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Research article

Temperature sensitivity of soil organic matter decomposition after forest fire in Canadian permafrost region

Heidi Aaltonen[a,*], Marjo Palviainen[a], Xuan Zhou[a], Egle Köster[a], Frank Berninger[b], Jukka Pumpanen[c], Kajar Köster[a]

[a] Department of Forest Sciences, University of Helsinki, PO Box 27 (Latokartanonkaari 7), Fi-00014, Finland
[b] Department of Environmental and Biological Sciences, University of Eastern Finland, PL 111, FI-80101 Joensuu, Finland
[c] Department of Environmental and Biological Sciences, University of Eastern Finland, PL 1627, FI-70211, Kuopio, Finland

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ABSTRACT

Climate warming in arctic/subarctic ecosystems will result in increased frequency of forest fires, elevated soil temperatures and thawing of permafrost, which have implications for soil organic matter (SOM) decomposition rates, the CO_2 emissions and globally significant soil C stocks in this region. It is still unclear how decomposability and temperature sensitivity of SOM varies in different depths and different stages of succession following forest fire in permafrost regions and studies on long term effects of forest fires in these areas are lacking. To study this question, we took soil samples from 5, 10 and 30 cm depths from forest stands in Northwest Canada, underlain by permafrost, that were burnt by wildfire 3, 25 and over 100 years ago. We measured heterotrophic soil respiration at 1, 7, 13 and 19 °C. Fire had a significant effect on the active layer depth, and it increased the temperature sensitivity (Q_{10}) of respiration in the surface (5 cm) and in the deepest soil layer (30 cm) in the 3-year-old area compared to the 25- and more than 100-year-old areas. Also the metabolic quotient (qCO_2) of soil microbes was increased after fire. Though fires may facilitate the SOM decomposition by increasing active layer depth, they also decreased SOM quality, which may limit the rate of decomposition. After fire all of these changes reverted back to original levels with forest succession.

1. Introduction

Permafrost soils cover 24% of the land area in the northern hemisphere, and these soils store around 50% of the total global soil carbon (C) pool (Tarnocai et al., 2009). Climate warming has been greatest in high latitudes (IPCC, 2013), and it is estimated that 25% of the permafrost area will thaw by 2100 (Davidson and Janssens, 2006). Rising soil temperatures and thawing permafrost may increase soil organic matter (SOM) decomposition and release of C from the soil, which may further amplify climate warming (Allison and Treseder, 2011). However, the amount of C potentially released from permafrost due to global warming is still uncertain (Moni et al., 2015). C stored in permafrost may be relatively labile since it is not necessarily protected by physical barriers, such as microaggregates, or stabilized by humification (Michaelson et al., 2004). Yet, the lability of SOM is not only dependent on stabilization or physical protection, but also on the molecular structure, which is affected, for example, by the origin of the SOM (Schmidt et al., 2011).

Climate warming is predicted to increase the frequency of boreal and Arctic wildfires (Flannigan et al., 2009). The effects of fires on permafrost soils depend on the fire intensity (and through that the severity) and on the time since the fire (Taş et al., 2014). Fires change the physical properties of soil and vegetation, leading to permafrost thaw and an increase in the depth of the active layer (the seasonally freezing and thawing layer above the permafrost), exposing previously frozen SOM to decomposition (Jiang et al., 2015). On the other hand, forest fires decrease soil microbial biomass (Dooley and Treseder, 2012; Zhou et al., 2018), change microbial community structure (Sun et al., 2015), and alter SOM quality by producing recalcitrant pyrogenic compounds (Certini, 2005; Knicker, 2007), all of which may slow down SOM decomposition (Köster et al., 2014).

Laboratory incubation measurements provide information about the temperature sensitivity of SOM decomposition. The Q_{10} value of respiration (change of respiration rate with a 10 °C temperature increase) has been commonly used to measure the temperature sensitivity of SOM decomposition, which depends on environmental conditions, the physiology of soil microbes and the characteristics of SOM (Gershenson et al., 2009). The Q_{10} of soil layers may vary because it may be affected

* Corresponding author.
E-mail address: heidi.m.aaltonen@helsinki.fi (H. Aaltonen).

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Table 1
Biomass of trees and ground vegetation and coverage of ground vegetation in the $FIRE_3$, $FIRE_{25}$ and $FIRE_{100}$ areas. Values given are averages of plots from three sample lines (two for $FIRE_{100}$) with standard error following.

Area	Tree biomass (kg m^{-2})	Ground vegetation biomass (kg m^{-2}) (vascular plants/moss and lichens)	Ground vegetation coverage (%) (vascular plants/moss and lichens)
$FIRE_3$		0.3 ± 0.1/0.2 ± 0.0	15.5 ± 3.0/4.0 ± 1.5
$FIRE_{25}$	0.09 ± 0.02	0.7 ± 0.1/0.7 ± 0.0	33.4 ± 5.5/66.1 ± 6.7
$FIRE_{100}$	5.50 ± 0.42	0.6 ± 0.1/1.2 ± 0.2	35.3 ± 5.8/86.3 ± 5.0

by chemical recalcitrance of the decomposing material (Karhu et al., 2010). Recalcitrant SOM has been found to have higher temperature sensitivity compared with labile SOM (Karhu et al., 2010; Yan et al., 2017), but other studies have also reported opposite findings and the temperature sensitivity of recalcitrant versus labile matter is still under discussion (Conant et al., 2011). The temperature sensitivity of permafrost layers has been studied quite actively in recent years, but the results have varied. The permafrost layers have been found to have both relatively lower and higher temperature sensitivities than the active layer (Bracho et al., 2016; De Baets et al., 2016; Waldrop et al., 2010).

