinstalled on each plot before measurements. After each measurement, the chamber was well ventilated to make sure that the initial CO<sub>2</sub> concentration in the chamber headspace was close to ambient concentration. The ventilation process took much more time and was much more troublesome during nighttime campaigns, when the atmospheric conditions were stable.

The number of nighttime and daytime measurements of CO<sub>2</sub> fluxes varied across all microsites and was different for each campaign within the period analyzed. In total, 565 single measurements were carried out during 9 nighttime campaigns and 963 measurements were conducted in daytime conditions (21 campaigns). Detailed characteristics of the atmospheric and meteorological conditions during chamber measurements are presented in Table 1.

### CO<sub>2</sub> Flux Calculations

CO<sub>2</sub> fluxes were calculated on the basis of CO<sub>2</sub> concentration changes in the chamber headspace over time. The total chamber headspace for flux calculation was computed as the sum of the chamber volume and the volume of an individual collar. The linear approach was applied for flux calculations by fitting a linear regression function that determines the average rate of concentration changes over closure time. The collected time series were validated in terms of temporal linearity of CO<sub>2</sub> concentration. The determination coefficient ( $r^2$ ) was calculated for each series and, if  $r^2 > 0.8$ , then CO<sub>2</sub> flux rate ( $F_{CO_2}$ ) was calculated and used for modeling. The linear Münchmeyer [53] equation was applied for CO<sub>2</sub> flux calculation:

$$F_{C-CO_2} = \frac{M \cdot P \cdot V \cdot \delta v \cdot f_1}{R \cdot T \cdot t \cdot A} \quad (1)$$

...where  $F_{C-CO_2}$  is CO<sub>2</sub> flux density [ $\mu\text{g}\cdot\text{CO}_2\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ],  $M$  is molar mass [ $\text{g}\cdot\text{mol}^{-1}$ ] of CO<sub>2</sub>,  $P$  is atmospheric pressure [Pa],  $\delta v$  represents CO<sub>2</sub> concentration changes in the chamber headspace over closure time [ppm(v)/h],  $V$  is total volume of the chamber headspace and the collar [ $\text{m}^3$ ],  $R$  is gas constant [ $\text{m}^3\cdot\text{Pa}\cdot\text{K}^{-1}\cdot\text{mol}^{-1}$ ],  $T$  is air temperature in the chamber [K],  $t$  is closure time [h],  $A$  is the chamber area [ $\text{m}^2$ ], and  $f_1$  is the factor used for calculation of C atoms in CO<sub>2</sub> molecule (12 g/44 g).

### Goodness-of-Fit Analyses

Ecosystem respiration was empirically modeled for each microsite, and separately for each of the three plots on each microsite, on the basis of the first-order exponential Lloyd and Taylor [54] equation. By using the measured CO<sub>2</sub> fluxes and temperatures of air (30 cm) and peat at the depths of 2, 5, and 10 cm, the exponential relationship between both parameters was identified and statistically analyzed (on the basis of residuals) in order to select for modeling those parameters of the exponential function that best fit the measured data set and propagate the smallest error. Several goodness-of-fit criteria were taken into consideration and calculated on the basis of the residuals of the fitted  $R_{eco}$  exponential function: mean absolute error (MAE), root mean square error (RMSE) and normalized root mean square error (%NRMSE). Only those parameters of the analyzed exponential function were used for seasonal  $R_{eco}$  flux modeling, which represents the relationships between  $R_{eco}$  and different soil and air temperatures with the smallest MAE, RMSE, and NRMSE, and the highest determination coefficient.

### Modeling Ecosystem Respiration ( $R_{eco}$ )

$R_{eco}$  fluxes were modeled at 30-min intervals from 1.06.2008 to 31.05.2009 in order to cover the whole 12-month period. For each microsite, the microsite specific soil and air temperatures were first modeled on the basis of the linear regression functions found between temperatures measured during chamber campaigns and automatically recorded temperatures of a climate station (distance from chamber microsites: 20 to 250 meters).

The Lloyd and Taylor [54] respiration model was parameterized on the basis of the data set from the whole measuring period, separately for each plot of all microsites, a microsite as a whole, and day and nighttime fluxes (with and without turbulence in the atmosphere). The  $u^*$  threshold of 0.15 m·s<sup>-1</sup> was applied in order to screen the campaign fluxes and separate nights with a low and well-developed turbulence in the atmosphere. Only the most significant regressions of  $R_{eco}$  and temperatures with the determination coefficient ( $r^2$ ) between 0.74 and 0.90 were considered for modeling.

The Lloyd and Taylor [54] exponential function used for modeling  $R_{eco}$  fluxes is as follows:

$$R_{eco} = R_{ref} \cdot \exp\{E_0[1/(T_{ref}-T_0)-(1/(T_{peat}-T_0))]\} \quad (2)$$

...where  $R_{eco}$  is the ecosystem respiration [ $\text{mg}\cdot\text{CO}_2\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ],  $T_{peat}$  is peat temperature [K] at 5-cm depth (measured at the time of CO<sub>2</sub> flux measurements),  $R_{ref}$  is peat respiration [ $\text{mg}\cdot\text{CO}_2\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ ] at the reference temperature, and  $T_{ref}$  of 283.15 K (10.0°C). Parameter  $E_0$  is activation energy [K] and depicts the temperature sensitivity of respiration processes. Parameter  $T_0$  is the minimum temperature at which respiration reaches zero and equals 227.13 K (-45.6°C) [54].

Table 1. Description of the atmospheric and meteorological conditions of daytime and nighttime chamber campaigns and average  $R_{eco}$  fluxes measured on all sites in period July 2008-May 2009.

