

IN SITU MEASUREMENTS OF SEASONAL PRODUCTIVITY DYNAMICS IN TWO SPHAGNUM DOMINATED MIRES IN HUNGARY

Evelin Ramóna PÉLI^{1*}, János NAGY² & Dániel CSERHALMI³

¹MTA-SZIE Plant Ecology Research Group, Szent István University, Institute of Botany and Ecophysiology, 2103 Gödöllő, Páter K. 1. Hungary

²Szent István University, Institute of Botany and Ecophysiology, Faculty of Agricultural and Environmental Sciences, 2103 Gödöllő, Páter K. 1. Hungary

³Szent István University, Institute of Biology, Department of Botany, Faculty of Veterinarian Sciences, H-1078 Budapest, Rottenbiller 50. Hungary

*Corresponding author: Tel.: +36 06 28 522 075; fax: +36 06 28 410 804. E-mail: Peli.Evelin@mkk.szie.hu

Abstract: Climate change sensitively concerns peatlands as ecosystems which represent significant stores of soil carbon globally. Differences in the carbon balance of peatlands seem to be long-term variations of carbon accumulation that appears in climate change but also it is particularly useful to study the short-term seasonal ecological function of small mires located in the frontier zone of *Sphagnum*-dominated peat bogs in the plains of Europe. The aim of the study is to provide a seasonal overview of functional physiological mechanisms of a unique and isolated peat moss dominated area in Hungary. Net ecosystem exchange (NEE) of carbon dioxide, Normalized Difference Vegetation Index (NDVI values), chlorophyll fluorescence parameter (Fv/Fm) of dominant *Sphagnum* and vascular plant species were measured seasonally in two Hungarian *Sphagnum* dominated mires under *in situ* field conditions. NEE ranged from -1.08 to -2.89 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the spring and autumn but fell to 0.68 to -2.52 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (a negative value indicates ecosystem uptake) under higher light flux density (PPFD of 1100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) during the summer period. NDVI values showed the highest rates in summer (between 0.756-0.882) and the lowest rates were measured in spring (between 0.426-0.612) in all investigated microhabitats. The maximal photochemical activity (Fv/Fm) of the dominated species reflected the seasonal and microclimatic adaptation; showed lower values in spring and autumn (0.505-0.847) while these parameters are characterized by higher values (0.8-0.857) in all dominated species in summer. Our study shows that functional differences can also exist within relatively small mire not only seasonally but also depending on microsites or types of plant communities. These results contribute to our understanding of dynamic changes of peatlands, mire ecosystem functioning at the edge of their distribution and predict ecosystem responses to climate change, which can be potential factors both on global carbon cycle and global change.

Keywords: peat bog, net ecosystem exchange, chlorophyll fluorescence, normalized difference vegetation index

1. INTRODUCTION

Investigations of peatland and wetland ecosystems are very important as their role in the global carbon cycle is considerable and they compose a significant part of the global climate systems as the reservoirs of carbon sources (Zoltai & Martikainen, 1996; Wieder, 2001; Zhaojun et al., 2011). Peat bogs can form and store atmospheric CO₂ to significant amount of organic C, otherwise, a

degree of these processes is influenced by regional factors, namely climate, local and hydrological conditions. The two most important factors that influenced the biological and physicochemical processes of these ecosystems are water conditions (including quantities, chemistry, fluctuation and flow system of water) and ratios of species composition (mainly peat mosses) (Vitt, 2005). Below ground layers of peat moss dominated area have a critical role in the carbon scale of peat bogs

and the prevention of desiccation of above ground layers (Bu et al., 2013). Net primer production of peat bogs is significantly determined by the water availability and the repeated desiccation-rehydration cycles, therefore it is supposed that carbon storage capacity of peat bogs may be in danger with decreasing water availability of above ground areas (McNeil & Waddington 2003; Bortoluzzi et al., 2006; Bu et al., 2013). At the same time, due to the drought processes and the decrease of freshwater resources resulting from the global climate change, the present ecological function of these areas has become endangered (Zhaojun et al., 2011; Cizkova et al., 2013). As a result, they can easily become sources. These sensitive ecosystems showed a large seasonal variation in photosynthetic/respiratory activity (Syed et al., 2006) and the 'quality' of seasons - such as warmer spring, longer growing season - will result in a shift of CO₂ gas exchange, which will affect the whole carbon cycle. Nevertheless, the significance of the different mires within a certain ecosystem is largely defined by the local environmental factors that unambiguously influence their functionality (Strilesky & Humphreys, 2012). Changes of present role of our studied areas are mainly effected by local environmental factors where the most important aim is to assure natural vegetation surrounding the mires and to keep the optimal water level in order to maintain this exceptional, ancient vegetation formation in Hungary.

Although the full CO₂ exchange (source and sink) between the surface and the atmosphere of these ecosystems are significantly smaller than in grasslands (Frolking et al., 1998; Gilmanov et al., 2007), their capability to carbon accumulation is significantly higher (Gorham, 1991; Clymo et al., 1998). Large differences were reported (Heijmans et al., 2004) between understory vegetation types of boreal forests, the midday net CO₂ uptake rate in *Sphagnum* dominated vegetation were similar to rates measured in sites dominated by vascular plants. As the natural climatic and environmental circumstances (i.e. hydrological conditions) of our investigated mires are basically different from other enormous northern peatland ecosystems, it has a great importance in knowing the rates of CO₂ exchange and their roles in the ecological and climatic controls. Investigated mires are unique and special ecosystems in Hungary which represented the boundaries of the southeast spread of *Sphagnum*-dominated bogs in the plains of Europe boundary area at the edge of peatlands distribution therefore the understanding their ecological functioning is also very valuable.