SOM quality and the soil microbial biomass are linked in several ways, especially since the SOM quality is much affected by microbial reworking. The effectiveness of microbial C assimilation in soil can be measured with microbial carbon use efficiency (CUE) and the metabolic quotient (qCO_2) (Rutigliano et al., 2007), the respiration rate per microbial biomass C. The latter is an indicator of stress in soils (Anderson and Domsch, 1993) and describes the efficiency with which microbes acquire C (Pinzari et al., 2017). When qCO_2 values are low and CUE is high the microbial growth is efficient and only a low amount of C is released as respiration (Manzoni et al., 2012; Rutigliano et al., 2007). Previously, qCO_2 has been observed to increase after burning (Fritze et al., 1993; Rutigliano et al., 2007) and higher values have been attributed to microbial pioneer species having high respiration rates (Pietikäinen and Fritze, 1995).

Even though there are previous studies dealing with decomposability and Q_{10} in permafrost soils after fire (De Baets et al., 2016; O'Donnell et al., 2011), it is still unclear how these vary in different stages of succession after forest fire. The aim of this study was to determine how heterotrophic soil respiration (R_h), originating from the decomposition of SOM, and the Q_{10} of this process vary between different depths over the years following a forest fire in permafrost-affected soils. We also studied how the microbial biomass and qCO_2 are affected by the fire. Finally, we investigated what the most important factors affecting the Q_{10} of SOM decomposition are. We hypothesized that forest fires decrease R_h and change the Q_{10} of SOM decomposition, because a large amount of SOM is combusted or turned into decomposition resistant pyrogenic C (Knicker, 2007) and these changes can be observed with proceeding succession in the years following the fire. We also expected to see possible increases in the qCO_2 of microbes as found by earlier studies (Fritze et al., 1993; Rutigliano et al., 2007).

2. Methods

2.1. Study site description

Our study areas were located in the continuous permafrost zone along the Dempster Highway, close to Eagle Plains (66° 22′ N, 136° 43′ W) in Yukon, Canada (Fig. A1, supplementary material).

In the summer of 2015 a fire chronosequence was established, with forest areas with three different times since the last stand-replacing fire: 3 years ago ($FIRE_3$), 25 years ago ($FIRE_{25}$) and an area with no fire for at least the last 100 years ($FIRE_{100}$). The fire years were taken from fire maps published by the Canadian Forest Service (Canadian Forest Service) and confirmed by analysing tree rings from core samples taken from the trees in the studied areas. All the fires in our research areas were stand-replacing. The severity of the fire could be seen from post-fire mortality: there were no living trees from pre-fire succession, indicating high severity, stand-replacing fires. The tree ring measurements through all fire chronosequence areas showed that the stands were even aged – no older trees were found from any areas – meaning that the fires were similarly stand-replacing through the entire fire chronosequence used in this study.

The ecosystem where our study areas were located is taiga dominated by evergreen coniferous trees, mainly *Picea mariana* (Mill.) BSP and some specimens of *Picea glauca* (Moench) Voss. The ground vegetation consisted mainly of *Sphagnum* sp., *Cladonia* sp., *Cladina* sp., L., *Rhododendron groenlandicum* (Oeder), *Rubus chamaemorus* L. and *Vaccinium uliginosum* L. (Köster et al., 2017). Tree biomass and ground vegetation coverage are presented in Table 1. All the areas were gently sloping, and tree remains in the younger fire areas indicated a similar stand density to those in the older areas.

The soils in the study areas can be classified as silt loam with underlying permafrost, and the soils, therefore, were classified as cryosolic soils (Stanek, 1982) or relict cryosols (Michaelson et al., 2004) in the $FIRE_3$ area, where the active layer is deeper than 100 cm. The active layer thickness and other soil characteristics in the areas are presented in Tables 2 and 3.

2.2. Sampling

We established three 150 m long lines in the $FIRE_3$ and $FIRE_{25}$ areas, each line having three sampling plots 50 m apart from each other. The

Table 2
Soil pH, electrical conductivity (EC), soil temperature (at the time of sampling) and water filled pore space (WFPS). Values given are averages of plots from three sample lines (two for $FIRE_{100}$) with standard error following.

Area	Depth (cm)	pH	EC (μS)	Soil temperature (°C)	WFPS	Soil type
$FIRE_3$	5	4.5 ± 0.1	47.8 ± 5.1	7.2 ± 0.6	0.6 ± 0 .1	Organic
	10	4.7 ± 0.1	58.0 ± 12.8	6.8 ± 0.5	1.0 ± 0 .1	Mineral
	30	5.2 ± 0.2	44.7 ± 10.2	4.0 ± 0.6	1.0 ± 0.0	Mineral
$FIRE_{25}$	5	4.8 ± 0.2	41.4 ± 6.1	7.1 ± 0.4	0.6 ± 0.1	Organic
	10	5.2 ± 0.1	25.0 ± 4.3	7.7 ± 0.6	0.9 ± 0.2	Organic
	30	5.3 ± 0.2	34.7 ± 3.7	3.6 ± 0.9	1.0 ± 0.2	Mineral
$FIRE_{100}$	5	4.8 ± 0.4	51.2 ± 13.3	6.7 ± 0.5	0.4 ± 0.1	Organic
	10	5.3 ± 0.3	33.8 ± 6.6	4.3 ± 0.5	0.9 ± 0.2	Organic
	30	5.8 ± 0.4	75.85 ± 8.0	−0.1 ± 0.2	1.0 ± 0 .1	Mineral

