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Aerobic and anaerobic respiration in profiles of Polesie Lubelskie peatlands

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A b s t r a c t. Soil respiration is a very important factor influencing carbon deposition in peat and reflecting the intensity of soil organic matter decomposition, root respiration, and the ease of transporting gases to the surface. Carbon dioxide release from three different peat soil profiles (0-80 cm) of the Polesie Lubelskie Region (Eastern Poland) was analyzed under laboratory conditions. Peat samples were incubated at 5, 10, and 20°C in aerobic and anaerobic environments, and their CO_2-evolution was analyzed up to 14 days. The respiration activity was found to be in the range of 0.013-0.497 g CO_2 kg^{-1} DW d^{-1}. The respiratory quotient was estimated to be in the range of 0.51-1.51, and the difference in respiration rates over 10°C ranged between 4.15 and 8.72 in aerobic and from 1.15 to 6.53 in anaerobic conditions. A strong influence of temperature, depth, the degree of peat decomposition, pH, and nitrate content on respiration activity was found. Lack of oxygen at low temperature caused higher respiration activity than under aerobic conditions. These results should be taken into account when the management of Polish peatlands is considered in the context of climate and carbon storage, and physicochemical properties of soil in relation to soil respiration activity are considered.

K e y w o r d s: peat ecosystem, aerobic and anaerobic respiration, carbon dioxide

INTRODUCTION

Soils store twice as much carbon as there is in the atmosphere (Kellman *et al*., 2007). In the carbon cycle, soil rhizosphere respiration and photosynthesis play a crucial role, making it a multidisciplinary subject for study that is of concern not only to ecologists, soil scientists, microbiologists, and agronomists but also to atmospheric scientists and biogeochemists. Carbon dioxide is releazed from soil *via* roots and microbial respiration in an ecosystem biological process. Respiration of soil organic matter is an important but poorly understood part of the carbon (C) budget of peatlands due to much higher heterogeneity of peatlands in the world. It is estimated that as a result of soil respiration, about 75-80 Gt of carbon per year is emitted globally to the atmosphere, which is nearly one half of the gross primary productivity of terrestrial ecosystems and about 10% of the total atmospheric carbon (Drake *et al*., 2012). Organic matter is decomposed to CO_2 under aerobic conditions and therefore the rate of CO_2 efflux is commonly used as a measure of total soil respiration in terrestrial ecosystems. Laboratory CO_2 production potentials can isolate soil microbial respiration (often referred to as heterotrophic respiration) from respiration of living roots and rhizomes, and provides a direct measurement of decomposer activity. Removal of plants and plant roots from investigated soils connected with controlling CO_2 concentration in the headspace gives a view of microbial activity in these soils (Drake *et al*., 2012; Minkkinen *et al*., 2007). In that approach, CO_2 production is one of the biological indicators of soil conditions because organic matter hosts microbial activity. Aerobic and anaerobic decomposers use organic matter as a source of nutrients and energy for their growth and functioning (Gajda and Przewłoka, 2012., Gajda *et al*., 2013; Šantrůčková *et al*., 2010).

Studies on the processes and factors controlling soil carbon cycling and gaseous end products in soil, and especially in peatlands, which mainly consist of carbon (40-60%), can serve as useful analogues to potential changes in soils under a warming climate because relatively small changes in soil respiration rates may alter the atmospheric concentration of CO_2 as well as the rates of soil carbon sequestration.

In submerged soils, low oxygen diffusion limits oxic and enhances anoxic zones. In peat soils, deeper layers of the profile stay anoxic. Aerobic microorganisms are believed to be capable of decomposing organic matter completely,

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while in anaerobic decomposition mutualistic consortia participate because no single type of anaerobic bacteria seems to be capable of complete mineralization. Submerged conditions cause slower mineralization of organic matter in comparison to aerobic conditions. Some researchers have shown that in anoxic conditions degradation of organic matter was 5 to 10 times slower than in an oxic environment (Kristensen and Holmer, 2001). When there is a lack of oxygen, some microorganisms can utilize alternative electron acceptors, such as a SO_4^{-2}, NO_3^-, Fe_3^+ and Mn_4^+, or humic substances contained in dissolved organic matter (Keller and Takagi, 2013), in the process of soil carbon mineralization (Dilly, 2003; Kristensen and Holmer, 2001). An increase in soil temperature is connected with an increase in the soil respiration activity. The temperature response of CO_2 is modified by substrate quality, which means how easily carbon in the soil organic matter can be mineralized. Generally, two kinds of carbon substrates in soil are distinguished: labile (easily mineralized) and recalcitrant. A more common theory based on thermodynamic considerations is that the decomposition of recalcitrant soil organic matter should have higher temperature sensitivity than labile, because recalcitrant soil organic matter requires higher activation energy and a larger number of enzymatic steps than labile forms (Gershenson *et al*., 2009).

Most studies focused on CO_2 release from peatlands do not examine the peat profile from the surface to below the water table but only from the surface level, meanwhile CO_2 emission from peat is to a greater or lesser extent a result of respiration of organisms inhabiting the whole profile. In peatlands, the groundwater table is changeable because of weather conditions and human activity (agriculture, drainage, soil cultivation in adjacent areas). As a result, some parts of profiles become aerated whilst other remain anaerobic during the year. Peatlands from the different sites of the world are the subject of many investigations. There is still insufficient data about microbiological processes in Polish peatlands that describe their state and changes. Understanding the mechanisms controlling aerobic and anaerobic respiration at small scales is particularly valuable because it allows us to improve our predictions of the tendency to atmospheric carbon storage and potential effects of climate changes. The potential for carbon release in objects even from a small-area region can be very diverse, despite the small distance from each other.