Months	Dates of chamber campaigns (YY-MM-DD)			$T_{air}$ avg	$u^*$	$WS$	$N_{day}$	$N_{night}$	F(CO <sub>2</sub> )_avg campaign			
	Night	Day		°C	m·s <sup>-1</sup>	m·s <sup>-1</sup>			μmol·m <sup>-2</sup> ·s <sup>-1</sup>			
	S1-S4	S1-S2	S3-S4				963	565	S1	S2	S3	S4
July			2008-07-02	24.5	0.32	1.6	62				5.2	8.6
			2008-07-03	28.3	0.36	2.5	64		12.0	7.6		
			2008-07-15	19.6	0.33	3.3	55		7.4	4.7		
			2008-07-16	21.0	0.29	2.8	43				3.0	7.0
		08-07-17/18		10.7	0.01	0.4		63	10.1	5.2	4.7	5.8
			2008-07-29	25.0	0.28	1.9	60				5.3	8.1
			2008-07-30	23.7	0.24	1.8	53		11.5	6.7		
August	08-08-07/08			21.6	0.16	2.1		84	12.1	2.7	5.6	3.0
			2008-08-19	25.1	0.28	2.7	49				3.7	4.7
		2008-08-21		20.3	0.25	2.5	63		6.3	3.3		
September	08-09-09/10			7.9	0.01	0.2		81	6.7	1.9	3.1	4.4
		2008-09-16	2008-09-16	9.0	0.33	2.7	39		3.1	2.1	1.5	2.2
October	08-10-01/02			9.5	0.34	3.4		81	2.8	0.9	1.7	1.9
			2008-10-09	10.1	0.18	1.4	55				0.8	0.9
		2008-10-16		13.9	0.38	3.8	30		1.6	1.1		
		2008-10-20		12.4	0.23	2.3	26		1.3	0.7		
			2008-10-21	17.8	0.36	3.3	66				0.9	1.1
November	08-11-04/05			10.1	0.15	1.6		49	1.4	0.2	1.0	1.2
December			2008-12-15	1.7	0.27	3.6	27				0.1	0.1
		2008-12-16		1.1	0.09	1.4	30		0.2	0.1		
		08-12-21/22		5.7	0.37	4.1		40	0.5	0.2	0.3	0.3
January	<i>Chamber measurements were not conducted</i>											
February		2009-02-19	2009-02-19	-2.3	0.17	1.9	38		0.0	0.0	0.0	0.0
March	09-03-04/05			6.3	0.31	4.1		36	0.5	0.9	0.4	0.5
		2009-03-18	2009-03-18	5.4	0.58	5.1	35		0.3	0.1	0.2	0.3
April			2009-04-01	11.7	0.21	1.2	51				1.0	1.4
		2009-04-02		7.0	0.27	3.2	38		1.0	0.3		
	09-04-06/07			4.9	0.01	0.3		60	1.7	6.9	1.3	2.2
			2009-04-16	14.4	-	-	41				1.6	1.9
		2009-04-21		12.3	0.30	2.6	38		2.4	1.6		
May	09-05-04/05			2.0	0.01	0.5		71	3.9	2.9	3.1	4.0

## Results

The regression analyses of the measured  $R_{eco}$  fluxes and different temperatures allow us to select the model that fits most appropriately the analyzed set of data and propagates

the smallest error. The analyses conducted for each plot individually and for the whole period indicated a smaller error than the analyses carried out for the whole microsite, where all CO<sub>2</sub> fluxes measured on all three plots were considered as one set of data and were correlated with temperatures.

These differences, however, were higher for nighttime regressions and not significantly different for daytime regressions. Daily measured  $R_{eco}$  fluxes correlate best for the whole microsites with peat temperature at 5-cm depth, while nighttime  $R_{eco}$  fluxes correlate best with peat temperature at 10-cm depth (Fig. 2). The determination coefficient ( $r^2$ ) for the selected models was in most cases higher than 0.8. The normalized root mean square error (NRMSE) was also the smallest in the examples mentioned above, having significantly smaller values for nighttime regression models with peat temperature at 10-cm depth, than for daytime regression models. The differences were statistically significant ( $p < 0.05$ ).

Individual specific behavior of respiration processes between the microsites are reflected by different levels of activation energy ( $E_o$ ) and respiration at the reference temperature of 10°C. Reference ecosystem respiration normalized at 10°C, varied between microsites, showing the highest values for S1 – *Carrex* dominated microsite (Fig. 3).  $R_{ref}$  at 10°C for S1 microsite reached  $2.5 \pm 0.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , depending on daytime or nighttime respiration, while for the other microsites it varied between  $1.3\text{--}1.7 \pm 0.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  when it was calculated for each plot separately. If  $R_{ref}$  is estimated for a data set specific for the whole microsite, then it seems to be slightly higher, but not significantly different from these estimated for the plot-specific data set. The only exception is S4 microsite, where these differences are significant ( $p < 0.05$ ). In this case  $R_{ref}$  is higher, at about 0.38 and  $0.84 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for day and nighttime regressions, respectively, when they are estimated for the whole set of data. However, there are not significant differences between  $R_{ref}$  values between day and nighttime measurements if they are calculated on the basis of the whole set of data for all campaigns, although  $R_{ref}$  for S2 and S3 microsites seems to be lower than for S1 and S4. Due to these differences in estimation of the model parameters for different data sets and different approaches, the result of modeling can be biased, as it depends on the estimation strategy of the model parameters.

The differences in values of activation energy ( $E_o$ ) of respiration processes, found on the basis of the analyses of Lloyed and Taylor [54], regressions for day and nighttime  $\text{CO}_2$  fluxes are much more significant ( $p < 0.001$ ).  $E_o$  for daytime regressions at the reference temperature of 10°C is between 330–430 K depending on the microsite, while  $E_o$  for nighttime conditions is much higher for each microsite and plots of a microsite and reaches from 430 to 730 K, depending on the microsite (Fig. 3). However, the difference between these parameters estimated on the basis of the microsite- or plot-specific data set is very characteristic, and is the most pronounced for S4 microsite.

The differences between the microsite-specific, as well as between day- and night-specific regressions of the measured  $R_{eco}$  fluxes versus temperatures (for the selected models) are presented in Fig. 4. The regressions were developed in this case for the whole site-specific set of the measured data (for all plots of the microsite altogether). As stated above, the activation energy ( $E_o$ ) at the reference tempera-

ture of 10°C for each microsite is much higher for nighttime regressions. However, the  $R_{ref}$  values for S1 and S4 microsites were similar or there were no significant differences between day and nighttime regressions. On the contrary, the  $R_{ref}$  estimated for daytime regressions for S2 was higher than for nighttime, while for S3 it was in reverse.

This means that there is no clear answer how the modeled nighttime  $\text{CO}_2$  fluxes can differ from the modeled daytime fluxes, as in the modeling process both  $R_{ref}$  and  $E_o$  parameters are considered. However, it can be hypothesized that, for the same temperature-dependent model,  $R_{eco}$  fluxes can be higher in nighttime conditions and at temperatures above 10°C (due to exponential fit and higher  $E_o$  parameter).

### Estimation of Differences between Daytime and Nighttime Ecosystem Respiration

In order to estimate the differences in  $R_{eco}$  fluxes measured in day and night conditions, the data from 9 nighttime and 21 daytime chamber campaigns were used (Table 1). We compared only the reference respiration ( $R_{ref}$ ) and activation energy ( $E_o$ ), calculated on the basis of the Lloyed and Taylor [54] model, for each plot-specific data series and for the whole measuring period. These parameters were calculated separately for regressions of  $R_{eco}$  and peat temperatures measured at 5 and 10 cm (used as regressor variables) in day- and nighttime conditions. Our study is limited because we did not measure  $R_{eco}$  fluxes over the whole 24-hour period during the day, but there were sometimes one- or two-week intervals between daytime and nighttime chamber campaigns. Hence, the measurements were conducted often at different temperature and hydrological conditions, which certainly had some influence on the analyses. However, considering the differences in daytime and nighttime peat temperatures, it can be assumed that the shifts of time, when the chamber campaigns were conducted, should have no significant effect on the analyses carried out for such a long measuring period.