Table 3
Active layer thickness, soil carbon (C) stocks (kg m^{-2}) and C/N ratios, as well as soil organic matter (SOM) concentrations (%) (based on soil C (%) and Van Bemmelen factor) at 5, 10 and 30 cm depth. Values given are averages of plots from three sample lines (two for $FIRE_{100}$) with standard error following. Uppercase letters denote statistical differences ($P < 0.05$) between different fire areas at the same soil depth (different letter indicates significant difference). If no letters are given, no significant differences were detected.

Area	Depth (cm)	Active layer thickness (m)	Organic layer thickness (cm)	Soil C (kg m^{-2})	Soil C/N	SOM (%)	Microbial C (mg g^{-1})
$FIRE_3$	5	1.01 ± 0.09^{A}	5.34 ± 1.2^{A}	2.61 ± 0.5	28.1 ± 2.9	43.7 ± 7.8	3.5 ± 0.5
	10			2.22 ± 0.2	14.4 ± 0.9	3.11 ± 2.3^{A}	0.13 ± 0.01
	30			7.74 ± 1.2	13.5 ± 1.1^{A}	5.1 ± 1.0^{A}	1.0 ± 0.4
$FIRE_{25}$	5	0.88 ± 0.10^{B}	10.2 ± 2.5^{AB}	7.46 ± 3.7	29.3 ± 6.4	39.7 ± 9.6	3.2 ± 0.9
	10			2.18 ± 0.5	25.3 ± 4.4	29.1 ± 9.6^{AB}	3.5 ± 1.6
	30			8.64 ± 1.3	17.9 ± 2.1^{AB}	14.2 ± 5.4^{AB}	0.2 ± 0.0
$FIRE_{100}$	5	0.29 ± 0.01^{B}	16.0 ± 1.4^{B}	8.30 ± 1.5	36.5 ± 3.2	64.2 ± 2.3	8.5 ± 2.4
	10			2.16 ± 0.2	23.0 ± 4.7	29.4 ± 15.0^{B}	3.3 ± 1.0
	30			6.40 ± 1.0	22.5 ± 0.9^{B}	28.2 ± 11.1^{B}	2.0 ± 0.9

lines were placed in as flat terrain as possible. Furthermore, all the lines were situated at least 100 m from the closest road to minimize the effects of the road on permafrost (snow cover, dust emissions, etc.) (Gill et al., 2014). To determine the effect of fire we compared areas of recent fire with areas which had not been exposed to fire lately by establishing a similar 150 m long line, with three sampling plots on each, in the vicinity of the $FIRE_3$ and $FIRE_{25}$ areas in old forest stands which had not been exposed to fire for the last 100 years. These lines together formed the area $FIRE_{100}$ used in the analysis. A soil sampling pit was excavated in the middle of each sampling plot and soil samples were collected from the soil profile at the depths of 5, 10 and 30 cm with a metal corer (6 cm in diameter and length). Simultaneously, the permafrost depth and soil temperature were determined from the soil pit. During transportation, soil samples were first stored in a cooler filled with ice to keep the temperature of the samples as close to the conditions prevailing in nature as possible.

Tree biomass and ground vegetation were determined at each area. We measured the ground vegetation biomass in four 0.20 × 0.20 m squares placed randomly within each sample plot, and in addition, species composition and coverage were determined in two 0.75 × 0.75 m squares. Tree characteristics (stem diameter at 1.3 m height or diameter at the base of trees lower than 1.3 m in height, the height of a tree, crown height and crown diameter) were also measured from all trees over 1 m tall. Tree biomass was determined according to the formulas of Lambert et al. (2005) and Wagner and Ter-Mikaelian (1999).

2.3. Temperature response measurements

Soil samples were sieved through a 2 mm mesh and visible roots were removed. The samples were pre-incubated before the temperature response measurements at 4 °C for 3 weeks. A subsample (25 ml) was taken, weighed and transferred to incubation bottles (500 ml). The temperature response measurements were performed as in Riikonen et al. (2017). The bottles were flushed with compressed air consisting of 21% oxygen and 79% nitrogen (N) (Technical air 320020, AGA, Finland) before each measurement and were immediately closed with rubber stoppers. Empty bottles were prepared accordingly and used as blanks. The bottles were then incubated for 24 h in a climate chamber (WEISS WK11 340, Weiss Klimatechnik, Germany) at each temperature level before gas sampling. The temperature levels used were 1, 7, 13 and 19 °C. The aforementioned temperatures were chosen based on the actual soil temperatures measured at the study sites. The temperature at the lowest part of the active layer (Table 2) was around 1 °C. At the soil surface temperatures averaged between 7 and 13 °C, and the warmest temperatures at the soil surface were between 17 and 24 °C. We used the 24 h measurement time to avoid long-term changes in substrate availability (Karhu, 2010) or possible changes to microbial community structure as we wanted to determine the instantaneous response of R_h to changes in soil temperature. A 50 ml gas sample was taken from each bottle with a 60 ml polypropylene syringe (BD Plastipak 60, BOC Ohmeda, Helsingborg, Sweden), injected into a 12 ml Exetainer vial (Labco, Lampeter, UK) and analysed with an Agilent Gas Chromatograph (GC 7890A Agilent Technologies, USA) equipped with an autosampler. The analyses were performed with a flame ionization detector (FID) using helium as a carrier gas, and synthetic air (450 ml min^{-1}) and hydrogen (40 ml min^{-1}) as flame gases. In addition, nitrogen gas (5 ml min^{-1}) was used as the make-up gas for the FID standard. The carbon dioxide (CO_2) concentrations were measured using a 4-point calibration curve determined with 433, 750, 1067 and 1500 ppm standard gas concentrations (Oy AGA Ab, Espoo, Finland). The analyser's oven temperature was set to 60 °C with the detector temperature being 300 °C.