Therefore, this study focused on laboratory experiments on peat soil respiration in three types of Polesie Lubelskie Region peatlands, which differ in terms of water conditions in situ. The objective of this study was to determine:

– the respiration activity (RA) of peat soils from the 0-80 cm profile in aerobic-natural moisture (AE) and anaerobic-flooded (AN) conditions,
– the difference in respiration rates over 10°C (Q10) as a temperature sensitivity ratio and respiratory quotient (RQ) values,
– the relative importance of forms of nitrogen, substrate (carbon) availability, acidity, salinity, temperature, and layer deposition in the peat profile to aerobic and anaerobic RA. This work provides useful information about the role of Polish eastern peatlands in carbon release into the atmosphere and gives arguments in the discussion about the future development of peatlands.

MATERIALS AND METHODS

The sampling points were located in the Polesie Lubelskie Region (Eastern Poland). The sites were chosen to represent the genetically different types of peatland characteristics for the territory of Poland and, according to the Polish classification, belonging to low, transition, and high moor peatlands.

The Garbatówka site (51° 21' N, 23° 6' E) was selected as a representative of low moor peat (L), with numerous pools and a high groundwater level (from -10 to 0 cm) for a greater part of the year. The vegetation mainly comprises *Carex* spp., *Juncus* spp., *Schoenoplectus* spp., and various non-sphagnum mosses, in contrast to trees and shrubs, which were represented by *Betula* spp. and *Salix* spp.

Orłowskie Peatland (51° 25' N, 23° 3' E), representing a transition moor peat (T), is characterized by water supply mainly from rainfall and from the adjoining Lake Łukie (ground water at -20 cm). The commonly present species include *Poa pratensis, Festuca rubra, Deschampsia caespitose, Rumex acetosa* and, locally, shrubs with *Salix lapponum* and *Salix myrtilloides*.

High moor peat (H) of lacustrine origin was located in the centre of a palustrine forest adjoining Lake Moszne (51° 27' N, 23° 6' E), where water is only supplied by rainfall, so that in the warm season a decline in moisture is observed in the surface layer (groundwater level below the depth of 30 cm). The vegetation is dominated by *Vaccinium uliginosum, Ledum palustre, Eriophorum vaginatum*, a great number of peat mosses (*eg Sphagnum acutifolium, Sphagnum magellanicum*), shrubs and trees such as *Pinus sylvestris, Betula pubescens, Quercus robur, Populus tremula*, *Betula pendula* (Wojciechowski and Szczurowska, 2002).

Peat material was collected in summer 2007 from three representative plots in every peatland. After removing plants from the soil surface, peat samples (large blocks) were taken from the soil profile by excavating the soil pit and removing layers of 20 cm thickness from the surface to the depth of 80 cm, which gave samples from the 0-20, 20-40, 40-60, and 60-80 cm layers (a total of nine pits were made). Peat portions were placed in plastic containers and tightly closed. The samples were stored in the laboratory at 4°C in the dark, and after a few days were subjected to analyses.

pH, decomposition of organic matter, salinity, water content, total organic carbon, and bioavailable nitrogen forms were analyzed in the collected samples.

The dry mass of the peat material and its water content (n=3 for each layer) were determined by weighing peat before and after drying at 105°C for 48 h (Szafranek-Nakonieczna and Bennicelli, 2010). The decomposition degree of peat was classified from H_1 (peat being pristine, unrecompensed, and fibrous) to H_{10} (fully decomposed, humified peat) on the basis of the von Post scale (Glatzel *et al*., 2004). Soil pH was determined in aqueous solution (1:1 (w/v) soil to water ratio), after 30 min of shaking and free sedimentation of soil particles (1 h) according to EPA SW-846 Method 9045 (Szafranek-Nakonieczna and Bennicelli, 2010). Electrolytic conductivity (EC) was measured by connecting an electrode p/n 51970-00 with a pIONeer 65 meter (Radiometer Analityca S.A.), and expressed as μS cm^{-1}. Bioavailable forms of nitrogen (nitrate, ammonia) were measured in peat extracts using an AA3 (Braun+Luebbe, Germany) analyzer, after filtering through filter paper (Munktell, grade 390, Germany). In order to determine NO_3-N, peat-water (1:3) extraction was prepared after shaking for 2 h. In the case of NH_4-N, 0.2 mol NaCl was used as an extractant (3:1 extractant-to-peat, 2h shaking) (Banach *et al*., 2009). Total organic carbon was determined in dry peat samples by TOC-VCSH with a SSM-5000A module (Shimadzu, Japan).

Peat samples from each sampling point and layer were incubated under atmospheric conditions and natural moisture (AE), as well as under a helium atmosphere associated with flooded conditions (AN) at three temperatures: 5, 10, and 20°C for 14 days. The incubation temperatures were selected on the basis of mean air seasonal temperatures to test the peat soil efficiency in carbon release in particular seasons of the year (spring 12, autumn 6, and summer 19°C) in the investigated region (Szafranek-Nakonieczna and Bennicelli, 2010).

