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Original Research

Sedge Community (*Caricetum elatae*) Carbon Dioxide Exchange Seasonal Parameters in a Wetland

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Abstract

Our paper presents the results of simultaneous measurements of carbon dioxide fluxes using non-steady state non-through flow chamber method and the amount of green biomass above the ground surface in the sedge community *Carex elatea*. The comparison of the results of the research allowed us to estimate the amount of carbon dioxide accumulated in green plant biomass. It was concluded that a maximum of 28% of carbon absorbed in the process of photosynthesis was accumulated in green part biomass. The carbon uptake per unit of carbon of green biomass at the beginning of the vegetative season amounted to 491.2 $\mu g \cdot g^{-1} \cdot MJ^{-1} \cdot d^{-1}$, whereas at the end of the vegetative season it dropped to 49.1 $\mu g \cdot g^{-1} \cdot MJ^{-1} \cdot d^{-1}$.

Keywords: sedge, green biomass, gross primary production, chamber technique

Introduction

Physical (e.g. global warming) and chemical (e.g. increase of CO_2 concentration) changes in the atmospheric features influence the functioning of the whole biosphere of earth [1]. Simultaneously, physical features of the atmosphere as well as the condition of plant cover significantly influence the processes of mass and energy exchange between the ground surface and the atmosphere [2-5].

Global warming is often described in literature influences, among other things, as the carbon circulation between the earth and the atmosphere [6]. Wet ecosystems play an important role in global carbon balance because the soils of organic environments of the northern hemisphere accumulate about 30% of the whole soil C [7, 6], although they occupy an insignificant part of the land [8].

Wetlands seem to be particularly sensitive to climate change because of the complexity of both biomass growing and decomposition processes [9-14].

Consequently, studying gas exchange between wetland and the atmosphere is important in the context of rapid growth of concentrations of such gases as carbon dioxide and methane in the atmosphere [1]. The currently observed climate changes will most likely cause changes in wetland activity by altering the heat and water balance of their surface, among others [15].

Understanding and parameterization of the exchange processes (assimilation and emission) of CO_2 are crucial to describe the present balance and direction of changes that will take place in these environments in the future.

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This knowledge can be very useful for systemic understanding of the environment [16].

The sedge (*Carex*) is one of the basic peat-forming plants [17]. Therefore, investigating the dynamics of biomass growth of these plants and simultaneously the assessment of CO_2 exchange rate are of crucial importance for the quantitative description of the development processes taking place in a sedge peat bog.

The sedge (*Carex*) is well adapted to survive in high groundwater table conditions and one of the adaptations is the occurrence of Aerenchyma tissue in organisms of these plants. This type of air channels allows for air exchange between shoots and roots located below the water table [18]. The process is so efficient that it works even at 230 cm below ground level [19]. There is literature proving the influence of climate change on the development of this plant genus [20].

Peatland plants absorb CO_2 from the atmosphere in the process of photosynthesis, and this flux is known as gross primary production (GPP) [21]. The absorbed carbon is accumulated in plant biomass in its various parts and in various chemical forms [22].

Simultaneously the processes of decomposition take place in each peatland such as autotrophic respiration (R_{aut}) or decomposition of organic matter accumulated in substrate, namely heterotrophic respiration (R_{het}). Both processes lead to releasing CO_2 into the atmosphere and their sum is known as ecosystem respiration (R_{ECO}) [23].

Thus, the GPP value can be described using the following formula [21].

$$GPP = NEP + R_{ECO} \tag{1}$$

...where:
GPP – gross primary production [$g \cdot m^{-2} \cdot d^{-1}$]
NEP – net ecosystem production [$g \cdot m^{-2} \cdot d^{-1}$]
R_{ECO} – ecosystem respiration [$g \cdot m^{-2} \cdot d^{-1}$]

In the following paper all fluxes coming into the studied surface of the ecosystem are marked by "+", whereas all fluxes going out are marked by "-."

The main goal of this paper was to derive characteristics of CO_2 absorption by the sedge community in the wetland area in Rzecin.

Materials and Methods

Study Site Description (Rzecin Wetland)

Research described in this paper was conducted on a wetland site in the area of Rzecin village, 70 km northwest of Poznan (western Poland). The peatland is situated amidst the biggest Polish forest complex, namely Nadnotecka Primeval Forest. The research area is extremely valuable in terms of its flora and its values stem, among others, from the ongoing process of lake overgrowth taking place there [24]. Specific isolation and lack of human activity in the area have made it a unique place in this part of Europe.