The incubated soil samples were dried (105 °C, 24 h), ground with a mortar grinder (Retsch RMO Mortar Grinder, Retsch, Germany), and their C and N concentrations measured with an elemental analyser (Vario Max CN, Elementar Analysensysteme, Germany). Bulk densities were calculated from the fresh and dry weights of the samples and, based on this, we determined also the porosity of the samples (Eq. (1), Table 2). The water-filled pore space (WFPS, volumetric water content to porosity ratio) (e.g. Linn and Doran, 1984) of the soil was determined based on volumetric water content and porosity of the samples and is here expressed as:

$$WFPS = \theta_v/\varepsilon \quad (1)$$

where θ_v is the volumetric water content ($m^3\ m^{-3}$) and ε is the porosity ($m^3\ m^{-3}$).

2.4. Determination of soil characteristics

The soil C content (kg m^{-2}) was calculated based on the soil C (%) concentration, while SOM (%) was calculated based on van Bemmelen factor (1.724) and soil C (%) (Table 3). Soil pH and electrical conductivity were measured by preparing a 1:2.5 (v/v) soil/water solution (Table 2). The solution was allowed to set overnight and pH and conductivity were then measured using a pH meter (PHM210, Radiometer Analytical, France) and conductivity meter (JENWAY 4010 Conductivity, TER Calibration, Wigan, UK), respectively. Soil particle size distribution was determined with a laser diffractor (LS 230, Beckman Coulter, USA) from oven dried and sieved (< 2 mm) samples.

2.5. Microbial biomass carbon and microbial carbon use efficiency

The microbial biomass C was determined with the chloroform fumigation-extraction method by Vance et al. (1987). The extracted microbial biomass C was measured with a total organic carbon analyser (TOC-V CPH, Shimadzu, Kyoto, Japan) and the results were calculated following Beck et al. (1997). We also calculated microbial metabolic quotient (qCO_2), which is defined as the microbial respiration per unit microbial biomass C and is a measure of the ecophysiological status of

the soil microbes (Anderson and Domsch, 1993; Spohn, 2015).

2.6. Q_{10} fitting and statistical analyses

The CO_2 respiration rate per hour was calculated as the difference between the incubated and blank samples after 24 h of incubation and was expressed on an organic matter basis ($\mu gCO_2\ gC^{-1}\ h^{-1}$). The Q_{10} values were then calculated by fitting a model (Eq. (2)) to the CO_2 respiration data with the Python programming software (Python Software Foundation, version 2.7).

Q_{10} values were calculated from the flux data by fitting Eq. (2) to the data (using the least squares method) which gives out the Q_{10} as a parameter (Ito et al., 2015):

$$R_h = R_{ref} Q_{10}^{\frac{T-T_{ref}}{10}} \quad (2)$$

where R_h is the measured heterotrophic respiration rate ($\mu gCO_2\ gC^{-1}\ h^{-1}$) at different temperatures T (°C), and R_{ref} is the reference respiration at the reference temperature T_{ref}.

A linear mixed model was used to compare soil heterotrophic respiration R_h and Q_{10} values between the age classes. The models were as follows:

$$X = a + bY + cRDM \quad (3)$$

where X is either Q_{10} or R_h, Y is time since fire or soil depth, respectively, a is the model intercept, b and c are regression coefficients and RDM is the random effect (sampling line). Both variables (R_h and Q_{10}) were tested in separate models between times since fire and depths (within time since fire) with Bonferroni correction. Here, depending on the tested variable, the dependent variable was either Q_{10} or respiration rate, and the fixed factor was either time since fire or soil depth. Sample line was added as a random factor to take into account the possible dependency of soil depth and areas on each other. For this we used SPSS Statistics 24.0 (IBM Corporation, Armonk, New York, USA).

We also used a linear mixed model to determine which of the measured factors explained Q_{10} and R_{ref} (Eq. (4) and Eq. (5)). The model included all areas and depths:

$$Q_{10} = a + bMC + cDepth + dCN + eAD + fBiomass\_t + gBiomass\_g + hM + iPh + j(AD \times T) + kRDM \quad (4)$$

$$R_{ref} = a + bMC + cDepth + dCN + eAD + fBiomass\_t + gBiomass\_g + hM + iPh + j(AD \times T) + kRDM \quad (5)$$

where MC is the microbial biomass C (mg g^{-1}), $Depth$ is the sampling depth (cm), CN (%) is the soil C:N ratio, AD (m) is the depth of the active layer, $Biomass\_t$ (kg m^{-2}) is the above-ground biomass consisting of living trees, $Biomass\_g$ (kg m^{-2}) is the ground vegetation biomass (shrubs, grasses, mosses and lichens), M is the soil moisture (%), Ph is the soil pH, $AD \times T$ is the cross effect of the active layer depth and soil temperature, and RDM is the random effect (sample line). a is the model intercept and b–k are regression coefficients.