Reference respiration seems to be about 33% higher for nighttime than for daytime periods, when the  $R_{ref}$  is calculated for day and nighttime conditions on the basis of peat temperatures measured at 5-cm depth (Fig. 5). The differences between day and nighttime  $R_{ref}$  values are statistically significant ( $p < 0.001$ ). On the other hand, the  $R_{ref}$  parameter is about 13% lower in nighttime conditions when the  $R_{ref}$  is calculated for day and nighttime conditions on the basis of peat temperatures measured at 10-cm depth. The differences between these parameters are also statistically significant ( $p < 0.001$ ). Following the results of the goodness-of-fit analyses of the regressions between the measured  $R_{eco}$  fluxes and different temperatures (Fig. 2), we compared in the next step the  $R_{ref}$  parameters found for daytime conditions for peat temperatures at 5-cm depth and for nighttime conditions for peat temperatures at 10-cm depth. The result is that the  $R_{ref}$  calculated for daytime periods is about 3% higher than for nighttime conditions.

The differences between daytime and nighttime  $E_o$  parameters are more pronounced and more significant. Irrespective of the chosen regressor variable, the  $E_o$  parameter is always higher in nighttime conditions. The  $E_o$  is about 37% and 16% higher when peat temperature values at 5-cm and 10-cm depths are used respectively as the

regressor variables for both day and nighttime conditions. On the other hand, this difference is even much bigger if we compare the  $E_o$  parameters calculated on the basis of the best-fitting regressor temperatures (as described above). In this case, the  $E_o$  calculated for nighttime periods is about 62% higher than for daytime conditions.

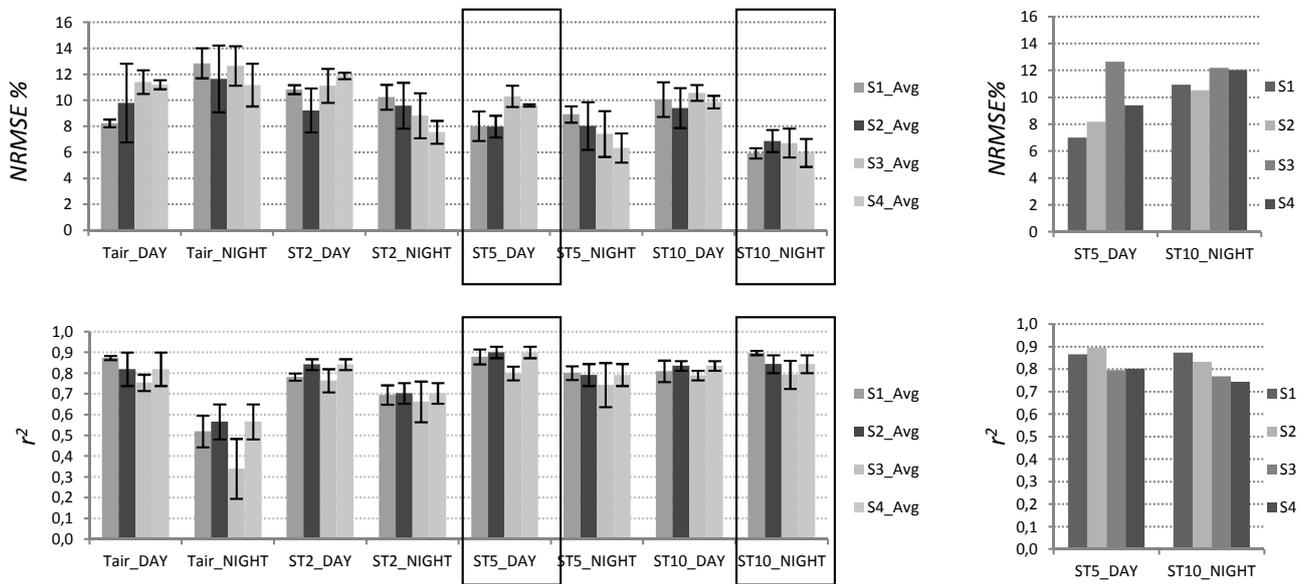


Fig. 2. Goodness-of-fit statistics of the regression analyzes for the measured  $R_{eco}$  fluxes and different air and peat temperatures. S1\_avg-S4\_avg represent the average value of a given parameter for the microsites, these are the average values of the statistics calculated separately for each plot of the microsite, while S1-S4 – statistics are calculated for the microsites as a whole. Tair – air temperature at 30 cm height, ST2, ST5, ST10 – peat temperatures at 2, 5, and 10-cm depth, respectively.

