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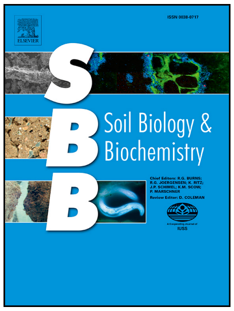

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Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change

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Highlights

- Temperature increased respiratory activity until optimum temperature then declined
- More decomposed peat decreased the amount of microbes but not respiratory activity
- Q_{10} of aerobic respiration increased by 14 % at 35-40 cm than 5-10 cm peat layer
- Depth dependent Q_{10} in peat profile can be applied in modelling peat decomposition

Abstract

The effect of climate change on peatlands is of great importance due to their large carbon stocks. In this study, we examined microbial biomass and effect of temperature and O_2 availability on soil respiration of surface and subsurface *Sphagnum* peat. The interactive effect of biotic and abiotic factors significantly affects soil respiration. Increasing temperature enhanced the microbial respiratory activity and thus the soil respiration, while there is a temperature threshold. The more decomposed subsurface peat showed a lower CO_2 production due to less labile carbon and lower microbial biomass, but a higher temperature sensitivity. Q_{10} of aerobic respiration increased from 1.93 ± 0.26 in surface to 2.20 ± 0.01 in subsurface peat. The linear relationship between Q_{10} and depth in the uppermost 50 cm peat section can be used to improve the estimation of CO_2 production in peat profiles.

Peatlands play a crucial role in global carbon cycle, with a storage of about 30 % of global soil carbon (C) in 3 % of the earth's land surface (Gorham, 1991). However, global climate change may alter the cold and wet conditions which favorable to their C sink function (Page and Baird, 2016; Waddington and Roulet, 1996). Soil respiration, being an important efflux of carbon dioxide (CO_2) from peatlands to the atmosphere, is largely controlled by abiotic factors: temperature, soil moisture and O_2 availability (Szafranek-Nakonieczna and Stepniewska, 2014; Wang et al., 2010). In addition, soil organic matter (OM) quality in terms of the proportion of labile or complex C compounds (referred to high and poor quality respectively; Dieleman et al., 2016), also affects respiration and temperature sensitivity. These factors vary in vertical peat profile with temperature variability, O_2 availability and OM quality decreasing with depth. Thus, in the context of climate change, it is crucial to understand the response of soil respiration in different depths to realistic and expected changes in temperature and water table depth (WTD) that determines O_2 availability. The quality of OM is a key factor in the response of ecosystems to increase temperature. Poor-quality OM decomposes slowly, resulting in lower CO_2 production, while it has been reported to be more sensitive to temperature change (Conant et al., 2008b; Davidson and Janssens, 2006). Effects of abiotic factors on CO_2 production in peat was frequently studied (e.g. Hilasvuori et al., 2013; Leifeld et al., 2012; Treat et al., 2014), while as the soil respiration was regulated by the biological processes, the constrains are both abiotic, biotic and interactive. To address this gap, we conducted a short-term incubation of peat from a site presenting a sharp decrease of OM quality with depth to examine soil respiration under various environmental conditions. Our objectives were to (1) determine the effect of temperature, O_2 availability, OM quality and microbial biomass (MB) in regulating soil respiration; (2) investigate the temperature sensitivity of peat decomposition at two different degradation states.

Peat samples were taken from a near soil surface layer (5-10 cm) and a subsurface layer (35-40 cm) at four different *Sphagnum* locations about 20 m apart under *Sphagnum rubellum* hummocks on April 2019 in La Guette peatland (a *Sphagnum* acidic fen in France, Gogo et al., 2011). The samples from these four locations were used as replicates. The two layers corresponded to less and more decomposed peat respectively as the older and deeper litters has been exposed to decay for longer time (properties described in Table 2; Hilasvuori et al., 2013). Eight collected samples were homogenized separately and stored at 4 ^{o}C for two weeks before incubation. Subsamples of 10g from 5-10 cm depth and 30 g from 35-40 cm depth were transferred into 250 mL jars, sealed and vacuumed, then flushed with pure nitrogen (N_2) or air for anaerobic and aerobic incubation (16 for each condition including 2 replicates for each of the 8 collected samples), respectively. The jars were incubated at constant temperature in FitoClima 1200 incubator (Aralab) for 7 days. Each day, 5 mL gas was collected and CO_2 concentration was analyzed by LGR Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, Inc. CA) and replaced by same volume of N_2/air to maintain pressure. These processes were reproduced every week under 7 temperatures between 4 and 28 °C, in 4 °C step. The CO_2 production rate was calculated by the linear regression of CO_2 concentration versus time. Temperature sensitivity (Q_{10}) of CO_2 production was determined following Lloyd and Taylor, (1994).