The best model was selected based on Akaike's information criterion (Chambers and Hastie, 1992). For this we used the lme4 package (Bates et al., 2015) in R (R 1.1.383). Normality of residuals was checked with the Shapiro-Wilk test, and if the requirements of a parametric test were not met, the data were log transformed.

3. Results

Fire increased the active layer depth along the fire chronosequence so that in the $FIRE_{100}$ area the active layer depth was 0.30 m, while in $FIRE_{25}$ it was 0.88 m and in $FIRE_3$ 0.88 m (Table 3). The changes to the active layer depth resulting from fire were also reflected in the temperature response of soil respiration which varied from 1.7 to 3.0 in our study areas (Fig. 1). The fire also, to some degree, decreased the soil C values (kg m^{-2}) in $FIRE_3$ compared with other areas (Table 3), but the difference was not statistically significant ($P > 0.05$). In addition, the soil organic layer thickness was reduced in $FIRE_3$ compared with $FIRE_{100}$ ($P < 0.05$) but not compared with $FIRE_{25}$ (Table 3).

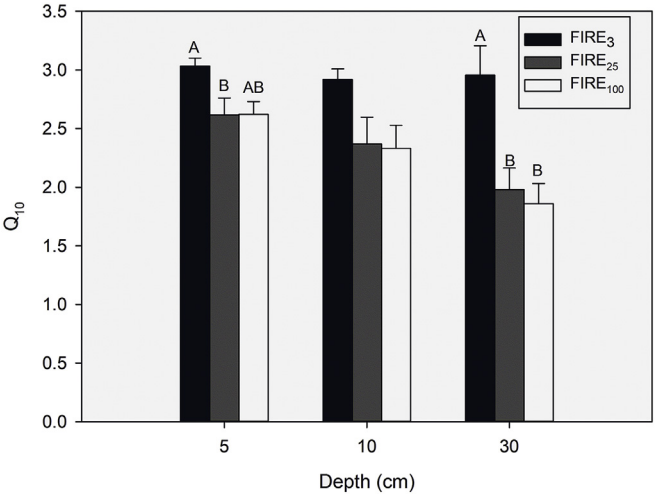

Fig. 1. Mean (± SE) soil temperature sensitivities (Q_{10}) of samples from 5, 10 and 30 cm depths. Within a given group (between fire areas), bars with the same uppercase letter at their top do not differ statistically. If no letters are given, no significant differences were detected.

The fire seemed to increase Q_{10}, especially in the deepest soil layer (30 cm) where the most recently burned area $FIRE_3$ had higher Q_{10} than $FIRE_{25}$ and $FIRE_{100}$ ($P < 0.05$) (Fig. 1). Similarly, at 5 cm depth, higher Q_{10} values were observed for $FIRE_3$ than $FIRE_{25}$ ($P < 0.05$) and nearly significantly higher values than for $FIRE_{100}$ ($P = 0.06$). There were no differences in the Q_{10} values between areas $FIRE_{25}$ and $FIRE_{100}$. Further, at 10 cm soil depth, there were no significant differences between any of the areas. The depth-wise comparison showed that there were no significant differences in Q_{10} between different soil depths in the most recently burned area $FIRE_3$ and area $FIRE_{25}$, but in $FIRE_{100}$ the Q_{10} values at 5 cm depth were significantly higher than those at 30 cm depth ($P < 0.05$).

$FIRE_3$ and $FIRE_{25}$ showed a trend of lower R_h values at the 5 cm soil depth compared with $FIRE_{100}$ (Fig. 2) at all temperatures, but despite this trend, the difference was not statistically significant ($P > 0.05$). The lowest values at the 5 cm soil depth were found in area $FIRE_3$. At the 10 and 30 cm soil depths we observed no clear trends or significant differences between the fire areas. In all age classes, R_h was significantly higher at the 5 cm soil depth than at the 30 cm soil depth ($P < 0.05$).

The linear mixed effects model showed that Q_{10} was best explained (43%) by the soil depth and ground vegetation biomass. Q_{10} decreased with increasing soil depth and ground vegetation biomass (Table A1, supplementary material). Both factors contributed significantly to the model ($P < 0.05$, Table A1, supplementary material). R_{ref} was best described by microbial biomass C, soil depth and the active layer depth, which together explained 54% of the variation in R_{ref}. R_{ref} decreased with increasing sampling and active layer depths, while microbial biomass C increased with R_{ref} (Table A2, supplementary material). All aforementioned factors contributed significantly to the model ($P < 0.05$, Table A2, supplementary material).