The plant community studied in respect to biomass and gas exchange was the sedge community *Caricetum elatae* (W. Koch 1926), which belongs to the *Magnocaricion* systematic group [25].

The following species were found on this site: *Lysimachia thyrsiflora*, *Eqiusetum arvense*, *Equisetum palustre*, *Equisetum fluviatile*, *Polygonum persicaria*, *Polygonum nodosum*, *Galium aparine*, *Galium palustre*, *Stellaria palustris*, and *Alisma plantago-aquatica*.

The tufted sedge (*Carex elata* All.) is the most common species at this location. It creates hillocks and dominates the total standing biomass of living flora on the site [26]. At the beginning of the vegetation season the sedge made up 100% of green standing biomass and at the end of this season it was still quite a lot, which means 88.8% (Fig. 1).

The occurrence of this type of community indicates eutrophic character of the studied environment [25].

Meteorological Measurements

The measuring station in Rzecin peatland has been operating since 2004. It was built to assess mass and energy exchange between the wetland surface and the atmosphere [27-31]. A wide range of measurements have been conducted at this station, including both micrometeorological (Eddy covariance, chamber measurements) and meteorological, e.g. air temperature (Humidity and Temperature Transmitter HMD50Y, Vaisala, Finland), global radiation (pyranometer CM3 Kipp&Zonen, The Netherlands) or precipitation (heated tipping bucket rain gauge RG2-M, Onset, USA). All measurements were conducted automatically and most of the parameters are stored in a field computer memory [32].

Chamber Measurements

The non-steady state flow-through chamber technique [33] was applied to measure carbon dioxide exchange between the sedge community and the atmosphere. This technique is commonly used in the research of gas exchange between surfaces of various ecosystems and the

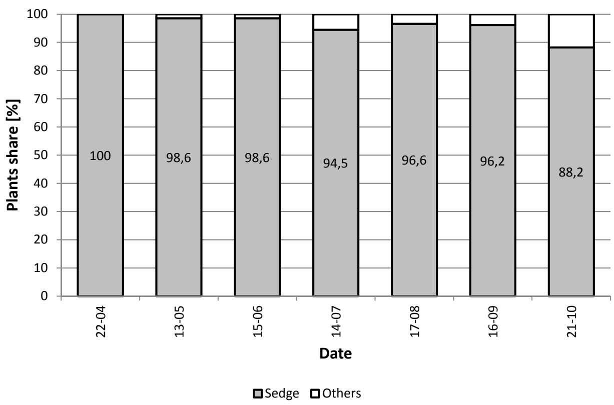

Fig. 1. Seasonal average share of sedge (darker part of bar) in the total standing green biomass run of sedge community at Rzecin wetland in 2009 [26].

Table 1. Green biomass amounts at Rzecin in 2009.

Date	No.	Mean	STD	VC
		$g \cdot m^{-2}$	$g \cdot m^{-2}$	%
22.04.2009	3	25.25	12.88	51
13.05.2009	3	68.57	17.08	25
15.06.2009	9	229.27	79.39	35
14.07.2009	9	315.89	60.32	19
17.08.2009	9	399.49	80.39	20
16.09.2009	3	356.48	67.28	19
21.10.2009	3	109.57	8.19	7

No. – number of samples, Mean – mean amount of green biomass, STD – standard deviation, VC – variability coefficient

atmosphere. One of the basic advantages of this technique is its simplicity and relatively small measurement spatial scale (about 1 m^2) [34]. The measurements were conducted both by applying transparent (NEP), and non-transparent (R_{ECO}) measuring cuboid-shaped chambers of the size 77 cm×77 cm×50 cm.

In order to apply the measurement technique described above in the studied sedge community, three neighboring collars (soil seals) were installed in the substrate 10 cm below the surface (52º45' 35.430 N/16º18' 34.948 E – coordinates of the middle collar). The application of collars prevents carbon dioxide leakage from the chamber during measurements.

The carbon concentration changes in air was measured with a CO_2 infrared gas analyzer (LI-820, Licor, USA) with flow rate of 600 $ml \cdot min^{-1}$ [35].

The measurements on this site were conducted at irregular intervals (about every 3 weeks), because the interpolation methodology for periods between the measurements required that observations should be carried out in cloudless weather conditions. The parameters obtained on sunny days were used for modeling fluxes in the periods between the measurement sessions [36].