Total carbon and nitrogen contents (TC, TN) of the eight collected samples were measured by an elemental analyzer (Thermo-126 FLASH 2000 CHNS/O Analyzer). Microbial biomass of the eight collected samples and samples after incubation was determined by the chloroform fumigation extraction method (Jenkinson and Powlson, 1976). Water extractable organic carbon (WEOC) corresponded to the organic carbon concentration of non-fumigated samples. Normality of distribution, homogeneity of variance of data were tested, three-way ANOVA was used to determine effect of the temperature, O_2 availability and OM quality on the CO_2 production rate. One-way ANOVA was used to determine the difference of soil properties and Q_{10}.

CO_2 production rate/gram dry peat continuously increased with increasing temperature (Fig 1a and b). Whereas CO_2 production rate/gram MB increased with elevated temperature until 24 °C, then declined at 28 °C (Fig 1c and d), suggesting an optimum temperature between these two temperatures. The contrary trend observed at 28 °C could be attributed to the higher amount of MB at 28 ^{o}C than at 24 ^{o}C (43.3 % and 197.2 % higher in 5-10 cm, 186.6 % and 99.2 % higher in 35-40 cm under aerobic and anaerobic, respectively). Therefore, temperature increased the microbial respiratory activity and thus the soil respiration rate, but there is an optimum temperature between 24 and 28 ^{o}C. When above this threshold temperature, the increasing soil respiration could be attributed to the larger MB amount.

Low O_2 availability restricts microbial activities (Yavitt et al., 1997). Our study confirmed that aerobic condition enhanced soil respiration and this effect depends on temperature (Fig. 2; Table 1). At 28 ^{o}C, anaerobic incubation reduced CO_2 production rate compared with aerobic conditions (decrease of 25.5 % and 35.5 % for 5-10 and 35-40 cm, respectively), while significant difference was only observed in 35-40 cm (p<0.001). No significant effect of O_2 availability was found at 4 ^{o}C

The decreasing C:N with depth (Table 2) suggested an increased decomposition degree, as microbes consume C-rich OM while recycle N, resulting in higher relative N concentration in more decomposed soil (Biester et al., 2014; Broder et al., 2012; Kuhry and Vitt, 1996). Additionally, WEOC also declined with depth (Table 2), suggesting a decreased availability of labile substrates (Biester et al., 2006; Kalbitz and Geyer, 2002). These results showed that the gradient of decomposition degree is steep in our site. CO_2 production rate/gram MB was higher for 35-40 cm than 5-10 cm at 16-24 ^{o}C under aerobic, while it was similar under anaerobic incubation (Fig 1 c and d). This could be related to the decline of fungi to bacteria ratio with peat depth found by Zocatelli et al (article in preparation) of our samples and in other studies (Sjögersten et al., 2016). Each unit cell mass of fungi release less CO_2 than bacteria due to the lower surface-to-volume ratio. Thus the lower relative abundance of fungi in 35-40 cm leads to higher respiration rate/gram MB (Blagodatskaya and Anderson, 1998). However, a lower MB was observed in 35-40 cm compared to 5-10 cm both before (Table 2; p=0.08) and after incubation (average of all incubation conditions: 0.80 ± 0.51 vs. 2.70 ± 1.41 mgC g^{-1}dw; p <0.001). Therefore, these results suggested that the decreasing CO_2 production rate with depth (Fig. 1a and b) was linked to the lower available labile C substrate and less MB, but not the microbial respiratory activity.