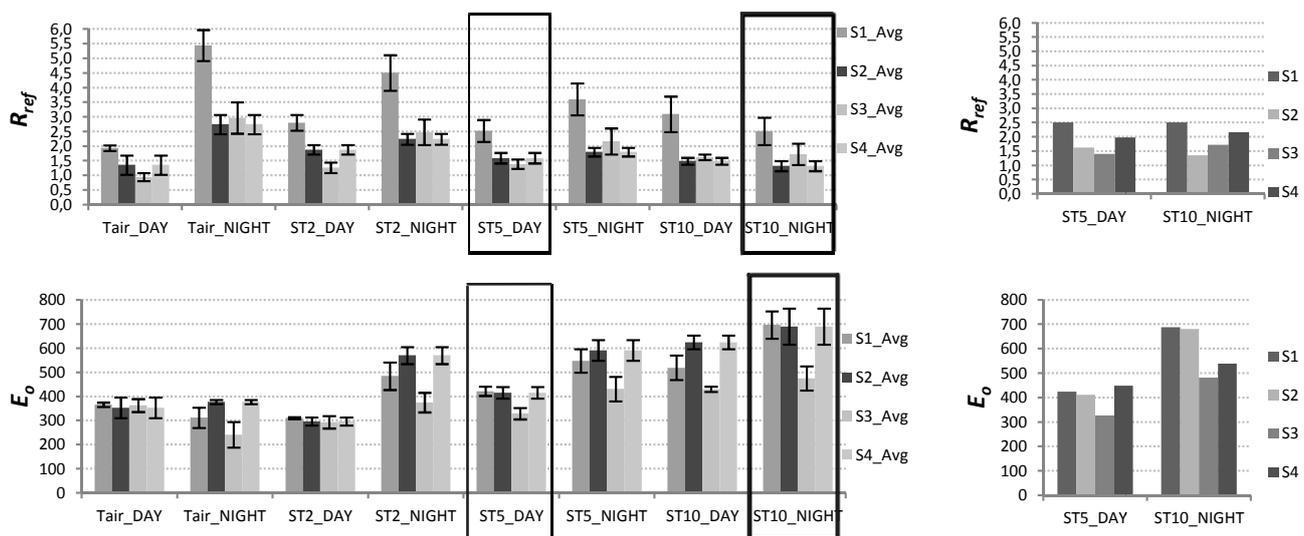


Fig. 3. Reference ecosystem respiration ( $R_{ref}$ ) normalized at 10°C as well as activation energy ( $E_o$ ) of the respiration processes taken from the regressions analyzes of the dependences of the measured  $R_{eco}$  fluxes with different temperatures on the basis of Lloyed and Taylor [53] exponential model.  $R_{ref}$  is given in  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and  $E_o$  in K. In the left part of the graph there are average values of  $R_{ref}$  and  $E_o$  with standard deviations for regressions developed for each plot of the microsite separately. On the right, there are  $R_{ref}$  and  $E_o$  parameters estimated on the basis of the whole microsite specific data.

S1\_avg-S4\_avg represent the average value of a given parameter for microsites (they were calculated separately for each plot of the microsite), while S1-S4 – represent the same parameters as above, but calculated for microsites as a whole. Tair – air temperature at 30 cm height, ST2, ST5, ST10 – peat temperatures at 2, 5, and 10-cm depth, respectively.

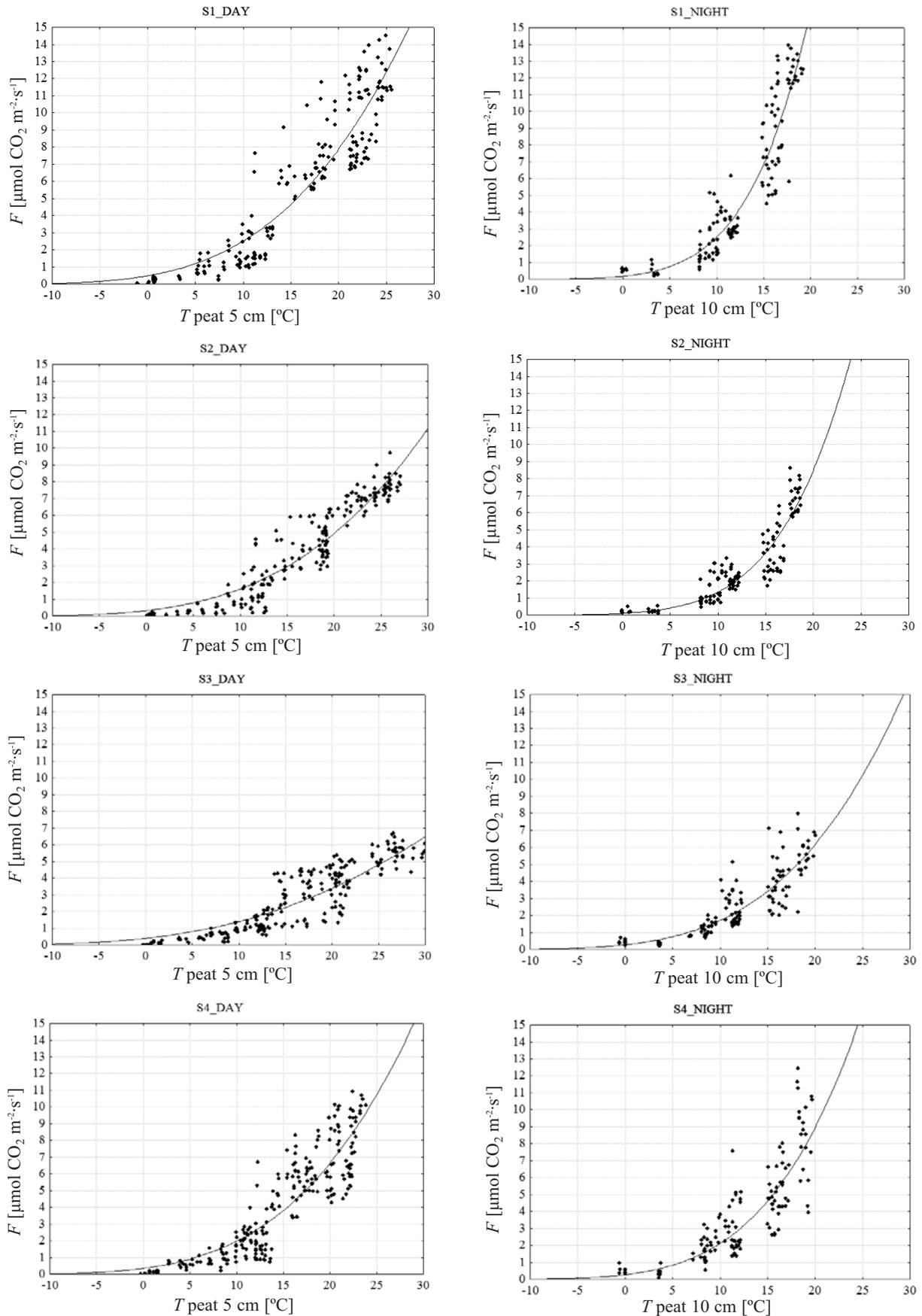


Fig. 4. The best-fitting relationships of the measured ecosystem respiration ( $R_{eco}$ ) with selected temperatures: Lloyd and Taylor [53] exponential function fits in with the individual data set for each site and for the whole measuring period from 01.06.2008 to 31.05.2009. For nighttime regressions,  $R_{eco}$  was correlated with peat temperature at 10-cm depth, while for daytime conditions  $R_{eco}$  was best correlated with peat temperature at 5 cm (see Figs. 2 and 3).

The differences in modeling parameters estimated for day and nighttime conditions and for different regressor variables should be taken into account in the modeling process. In this case, the transparent and objective procedures should be applied in estimation of these parameters in order to minimize biases in assessment of the modeling variables.

### Modeling Ecosystem Respiration ( $R_{eco}$ ) for Daytime and Nighttime Conditions (with Low and Well-Developed Turbulence)

$R_{eco}$  was modeled on the basis of the best fitted models parameterized for each plot of the four analyzed microsites, separately for the measured daytime and nighttime  $CO_2$  fluxes. The nighttime data were screened to separate campaigns conducted in turbulent and stable atmospheric conditions (the  $u^*$  of  $0.15 \text{ m}\cdot\text{s}^{-1}$  was used as a threshold of stability criteria). The  $R_{eco}$  model was parameterized additionally for nighttime fluxes measured in turbulent and stable atmospheric conditions. As mentioned above, nighttime  $R_{eco}$  was modeled on the basis of peat temperature at 10-cm depth (whatever conditions were considered), while daytime  $R_{eco}$  was modeled on the basis of peat temperature at 5-cm depth. The parameters of the best fitted regressions as well as goodness-of-fit statistics are shown in Table 2.