The qCO_2 values showed that the youngest fire area ($FIRE_3$) differed significantly from the other two areas (Fig. 3). At 5 cm depth, it had overall higher qCO_2 than the two other fire areas ($P < 0.05$) except for 13 °C temperature where no differences were observed. At 10 cm depth, the area $FIRE_3$ had higher qCO_2 at all temperatures than the other two areas $FIRE_{25}$ and $FIRE_{100}$ ($P < 0.05$). Finally, at 30 cm depth, the differences were again significant between $FIRE_3$ ($P < 0.05$) compared with $FIRE_{25}$ and $FIRE_{100}$ at the 13 and 19 °C temperatures, while at the

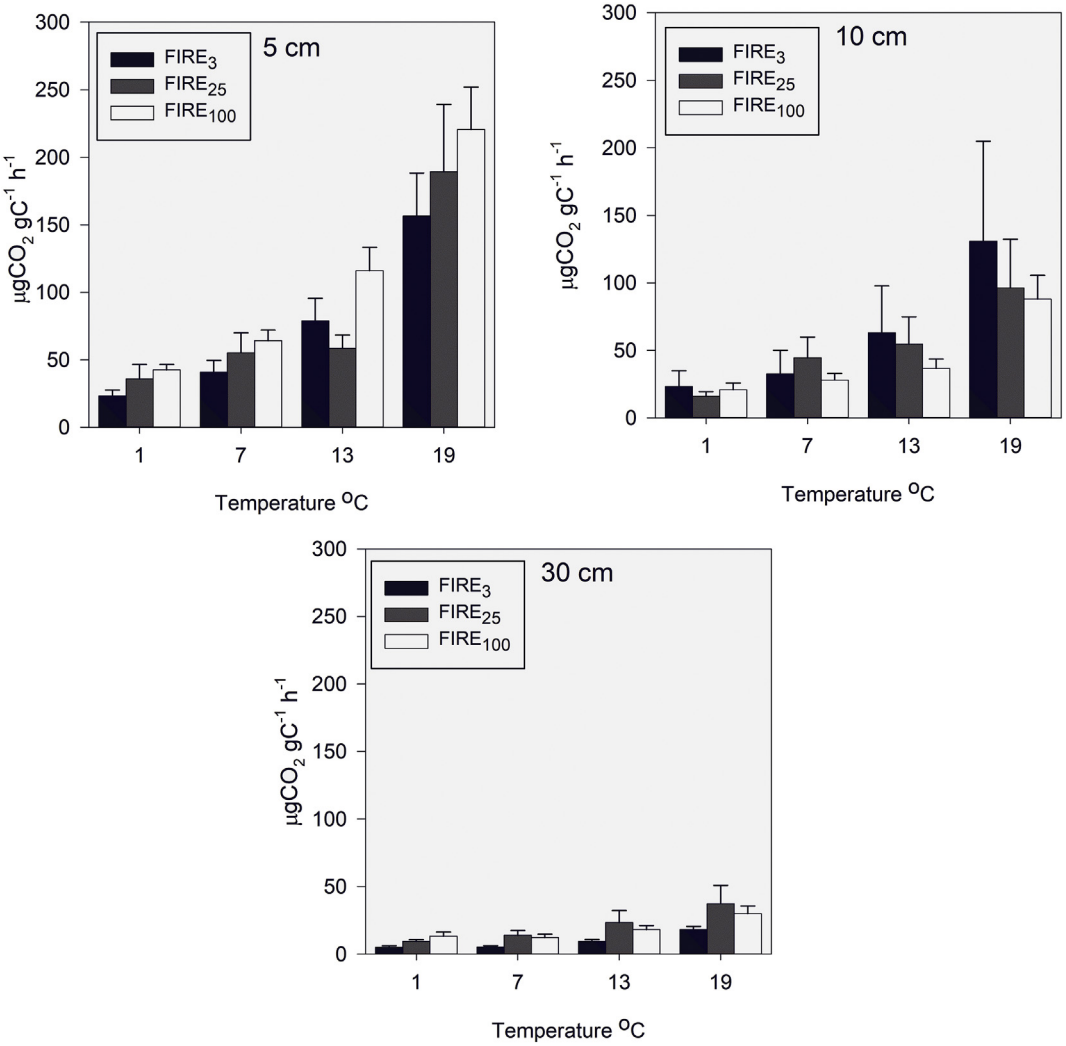

Fig. 2. Mean (± SE) soil heterotrophic respiration rates of samples from 5, 10 and 30 cm depths after 24 h incubation periods in 1, 7, 13 and 19 °C. Within a given group (between fire areas), bars with the same uppercase letter at their top do not differ statistically. If no letters are given, no significant differences were detected.

two lowest temperatures (1 and 7 °C) the differences were mostly not significant (Fig. 3). $FIRE_{25}$ and $FIRE_{100}$ did not differ from each other at any temperature at the three sampling depths.

4. Discussion

Our results indicated that fire had a substantial effect on the temperature response of soil respiration in boreal forests with underlying permafrost, while there were no significant differences in the heterotrophic respiration levels between the age classes. The fire also increased the active layer depth (Köster et al., 2017) and decreased the organic layer thickness. We observed a trend of decreased, although not significant, soil C stocks especially in the 5 cm soil horizon after the fire. In addition to soil C stocks, also the quality of organic matter changes in the fire (Certini, 2005). Organic C and N in SOM are partly combusted and partly turned to pyrogenic C ('black C') and N ('black N') resistant to decomposition (Knicker, 2007). The formed recalcitrant SOM can be considered to have higher temperature sensitivity than labile SOM (Karhu et al., 2010; Yan et al., 2017), although the temperature sensitivity of labile and recalcitrant matter remains under discussion (Conant et al., 2011).