Fresh peat subsamples (10 g of hand-mixed 20 cm layers of peat with roots removed, from three pits in each of the tested peatland) were placed in dark, sterile bottles (60 ml) and tightly closed. For the anaerobic combinations (AN), air was removed by flushing with helium (15 min, 4.5 N, Praxair, Poland) and complete flooding with deionized water. For each combination, three replications were prepared. Throughout the experiment, the bottles remained closed, which prevented air change and water evaporation.

In the AE combinations, the O_2 concentration decreased during the time of the experiment, but at the end, it did not drop below 5% (v/v), which guaranteed that soil respiration was not hampered by lack of oxygen.

The levels of accumulated CO_2 and O_2 were analyzed in the head space by means of a gas chromatograph (Varian CP-3800, USA, equipped with a thermal conductivity detector – TCD (120°C) and two types of columns: Poraplot Q (25 m) and a molecular sieve 5A (30 m) connected together and at 40°C) at the start of the incubation and then after 3, 7, 10, and 14 days, always in triplicate (Bennicelli *et al*., 2009; Szafranek-Nakonieczna and Bennicelli, 2010).

Respiration activity (RA) was expressed as a mass of produced carbon dioxide per mass of dry peat used in the experiment and per unit of time (g CO_2 kg^{-1} DW d^{-1}). Q10 values, representing the difference in respiration rates over a 10°C temperature interval, were calculated according to equation:

$$Q10 = (R2/R1)^{10/(T2-T1)}$$

where: R1 and R2 are measured respiration rates at temperatures T1 and T2, respectively (Graf *et al*., 2008).

The RQ for peat incubated aerobically was calculated as the ratio of mole CO_2 evolved to O_2 consumed (Brzezińska, 2006; Dilly, 2003).

Statistical analyses of the data obtained (ANOVA, analysis of regression) were performed using Statgraphics Plus 3.0.

RESULTS

Data from the physicochemical analyses are presented in Table 1. The investigated layers of peat profiles differ from each other in the particular peats in almost all of the tested parameters.

The highest decomposition degree of peat characterized the material from Orłowskie Peatland (transition) and ranged from H_4 to H_7 in the Von Post ranking, while the freshest peat was found at Garbatówka (low peatland). The most acidic peat occurred at the high peatland, where the average pH reached 3.4, while the others were around 6.4 (transition) and 6.8 (low). Water content generally increased with depth; the highest differences between the layers were observed at the high peatland where, in the deepest layer (60-80 cm), the moisture was 24% lower than at the surface (0-20 cm). In the transition peatland, it was only 13% lower, whereas in the low peatland the difference was very small. The highest content of total organic carbon (TOC) was found in the layers of the high peatlands; in the low peatland, it was by about 20% lower. All the layers differed in salinity, which was strong at the surface level at the transition and high peatlands and at the subsurface in the low peatland. In the case of bioavailable forms of NO_3-N, very high values were found in the low peatland - from the layers of 40-60 and 60-80 cm, *ie* double that at depths of 0-20 and 20-40 cm, 2-3 times higher than in the transition peatland, and 11-34 times more than in the particular layers of the high peatland. A surprisingly high NH_4-N content was observed in the high peatland, where it was 6 times higher than in the low and transition peatlands, where NH_4-N was at a comparable level.

After two weeks of incubation, respiration activities were calculated. The results are presented in Table 2. RA ranged from 0.018 to 0.497 and from 0.013 to 0.227 g CO_2 kg^{-1} DW d^{-1} in the aerobic and anaerobic conditions, respectively.

Anaerobic conditions in most cases caused a considerable, statistically significant reduction of respiratory processes (Table 3). When peat soil microorganisms had free

T a b l e 1. Characteristics of the peat profiles

Type of peatland	Depth (cm)	Von Post ranking	pH (H_2O)	Water content (g kg^{-1})	TOC (g kg^{-1} DW)	EC (μS cm^{-1})	NO_3-N	NH_4-N
							(mg kg^{-1} DW)	
L	0-20	H_2a	6.93c	855.69c	427.00c	185.70a	4.34a	5.62a
	20-40		6.80b	841.29a	392.00a	268.30d	4.79a	5.84a
	40-60	H_3b	6.83b	853.45b	449.10d	211.00c	8.36b	5.63a
	60-80		6.7a	869.76d	418.20b	205.00b	9.9b	5.18a
T	0-20	H_4a	6.17a	739.44a	411.51a	278.30d	4.30c	5.8a
	20-40	H_5b	6.44b	800.18b	467.32b	159.20b	2.93a	5.61a
	40-60	H_6c	6.52c	849.19c	517.43c	145.00a	3.09a	5.46a
	60-80	H_7d	6.53c	851.44d	510.63c	182.70c	3.87b	5.74a
H	0-20	H_3a	2.87a	664.08a	501.11a	320.70d	0.29b	44.53c
	20-40	H_4b	2.98b	758.85b	513.74b	309.30c	0.46a	24.05a
	40-60	H_5c	3.36c	869.61c	541.70d	190.70b	0.45a	17.87a
	60-80	H_6d	3.43d	877.89d	528.82c	109.00a	0.79c	32.65b
All profiles	L	$H_{3.5}$a	6.83c	855.05a	421.83a	217.50a	6.86c	5.57a
	T	$H_{5.5}$b	6.42b	810.06a	476.72b	191.32a	3.55b	5.70a
	H	$H_{4.5}$b	3.16a	792.79a	521.34c	232.42a	0.50a	29.80b

L – low moor, T – transition peatlands, H – high peatlands. Figures followed by the same letter do not differ significantly ($p>0.05$).