Application of chamber methods for measuring spatial and temporal micro scale variability of CO₂ fluxes general in northern hemisphere peatlands (Crill, 1991; Carroll & Crill, 1997; Lafleur et al., 1997, 2001; Aurela et al., 1998; Soegaard & Nordstroem 1999; Vourlitis & Oechel 1999; Hargreaves et al., 2001; Frolking et al., 2002; Maanavilja et al., 2011; Schneider et al., 2012). As peatlands are very sensitive to environmental changes, they would be suitable to estimate the short-term effects of the global changes on natural ecosystems by measuring CO₂ gas exchange (Zhaojun et al., 2011). On the basis of daily CO₂ gas exchange measurements of northern hemisphere peatlands (Kettunen, 2000) daytime characterized by sink while nights by source function. Diurnal hydrological gradients and vegetation patterns had significant role in carbon fixation rate (Bubier et al., 1998, 1999; Frolking et al., 1998; Christensen et al., 2000). Respiratory rates are basically determined by water table stands (Silvola et al., 1996) in case of its level close to moss surfaces the daily CO₂ fluxes appeared as source function. Otherwise, temporary changes in environmental factors significantly and instantly influenced the CO₂ fluxes of peat mosses hereby considerably affected the yearly carbon budgets (Bubier et al., 1998, 1999; Griffis et al., 2000; Soegaard et al., 2000). Measurements of NDVI and Fv/Fm fluorescence parameters well accepted to measure with CO₂ gas exchange for monitoring changes in net ecosystem exchange because aboveground carbon storage well correlated with the chlorophyll content of the vegetation and aboveground plant biomass (Boelman et al., 2005; Gaalen et al., 2007).

Our aim is to present how plant communities and rates of C accumulation can vary over time by measuring physiological changes of the vegetation, which can indicate variations in climate and local circumstances changes. Our main questions were: (1) the change of which abiotic environmental factor can affect the physiological function of the investigated habitats and to what extent; (2) what differences in the seasonal physiological dynamics can be noticed on the various environmentally adapted microsites; (3) how seasonal changes can refer to the plasticity/tolerance level related to changing environmental agents.

The objective of the present work was to reveal *in situ* seasonal dynamic changes of the main determining production processes by using ecophysiological methods in two Hungarian *Sphagnum* dominated mires. As all *Sphagnum* covered mire ecosystems are very sensitive to any environmental changes (especially small ones)

therefore they can indicate any changes very rapidly with their physiological responses. Its importance in the complex climatic cycle and their responses to global and local climate changes are reflected by *in situ* ecophysiological measurements which are very informative not only for the local environmental conditions but they can also refer to large scale changes.

2. MATERIALS AND METHODS

2.1. Site description

The study area is two *Sphagnum* dominated mires (Nyíres-tó and Báb-tava), which are situated in the Bereg-plain (NE Hungary) (Fig. 1). The mires were first mentioned by Simon (1953) who made the first vegetation maps (Simon, 1960) and described their plant associations. Open peat bog and alder carr were dominant in the middle of the bed. The dominant peat mosses were *Sphagnum angustifolium* and *Sphagnum palustre*. Due to arid years and human effects the cover of tree-dominated associations increased and the habitats of protected rare species decreased (Simon, 1992a). After the artificial flooding of the mires, degradation processes slowed down and quick regeneration started (Cserhalmi et al., 2011).

The study area was the peaty bed of Nyíres-tó (48°11'3"N, 22°30'6"E) and Báb-tava (48°11'16"N, 22°29'0"E) mires. The presence of raised bog associations on the Bereg-plain is its southernmost occurrences in the plains of Europe (Simon, 1992a). The average annual sunshine is *ca* 1950 hours and mean annual temperature is 9.4 – 9.5 °C. The annual rainfall is 630 – 660 mm, of which 370 – 380 mm falls during the vegetation period (Marosi & Somogyi 1990) and the climate is moderately warm with cold winter. Average sizes of these ox-bows were less than 5 hectares. The mires are situated within the Hortobágy National Park. The mires have had artificial water supply since 1986 (Simon, 1992a).

The structure of the mires are characterised by three different habitats: open peat bog, poor fen and alder carr. Open peat bog covers the middle parts of the mires. For species names we used the nomenclature of Simon (1992b). Dominant vascular plants are *Eriophorum vaginatum*, *Eriophorum angustifolium*, *Juncus effusus*, *Carex lasiocarpa* and *Vaccinium oxycoccos*. In Báb-tava mire the most common peat mosses are still *Sphagnum palustre* and *Sphagnum angustifolium* the same as in Nyíres-tó (Szurdoki & Nagy 2002). The average pH value of pore water was 3.7 (Nagy, 2006). The poor fen habitat had almost the same characteristic species

with a higher cover of *Eriophorum angustifolium*. The cover of trees and shrubs were very low, only plenty of dried *Betula pubescens* trees were present. Dominant peat mosses were *Sphagnum palustre* and *Sphagnum fallax*. Average pH value was 3.48 (Nagy, 2006). The third habitat (alder carr) has closing canopy with approximately 80 % of tree cover. The main stand former species was *Alnus glutinosa* with a lower cover of *Frangula alnus* or *Betula pubescens*. Dominant herbs were *Carex elongata*, *Lysimachia vulgaris* and different mosses like *Sphagnum angustifolium* and *Sphagnum fimbriatum*. The cover of moss layer was only 10-20 %, peat mosses covered only 1-5 %. The average pH value is 6.02 (Nagy, 2006).

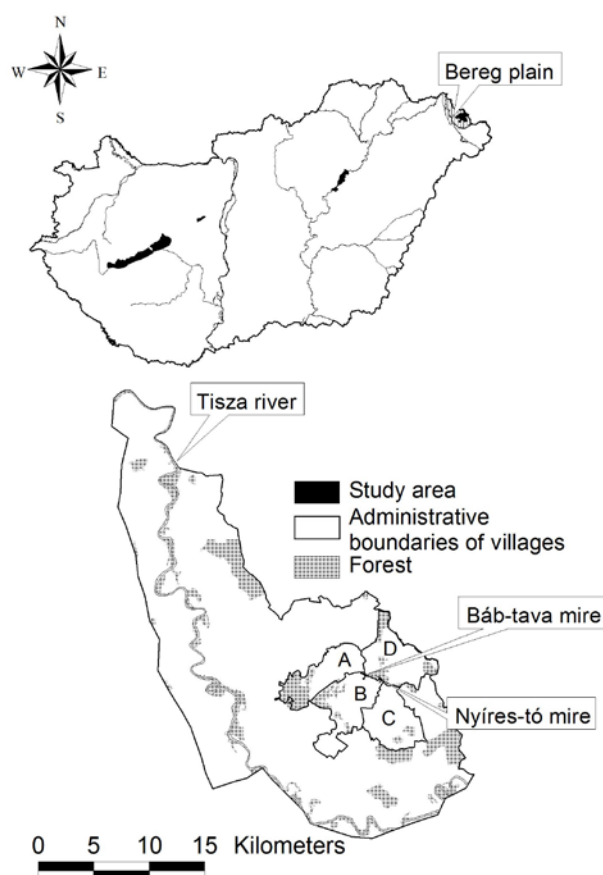


Figure 1. Relative locations of the investigated mires in Hungary showing four surrounding villages (A:Gelénes, B:Csaroda, C:Márokpapi, D:Beregdaróc).

Investigated microhabitats size were approx. 2.5-3 m² respectively, sunny and shady ones; both of them are situated in the open peat bog region with *Sphagnum* dominated covering. Microsites were close to each other differed in sun exposition, means in degree of radiation (PAR).

2.2. CO₂ flux measurements

Two different microhabitats were investigated

in both mires for seasonal measurements. One of them was a sunny and opened place while the other was a shaded microhabitat; both of them are located in the open peat bog region of the mires.

Stand Net Ecosystem Exchange (NEE) measurements of CO₂-fluxes were done seasonally in each microsite. At the same time, radiation and air temperature values within the chamber were recorded. Most often the measurements were carried out on the most characteristic days of every seasonal period at the actual *in situ* temperature. CO₂ concentration (ppmv) was measured with a portable infrared CO₂ gas analyzer (LCA-2, ADC Systems, Hoddesdon, UK) operating in an open system using a round shape water-clean perspex-chamber with a diameter of 30 cm (sample size). The light and mobile chamber system was equipped with a battery-operated fan, which ensured that the air was mixed inside the chamber. Methods and NEE rates were calculated from differences in CO₂ concentration in the chamber headspace and the outside air with respect to the chamber volume and temperature; the calculations were carried out according to Czóbel et al., (2005), Juhász et al., (2005) and Balogh et al., (2007). The air was blown through the chamber by an outer fan using constant flow rate to decrease the chamber effects operating as a cooling system to prevent excessively temperature, radiation and moisture condensation increases inside the chamber. *Sphagnum* covering under the chamber, namely the patterned surface (sampled area), was 100 %. Chamber methods were used for measurements in 4-5 plots by seasonal measurement campaigns during the growing season in two microhabitats of both mires. CO₂ concentration was sampled and recorded by 60 s intervals and measurements were carried out continuously in the daytime. Mean values of NEE were calculated by three daytime measurements in all microsites, respectively. The photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and temperature (°C) were measured by a quantum and temperature sensor (HOBO MicroStation; Massachusetts, USA) located on the surface of the peat moss cushion under the chamber.

2.3. NDVI (Normalized Difference Vegetation Index) measurements

CO₂ fluxes were measured using chamber method together with NDVI measurements at all microsites. NDVI pictures were carried out using an agricultural digital camera (ADC, Dycam Inc., Chatsworth, CA, USA) to take pictures of vegetation in the red and near infrared part of the spectrum. The amount of chlorophyll in the vegetation can be

calculated using these images according to one of the standard vegetation indices such as NDVI. The calculations used to generate NDVI index are based on the intensity of red (Rpixel) and infrared (IRpixel) values at each point in the image (White et al., 2000). Calculation of NDVI is: $\text{NDVI} = (\text{IRpixel} - \text{Rpixel}) / (\text{IRpixel} + \text{Rpixel})$. BRIV 32 software (Heinold, 2000) was used to calculate NDVI for each pixel and produce mean values for each image.

2.4. Chlorophyll fluorescence measurements

The maximum quantum yields of PSII photochemistry (Fv/Fm) of dominant peat mosses and herbaceous plants selected randomly from the entire area of both mires were measured in all seasons. Chlorophyll fluorescence was measured using a portable PEA (Hansatech Inst., Norfolk, England) fluorometer. Plant leaves were dark adapted for 25 minutes before starting the measurements using lightweight leaf clips. F₀ level of fluorescence was determined by switching on measuring light (PPFD less than $1 \mu\text{mol m}^{-2} \text{s}^{-1}$). The maximum fluorescence yield Fm in the dark adapted state was measured by applying a 0.7 s pulse of white light (PPFD of $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$). The Fv/Fm parameters were calculated from the induction kinetics at all measuring points. Calculation of fluorescence parameters and conventions for symbols follow Schreiber & Bilger (1993), in equations: $\text{Fv/Fm} = (\text{Fm} - \text{F}_0) / \text{Fm}$. Measurements were carried out in five replicates of each plant species per seasons.

2.5. Statistical analyses

The data were analyzed by the Student's *t*-test and analyses of variance (ANOVA). Effects of periods, habitats and their interactions were analyzed using a two-way of ANOVA. Differences were calculated between NEE and PPFD parameters of Nyíres-tó and Báb-tava mires by two-way ANOVA test. Two independent variables were periods (seasons) and habitat types (shady and sunny). Changes of seasonal fluorescence parameters (Fv/Fm) were compared using Student's *t*-test. Differences are considered to be significant at a level of $P < 0.005$.

3. RESULTS

3.1. CO₂ gas exchange measurements

Differences in seasonal dynamics between sunny and shady microhabitats are well represented in case of Nyíres-tó and Báb-tava mires (Table 1). The mean temperature during NEE measurements were

10.4°C/22.38°C/10.5°C of spring/summer/autumn time in Nyíres-tó mire while they were 8.6 °C/18.22 °C/6.34 °C of spring/summer/autumn time in Báb-tava mire. Higher radiation values of sunny microhabitat of Nyíres-tó in summer time were not productive of salient CO₂ uptake rate while lower radiation of spring and autumn periods resulted in a similar uptake. Both mires showed less negative NEE values on shady microhabitats under lower radiation in summer period while the mires bounded CO₂ (sink) under similarly low light conditions in spring and autumn terms. The summer sunny habitat of Báb-tava mire showed extremely low light radiation (51.34 $\mu\text{molm}^{-2}\text{s}^{-1}$ PPFD) due to cloudy weather resulting in positive NEE (0.68 $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and implying a source function of the mire. Based on seasonal NEE values autumn proves to be the most productive period (Tab. 1) that means mires showed the highest CO₂ uptake in the case of both microhabitats – NEE fluxes were -2.43 or -1.98 $\mu\text{molm}^{-2}\text{s}^{-1}$ (sunny) and -2.89 or -1.25 $\mu\text{molm}^{-2}\text{s}^{-1}$ (shady) on Nyíres-tó and Báb-tava mires severally. Besides higher radiation in summer period daily NEE values were significantly lower or similar -2.52 or 0.68 $\mu\text{molm}^{-2}\text{s}^{-1}$ (sunny) and -0.16 or -1.00 $\mu\text{molm}^{-2}\text{s}^{-1}$ (shady) on Nyíres-tó and Báb-tava mires, respectively. Sensitivity of CO₂ uptake of different *Sphagnum* dominated microhabitats increased with daily rising radiation (Table 1). NEE values of sunny exposed *Sphagnum* dominated plots reacted more sensitively to changes of daily radiation than in shady microhabitats. Variability of NEE values was smaller under lower radiations of spring and autumn periods while they showed lower (more positive) NEE values under lower radiations during summer. The statistical analysis confirmed significant variations among habitats and periods (Table 2).

3.2. Changes in NDVI values and fluorescence parameters

Based on the seasonal variation of NDVI values, the highest ones (0.76-0.88) were observed in summer season in all investigated microhabitats (Fig. 2). These were the same 4-5 plots of sunny and shaded

microhabitats where CO₂ flux measurements were carried out. The values of summer period were higher on average with 15 % and closely 40 % compared to autumn and spring periods, respectively. The lowest values (0.43 and 0.44) were measured in the sunny site of Nyíres-tó mire and in the shady plot on Báb-tava mire, both in spring time. The highest values (0.61 and 0.8) of spring and autumn periods were measured in the sunny microhabitat of Nyíres-tó mire. Fv/Fm fluorescence parameters were also higher in both peat mosses and vascular plants in summer period, which is especially expressed in the case of vascular plants (Table 3). Values of spring and autumn periods showed lower and similar ranges due to a more active life period following winter and also because of launching senescence processes in autumn. If we compare the *Sphagnum* species in the case of *S. angustifolium* the Fv/Fm parameters showed significant differences between spring and summer periods in both mires while *S. palustre* (in Báb-tava mire) confirmed it between summer and autumn. Otherwise, changes in Fv/Fm parameters in different seasons were not as considerable for peat mosses as for vascular plant species.

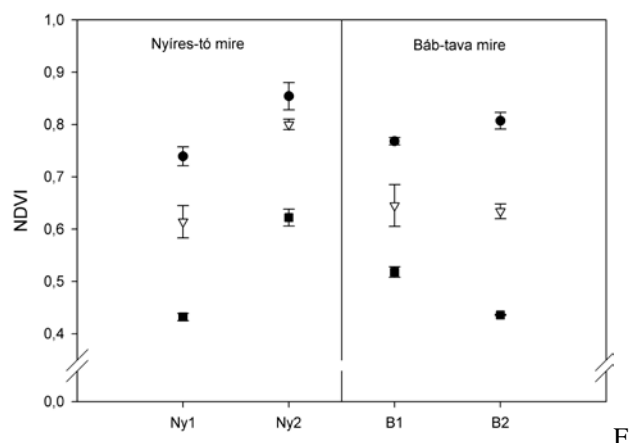


Figure 2. Seasonal changes of NDVI values in spring (■), summer (●) and autumn (▽) periods on four investigated microhabitats of Nyíres-tó (Ny1-opened and sunny; Ny2-shady) and Báb-tava (B1-opened and sunny; B2-shady) mires.

Table 1. Seasonal changes of the daily average and variance values of NEE ($\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and PPFD ($\mu\text{molm}^{-2}\text{s}^{-1}$) parameters on two microsites (sunny and shady) of Nyíres-tó and Báb-tava mires. Negative NEE values indicate carbon uptake as photosynthesis while positive values reflect the release of CO₂ as respiration.

Site		Spring		Summer		Autumn	
		Sunny	Shady	Sunny	Shady	Sunny	Shady
		NEE/PPFD	NEE/PPFD	NEE/PPFD	NEE/PPFD	NEE/PPFD	NEE/PPFD
Nyíres-tó mire	Average	-2.73/368.8	-1.87/202.08	-2.52/570.73	-0.16/76.26	-2.43/161.71	-2.89/159.09
	Variance	0.34/5002.5	0.06/3843.65	0.88/154731	1.08/6011.14	0.33/1063.16	0.58/5966.48
Báb-tava mire	Average	-1.08/595.29	-1.38/292.27	0.68/51.34	-1.00/109.46	-1.98/81.96	-1.25/56.22
	Variance	0.15/74374.35	0.02/2178.49	6.27/35.22	1.22/1227.22	1.91/3577.23	1.10/235.51

Table 2. Differences between NEE ($\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$) and PPFD ($\mu\text{molm}^{-2}\text{s}^{-1}$) parameters of Nyíres-tó and Báb-tava mires by two-way ANOVA test. Two independent variables are periods (seasons) and habitat types (shady and sunny). Df – degree of freedom; SS – sum of squares; MS – mean squares; F – value of Fisher test; all data are significant at $p < 0.001$.

Site	Factors and effects		df	SS	MS	F	p
Nyíres-tó	NEE	habitat	1	77.25	77.25	141.45	<0.0001
	[$\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$]	period	2	113.64	56.82	104.04	<0.0001
		habitat x period	2	121.31	60.65	111.06	<0.0001
	PPFD	habitat	1	4479898	4479898	152.19	<0.0001
	[$\mu\text{molm}^{-2}\text{s}^{-1}$]	period	2	1776444	888221.8	30.17	<0.0001
		habitat x period	2	3825274	1912637	64.98	<0.0001
Báb-tava	NEE	habitat	1	17.00	17.00	9.56	0.002139
	[$\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$]	period	2	145.76	72.88	40.97	<0.0001
		habitat x period	2	93.50	46.75	26.28	<0.0001
	PPFD	habitat	1	781204.2	781204.2	50.57	<0.0001
	[$\mu\text{molm}^{-2}\text{s}^{-1}$]	period	2	11629348	5814674	376.44	<0.0001
		habitat x period	2	2286153	1143076	74.00	<0.0001

Table 3. Seasonal changes of the maximal photochemical efficiency (Fv/Fm) parameters of dominated plant species on Nyíres-tó and Báb-tava mires. Results are shown \pm the standard error of the mean; n=5. Different superscript letters indicate statistically significant differences at $p < 0.005$ level.

Site	Species	Season		
		Spring	Summer	Autumn
Nyíres-tó	<i>Sphagnum angustifolium</i>	0.755 \pm 0.038 ^a	0.827 \pm 0.012 ^b	0.767 \pm 0.051
	<i>Carex riparia</i>	0.789 \pm 0.013 ^a	0.843 \pm 0.008 ^b	0.763 \pm 0.020 ^a
	<i>Juncus effusus</i>	0.799 \pm 0.020	0.824 \pm 0.014	-
	<i>Vaccinium oxycoccos</i>	0.741 \pm 0.071	0.846 \pm 0.008	0.766 \pm 0.050
	<i>Carex lasiocarpa</i>	-	0.815 \pm 0.029	0.800 \pm 0.009
	<i>Lysimachia vulgaris</i>	-	0.857 \pm 0.002 ^a	0.505 \pm 0.070 ^b
	<i>Frangula alnus</i>	-	0.833 \pm 0.003 ^a	0.593 \pm 0.070 ^b
Báb-tava	<i>Sphagnum angustifolium</i>	0.686 \pm 0.032 ^a	0.815 \pm 0.020 ^b	0.847 \pm 0.015 ^b
	<i>Sphagnum palustre</i>	0.717 \pm 0.047	0.800 \pm 0.019 ^a	0.740 \pm 0.019 ^b
	<i>Eriophorum vaginatum</i>	0.798 \pm 0.032	0.837 \pm 0.030	0.830 \pm 0.017

Significant difference at $P < 0.005$

4. DISCUSSIONS

Our study provided a comparison of the variability of two similar mires during three periods of growing seasons to understand the mire ecosystem functioning at the edge of the area of their distribution. *Sphagnum* cushions showed a very fast reply for changing radiation independent from the level of light adapted state of the microhabitat (sunny or shady), which was immediately reflected in their physiological, mainly in photosynthetic functioning. The opened, sunny microsites showed higher values of NEE than shady ones, which can be influenced by the species composition (Hájek & Vicherová 2013) and vegetation characteristics (Glenn et al., 2006; Schneider et al., 2012). CO_2 exchange in *Sphagnum* plots was mostly related to light condition which was confirmed by different seasonal patterns (Heijmans et al., 2004) such as the

unique microclimatical conditions. The differences in daily NEE values between the microhabitats (sunny and shady) were less considerable in autumn time on both mires (Table 1). Different microsites can show similar ecological adaptation levels due to less solar radiation at the end of the growing season which is reflected in such NEE values. Daily temperature can be much rather considered as a constant environmental factor in a peat bog ecosystem fluctuating less during the day compared to radiation, which can be attributed to special microclimate and exceptional, unique life communities. Nevertheless, slight differences in daily average temperature between two mires during seasonal measurements expressed differences in daytime NEE values since mean temperature was consistently lower at Báb-tava mire than Nyíres-tó mire. The third essential abiotic environmental factor which basically determines the physiological

function of peat bog is water. In our case it can be considered as a less changing parameter due to the artificial regulation of flood. The differences in the seasonal physiological dynamics on the various environmental adapted microsites showed that the typical function is adequate to light adapted conditions (Heijmans et al., 2004). Especially in spring period when the vegetation period starts the higher NEE values are coupled with lower NDVI values and inversely also, to reflect more photosynthetic pigment presence under less available light condition due to the seasonal radiation supply. Summer and autumn times consequently higher NDVI values observed in both shady microhabitats can be attributed to the closure of upper canopy layer. Otherwise, in these latter vegetation periods the NEE values are less following unanimously the changes of NDVI values which can be caused by the presence of the higher vascular plants covering on the *Sphagnum* cushion surfaces and changing ratio of direct and indirect light conditions on the microhabitats. Overwintering leaves of evergreen species can afford an ecological advantage in spring for the production and compensate the lower growth rates during the summer time (Greulich & Bornette 2003; Wilson, 2007). The seasonal changes with varying environmental agents can develop different level of tolerance of *Sphagnum* species which can rearrange the peat bog structure (Hájek & Vicharová 2013).

Based on NEE values the most photosynthetically inactive period is the summer term in Hungarian bogs similarly to the other peat bogs of various ecosystems and climatic conditions, namely, Canadian bogs and the arctic region (Bubier et al., 2003). The highest respiratory activity was measured in summer period. The seasonal pattern of net CO₂ exchange in *Sphagnum* dominated plots was extremely related to light conditions. Both mires showed higher productivity compared with the northern peatlands due to the special microclimatic condition and the four seasons of a year. Due to the seasonal variation of four seasons in the temperate zone the highest amount of light that reaches the *Sphagnum* moss surfaces was measured in spring and autumn periods in the opened, sunny microhabitat of Báb-tava. Due to the higher tree cover of Báb-tava, the canopy extends in the summer period, and the shading effect is higher. Nyíres-tó remains sunny even in summer due to lower tree cover. Decreased NEE values of summer period affirmed that the most active periods concerning CO₂ occlusion of the investigated Hungarian bogs are the spring and autumn periods also reported by Heijmans et al., (2004) and

Schneider et al., (2012). Investigating microscale species can show significantly different production in microtopography (Weltzin et al., 2001; Wu et al., 2011; Hájek & Vicharová 2013).

NDVI values are very good indicators of photosynthetic processes and show a strong correlation with the chlorophyll content of plants or vegetation. Summer period showed higher NDVI values due to the higher cover of vascular plants (*Vaccinium oxycoccus*, *Carex lasiocarpa*, *Lysimachia vulgaris*, *Eriophorum vaginatum*) on the *Sphagnum* surfaces. Otherwise, increased water content of peat mosses showed a positive correlation with NDVI values (Douma et al., 2007). In case of Hungarian mires the artificial water supply in summer increased the water level of mires which also reflected higher NDVI values of vegetation. Relatively low NDVI and Fv/Fm values of spring period can be attributed to lack or inactive state of vascular plants on *Sphagnum* cushions and lower chlorophyll content of peat mosses on the mire surface. Photosynthetic activity of *S. palustre* in spring – living in drier microhabitat (hummock) – exceed *S. angustifolium* – adopted to wetter microhabitat (hollow) – while their Fv/Fm values were similar in summer (0.8 ± 0.02 and 0.815 ± 0.02 respectively). On the other hand, the vascular plant roles on the peat bogs are essential for *Sphagnum* species diversity and composition – especially in drier hummock regions of peat bogs - mainly their microclimatic effects and reducing abiotic stress (Malmer et al., 2003; Pouliot, 2011). The main vegetation period of these vascular plants is summer time when their photosynthetic capacity showed maximum values. It is reflected by Fv/Fm parameters of higher plants to contribute to the development of peat bog microtopography since increasing vascular plant cover reduces the availability of light and water supply for *Sphagnum* species (Berendse et al., 2001; Pauli et al., 2002). Fv/Fm values of *Sphagnum* species are not changed significantly in summer and autumn time (Table 3) due to the increasing shade of vascular plants while their productivity (NEE) significantly decreased in summer time also on the sunny and shady microhabitats of both investigated mires (Table 3). Even though both study sites were located in a relatively small area and very close to each other, they are characterized by different microclimatic conditions, which might explain the differences in measured parameters. Our study shows that the CO₂ flux estimation is also important to calculate on a microscale, not only on the ecosystem and regional scales because data showed different dispersion between different mires and within different

microhabitats of the same mire. These results contribute to our understanding of dynamic changes of peatlands, mire ecosystem functioning at the edge of their distribution and predict ecosystem responses to climate change, which can be potential factors both on global carbon cycle and global change.

Further studies exploring the vegetation composition at micro-scale imply the classification of certain peat moss species based on microtopography (hollow, hummock forming); mapping of the degree of desiccation tolerance of *Sphagnum* species; describing the limit values of water status and temperature on the degree of regeneration ability; different desiccation-rehydration dynamics of Hungarian *Sphagnum* species versus microtopography; all of which would enhance our understanding of the physiological mechanisms of these ecosystems e.g. the lateral hydrological dynamics, annual NEE dynamics, decomposition, differences in nutrients and soil chemistry.

ACKNOWLEDGEMENTS

This study was supported by the Hortobágyi National Park (Debrecen), János Bolyai Research Scholarship of the Hungarian Academy of Sciences and the Hungarian Scientific Research Fund (OTKA-PD 109445).

REFERENCES

- Aurela, M., Tuovinen, J.P. & Laurila, T., 1998. Carbon dioxide exchange in a subarctic peatland ecosystem in northern Europe measured by eddy covariance technique. *J Geophys Res*, 103, 11289-11301.
- Balogh, J., Nagy, Z., Fóti, SZ., Pintér, K., Czóbel, SZ., Péli, E.R., Acosta, M., Marek, M.V., Csintalan, Zs. & Tuba, Z. 2007. Comparison of CO₂ and H₂O fluxes over grassland vegetations measured by the eddy-covariance technique and by open system chamber. *Photosynthetica*, 45, 288-292.
- Berendse, F., Van Breeman, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H., Wallén, B., 2001. Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Global Change Biol*, 7, 591-598.
- Boelman, N.T., Stieglitz, M., Griffin, K.L. & Shaver, G.R., 2005. Inter-annual variability of NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra. *Oecologia*, 143, 588-597.
- Bortoluzzi, E., Epron, D., Siegenthaler, A., Gilbert, D. & Buttler, A., 2006. Carbon balance of a European mountain bog at contrasting stages of regeneration. *New Phytol*, 172, 708-718.
- Bu, Z.-J., Zheng, X.-X., Rydin, H., Moore, T. & Ma, J., 2013. Facilitation vs. competition: Does interspecific interaction affect drought responses in *Sphagnum*? *Basic Appl Ecol*, 14, 574-584.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T. & Lafleur, P.M., 2003. Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a Large Peatland in Ontario, Canada. *Ecosystems* 6:353-367
- Bubier JL, Crill PM, Moore TR, Savage K. & Varner R (1998) Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex. *Global Biogeochem Cy*, 12, 703-714.
- Bubier, J.L., Frolking, S., Crill, P.M. & Linder, E., 1999. Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *J Geophys Res*, 104, 27683-27692.
- Carroll, P. & Crill, P.M., 1997. Carbon balance of a temperate poor fen. *Global Biogeochem Cy*, 11, 349-356.
- Christensen, T.R., Friborg, T., Sommerkorn, M., Kaplan, J., Illeris, L., Soegaard, H., Nordstroem, C. & Jonasson, S., 2000. Trace gas exchange in a high-arctic valley 1. Variations in CO₂ and CH₄ flux between tundra vegetation types. *Global Biogeochem Cy*, 14, 701-714.
- Cizkova, H., Kvet, J., Comn, F.A., Laiho, R., Pokorný, J. & Pithart, D., 2013. Actual state of European wetlands and their possible future in the context of global climate change. *Aquatic Sci*, 75, 3-26.
- Clymo, R.S., Turunen, J. & Tolonen, K., 1998. Carbon accumulation in peatlands. *Oikos*, 81, 368-388.
- Crill, P., 1991. Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochem Cy*, 5, 319-334.
- Cserhalmi, D., Nagy, J., Kristóf, D. & Neidert, D., 2011. Changes in a wetland ecosystem: A vegetation change reconstruction study based on historical panchromatic aerial photographs and succession patterns. *Folia Geobot*, 46, 351-371.
- Czóbel, SZ., Fóti, SZ., Balogh, J., Nagy, Z. & Tuba, Z., 2005. Chamber series and space-scale analysis of CO₂ gas-exchange in grassland vegetation: A novel approach. *Photosynthetica*, 43, 267-272.
- Douma, J.C., Van Wijk, M.T., Lang, S.I. & Shaver, G.R., 2007. The contribution of mosses to the carbon and water exchange of arctic ecosystems: quantification and relationships with system properties. *Plant Cell Environ*, 30, 1205-1215.
- Frolking, S., 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 from northern peatlands. *Global Biogeochem Cy*, 12, 115-126.
- Frolking, S., Roulet, N.T., Moore, T.R., Lafleur, P.M., Bubier, J.L. & Crill, P.M., 2002. Modeling

- seasonal to annual carbon balance of Mer Bleu Bog, Ontario, Canada. *Global Biogeochem Cy*, 16, 4-21.
- Gaalen, K.E., Flanagan, L.B. & Peddle, D.R., 2007. Photosynthesis, chlorophyll fluorescence and spectral reflectance in *Sphagnum* moss at varying water contents. *Oecologia*, 153, 19-28.
- Gilmanov, T.G., Soussana, J.F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., Barcza, Z., Bernhofer, C., Campbell, C.L., Cernusca, A., Cescatti, A., Clifton-Brown, J., Dirks, BOM., Dore, S., Eugster, W., Fuhrer, J., Gimeno, C., Gruenwald, T., Haszpra, L., Hensen, A., Ibrom, A., Jacobs, AFG., Jones, M.B., Lanigan, G., Laurila, T., Lohila, A., Manca, G., Nagy, Z., Pilegaard, K., Pinter, K., Pio, C., Raschi, A., Rogiers, N., Sanz, M., Stefani, P., Sutton, M., Tuba, Z., Valentini, R., Williams, M.L. & Wohlfahrt, G., 2007. Partitioning European grassland net ecosystem CO₂ exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agric Ecosyst Environ*, 121, 93-120.
- Glenn, A.J., Flanagan, L.B., Syed, K.H. & Carlson, P.J., 2006. Comparison of net ecosystem CO₂ exchange in two peatlands in western Canada with contrasting dominant vegetation, *Sphagnum* and *Carex*. *Agric Forest Meteorol*, 140, 115-135.
- Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl*, 1, 182-195.
- Greulich, S. & Bornette, G., 2003. Being evergreen in an aquatic habitat with attenuated seasonal contrasts – a major advantage? *Plant Ecol*, 167, 9-18.
- Griffis, T.J., Rouse, W.R. & Waddington, J.M., 2000. Interannual variability of net ecosystem CO₂ exchange at a subarctic fen. *Global Biogeochem Cy*, 14, 1109-1122.
- Hájek, T. & Vicharová, E., 2013. Desiccation tolerance of *Sphagnum* revisited: a puzzle resolved. *Plant Biol*, Published online. DOI:10.1111/plb.12126.
- Hargreaves, K.J., Fowler, D., Pitcairn, C.E.R. & Aurela, M., 2001. Annual methane emission from Finnish mires estimated from eddy covariance campaign measurements. *Theo Appl Climat*, 70, 203-213.
- Heijmans, M.P.D., Arp, W.J. & Chapin, F.S. III., 2004. Carbon dioxide and water vapour exchange from understory species in boreal forest. *Agric Forest Meteorol*, 123, 135-147.
- Heinold, S., 2000 *BRIV32 Software*. Dycam Inc., Chatworth, CA, USA.
- Juhász, A., Balogh, J., Csintalan, Z. & Tuba, Z., 2005. The influence of the water content on the photosynthetic features and carbon-balance of the poikilohydric moss carpet vegetation. *Cer Res Comm*, 33, 235-237.
- Kettunen, A., 2000. Short term carbon dioxide exchange and environmental factors in a boreal fen. *Verhandlungen des Internationalen Verein Limnologie*, 27, 1-5.
- Lafleur, P.M., McCaughey, J.H., Joiner, D.W., Bartlett, P.A. & Jelinski, D.E. 1997. Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal wetland. *J Geophys Res*, 102, 29009-29020.
- Lafleur, P.M., Roulet, N.T. & Admiral, S.W., 2001. Annual cycle of CO₂ exchange at a bog peatland. *J Geophys Res*, 106, 3071-3081.
- Maanavilja, L., Riutta, T., Aurela, M., Pulkkinen, M., Laurila, T. & Tuittila, E-S., 2011. Spatial variation in CO₂ exchange at a northern aapa mire. *Biogeochem*, 104, 325-345.
- Malmer, N., Albinsson, C., Svensson, B.M. & Wallén, B., 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos*, 100, 469-482.
- Marosi, S. & Somogyi, S., 1990. *Magyarország kistájainak katasztere I-II*. MTA Földrajztudományi Kutató Intézete, Budapest, (in Hungarian).
- McNeil, P. & Waddington, J.M., 2003. Moisture controls on *Sphagnum* growth and CO₂ exchange on a cutover bog. *J Appl Ecol*, 40, 354-367.
- Nagy, J. 2006. Vegetation maps of Báb-tava, Navat-patak, Nyíres-tó, Zsid-tó, Kis-tó, Nagy-tó and Hamvas-tó. The detailed description of their plant communities with the list of the plant species. In: Magura T (eds) *Complex habitat rehabilitation of the Central Bereg Plain, Northeast Hungary*. Debrecen, pp 59.
- Pauli, D., Peintiger, M. & Schmid, B., 2002. Nutrient enrichment in calcareous fens: effects on plant species and community structure. *Basic Appl Ecol*, 3, 255-266.
- Pouliot, R., Rochefort, L., Karofeld, E. & Mercier, C., 2011. Initiation of *Sphagnum* moss hummock in bogs and presence of vascular plants: Is there a link? *Acta Oecol*, 37, 346-354.
- Schneider, J., Kutzbach, L. & Wilmking, M., 2012. Carbon dioxide exchange fluxes of a boreal peatland over a complete growing season, Komi Republic, NW Russia. *Biogeochem*, 111, 485-513.
- Schreiber, U. & Bilger, W., 1993. Progress in chlorophyll-fluorescence research: major developments during the past years in retrospect. *Prog Bot*, 54, 151-173.
- Silvola, J., Alm, J., Ahlholm, U., Nykänen, H. & Martikainen, P.J., 1996. CO₂ fluxes from boreal mires under varying temperature and moisture conditions. *J Ecol*, 84, 219-228.
- Simon, T., 1992b. *Magyarországi edényes flóra határozója (Field guide to the vascular flora of Hungary)*, Nemzeti Tankönyvkiadó Rt., Budapest. In Hungarian.
- Simon, T., 1953. *Torfmoore im Nordem des Ungarischen Tieflandes*. *Acta Biol Hun*, 4, 249-252. (in German)
- Simon, T., 1960. *Die Vegetation der Moore in den Naturschutz-gebieten des Nördlichen Alföld*. *Acta Bot*, 6, 107-137. (in German)

- Simon, T.**, 1992a. *Vegetation change and the protection of the Csaroda relic mires, Hungary*. Acta Soci Bot Pol, 61, 63-74.
- Soegaard, H. & Nordstroem, C.**, 1999. *Carbon dioxide exchange in a high-arctic fen estimated by eddy covariance measurements and modelling*. Global Change Biol, 5, 547-562.
- Soegaard, H., Nordstroem, C., Friborg, T., Hansen, B.U. & Christensen, T.R., Bay, C.**, 2000. *Trace gas exchange in a high-arctic valley 3. Integrating and scaling CO₂ fluxes from canopy to landscape using flux data, footprint modelling, and remote sensing*. Global Biogeochem Cy, 14, 725-744.
- Strilesky, S.L. & Humphreys, E.R.**, 2012. *A comparison of the net ecosystem exchange of carbon dioxide and evapotranspiration for treed and open portions of a temperate peatland*. Agric Forest Meteo, 153, 45-53.
- Syed, K.H., Flanagan, L.B., Carlson, P.J., Glenn, A.J. & Van Gaalen, K-E.**, 2006. *Environmental control of net ecosystem CO₂ exchange in a treed, moderately rich fen in northern Alberta*. Agric Forest Meteo, 140, 97-114.
- Szurdoki, E. & Nagy, J.**, 2002. *Sphagnum dominated mires and Sphagnum occurrences of North-Hungary*. Folia historico-naturalia musei Matraensis, 26, 67-84.
- Vitt, D.H.** 2005. *Peatlands: Canada's past and future carbon legacy*. In: Bhatti J, Lal R, Price M, Apps J (eds) *Climate change and carbon in managed forests*. Boca Raton, FL: CRC Press, pp 201-216.
- Vourlitis, G.L. & Oechel, W.C.**, 1999. *Eddy covariance measurements of CO₂ and energy fluxes of an Alaskan tussock tundra ecosystem*. Ecol, 80, 686-701.
- Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J. & Vonderharr, M.**, 2001. *Production and microtopography of bog bryophytes: response to warming and water-table manipulations*. Oecologia, 128, 557-565.
- White, M.A., Asner, G.P., Nemani, R.R., Privette, J.L. & Running, S.W.**, 2000 *Measuring fractional cover and leaf area index in arid ecosystems: digital camera, radiation transmittance, and laser altimetry methods*. Remote Sens Environ, 74, 45-57.
- Wieder, R.K.**, 2001. *Past, present, and future peatland carbon balance: an empirical model based on ²¹⁰Pb-dated cores*. Ecol Appl, 11, 327-342.
- Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K.A., Farrell, E.P. & Tuittila, E-S.**, 2007. *A high resolution green area index for modelling the seasonal dynamics of CO₂ exchange in peatland vascular plant communities*. Plant Ecol, 190, 37-51.
- Wu, J., Roulet, N.T., Moore, T.R., Lafleur, P. & Humphreys, E.**, 2011. *Dealing with microtopography of an ombrotrophic bog for simulating ecosystem-level CO₂ exchanges*. Ecol Model, 222, 1038-1047.
- Zhaojun, B., Joosten, H., Hongkai, L., Gaolin, Z., Xingxing, Z., Jinze, M. & Jing, Z.**, 2011. *The response of peatlands to climate warming: A review*. Acta Ecol Sin, 31, 157-162.
- Zoltai, S.C. & Martikainen, P.J.**, 1996. *The role of forested peatlands in the global carbon cycle*. Nato Asi Ser, 40, 47-58.

Received at: 18. 02. 2014

Revised at: 30. 01. 2015

Accepted for publication at: 10. 02. 2015

Published online at: 13. 02. 2015