The offset of regression functions expressed by  $R_{ref}$  parameters is higher in nighttime conditions (when all measurements are considered) for the S1 and S3 microsites, smaller for S2 and the same for the S4 microsite. However, the rate of  $R_{ref}$  is in each case significantly higher for regressions of nighttime measurements carried out during low turbulence in the atmosphere. When the fluxes measured at

a low turbulence are excluded from nighttime set of data, then, the  $R_{ref}$  parameter seems to be significantly smaller than for daytime regressions. What is especially noticeable,  $E_o$  parameter, which characterizes the nonlinear dependence of  $R_{eco}$  fluxes on peat temperature, was always much higher for nighttime regressions, especially when the fluxes measured in low turbulence conditions were excluded from the analyzed set of data. The  $E_o$  parameter is much smaller for regressions developed for nighttime conditions with a low turbulence in the atmosphere (in relation to the daytime regressions). In these cases,  $E_o$  parameters are half of the value of the parameters estimated for nights with turbulent conditions.

The selected models seem to be the best fitted to the measured fluxes for nighttime regressions, where the fluxes measured at a low turbulence in the atmosphere were excluded from the analyzed set of data. The determination coefficient ( $r^2$ ) reaches 0.85-0.98 in these cases (depending on the site), which is much higher than for nights with low turbulence in the atmosphere ( $r^2$  is between 0.48-0.73). The values of NRMSE are 2-3 times smaller for the model developed for nights with turbulent atmospheric conditions and they are also smaller in comparison to the daytime model. For daytime regressions, the determination coefficient is between 0.81-0.90.

The cumulated  $R_{eco}$  fluxes expressed in  $\text{g CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$  for all microsites and different modeling approaches (day/night, night turbulent/stable) for the whole 12-month period, between 01.06.2008 and 31.05.2009, are presented in Table 2. The highest cumulated  $R_{eco}$  was modeled for the S1 microsite dominated by *Caricetum elatae* plant communities, which in fact can be characterized by the highest amount of plant biomass and lowest groundwater depth

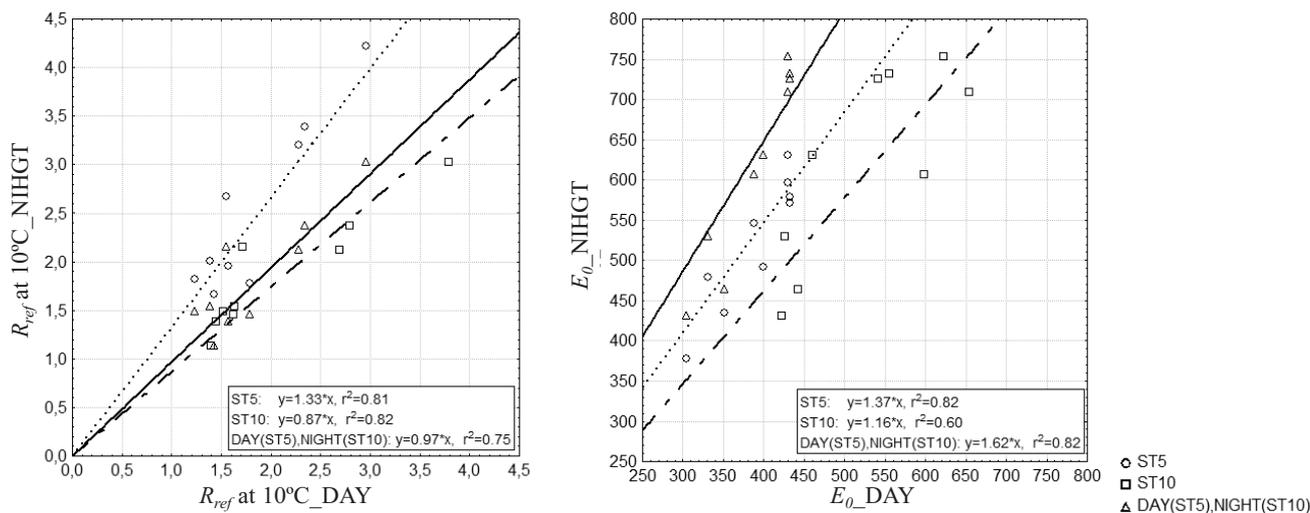


Fig. 5. Regression analyses of the relationships of the calculated plot-specific daytime and nighttime reference respiration ( $R_{ref}$ ) and activation energy ( $E_o$ ). These parameters were calculated on the basis of the Lloyed and Taylor [53] model, and for the whole measuring period from 01.06.2008 to 31.05.2009.  $R_{ref}$  values are expressed in  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , while  $E_o$  in K.

ST5 – peat temperature at 5-cm depth was used as regressor variable to estimate  $R_{ref}$  for day and nighttime data series.

ST10 – peat temperature at 10-cm depth was used as regressor variable to estimate  $R_{ref}$  for day and nighttime data series. DAY(ST5), NIGHT(ST10) – peat temperatures at 5 and 10-cm depths were used as regressor variables to estimate  $R_{ref}$  for day and nighttime data series, respectively.

Table 2. Model parameters: reference respiration at 10°C ( $R_{ref}$ )\* and activation energy ( $E_o$ )\*\*, goodness-of-fit statistics (RMSE, %NRMSE)\*\*\*, coefficient of determination ( $r^2$ ) of the best fitted regression functions between  $R_{eco}$  fluxes and peat temperatures at 5-cm depth for daytime and 10-cm depth for nighttime regressions, the modeled cumulated  $R_{eco}$  (for period 01.06.2008-31.05.2009), grouped into four microsite types by daytime/nighttime conditions, as well as by different turbulence status (for nights).