Previous studies have found that fire increases the temperature sensitivity of respiration in soils (Muñoz-Rojas et al., 2016). Our results also showed increased temperature sensitivity a few years after the fire. In the youngest fire area, Q_{10} was also affected down to 30 cm depth, although the direct effects (such as heat) of fire did not seem to reach this depth. The higher temperature sensitivity at 30 cm depth in the most recently burned area compared with other areas could be linked to two factors: translocation of pyrogenic compounds down the soil profile (Guggenberger et al., 2008) or ceased input of easily decomposable C in fresh litter and root exudates (Knicker, 2007) after fire. As the succession proceeds, more labile C can become available again (Chen and Shrestha, 2012) and the temperature sensitivity may decrease back to original levels, which in this case seemed to take less than 25 years. On the other hand, the low Q_{10} values of mineral soils in the older fire areas could be caused by the soil aggregate protection of otherwise recalcitrant SOM (Gillabel et al., 2010). Gillabel et al. (2010) observed that subsoil SOM, protected by the silt and clay fraction, had a lower Q_{10} than the topsoil SOM in the micro- and macroaggregates, attributing this difference to stronger protection of organo-mineral interactions in the silt and clay components compared with physical protection of larger aggregates (Six et al., 2002).

The origin of SOM is also reflected in the Q_{10} values. The ground vegetation affects the availability of labile C in the soil, which was also seen in the mixed model analysis for Q_{10}. The Q_{10} was significantly affected by ground vegetation biomass and soil depth. Increasing ground vegetation biomass led to lower Q_{10} values as the succession of ground vegetation, possibly producing labile soil organic C, proceeded

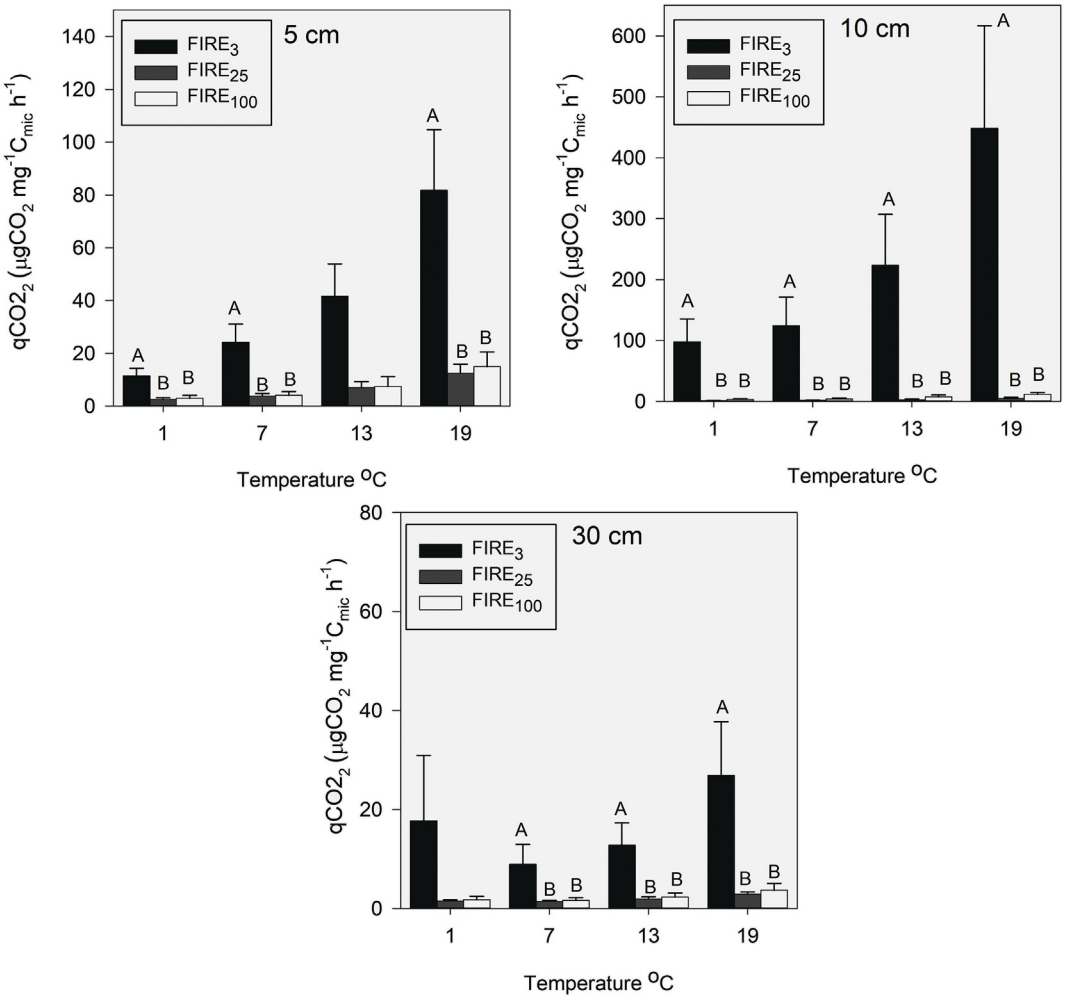

Fig. 3. The metabolic quotient qCO_2 of fire areas in the soil depths of 5, 10 and 50 cm. Within a given group (between fire areas), bars with the same uppercase letter at their top do not differ statistically. If no letters are given, no significant differences were detected.