T a b l e 2. Respiration activity (RA) of particular peat materials

Type of peatland	Depth (cm)	RA (g CO_2 kg^{-1} DW d^{-1})					
		AE			AN		
		5	10	20	5	10	20
		(°C)					
L	0-20	0.033c	0.057c	0.497d	0.032b	0.052c	0.127d
	20-40	0.035c	0.063d	0.424c	0.030ab	0.060d	0.101c
	40-60	0.026b	0.037a	0.225b	0.032ab	0.030b	0.052a
	60-80	0.020a	0.041b	0.170a	0.029a	0.013a	0.059b
T	0-20	0.044c	0.069c	0.443c	0.030c	0.037b	0.146d
	20-40	0.033b	0.069c	0.310b	0.023b	0.032a	0.116c
	40-60	0.028a	0.052b	0.218a	0.028c	0.042c	0.077b
	60-80	0.031b	0.038a	0.228a	0.019a	0.042c	0.049a
H	0-20	0.032c	0.051d	0.238b	0.025a	0.049b	0.227c
	20-40	0.024b	0.042c	0.253b	0.023a	0.019a	0.124b
	40-60	0.018a	0.037b	0.245b	0.041b	0.018a	0.113b
	60-80	0.023b	0.034a	0.154a	0.041b	0.016a	0.065a

AE – aerobic condition, AN – anaerobic condition (± SE, n=3) as a function of temperature. Other explanations as in Table 1.

T a b l e 3. Anaerobic respiration as a percentage of aerobic respiration and differences in respiration activity between the AE and AN treatments

Type of peatland	Depth (cm)	AN as % of RA in AE conditions		
		5	10	20
		(°C)		
L	0-20	97 n.s.	91*	26***
	20-40	86**	95**	24***
	40-60	123**	81***	23***
	60-80	145***	32***	35***
	0-80	113	75	27
T	0-20	68**	54***	33***
	20-40	70 n.s.	46***	37***
	40-60	100**	81***	35***
	60-80	61***	111***	21***
	0-80	75	73	32
H	0-20	78***	96 n.s.	95 n.s.
	20-40	96 n.s.	45***	49***
	40-60	227***	49***	46***
	60-80	178***	47***	45***
	0-80	145	59	59

Indicate statistically significant differences at *p<0.05, **p<0.01, ***p<0.001 levels. Other explanations as in Tables 1 and 2.

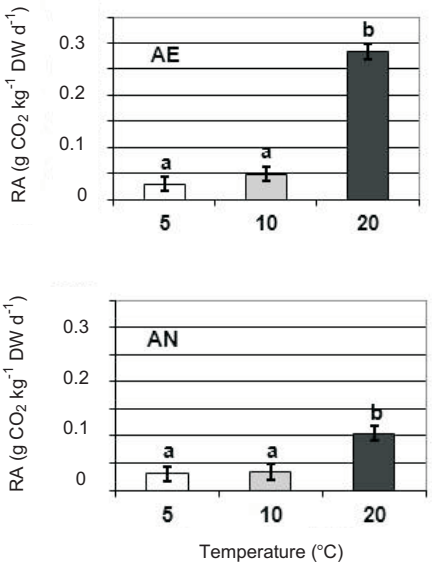

Fig. 1. Influence of soil temperature on respiration activity (RA) of peat material under aerobic (AE) and anaerobic (AN) conditions. Error bars indicate the 95% confidence interval. Figures followed by the same letter do not differ significantly (p>0.05).

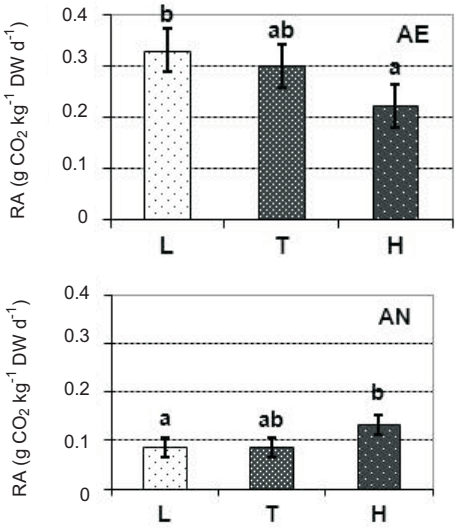

Fig. 2. Respiration activity of peat material (0-80 cm) under aerobic (AE) and anaerobic (AN) conditions at 20°C. Explanations as in Fig. 1.

access to atmospheric oxygen, the surface or subsurface layers were the most active in respiration, while under anaerobic conditions, in the transition (10°C) and high peatlands (5°C) higher respiration was found in a deeper layer (40-80 cm). At 20, 10, and 5°C anaerobic respiration corresponds to, on average, 39, 69, and 111% of aerobic respiration, respectively (Fig. 1).

Respiration activity at 20°C under aerobic conditions differed statistically only between the low and high peatland. The same pattern was found in anaerobic conditions. In aerobic conditions (20°C), the lowest potential for carbon mineralization and the highest potential in anaerobic conditions were found in the high peatland (Fig. 2). In both cases, the material from the transition peatland revealed intermediate values of respiration activity. More sensitive to changing aeration conditions (in 0-80 cm profile) was the material from the low peatland where, under anaerobic conditions, RA was reduced to about 74%. Peat from the transition peatland was slightly less sensitive – reduction to 68%, and the most resistant was peat from the high peatland where in anaerobic conditions RA constituted 78% of aerobic RA. There was a strong positive correlation between the aerobic and anaerobic respiration values (Fig. 3).

Both under aerobic and anaerobic conditions, a strong effect of temperature on RA (data analyzed together and separately from each peat material) was found (p<0.001), which was confirmed by high values of the R coefficient (Table 4). In all cases, the exponential function provided a better fit. Higher values of the R coefficient were found under aerobic conditions.

On the basis of the data from the incubations, RQ for aerobic incubation and Q10 for peat materials under aerobic and anaerobic conditions were calculated. The lowest value

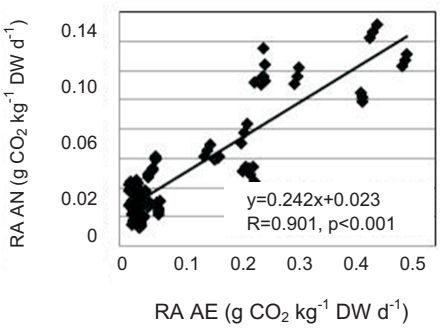

Fig. 3. Relationship between soil respiration potential of peat material under aerobic (AE) and anaerobic (AN) conditions (all data, n=108).

T a b l e 4. Correlation coefficient between temperature and respiration activity under aerobic (AE) and anaerobic (AN) conditions

Sampling sites	AE	AN
L	0.949	0.705
T	0.961	0.702
H	0.961	0.758
All data	0.946	0.716

All cases statistically significant differences at $p<0.001$ were noted (n=36). Explanations as in Tables 1 and 2.

of RQ, at the level 0.51, was found in the deepest layer of the high peatland (10°C), while the highest, 1.51, was noted in the subsurface layer (20-40 cm at 5°C) of the transition peatland (Table 5). The mean (for all levels of the profile) respiratory quotient increased with temperature in the low and high peatlands; in the transition peatland, the highest value of RQ was noted at 5°C; it decreased with temperature but was still above 1.

The peat soils were more sensitive to the temperature increase (Q10) when oxygen was available; cutting off oxygen resulted in a lower response at two-fold higher temperature. Under aerobic conditions, the value exceeded 8.7, whereas under anaerobic conditions it ranged between 1.17 and 6.53. In the low peatland, Q10 decreased with depth, whereas in the transition peatland higher values of Q10 were observed in the 0-20 and 60-80 cm layers. In the high peatland, higher values were noted in the layer of 20-60 cm (Table 5).

The further studies on factors affecting respiration activity were carried out using the data of RA at 20°C, because at that temperature, among others, the RA was the most efficient. The relationships between RA and the physicochemical parameters of the peat have a linear character; the R values are presented in Table 6.

Statistical analysis shows that pH, soil depth, peat decay, and NO_3-N content have a strong influence on RA of all the tested peat soils, both in anaerobic and anaerobic treatments. Salinity (expressed as electrolytic conductivity – EC)

T a b l e 5. Calculated values of RQ for the aerobic condition and Q10 for the aerobic and anaerobic condition

Type of peatland	Depth (cm)	RA (AE)			Q10 for 10 and 20°C	
		5	10	20	AE	AN
		(°C)				
L	0-20	0.65a	0.68a	1.04b	8.72b	2.44c
	20-40	0.71b	0.79b	0.99a	6.73c	1.68a
	40-60	1.28c	1.07d	0.94a	6.08a	1.73b
	60-80	0.72b	0.88c	1.10b	4.15d	4.54d
	Mean	0.84a	0.86a	1.02a	6.42b	2.60a
T	0-20	1.14a	1.15c	1.12b	6.42d	3.95d
	20-40	1.51d	1.18c	1.11b	4.49b	3.63c
	40-60	1.35c	0.99b	1.17b	4.19a	1.83b
	60-80	1.23b	0.88a	0.69a	6.00c	1.17a
	Mean	1.31b	1.05a	1.02a	5.28b	2.65a
H	0-20	1.12c	1.07b	1.16b	4.67b	4.63b
	20-40	1.21d	1.22d	1.16b	6.02c	6.53d
	40-60	0.62a	1.14c	0.97a	6.62d	6.28c
	60-80	0.96b	0.51a	1.26c	4.53a	4.06a
	Mean	0.98a	0.99a	1.14a	5.46a	5.38a

Values followed by the same letter within the peat type are not significantly different (ANOVA, $p>0.05$). Explanations as in Tables 1 and 2.

T a b l e 6. R values for the relationship between respiration activity and physicochemical parameters of peat soils at aerobic and anaerobic conditions (20°C, n=12)

Factors	AE				AN			
	L	T	H	All data	L	T	H	All data
pH	0.775***	-0.979***	-0.937***	0.335*	0.579*	-0.759**	-0.684*	-0.552***
Depth	-0.974***	-0.913***	-0.719**	-0.760***	-0.917***	-0.991***	-0.937***	-0.829***
Moisture	n.s.	-0.976***	-0.708*	n.s.	n.s.	n.s.	n.s.	n.s.
Salinity	n.s.	0.882***	0.793**	0.527**	n.s.	0.645*	0.810**	0.656***
Von Post ranking	-0.971***	-0.913***	-0.719**	-0.523**	-0.950***	-0.991***	-0.937***	-0.379*
TOC	n.s.	-0.993***	n.s.	-0.641***	n.s.	-0.924***	-0.734**	n.s.
NO_3-N	-0.897***	0.902***	-0.815**	0.404*	-0.830***	0.734**	0.793**	0.416***
NH_4-N	n.s.	n.s.	n.s.	-0.375*	n.s.	n.s.	0.604*	0.556***

Indicate statistically significant differences at *p<0.05, **p<0.01, ***p<0.001 levels. Other explanations as in Tables 1 and 2.

influenced RA in material from the transition and high peatlands as well as TOC in the transition peatland under aerobic conditions and the transition and high peatlands under anaerobic conditions. The influence of NH_4-N on RA was rather weak, particularly under aerobic conditions where significant correlations were found only in the case of all data collection and in anaerobic conditions in the high peatland and all experimental data.

The natural water content showed a negative effect on RA in the peat from the transition and high peatlands incubated under aerobic conditions (Table 6).

DISCUSSION

Even if the deeper layers of peat from the investigated profiles were exposed to aerobic conditions, the RA was lower than in the surface peat, which was confirmed by the statistically important and negative relationship between RA and depth ($p<0.01$, Table 6). The reduction of RA in aerobic conditions (20°C) between the depths of 0-20 and 20-40 cm was between 14 and 30% in peats from the low and transition peatlands, while in those from the high peatland, a statistically important decrease was observed only in the 60-80 cm layers (Table 2). Under anaerobic conditions, the decrease was stronger, ranging from 20 to 45%, and it intensified with depth to a maximum of 71%. The strong relationships both under aerobic and anaerobic conditions ($p<0.001$) in all the tested peat profiles separately as well as in the collective statistical analysis confirm the important influence of depth on RA (Table 6). A decrease in soil respiration with depth was observed both in organic and in mineral soils (Šantrůčková *et al*., 2010). Despite the accessibility of oxygen, the availability of substrate for decomposition decreased with depth. Fresh litter and partially decomposed plant material of the upper peat decompose at a faster rate than older peat material located in the deeper part of the profile (Keller and Takagi, 2013). The process of decomposition is initially fast, but slows down considerably as the supply of readily decomposable organic matter gets exhausted. Sugars, amino acids, lipids, and starches are decomposed first at rapid rates, while insoluble components such as cellulose, hemicellulose, lignin, and proteins, which constitute a major portion of soil organic matters, are decomposed rather slowly (Prescott, 2005). The degradation of cellulose and hemicellulose to oligomeric and monomeric sugars is considered one of the most important steps in anaerobic degradation of organic matter and it is catalyzed by a diverse set of hydrolytic extracellular enzymes produced by microorganisms. Further steps in the anaerobic degradation are the fermentative and methanogenic pathways (Tveit *et al*., 2012).

Bacteria, fungi and actinomycetes are involved in both aerobic as anaerobic degradation of organic matter, but fungi are more efficient than bacteria in degradation of highly recalcitrant organic matter because they produce a wider range of extracellular enzymes than bacteria. In anaerobic and waterlogged layers of peat soils, phenolic substances such as lignin are accumulated in high concentrations, partly owing to the low activity of phenol oxidases, which require oxygen for function. The inhibiting effect of phenolic substances has been suggested as a major factor for the low soil organic matter degradation rates in peat soils (Tveit *et al*., 2012).

The chemical quality of soil organic matter affects the values of RQ. The respiratory quotient is equal to 1 when the oxidized substrates have a carbohydrate character and is generally >1 (around 1.3) when the respiratory substrates belong to highly oxidized compounds such as organic acids. Oxidation of reduced substrates such as fatty acids or proteins results in RQ <1 (Brzezińska, 2006). A respiratory quotient < 1 may also be a result of incomplete oxidation of

carbohydrates or assimilation of formed CO_2. Nitrification also contributes to lower RQ values, when consumption of O_2 without CO_2 emission takes place (Dilly, 2003). In our investigation, RQ was frequently >1, indicating that oxidation of organic acids such as fulvic and humic acids took place (Table 5). The investigated peat was at the different steps of the organic matter decomposition, the von Post index was maximally 70% (Table 1), but the high RQ values indicated that substrates for respiration were of high quality. Aerobic as well as anaerobic CO_2 production was strongly negatively correlated with the values of von Post decomposition ranking ($P<0.01$, Table 6), which suggests that highly oxidized organic coupons are available in deeper layers but probably in a lower amount. Similar observations were made by Glatzel *et al*. (2004) on peat material from peatlands near Rivere-du-Loup, Québec, Canada. Results from thirteen sites indicated that humification significantly modified the soil RA. Generally, the greatest potential for CO_2 production arises in surface peat with the highest content of fresh organic matter derived from slightly decomposed plant litter.

In most cases, cutting off the access of oxygen resulted in reduction of peat soil RA at both 20 and 10°C, maximally to 77 and 68%, respectively, and to only 32% at 5°C. In some cases, the differences were not significant or, surprisingly, RA was higher in anaerobic than in aerobic conditions. High water content causes air displacement from soil pores, resulting in lower oxygen availability for soil microorganisms responsible for soil respiration. Soil moisture also hinders gas exchange between the soil and the atmosphere, because diffusion of gases in water is approximately 104 times slower than in air (Minkkinen *et al*., 2007). In our investigation, significant effects were observed in the material from the transition and high peatlands, in which the highest differences in moisture between the surface (less moist) and the deepest layers were observed (Tables 1 and 6). Comparable activity in both the aerobic as anaerobic treatments was observed in the material from the 0-20 cm layer (high peatland), both at 10 and 20°C (Table 3). This implies that the intensity of carbon release in this zone is independent of the water level. In this location, the high variability of the water level during the year resulted in cyclicity of aerobic and anaerobic conditions and created conditions for good adaptation of both aerobic and anaerobic microorganisms. It was reported that decomposition efficiency of organic matter is dependent on a cascade of aerobic and anaerobic steps (Tveit, 2012). In the other investigated sites in a low moor peatland, despite the high ground water level during almost the whole year, aerobic respiration was higher in aerobic than in anaerobic conditions. This activity can be affected by the presence of plant roots. In the investigated low moor peatland, the vegetation is dominated by *Carex* spp. plants with extensive root systems reaching around 50 cm and in some cases even 300 cm of depth and with a higher root density in the subsurface zone (Canadell *et al*., 1996). High moisture led to a deficit of oxygen for root respiration, plants had to transport it from the atmosphere via leaves and stems to the roots, which resulted in efficient aeration of the root zone. Consequently, soil aerobic microorganisms were active although the high moisture prevented diffusion of air from the atmosphere into the soil pores.

The data obtained show that the RA of the investigated peat soils is strongly influenced by soil temperature ($p<0.0001$) and the relationship has an exponential character (Table 4).

In the deeper investigated layers (below 40 cm) of the transition and high peatland profiles, at 5°C the RA was higher in the anaerobic treatment. This suggests that at low temperature in these zones degradation of organic matter was more efficient due to the presence of anaerobic organisms. It is known that low temperature hampers the activities of enzymes that participate in organic matter decomposition. However, anaerobic microorganisms inhabiting the investigated peat seem to be more resistant to the temperature decrease to 5°C. Temperature stimulates enzyme activities but on the other hand, it is possible that increased temperatures cause microbes to undergo physiological changes that result in reduced carbon use efficiency (Frey *et al*., 2013). When all data was grouped according to temperature (aerobic and anaerobic separately), statistical analysis revealed that RA between 5 and 10°C did not differ significantly either in aerobic or anaerobic conditions. A temperature increase to 5°C was not sufficient for considerable modification of the activity of organic matter decomposers (Fig. 1). Various substrates require different energy for activation of decomposition. For example, activation energy for lignin decay was reported as greater than for cellulose (Chapman and Thurlow, 1998). RQ values seem to be also dependent on the decomposition index and primarily on the species of plants that form particular layers of peat and differ in the content of carbon forms. Changes of temperature caused greater diversity of RQ values in the peat profiles from the Polesie Lubelskie Region, which suggests that temperature modified RQ in these cases probably by differences in adaptation of soil microorganisms to changes of temperature and by efficiency of utilization of carbon substrates and incomplete oxidation (Table 5). Our investigation shows that highly oxidized carbon compounds are still available in all the profiles, which confirms good protection of accumulated carbon. Because a decrease in temperature slows carbon mineralization, organic matter is better protected against breakdown at low temperature (Table 2). An increase in temperature to 20°C reduces the time of carbon oxidation up to 15 times in aerobic and even 9 times in anaerobic treatment. Therefore, the temperature rise contributes to reduction of the efficiency of carbon sequestration in the form of peat. The Q10 ratio provides insight into the impact of temperature on RA. Literature data indicate that the dependence of Q10 on soil types is variable. In two paired

pasture-forest sites in north-eastern Nova Scotia (Canada), it ranged between 2.17 and 2.52 and it was 0.25 greater in the paired pastures than in the paired forests incubated in aerobic conditions (Kellman *et al*., 2007). In ten peatlands from Scotland (Chapman and Thurlow, 1998), it ranged from 1.9 to 6.4.

In the present study, the peat samples incubated under aerobic conditions showed Q10 between 8.7 in the 0-20 cm layer and 4.15 at the depth of 60-80 cm in the profile of the low moor peatland. In the profiles from the low and transition peatlands, Q10 was significantly lower in anaerobic conditions while in the high peat Q10 had comparable values (Table 5). The results suggest that the samples from the high peatland, naturally overgrown by woodland and characterized by more stable thermal conditions, were more sensitive to temperature change than in the other two (low and transition) peatlands, which were not protected by woodland. Generally, aerobic processes were more sensitive to the temperature increase (Q10 equal on average 5.7) than anaerobic processes (Q10 equal only 2.9, Table 5).

The Q10 values in field measurements in the catchment basin of the Rur River increased with depth (Graf *et al*., 2008). Similar observations were made in a soil classified as a thermic pachic haploxeroll (Fierer *et al*., 2003). In none of our investigations were similar relations found either under aerobic or anaerobic conditions. Peats are a special type of soils with high organic carbon content, increasing with depth as a result of accumulation of plant litter and increased bulk density due to higher decomposition of organic matter expressed on the Von Post scale. Higher decomposition is connected with a longer time of the action of decomposers and a higher concentration of the recalcitrant form of carbon. In mineral soils, a reverse situation takes place, *ie* the carbon content decreases with depth. As mentioned earlier, not all organic forms of carbon are easily available for microorganisms but they might be an important factor modifying Q10. Surface soils in the temperate climate seem to be adapted to fluctuating temperature because they are exposed to atmospheric conditions. The amplitude of temperature during the day or year decreases with depth and microorganisms from deeper layers are adapted to a more narrow range of temperature. Perhaps the 14-day period of incubation was too short to adapt them to the increased temperature.