		DAY		NIGHT		NIGHT_ ( $u^*>0.15$ )		NIGHT_ ( $u^*<0.15$ )	
S1	$R_{ref}$	2.2	±0.16	2.5	±0.47	2.1	±0.16	2.9	±0.64
	$E_o$	413.1	±34.55	696.6	±56.66	766.6	±20.43	622.4	±84.84
	RMSE	1.0	±0.14	0.8	±0.08	0.7	±0.09	1.2	±0.07
	%NRMSE	7.5	±0.33	5.9	±0.39	5.7	±0.47	11.0	±0.11
	$r^2$	0.89	±0.01	0.90	±0.01	0.98	±0.01	0.73	±0.02
	$n$	288		141		71		70	
	$R_{eco\ cumulated}$ g CO <sub>2</sub> -C·m <sup>-2</sup> ·a <sup>-1</sup>	1225	±146	1414	±154	1317	±67	1485	±208
S2	$R_{ref}$	1.6	±0.18	1.3	±0.17	1.4	±0.11	1.8	±0.14
	$E_o$	415.8	±23.91	690.2	±75.07	709.8	±43.03	418.1	±41.97
	RMSE	0.6	±0.09	0.5	±0.06	0.5	±0.10	0.9	±0.05
	%NRMSE	8.0	±0.84	6.9	±0.85	6.1	±0.91	19.0	±2.42
	$r^2$	0.90	±0.03	0.84	±0.04	0.98	±0.02	0.48	±0.09
	$n$	261		149		79		70	
	$R_{eco\ cumulated}$ g CO <sub>2</sub> -C·m <sup>-2</sup> ·a <sup>-1</sup>	811	±66	733	±51	783	±59	736	±52
S3	$R_{ref}$	1.4	±0.24	1.7	±0.37	1.3	±0.18	2.2	±0.41
	$E_o$	368.2	±48.02	474.9	±50.27	591.7	±14.04	317.1	±36.17
	RMSE	0.6	±0.02	0.5	±0.12	0.6	±0.06	0.9	±0.11
	%NRMSE	9.9	±0.15	6.7	±1.11	8.6	±0.12	21.6	±3.98
	$r^2$	0.82	±0.01	0.79	±0.07	0.93	±0.01	0.49	±0.15
	$n$	282		137		71		66	
	$R_{eco\ cumulated}$ g CO <sub>2</sub> -C·m <sup>-2</sup> ·a <sup>-1</sup>	695	±84	845	±140	759	±98	913	±177
S4	$R_{ref}$	2.1	±0.32	2.1	±0.35	1.7	±0.23	2.9	±0.60
	$E_o$	476.1	±55.42	561.0	±39.14	661.6	±20.65	322.7	±62.34
	RMSE	1.0	±0.03	0.6	±0.10	0.9	±0.05	0.9	±0.05
	%NRMSE	9.5	±0.17	6.0	±1.07	7.7	±0.26	15.6	±1.82
	$r^2$	0.81	±0.01	0.82	±0.05	0.85	±0.05	0.58	±0.12
	$n$	284		140		73		67	
	$R_{eco\ cumulated}$ g CO <sub>2</sub> -C·m <sup>-2</sup> ·a <sup>-1</sup>	1010	±148	997	±171	911	±111	1129	±206

\*expressed in  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , \*\* expressed in K, \*\*\* related to values expressed in  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$

(not considered in this paper). The cumulated  $R_{eco}$  flux was  $1225\pm146$  gCO<sub>2</sub>-C·m<sup>-2</sup>·a<sup>-1</sup> when the daytime dependent model was applied. A slightly smaller cumulated  $R_{eco}$  was estimated for the S4 microsite (*Sphagno apiculati-Caricetum rostratae* plant communities), where the yearly value reaches  $1010\pm148$  gCO<sub>2</sub>-C·m<sup>-2</sup>·a<sup>-1</sup>. For the S2

microsite (dominated by *Calamagrostietum neglectae*),  $R_{eco}$  was close to  $811\pm66$  gCO<sub>2</sub>-C·m<sup>-2</sup>·a<sup>-1</sup>, and for S3 (dominated by *Menyantho-Sphagnetum teretis*) the cumulated  $R_{eco}$  was the smallest, at the rate of  $695\pm84$  gCO<sub>2</sub>-C·m<sup>-2</sup>·a<sup>-1</sup>. In all cases, however, the cumulated values of  $R_{eco}$  were estimated on the basis of the daytime-dependent regressions.

However, when the nighttime dependent model of  $R_{eco}$  is applied (all nights were included), then the cumulated  $R_{eco}$  seems to be significantly higher in comparison to the estimations carried out for daytime regressions for the S1 ( $1414 \pm 154 \text{ gCO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ) and S3 ( $845 \pm 140 \text{ gCO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ) microsites, smaller for S2 ( $733 \pm 51 \text{ gCO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ) and not significantly different for S4 ( $997 \pm 171 \text{ gCO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ). These results indicate that our  $R_{eco}$  model was extremely sensitive to  $R_{ref}$  parameters. When the  $R_{ref}$  was higher in day or nighttime conditions, the cumulative modeled  $R_{eco}$  was also higher and vice versa. What is more, the  $E_o$  parameter seems to be of much smaller importance within the range of peat temperatures used in the modeling, although this parameter was significantly higher for all microsites for nighttime-dependent regressions.

When  $\text{CO}_2$  fluxes measured during nights with low turbulence in the atmosphere are excluded from the analyzed set of nighttime data, then the cumulative modeled  $R_{eco}$  is much smaller for the S1, S3, and S4 microsites than for the nighttime-dependent  $R_{eco}$  model developed on the basis of

all nighttime data. The only exception is the S2 microsite, where the modeled  $R_{eco}$  is higher, when the low turbulence campaigns are excluded (this is related to a higher value of  $R_{ref}$  parameter). However, when the nighttime dependent  $R_{eco}$  model is parameterized on the basis of  $\text{CO}_2$  fluxes measured in stable atmospheric conditions, then the cumulated  $R_{eco}$  is higher for most of the microsites in comparison to the values estimated on the basis of the daytime dependent model.

In order to assess the differences between the modeled  $R_{eco}$  fluxes calculated for day and nighttime periods and for different atmospheric conditions, plot-specific (12 plots) cumulated  $R_{eco}$  cumulative fluxes were compared for the site as a whole and the results of this comparison are presented in Figs. 6A-E, respectively. The cumulative sums of nighttime  $R_{eco}$  cumulative, calculated by using all measurements, are about 15% higher when compared to daytime  $R_{eco}$  cumulative (Fig. 6A). These differences are even higher if nighttime cumulative sums of  $R_{eco}$  are restricted only to nights with stable atmospheric conditions ( $u^* < 0.15$ ) and, in this case, night-