along the fire chronosequence. Higher ground vegetation biomass also causes greater input of litter to the soil surface for the microbes to degrade, and this also is reflected in the quality of litter. The area $FIRE_{100}$ was characterized by a full moss cover (*Sphagnum* sp., *Pleurozium* sp.), shrubs (*Ledum groenlandicum* (Oeder), *Vaccinium vitis-idaea* L., *V. uliginosum*) and some *R. chamaemorus* L. In the area $FIRE_{25}$ the vegetation was similar to $FIRE_{100}$ but with some unvegetated patches and several *Cladonia* and *Cladina* species of lichens. In the area $FIRE_3$, the soil surface was still governed by many bare patches and the main vascular plant growing there was *Equisetum sylvaticum* L. (Köster et al., 2017). Consequently, the differences in the ground vegetation species composition affect the quality of the incoming litter in the fire areas. Forest fires have commonly been seen as having a decreasing effect on soil respiration because of a decrease in microbial biomass (Dooley and Treseder, 2012) and in the amount of SOM. Our previous study, carried out with portable chambers at our study sites (Köster et al., 2017), revealed that soil CO_2 efflux decreased immediately after fire but recovered during the following decades. In the current study, we did not observe a significant decrease in the soil heterotrophic respiration rates, although a trend towards decreased R_h was seen at the 5 cm depth in the youngest fire area. However, while the R_h values in our study were measured per mass of soil C without vegetation, the CO_2 efflux measured in Köster et al. (2017) represented the CO_2 production of the whole soil column below the chamber. Soil CO_2 efflux consists of two main fluxes: heterotrophic respiration originating from the decomposition of SOM and autotrophic respiration originating from roots and root-associated mycorrhizal fungi. The proportion of autotrophic respiration can be very high, up to 50% of the total soil CO_2 efflux in mature boreal forests (Högberg and Read, 2006; Pumpanen et al., 2015). As the trees and ground vegetation are killed in the fire, the autotrophic respiration component is lost and remains low during the first years after fire until the new vegetation starts to emerge in the area. As the measurements in this study represent the heterotrophic component of soil respiration, we did not observe this significant decrease in CO_2 efflux resulting from the loss of autotrophic respiration in the fire. Thus, our results are similar to those in the study by Hu et al. (2017), who also found that the decrease in soil respiration after fire was actually caused mainly by the reduced autotrophic respiration, while R_h was not significantly affected. In some studies, R_h has actually been found to increase following fire, which has been attributed to increased input of detritus following combustion of vegetation on the soil surface (Muñoz-Rojas et al., 2016).

While fire did not significantly reduce R_h in our study, the effects of fire on other factors could be seen in the mixed model analysis. Microbial biomass expectedly affected respiration: The mixed model analysis showed that R_{ref} ($\mu gCO_2\ gC^{-1}\ h^{-1}$) was positively affected by microbial biomass C and negatively affected by active layer depth and soil depth. The microbial biomass, and hence the heterotrophic soil respiration, is known to decrease with soil depth (Fierer et al., 2003; Zhou et al., 2018), thus affecting the heterotrophic soil respiration. Yet, some exceptions with soil respiration increasing with depth have been observed (Rovira et al., 2010).

The microbial biomass C showed some, but not a significant, decrease in area $FIRE_3$ compared with $FIRE_{100}$ (Table 3), while the qCO_2 of microbes was higher shortly after fire (in $FIRE_3$) compared with older areas. Other studies have also observed higher qCO_2 values after fire (De Marco et al., 2005; Fritze et al., 1993; Rutigliano et al., 2007). The reason for this decrease might be pioneering microbial species that have higher respiration rates (Pietikäinen and Fritze, 1995) or changes in the fungal to bacterial ratio, which has been observed to decrease following fire (Zhou et al., 2018). Fungi have a higher CUE and therefore lower qCO_2 (Sakamoto and Oba, 1994). Hence, it has also been found that qCO_2 decreased with an increase in the fungal to bacterial ratio (Sakamoto and Oba, 1994). Fungi are also more sensitive to fire than bacteria (Mataix-Solera et al., 2009), and thus in our previous study we observed a reduced fungal to bacterial ratio after fire in our measurement areas (Zhou et al., 2018), which could explain the higher qCO_2 values in the area $FIRE_3$. At the same time, the higher qCO_2 values could be the reason why soil heterotrophic respiration was not significantly reduced after fire at $FIRE_3$ compared with other areas, as the higher values indicate that microbes are using more C for respiration in the recently burned areas compared with the older areas. This means that the microbial efficiency is reduced after fire, but it returns to original levels by 25 years after fire.

5. Conclusions

We conclude that forest fires may facilitate the decomposition of permafrost SOM by increasing the active layer depth, but fire increased the temperature sensitivity of decomposition. Based on the Q_{10} values of the oldest fire area, the SOM in the permafrost surface was less temperature sensitive than the SOM in the soil surface. The post-fire decreases in ground vegetation were reflected in the SOM temperature sensitivity shortly after fire but seemed to return to original levels with forest succession. The fire also increased the microbial qCO_2, which could be related to changes in microbial population as the microbial community is changed from fungal dominated to bacterial dominated as a result of fire. The changes in microbial qCO_2 may also partly explain the lack of significant decrease in heterotrophic soil respiration after fire, as the microbes may use more C for respiration in the recently burned areas compared with the older areas. Even though fires increased the active layer depth, the decrease in SOM quality caused by fire may limit the decomposition rate to some degree.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2019.02.130.

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