The Q_{10} increased with depth in aerobic conditions, (Fig 1a and b, *p*=0.014) but not in anaerobic condition (*p*=0.072). These results indicated that the more decomposed OM is more sensitive to temperature change than labile ones, confirming previously reported results (Conant et al., 2008b, 2008a; Davidson and Janssens, 2006). These results showed that the combination of higher temperature and increase frequency of drought would generate most favorable conditions for CO_2 production. This would stimulate soil respiration in subsurface layer with more decomposed peat, especially this layer was only 40 cm apart from surface. Such a stimulation of old peat decomposition could significantly increase the CO_2 emission to the atmosphere with an increasing possibility of transforming this ecosystem into a net C source.

Calculation of Q_{10} with a limited temperature range or insufficient points affects the exponential fit and could cause large variations of results (e.g. Chen et al., 2010; McKenzie et al., 1998; Waddington et al., 2001). In our study, a large temperature range (4-28 ^{o}C) with reduced step (4 ^{o}C) was applied to get more reliable results. Our results were in the range of those from different studies that showed Q_{10} of CO_2 production mostly ranged between 1-2.5 (65.9 %; Table S1 and Fig. S1). A linear increase of Q_{10} with peat depth was observed (Fig. S2, R^2=0.66; *p*=0.004 without outliers). This relationship allows Q_{10} to be more finely adjusted in models instead of using a constant value.

In conclusion, the effect of temperature, O_2 availability, substrate quality and their interactions on soil respiration were identified (Table 1). Raised temperature, aerobic condition and high OM quality significantly increased the release of CO_2 . These factors regulate the respiratory activity or amount of MB with implications for peat decomposition. Our study emphasized the importance of integrating environmental parameters, substrate quality, and MB when evaluating the response of soil respiration to climate change. Q_{10} of soil respiration was higher in more decomposed peat and showed a vertical variation. As an important parameter in modeling carbon cycle of peatlands under global warming, the vertical heterogeneity of Q_{10} should be taken into account to improve the estimation of CO_2 production in peat profiles.

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Tables

Table 1 Effect of the organic matter (OM) quality, temperature, Aerobic/anaerobic condition and their interactions on CO_2 production rate (μgC g^{-1} dw h^{-1}). Significance levels of three-way ANOVA are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$ (n=8).

	CO_2 production rate (μgC g^{-1} dw h^{-1})
OM quality	***
Temperature	***
Aerobic/anaerobic condition	***
OM quality *Temperature	***
OM quality* Aerobic/anaerobic condition	
Temperature* Aerobic/anaerobic condition	*
OM quality* Temperature* Aerobic/anaerobic condition	

Table 2 Physical, chemical and biological properties of peat from 5-10 cm and 35-40 cm layer (n=4, mean ± SD). Significance levels of one-way ANOVA are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

	5-10 cm	35-40 cm	*p*
Water content (%)	85.17 ± 3.00	86.09 ±3 .10	
C:N	97.44 ± 13.29	21.94 ± 1.29	***
WEOC (mg C g^{-1} dw)	1.02 ± 0.14	0.54 ± 0.09	**
Microbial biomass C (mg C g^{-1} dw)	2.97 ±1 .36	1.39 ± 0.70	