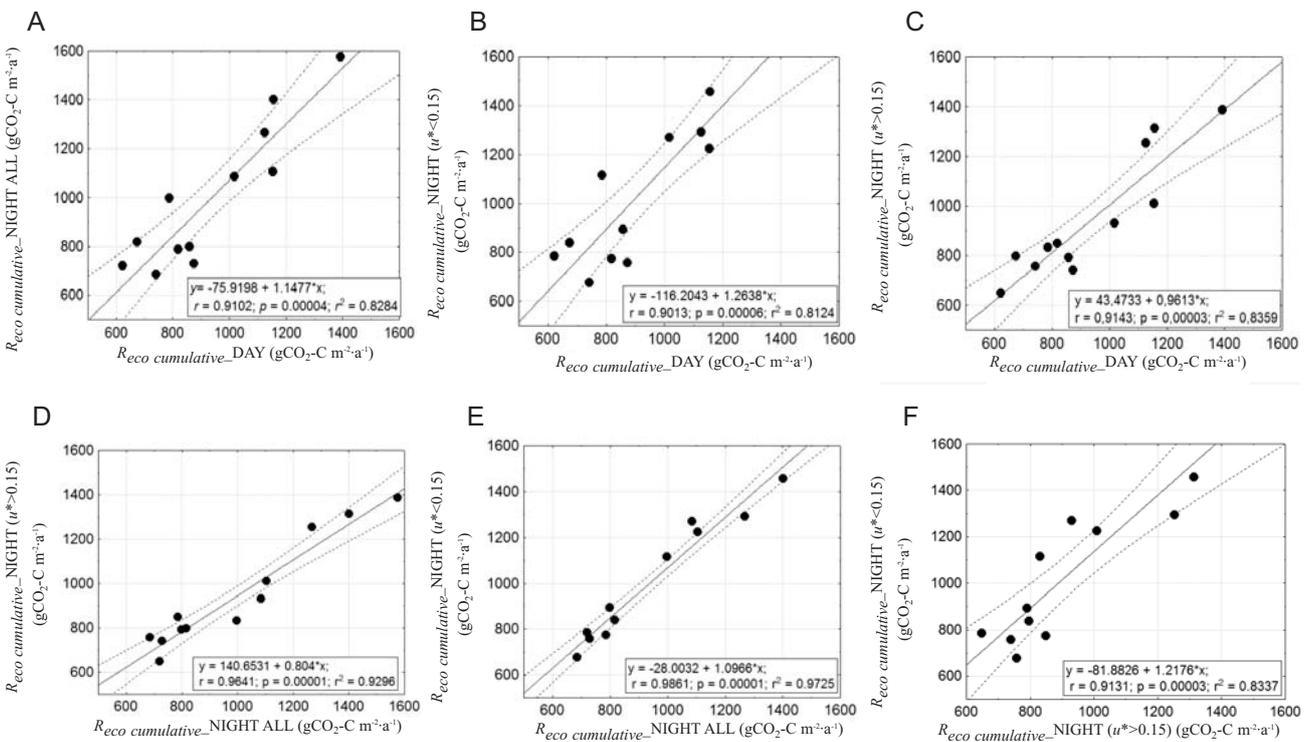


Fig. 6. Regression analyses of the relationship between the modeled plot-specific  $R_{eco}$  fluxes cumulated for the whole 12-month period (dash lines refer to 95% confidence intervals):

- A)  $R_{eco}$  cumulated for the model parameterized on the basis of daily regressions, versus  $R_{eco}$  cumulated for the model parameterized on the basis of all nighttime regressions.
- B) As above, but only nights with stable atmospheric conditions ( $u^* < 0.15$ ) were used in parameterization of the nighttime  $R_{eco}$  model,
- C) As above, but only nights with turbulent atmospheric conditions ( $u^* > 0.15$ ) were used in parameterization of the nighttime  $R_{eco}$  model.
- D)  $R_{eco}$  cumulated for the model parameterized on the basis of all nighttime regressions, versus  $R_{eco}$  cumulated for the model parameterized only on the basis of nights with turbulent atmospheric conditions ( $u^* > 0.15$ ).
- E)  $R_{eco}$  cumulated for the model parameterized on the basis of all nighttime regressions versus  $R_{eco}$  cumulated for the model parameterized only on the basis of nights with stable atmospheric conditions ( $u^* < 0.15$ ).
- F)  $R_{eco}$  cumulated for the model parameterized on the basis of regressions of nights with turbulent conditions ( $u^* > 0.15$ ), versus  $R_{eco}$  cumulated for the model parameterized only on the basis of nights with stable atmospheric conditions ( $u^* < 0.15$ ).

time  $R_{eco\ cumulative}$  values are 26% higher in comparison to daily values (Fig. 6B). Whereas there is nearly no difference between day and nighttime cumulative  $R_{eco}$  fluxes, if the nighttime regressions are restricted only to nights with turbulent ( $u^* > 0.15$ ) atmospheric conditions (Fig. 6C). What is more, the overestimation of the cumulative sums of nighttime  $R_{eco\ cumulative}$ , calculated by using all measurements, compared to nighttime  $R_{eco\ cumulative}$ , calculated on the basis of regressions restricted only to nights with well-developed turbulence conditions, is about 20% (Fig. 6D). On the other hand, the  $R_{eco\ cumulative}$ , calculated using all measurements, is underestimated by about 10%, if these values are compared to nighttime  $R_{eco\ cumulative}$  calculated on the basis of regressions restricted to stable atmospheric conditions (Fig. 6E). Nighttime  $R_{eco\ cumulative}$  restricted to nights with well developed turbulence is underestimated by 32% in relation to nighttime  $R_{eco\ cumulative}$  restricted to nights with stable atmospheric conditions. All the differences described above are statistically very significant ( $p < 0.001$ ).

### Discussion of the Results

In our paper, nighttime  $R_{eco}$  fluxes were compared to daytime  $R_{eco}$  fluxes, measured by means of the closed chamber technique in a natural wetland in Poland. This is most probably a unique comparative study of daytime and nighttime  $CO_2$  fluxes measured by chambers, as it is difficult to find any paper focusing on such studies in literature. There are only a few papers focusing on chamber measurements of nighttime  $CO_2$  fluxes on wetlands [20, 21, 55], but the results of such studies are difficult to compare.

Nighttime chamber measurements, carried out in calm and stable conditions, can be seriously biased [19-21, 56]. Schneider et al. [21] compared chamber fluxes measured during stable and turbulent nighttime conditions. They indicated that  $R_{eco}$  fluxes measured at nights under low turbulence conditions were biased and usually overestimated when compared to the  $CO_2$  fluxes measured during nights with a well developed turbulence in the atmosphere. Our results are in agreement with the conclusions of Schneider et al. [21]. We proved on the basis of cumulative modeled  $R_{eco}$  fluxes that cumulative sums of nighttime  $R_{eco}$ , calculated by using measurements restricted to stable atmospheric conditions are overestimated by 22% in comparison to the cumulative modeled  $R_{eco}$ , restricted to the nights with turbulent atmospheric conditions. Moreover, they are higher by about 10% when compared to sums of cumulative  $R_{eco}$  calculated by using all measured fluxes. The rate of this overestimation, found by Schneider et al. [21], was slightly higher and varied from 8% to 15.3%, depending on the microsite type, if the linear flux calculation method was used, and varied from 18% to 31% if the nonlinear flux calculation method was applied. In our study the  $CO_2$  fluxes were calculated on the basis of a linear approach, thus our results are in the range of the rate estimated by Schneider et al. [21].