Particular measurement sessions consisted of several single measurements. Each closure of the chamber lasted a few (1-3) minutes. These measurements were conducted throughout the whole day [37].

Such an approach aimed at obtaining the characteristics of CO_2 exchange processes between the sedge community and the atmosphere at various quantities of the shortwave radiation flux density and air temperature.

Biomass Sampling and Analysis

In order to obtain the information regarding the course of sedge community biomass growth 22 April to 20 October 2009, the following strategy of biomass sampling was applied. The analysis was carried out on the surface of the sedge community, not far from the wooden walkway, about 20 m from the chamber measurements site. The designated research area was located along the wooden walkway and consisted of 9 transects adjacent to one another, each of which was 1 meter wide and 4.5 m long. 5 plots of width 0.5 m and located 0.5 m apart were designated on each of the transects. Individual samples were obtained by aboveground biomass harvesting, from the plot of the size 50 cm × 50 cm. The number of plots harvested for biomass was 3 (April 22, May 13, September 16, October 21) or 9 (June 15, July 14, August 17) [26]. The mass samples were always collected from different plots (Fig. 2).

The collected biomass was split into species. Then, in the batches obtained in this way, living (green) and dead (brown) biomass were separated. The harvested biomass was dried to constant weight at 105ºC and weighed to determined the amount of biomass per m^2 (Table 1).

For each of the sample series from the particular collection date (i), average quantity of green biomass was calculated ($\overline{b}_i^G$).

The calculated average green biomass for the particular date in which the samples were collected was converted into carbon equivalent for each date of biomass measurement (i) according to the following formula:

$$c_i = \varphi_C \cdot b_i \tag{2}$$

c_i – green biomass carbon equivalent [$g \cdot m^{-2}$]
φ_C – carbon content 0.4362 [dimensionless]*
b_i – average green biomass [$g \cdot m^{-2}$]
*no carbon content for *Carex elatea* was available, therefore φ_C value for *Carex acutiformis* (0.4362) was used in order to calculate it [38].

Growing Season Carbon Flux Calculations

Chamber measurements provided data that was a basis for calculating the parameters of a hyperbolic function that

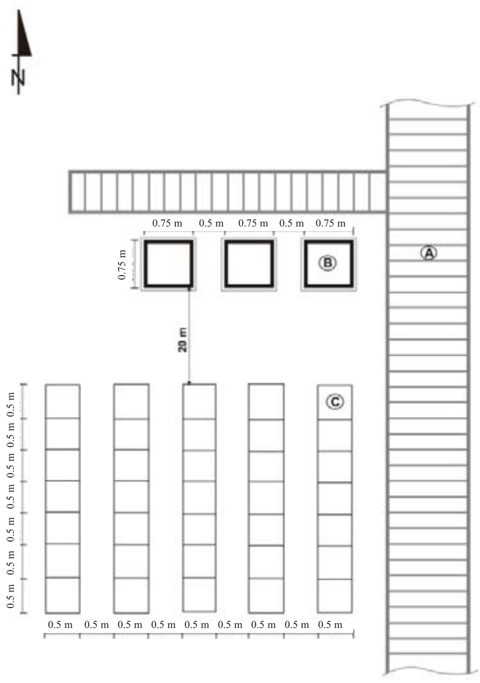

Fig. 2. Map of study site (A – wooden walkway, B – collar, C – biomass plot).

enables us to assess the amount of net ecosystem exchange flux density (NEE) on the basis of PPFD [36]. Also, the parameters of Lloyd & Taylor function [39] were calculated, the one which was applied to describe the relationship between R_{ECO} value and soil temperature between measuring sessions [35].

The parameters of individual equations of CO_2 exchange for the studied sedge community obtained in this way for each session were interpolated (by application of the linear function) for the periods between individual chamber measurement sessions.

Mean half-an-hour values of temperature, soil, and PPFD gathered at the meteorological station in Rzecin were used to calculate individual values of NEE and R_{ECO} fluxes for the period between the measurement sessions.

The obtained data were applied to calculate average daily sums of NEE, R_{ECO}, and GPP. Cumulated GPP (GPP_{cum}) sum was calculated for the whole year and sums of daily GPP (C_i^{GPP}) quantities for the periods between each biomass sampling sessions (i) were calculated according to the following formula:

$$C_i^{GPP} = \sum_{i-1}^{i} GPP \quad (3)$$

...where: C_i^{GPP} – carbon absorbed from the air between i–1 and i chamber measuring sessions [g·m^{-2}].