Figures

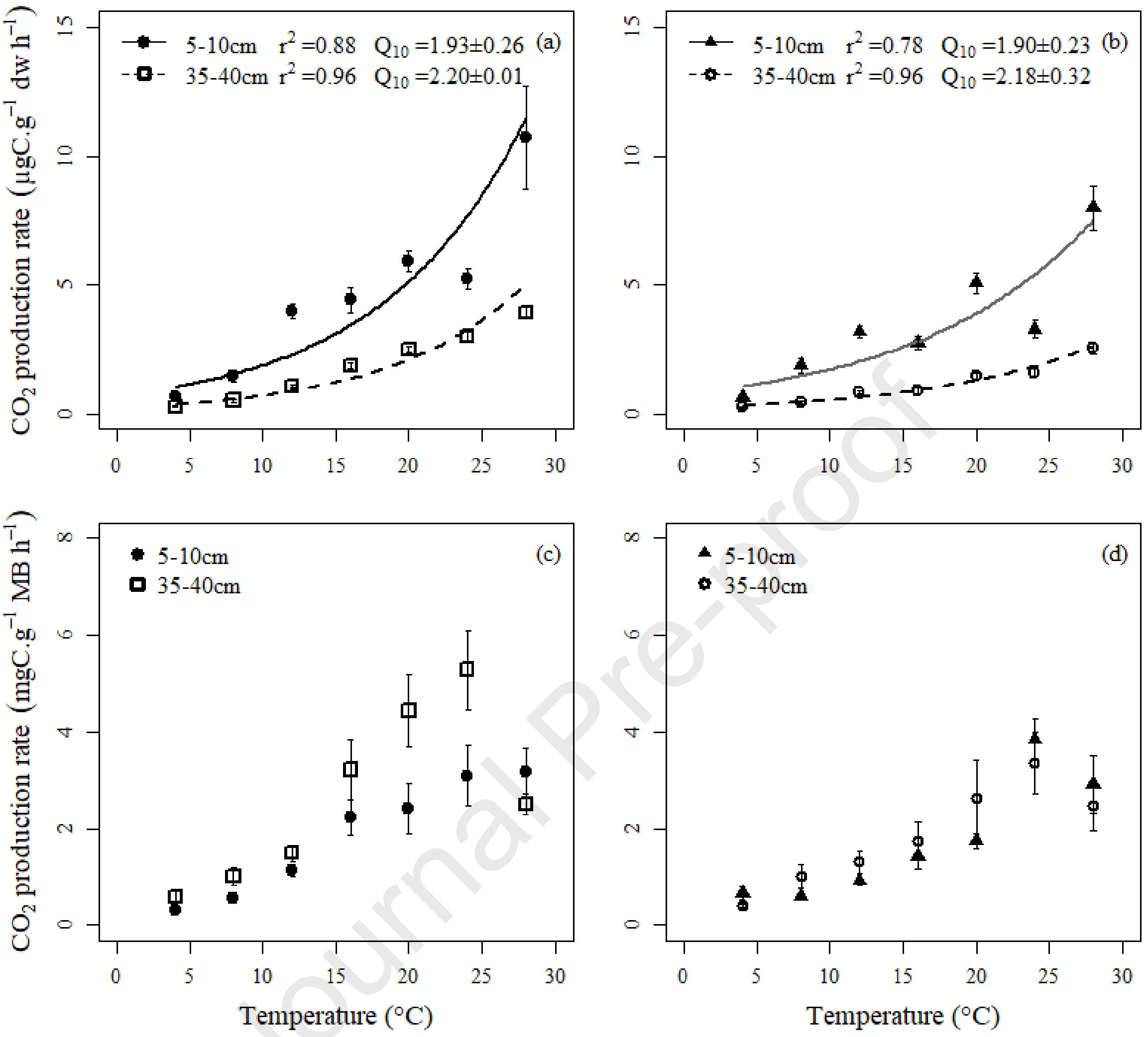


Fig. 1 CO_2 production rate (µgC g^{-1} dw h^{-1}) under (a) aerobic and (b) anaerobic conditions; and CO_2 production per gram microbial biomass (mgC g^{-1} MB h^{-1}) under (c) aerobic and (d) anaerobic conditions as a function of temperature for peat from 5-10 cm and 35-40 cm layer. The lines in panels a and b correspond to the model fitted to the measurements.