A strong correlation between aerobic and anaerobic CO_2 production was found (Fig. 3). The same pattern was found earlier in peatlands at different stages of degradation and in natural peatlands located in Canada (Glatzel *et al*., 2004). This result suggests that both aerobic and anaerobic bacteria, fungi and actinomycetes are incorporated in the investigated profiles.

In general, the pH of the investigated layers did not differ for the particular peatlands by more than about 0.56 unit. Usually, at the aerobic treatment (for all the studied peatlands), the highest activity was noted in material at pH close to neutral, while it was significantly lower at acidic pH. Generally, pH positively influenced RA under aerobic conditions (Table 6), whilst a reverse tendency was observed in the anaerobic incubations. These results confirmed the hypothesis that soil acidity would support accumulation of soil organic matter due to the reduced rate of microbial mineralization, but only in aerobic conditions. When there is a lack of oxygen, anaerobic fungi, which constitute even above 50% of microorganisms in peat soils and are active even at low pH, can play a crucial role in breakdown of organic matter (Schneider *et al*., 2010).

It has been reported that an increased concentration of salts can lead to a slower rate of organic matter mineralization and low respiration activity due to the detrimental effect of high salinity on the type and number of microorganisms. Salinity has adverse effects on enzyme activities, which are crucial for decomposition of organic matter, and is a source of osmotic stress for microbial cells. Researchers studying the effect of salinity on soil respiration potential demonstrated that soil respiration decreased with an increase in salinity, as low salinity values below 5 S m^{-1} were considered (Rietz and Haynes, 2003). In the transition and high peatland profiles, in layers with higher natural salinity, CO_2 production was also higher ($p<0.001$) while no influence was found in the low peats (Table 6). The investigated objects were characterized by very low salinity, not exceeding 0.32 S m^{-1} (Table 1). Such conditions had rather a negligible effect of organic matter decomposers.

Organic carbon was the only form of carbon in the investigated peatlands. The content of organic carbon did not always clearly influence peat respiration and if it did, it had a negative effect (Table 6). Generally, the content of TOC increased with depth, similarly to moisture, especially in the transition and high peatlands. As mentioned earlier, not all forms of carbon are easily available for organic matter decomposers and this was the reason of the negative effect of TOC.

Some researchers found that nitrogen can inhibit the decomposition of litter and the RA in the surface layer of soils, as observed in warm-temperate soils in a pine forest (*Pinus taeda*) in Chapel Hill (NC, USA) (Drake *et al*., 2012). In other research, the influence was positive, as in the case of forest soils (Harvard Forest) investigated by Bowden *et al*. (2004). In some cases, no changes in soil respiration were observed, as shown by Włodarczyk *et al*. (2002) during investigation of peaty-muck soils. In the presented data, the trends were not clear in the particular peatlands but, generally, regression analysis data from the AE and AN incubations indicated a positive effect of NO_3^- on RA ($p<0.05$), while the NH_4^+ impact was not clear (Table 6). Nutrients in water and soil, mainly in inorganic forms, may be used by microbial decomposers to supplement the nutrient pool within the organic substrate (Debusk and Reddy, 2005). The presence of nitrogen can affect organic matter mineralization in two different ways:

– by acting as an electron acceptor in the form of NO_3^- and increasing soil respiration and
– the presence of nitrogen in the form of NH_4^+ may decrease the soil organic matter decomposition rate by decreasing the C:N ratio and also decrease emission of CO_2 and CH_4, as shown in peat soil and paddy soil (Aerts and Toet, 1997; Huang *et al*., 2002).

CONCLUSIONS

1. Respiration activity of the peat material under aerobic and anaerobic conditions varied in the range of 0.018-0.497 and 0.013-0.227 g CO_2 kg^{-1}DW d^{-1}, respectively. The rate of CO_2 production at 20°C was almost 3 times higher under aerobic than anaerobic conditions.

2. In most cases, lack of oxygen reduced respiration activity of microorganisms inhabiting peat (up to 77%), but in some cases (layer 0-20 cm of H peatland, 20°C) was comparable whilst in others (below of 40 cm in the low, transition and high peatland, at 5°C) higher respiration acitivity was found in anaerobic conditions.

3. There were positive linear relationships between soil respiration potential of the peat material under aerobic and anaerobic combinations, but the comparison of respiration activity of the peatland (in the tested depth of 0-80 cm) showed that high peat had the lowest respiration activity under aerobic but the highest under anaerobic conditions.

4. The temperature sensitivity ratio and respiratory quotient value at 20°C in all the profiles (0-80 cm depth) was around or higher than 1, which suggests efficient distribution of highly oxidised compounds in the profiles despite the different degree of organic matter decomposition.

5. The peat soils from the low and transition peatlands showed high sensitivity to the temperature increase (the difference in respiration rates over 10°C) when oxygen was available; cutting off the oxygen input resulted in two-fold lower response to temperature. In the samples from the high peatland, the response to an increase in temperature was similar despite the aerobic conditions.

6. Temperature, oxygen availability, and salinity had the most statistically significant positive influence on respiration activity, whilst the degree of peat decomposition, depth of soil profile, total organic carbon content, and water regime had a negative effect.

7. Our investigation has revealed that peat soils from a small area can differ in their capability of CO_2 release and response to water conditions. Respiration activity in the profiles of these three types of peatlands may be affected by a few factors (temperature, depth, peat decomposition degree, pH, salinity, nutrient availability). It is also possible that these factors interact and the relationships of only the strongest factors, such as temperature, depth, and peat decomposition degree are visible.

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