Calculations of Green Biomass Carbon Uptake

Average green biomass carbon equivalent was calculated for individual periods between each biomass sampling session (i)

$$\bar{C}_i = \frac{c_{i-1} + c_i}{2} \quad (4)$$

...where: $\bar{C}_i$ – average green biomass carbon equivalent increment for period between each biomass sampling [g·m^{-2}].

The sum of global radiation that reached the sedge community surface in the period between each biomass sampling, calculated using the following equation:

$$R_i^g = \sum_{i-1}^{i} r_d^g \quad (5)$$

R_i^g – sum of global radiation for period between each biomass sampling [MJ·m^{-2}]

r_d^g – daily sum of global radiation [MJ·m^{-2}·d^{-1}].

The increase of green biomass carbon in the total carbon accumulated in that time in the process of its absorption from the atmosphere (α_i^C) was calculated as follows:

$$\alpha_i^C = \frac{c_{i-1} + c_i}{C_i^{GPP}} \quad (6)$$

We assumed that the sum of carbon absorbed by plants (C_i^{GPP}) in a given area is proportional to the average amount of green biomass ($\bar{C}_i$), the sum of global radiation energy reaching the surface (R_i^g), and the length of the period in which the process takes place (D_i).

$$C_i^{GPP} = \beta_i^C \cdot \bar{C}_i \cdot R_i^g \cdot D_i \quad (7)$$

...where:

β_i^C – green biomass carbon uptake efficiency [μg·g^{-1}·MJ^{-1}·m^{-2}·d^{-1}]

D_i – the length of period between each biomass collection [day]

The capacity of carbon absorption by green biomass (uptake efficiency) is described in the formula above by the value of green biomass carbon uptake efficiency (β_i^C). Its value was calculated by applying the following formula:

$$\beta_i^C = \frac{10^6 \cdot C_i^{GPP}}{\bar{C}_i \cdot R_i^g \cdot D_i} \quad (8)$$

The β_i^C describes the carbon uptake capacity of one gram of green biomass carbon found on one square meter, at the moment when 1 MJ of energy in the form of global radiation reaches it.

This methodology is similar to the commonly used light use efficiency (LUE) approach, but β_i^C describes rather carbon uptake capacity in relation to green biomass of studied vegetation type at different stages of development, while LUE is net ecosystem exchange parameter related to leaf area index (LAI).

Results

Meteorological Conditions

For the studied period in 2009 the following monthly average values were calculated: air temperature ($t^a_{m,2009}$), sum of global radiation ($R^g_{m,2009}$), and sum of precipitation ($P_{m,2009}$), which were compared with corresponding multiannual average values (Table 2). The year 2009 can be described as wet and the sum of precipitation of 705.2 mm significantly exceeds the average annual (calculated for 1951-2000 period) value (566 mm). Average annual temperature in 2009 (8.2ºC) is very close to the multiannual (calculated for 1971-2000) average temperature (8.0ºC), thus the studied year can be considered mild in terms of temperature. The sum of radiation 3845.4 MJ·m^{-2} in 2009 significantly exceeds multiannual (calculated for 2004-10) sum of radiation 3589.3 MJ·m^{-2}. Therefore, 2009 can be considered as favorable for plants in terms of radiation (Table 2).

July was the only month in the studied period in which monthly sum of radiation, average temperature, and sum of precipitation were higher than multiannual average values.

Average monthly temperature and global radiation were higher than corresponding multiannual values in April, August, and September. The sums of both radiation and precipitation in May, while only sums of precipitation in June and October, were higher than average climatic values. The remaining monthly values of the meteorological characteristics were lower than climatic ones.

Table 2. Climatic and meteorological data for Rzecin site.

Month	t_m^a**	$t_{m,2009}^a$	t	R_m^g***	$R_{m,2009}^g$	*R*	P_m****	$P_{m,2009}$	*P*
	°C	°C		MJ·m^{-2}	MJ·m^{-2}		mm	mm	
1	-1.3	-3.2	-	60.1	80.5	+	38	26.4	-
2	-0.5	-0.7	-	92.1	89.9	-	31	52.8	+
3	2.8	3.4	+	251.9	230.3	-	34	74.4	+
4	7.2	10.5	+	456.8	602.4	+	37	19.6	-
5	13.0	12.5	-	553.5	556.8	+	52	92.0	+
6	16.1	15.0	-	577.3	503.4	-	67	102.4	+
7	17.9	18.7	+	539.2	549.5	+	75	90.0	+
8	17.2	18.0	+	446.0	567.0	+	60	41.8	-
9	12.6	13.9	+	330.5	380.3	+	46	42.4	-
10	7.9	6.6	-	176.1	149.0	-	39	68.6	+
11	3.0	5.6	+	68.7	95.5	+	40	50.2	+
12	0.3	-1.1	-	37.1	40.8	+	47	44.6	-
Year	8.0	8.2	+	3589.3	3845.4	+	566	705.2	+

t_m^a – monthly average air temperature, $t_{m,2009}^a$ – monthly average air temperature for 2009, R_m^g – monthly sum of global radiation, $R_{m,2009}^g$ – monthly sum of global radiation for 2009, P_m – monthly total precipitation, $P_{m,2009}$ – monthly total precipitation for 2009 (gray background indicates comparison 2009 values with climatic one).
** – temperature values were calculated 1971-2000
*** – radiation values were calculated 2004-2010
**** – precipitation values were calculated 1951-2000
'+' – the 2009 average value higher than climatic average
'-' – the 2009 average value lower than climatic average

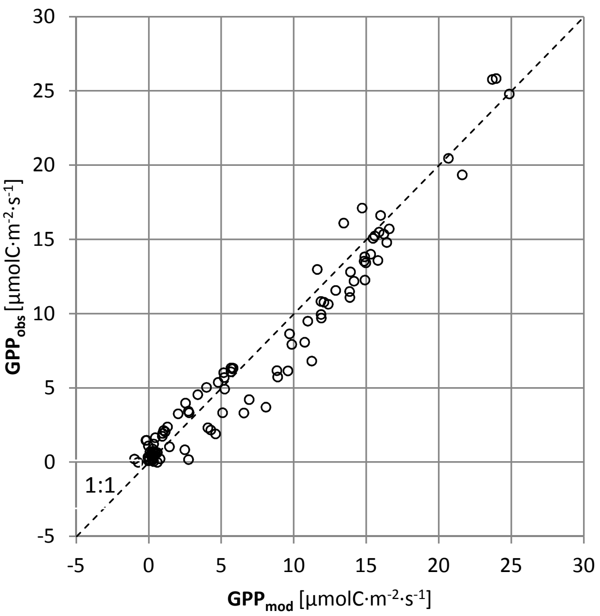

Fig. 3. Modeled (GPP$_{mod}$) versus observed (GPP$_{obs}$) half hour average Gross primary production values of sedge community at Rzecin wetland in 2009.

Chamber Measurements

The carbon fluxes of the studied sedge community were calculated for 2009 since the good agreement between modeled and measured GPP values were found (Fig. 3). The highest values of GPP was 13.50 g·m^{-2}·d^{-1}, while the lowest R_{ECO} was equal to -10.64 g·m^{-2}·d^{-1}. The GPP values are higher in the first half of the vegetation season, while R_{ECO} was higher in the second half of this period.

This resulted in positive (maximum 5.57 g·m^{-2}·d^{-1}) values of NEP in the first half of the vegetation season and negative (minimum -3.73 g·m^{-2}·d^{-1}) in the second half (Fig. 4).

Green Biomass Production and GPP

The seasonal course of green biomass carbon equivalent values in the sedge community is typical for plants and its highest value was observed during the measurements conducted on 17 August 2009 (174.26 g·m^{-2}). Culmination of GPP was observed earlier, i.e. at the beginning of July (3 July 2009 13.48 g·m^{-2}·d^{-1}). Since the beginning of July (most likely since blossoming), GPP decreases despite further increases of green plant biomass (Fig. 2).

Table 3. Sedge community characteristics during 2009 vegetation season at Rzecin wetland.

Date	GPP_{cum}	C_i^{GPP}	b_i	B_i	c_i	C_i	R_i^g	D_i	α_i^C	β_i^C
	g·m-2	g·m-2	g·m-2	g·m-2	g·m-2	g·m-2	MJ·m-2	d	g·g-1	μg·g-1·MJ-1·m-2·d-1
22.04.09	38.8		25.25		11.02					
13.05.09	126.8	88.08	68.57	43.32	29.91	20.46	417.32	21	0.21	491.2
15.06.09	375.1	248.27	229.27	160.70	100.01	64.96	575.86	33	0.28	201.1
14.07.09	679.8	304.72	315.89	86.62	137.79	118.90	505.06	29	0.12	175.0
17.08.09	930.7	250.90	399.49	83.60	174.26	156.03	618.04	34	0.15	76.5
16.09.09	1059.0	128.28	356.49	-43.00	155.50	164.88	447.95	30	-0.15	57.9
21.10.09	1112.2	53.21	109.57	-246.92	47.80	101.65	304.31	35	-2.02	49.1

GPP_{cum} – cumulated GPP since 1 January 2009 [g·m^{-2}]; C_i^{GPP} – carbon absorbed from the air between i–1 and i chamber measuring sessions [g·m^{-2}]; b_i – average green biomass [g·m^{-2}]; B_i – average green biomass increment for period between biomass sampling [g·m^{-2}]; c_i – green biomass carbon equivalent [g·m^{-2}]; C_i – average green biomass carbon equivalent increment for period between each biomass sampling [g·m^{-2}]; R_i^g – sum of global radiation for period between biomass sampling [MJ·m^{-2}]; D_i – period between each biomass sample collection [d]; α_i^C – green biomass carbon equivalent share in accumulated GPP for period between biomass sampling [g·g^{-2}]; β_i^C – green biomass carbon uptake efficiency [μg·g^{-1}·MJ^{-1}·m^{-2}·d^{-1}]

Values of the coefficient that describe the amount of carbon absorbed in the process of photosynthesis and accumulated in green biomass α_i^C (green biomass carbon equivalent share in accumulated GPP) fluctuate in the vegetation season. Maximum value of this coefficient was noticed in June (0.28), and since then a distinctive and significant downward trend of α_i^C value was observed. In September and October values of this coefficient are negative, which stems from the decrease of green biomass amount (Table 3).

The parameter describing the carbon absorption capacity of one gram of carbon in the form of biomass β_i^C (green biomass carbon uptake efficiency) was also calculated. For individual periods between biomass sampling it was concluded that plant absorption capacity of green biomass β_i^C decreases during the whole vegetation season from 491.2 to a value tenfold lower at the end of the vegetative season 49.1 μg·g^{-1}·MJ^{-1}·m^{-2}·d^{-1} (Table 3).

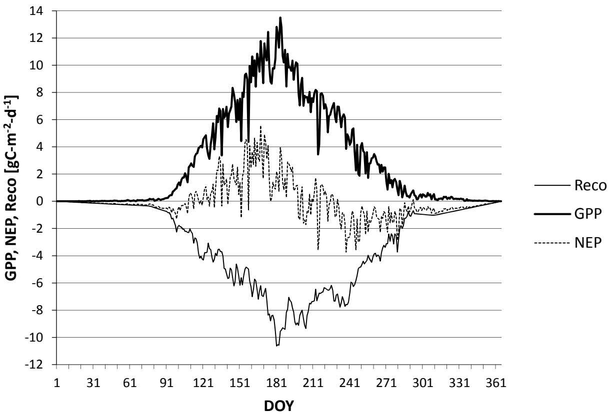

Fig. 4. Yearly run of modeled daily carbon fluxes exchange between sedge community and the atmosphere at Rzecin wetland in 2009 (Reco – Ecosystem respiration, GPP – Gross primary productivity, NEP – Net ecosystem productivity, DOY – Day of the year).

The biomass was sampled only during one year. The multiannual studies of Rzecin sedges could not be carried out longer because of field labor limitations.

Discussion

The accuracy of chamber measurements has been widely discussed both in the context of the measurement technique [40-42] and methodology of calculation [43]. However, it is widely recognized as a valuable technique for gas exchange estimation [33].

The value of α_i^C expresses the quantity of green biomass carbon equivalent share accumulated in green plant biomass. Values of α_i^C in the period from April to August were positive, which indicated the increase of green biomass amount in the environment. Carbon that accumulated in shoots did not exceed 28% of the total carbon absorbed from the atmosphere in that time. The smallest positive quantity was 15%, which means that 85% of carbon absorbed in that time was most probably accumulated in root mass or was used for autotrophic plant respiration processes. From August to October the value of α_i^C is negative, which indicates (lack of growth) the green biomass amount decrease. Therefore, considerations regarding accumulation of carbon from the atmosphere in green plant parts in that period are pointless. However, in that period the absorption of carbon from the air was still taking place (positive values of GPP) and it seems that the total amount of carbon bound by plants in the process of photosynthesis was accumulated in root mass and used for autotrophic respiration (preparation for winter).

The other coefficient calculated on the basis of field measurements was β_i^C, during the whole studied vegetation season the decrease of its value was observed. This may stem from the following reasons:

- Mutual reduction of access of individual shoots to radiation energy resulting from the growth of shoot mass.

  Young shoots grow in conditions of relatively small shade because shoots that grew in the previous year are strongly bent down after winter (horizontal position). The increase of green biomass causes light completion among the shoots, which may be an explanation for the β_i^C value decrease.
- Running out of mineral compounds in the environment.

  While changes in shoot growth dynamics are caused by a decrease of nitrogen compounds in the environment [22], the influence of the same factor (nitrogen limitation) on the Rzecin sedge community biomass capacity to absorb CO_2 from the atmosphere is disputable due to the lack of available nitrogen-related data.
- Water stress of plants.

  It seems that water stress is an unlikely cause of the decrease in β_i^C decrease. This assumption results from two facts: sedge communities are usually well adapted to high fluctuations of the groundwater table, although the sum of precipitation in the sedge community in August was lower than the multiannual average, and June and July turned out to be very wet months. Therefore, it seems that this factor did not limit the capacity of plants in the sedge community to absorb CO_2 from the atmosphere.
- Aging of shoots.

  This process seems to be the most probable explanation for the phenomenon of decreased β_i^C during the vegetative season. With age, individual shoots lose their capacity of binding CO_2 from air in the process of photosynthesis. Although it is still unknown what might be the cause [44] of this phenomenon, it seems to be the most important factor leading to a decrease in CO_2 uptake by this plant community.

Both α_i^C and β_i^C values can vary, since green biomass variability (even 51%) (Table 1) and all applied environmental characteristic variabilities need further study.

Conclusions

The obtained measurements lead to the conclusion that in the Caricetum elatae community only a small part of carbon absorbed during photosynthesis is accumulated in green aboveground biomass (maximum α_i^C for growing green biomass was 0.28).

The capacity of CO_2 absorption by the studied sedge community during the vegetative season decreases tenfold from 491.2 to 49.1 $\mu g \cdot g^{-1} \cdot MJ^{-1} \cdot m^{-2} \cdot d^{-1}$. The most likely explanation of this fact seems to be aging of shoots.

The proposed method of the systematic description of plant community capacity to absorb carbon dioxide may be successfully applied for research in other environments of this kind. It seems that the application of β_i^C may be the basis of modeling and remote sensing assessment of plant communities' capacity to absorb CO_2 from air.

Units and Terminology

GPP – gross primary production [$g \cdot m^{-2} \cdot d^{-1}$]
GPP_{cum} – cumulated GPP since 1 January 2009 [$g \cdot m^{-2}$]
NEP – net ecosystem production [$g \cdot m^{-2} \cdot d^{-1}$]
R_{ECO} – ecosystem respiration [$g \cdot m^{-2} \cdot d^{-1}$]
c_i – green biomass carbon equivalent [$g \cdot m^{-2}$]
C_i – average green biomass carbon equivalent increment for period between biomass samplings [$g \cdot m^{-2}$]
φ_C – carbon share 0.4362 [dimensionless]
$\overline{b}_i$ – average green biomass [$g \cdot m^{-2}$]
C_i^{GPP} – carbon absorbed from the air between i–1 and i chamber measuring sessions [$g \cdot m^{-2}$]
R_i^g – sum of global radiation for period between biomass samplings [$MJ \cdot m^{-2}$]
r_d^g – daily sum of global radiation [$MJ \cdot m^{-2} \cdot d^{-1}$]
α_i^C – green biomass carbon in accumulated GPP for period between biomass sampling [$g \cdot g^{-1}$]
β_i^C – green biomass carbon uptake efficiency [$\mu g \cdot g^{-1} \cdot MJ^{-1} \cdot m^{-2} \cdot d^{-1}$]
t_m^a – monthly average air temperature [ºC]
$t_{m,2009}^a$ – monthly average air temperature for 2009 [ºC]
R_m^g – monthly sum of global radiation [$MJ \cdot m^{-2}$]
$R_{m,2009}^g$ – monthly sum of global radiation for 2009 [$MJ \cdot m^{-2}$]
P_m – monthly total precipitation [mm]
$P_{m,2009}$ – monthly total precipitation for 2009 [mm]

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