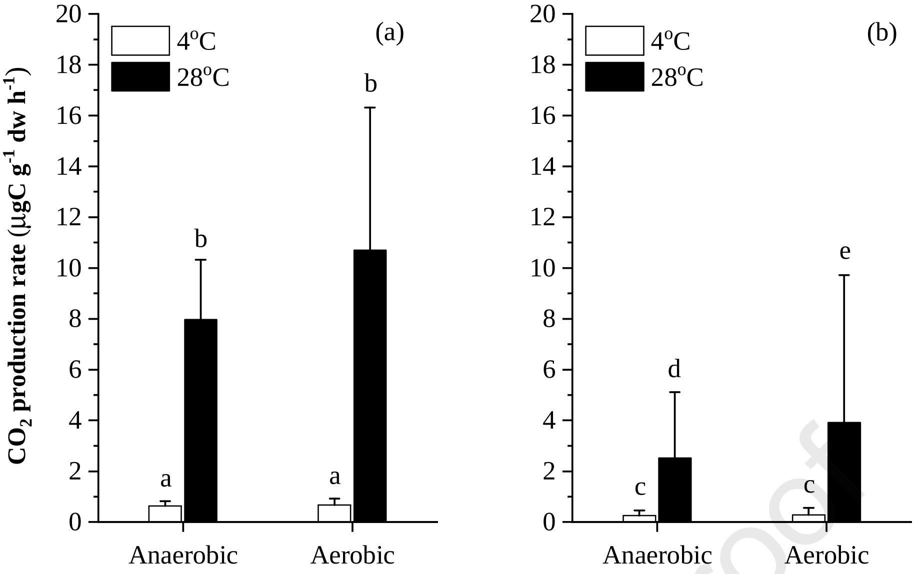
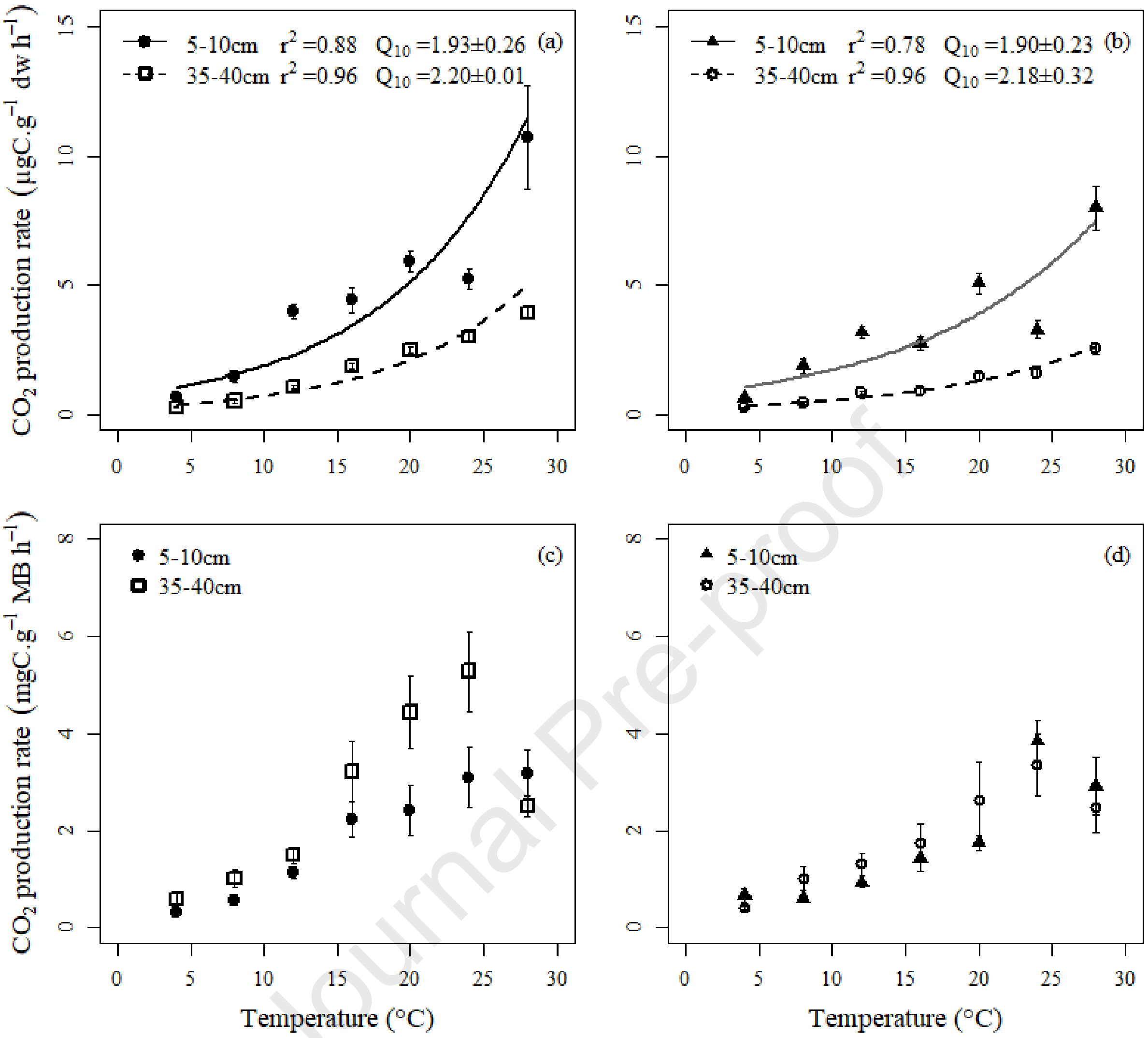
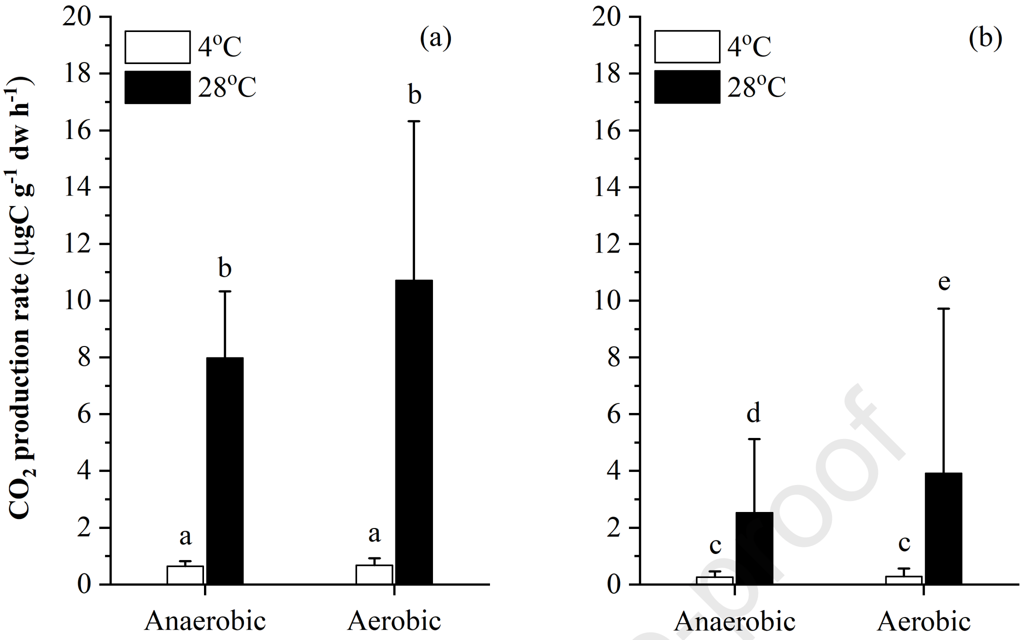