However, what is more important, we found significant differences between cumulative  $R_{eco}$  fluxes, which were modeled for daytime and nighttime periods, by using models parameterized independently for day and nighttime data series. The daytime fluxes were lower by about 15% than nighttime fluxes if all nighttime data were used for modeling. This difference was much higher (26%) if nighttime fluxes were restricted only to nights with stable atmospheric conditions and can be even higher if the nonlinear flux calculation method would be applied, as was proved by Schneider et al. [21] and Kutzbach et al. [57]. The range of daytime flux underestimation is in the rate of possible underestimation of the leaf respiration which is reported to be partly inhibited in the light conditions [36-41]. The inhibition degree of autotrophic respiration can differ from 16% to even 77%, depending mostly on the plant species, age of leaves and N content in plants [36-41]. However, it seems that this effect has no impact on the fluxes measured in our wetland, as there is nearly no difference between daytime and nighttime cumulative modeled  $R_{eco}$ , if the nighttime  $R_{eco}$  model is restricted to nights with turbulent atmospheric conditions. In this case, the daytime cumulative  $R_{eco}$  is even 3% higher than nighttime cumulative  $R_{eco}$ . Hence, the assessed differences between the day and nighttime  $R_{eco}$  can be the effect of the disturbance of the stratified air, typical for low-turbulence atmospheric conditions, caused by the deployment of the closed chambers. This effect was also indicated by Schneider et al. [21] and is related to the disturbance of diffusion which is the main gas exchange process in the soil and the near-surface atmosphere during stable atmospheric conditions. The deployment of a chamber with a fan inside the chamber headspace leads to an enhanced gas exchange rate due to disturbance of the  $CO_2$  gradient in the near-surface atmosphere and increase measured gas fluxes [58-59].

All the differences described above are significant and should be considered in any seasonal  $R_{eco}$  model, as they can greatly influence the whole carbon balance of the site. This statement shall be considered especially for the sites where the automatic transparent chamber systems operating 24-hours per day are the only source of information about the  $CO_2$  exchange rates. For these sites, the daily  $R_{eco}$  rates are estimated on the basis of the nighttime  $R_{eco}$  regression models and consequently the daytime  $R_{eco}$  and  $GPP$  can be seriously overestimated. Furthermore, chamber nighttime fluxes measured during stable atmospheric conditions are sometimes used to replace the eddy covariance  $CO_2$  fluxes that are supposed to be underestimated in such conditions [15-17]. If the nighttime  $R_{eco}$  models used for modeling of daytime  $R_{eco}$  fluxes were developed for  $CO_2$  fluxes measured by chambers at all nights (both during stable and turbulent atmospheric conditions), then these models can lead again to overestimation of daytime  $R_{eco}$  and  $GPP$  fluxes.

In order to reduce biases and uncertainties in estimation of daily  $R_{eco}$  fluxes on the basis of the nighttime chamber measurements we suggest screening the measured fluxes

and restricting the nighttime  $R_{eco}$  models only to the fluxes that were measured in turbulent atmospheric conditions. In these cases, we proved that the differences between the day and nighttime fluxes are the smallest. What is more, the regressor variable used in the  $R_{eco}$  model shall be objectively chosen, separately for daytime and nighttime regressions, on the basis of goodness-of-fit analysis, as in this paper. We proved that the  $R_{eco}$  fluxes correlated best to the peat temperature at 5 cm depth for daytime measurements and to the peat temperature at 10 cm depth for nighttime regressions and these temperatures were used in modeling daytime and nighttime  $R_{eco}$  fluxes. Wrongly chosen regressor variable used in modeling can lead to significant differences in estimated values of model parameters (Fig. 5). This may have a strong effect, especially on the reference respiration at 10°C ( $R_{ref}$ ), which refers to offset of the exponential regression function in the model of Lloyd and Taylor [54]. As shown, the  $R_{ref}$  parameter can be higher or smaller for daytime and nighttime regressions, depending on the chosen regressor temperature. The activation energy of respiration processes ( $E_o$ ) was always higher for nighttime than for daytime regressions, independently on the chosen regressor variable. These differences have a significant effect on the modeled  $R_{eco}$  fluxes. Thus, we suggest estimating the model parameters separately for day and nighttime conditions and for different temperatures, and to choose for modeling the model that correlates best with the measured data series and propagate the smallest error (expressed in our case by NRMSE).

### Conclusions

Our study indicated that there are significant differences between daytime and nighttime  $R_{eco}$  fluxes if all measured nighttime fluxes are considered in the analyses. These differences are much higher when the nighttime fluxes are restricted only to nights with stable atmospheric conditions. In these cases, the nighttime sums of cumulative  $R_{eco}$  are much higher than the one estimated for daytime conditions. Whereas there is nearly no difference between daytime and nighttime sums of cumulative  $R_{eco}$  when the nighttime fluxes are restricted only to nights with turbulent atmospheric conditions. Consequently,  $R_{eco}$  models developed for nighttime data series can overestimate  $CO_2$  fluxes, when they are used to estimate daytime respiration. This may happen, for example, in the case of automatic transparent chambers operating 24 hours per day, which are used to estimate the net ecosystem exchange ( $NEE$ ). In these cases, the gross primary production ( $GPP$ ) is calculated on the basis of the measured daytime  $NEE$  and modeled  $R_{eco}$  fluxes, which in turn are calculated on the basis of nighttime regressions of  $R_{eco}$  to temperature and, finally, leading to overestimation of the calculated  $GPP$ . It has to be noted here that chamber measurements are often used to support the gap filling of the eddy covariance data series, as well as to quantify  $CO_2$  flux underestimation by eddy covariance (EC) systems in

stable atmospheric conditions. If  $R_{eco}$  models developed for calm nights on the basis of chamber measurements are applied to correct EC data, then the modeled  $R_{eco}$  fluxes can be overestimated again, leading to the overall overestimation of the cumulated ecosystem respiration and to underestimation of the net ecosystem exchange and C sequestration. In order to reduce biases and uncertainties in estimation of daily  $R_{eco}$  fluxes on the basis of the nighttime chamber measurements, the nighttime  $R_{eco}$  models should be restricted only to the fluxes that were measured in turbulent atmospheric conditions.

The biases in nighttime chamber measurements (especially when conducted during stable atmospheric conditions), as well as differences in estimated daytime and nighttime  $R_{eco}$  fluxes (if they are not considered) can have a significant effect on assessment of global carbon balances of the terrestrial ecosystems. Thus, it is necessary to better quantify the differences of  $R_{eco}$  fluxes in day and night conditions for different ecosystems, and develop more advanced  $R_{eco}$  models that would consider these differences in order to minimize biases in the estimation of global respiration and carbon balances.

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