Fig. 2 CO$_2$ production rate (μgC g^{-1} dw h^{-1}) of peat from (a) 5-10 cm layer and (b) 35-40 cm layer incubated at 4 and 28°C during 7 days incubation under anaerobic and aerobic conditions. Different letters represent significant differences by ANOVA in each panel and error bars represent the standard error.


CO$_2$ production rate (µgC.g^{-1} dw h^{-1})
5-10cm r^2 =0.88 Q$_{10}$ =1.93±0.26 (a)
35-40cm r^2 =0.96 Q$_{10}$ =2.20±0.01
5-10cm r^2 =0.78 Q$_{10}$ =1.90±0.23 (b)
35-40cm r^2 =0.96 Q$_{10}$ =2.18±0.32
0
5
10
15
CO$_2$ production rate (mgC.g^{-1} MB h^{-1})
5-10cm
35-40cm
(c)
5-10cm
35-40cm
(d)
0
2
4
6
8
0
5
10
15
20
25
30
Temperature (°C)
Temperature (°C)


CO$_2$ production rate (μgC g^{-1} dw h^{-1})
20
18
16
14
12
10
8
6
4
2
0
4°C
28°C
(a)
(b)
a
b
a
b
c
d
c
e
Anaerobic
Aerobic
Anaerobic
Aerobic

Highlights

- Temperature increased respiratory activity until optimum temperature then declined
- More decomposed peat decreased the amount of microbes but not respiratory activity
- Q_{10} of aerobic respiration increased by 14 % at 35-40 cm than 5-10 cm peat layer
- Depth dependent Q_{10} in peat profile can be applied in modelling peat decomposition

Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: