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Transplanting boreal soils to a warmer region increases soil heterotrophic respiration as well as its temperature sensitivity

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ABSTRACT

Under a warming climate, the boreal forest could become one of the largest terrestrial net CO_2 sources, as increasing disturbances and soil organic matter decomposition rates (heterotrophic respiration, Rh) could offset net primary production. Since soil represents the boreal forest's largest C pool, it is critical of correctly predicting future changes in Rh, as well as its sensitivity to temperature (Q_{10} of Rh). We simulated a soil warming by transplanting soil cores from boreal balsam fir (*Abies balsamea*, BF) and black spruce (*Picea mariana,* BS) stands to a more southern Eastern hemlock stand (*Tsuga canadensis*, EH). We measured Rh and soil properties over 3 years, from June to October. Over three snow-free seasons, soil temperature (first 10 cm, including the FH organic layers) and Rh increased for BF (+3.2 °C, +60% of Rh) and BS cores (+2.3 °C, +27% of Rh). Microbial C concentration decreased by 54–73% in the FH layers of warmed and control cores relative to initial values, despite unchanged chemically labile C, probably due to excised roots and mycorrhizal hyphae. This suggests a possible underestimation of Rh during the experiment. In BF soils only, the increase in Rh was accompanied by an increase in its sensitivity to temperature. Under a +5 °C soil warming, mean predicted Rh of BF soils would increase by 83% rather than by 56%. Relative to BS soils, such increase in sensitivity could be partly due to a higher fraction of chemically labile C (+52%) in the FH layers and a higher mean warming effect. It suggests that for BF forest soils, predicting decomposition rates for a warmer climate based on current temperature sensitivities could be inadequate. However, longer-term studies are needed to see if this increase in Q_{10} of Rh for BF soils would be maintained for longer periods.

1. Introduction

The boreal forest plays a key role in the global level of carbon dioxide (CO_2), as its net CO_2 uptake during northern summers is the main cause of the global seasonal variations in CO_2 concentration (IPCC, 2013). From 1990 to 2007, the boreal forest stored 32% of the world forests' C stock and represented 21% of their C sink (Pan et al., 2011). In addition, boreal soils contain three times more C than forest biomass (Pan et al., 2011). Under a warming climate, the boreal forest could become a large annual net source of CO_2, because projected increases in net primary production could be offset by even larger increases in disturbance extremes (e.g. fires, insect outbreaks, drought) and in soil organic matter (SOM) decomposition (heterotrophic respiration, Rh) (Kurtz et al., 2013; Metsaranta et al., 2011). Among these potential sources of CO_2, future changes in Rh are the most uncertain, because very little is known about the temperature sensitivity of Rh (Q_{10}, i.e., the factor by which the rate of Rh increases with a 10 °C rise in temperature). We thus estimated the temperature sensitivity of Rh in the boreal forest of the province of Quebec.

Our current knowledge regarding the temperature sensitivity of Rh is mostly based on laboratory incubations. Studies show that Rh increases with warming, and that its Q_{10} is greater at lower temperatures (Dalias et al., 2001; Tuomi et al., 2008) and for slowly decomposing (recalcitrant) substrates, as long as C substrates are available for depolymerisation (e.g., for boreal soils: Hartley and Ineson, 2008; Karhu et al., 2010a,b; Laganière et al., 2015; Vanhala et al., 2008). However, these soil incubation studies have been criticized because they depart from *in situ* conditions. Indeed, they are unable to reproduce simultaneously seasonal fluctuations of temperature, relative humidity, wind, air pressure and sunlight (Wang et al., 2014). Furthermore, the use of separated soil horizons rather than intact multiple-horizon cores limits the exchange of substrates among soil horizons, and thus may limit

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stimulation of microbial activity (Podrebarac et al., 2016). As a result, laboratory incubation experiments with separated soil horizons could significantly underestimate the Q_{10} of Rh of *in situ* multiple-horizon cores (Podrebarac et al., 2016).

During field warming experiments, total soil respiration (Rs) is more often monitored than Rh (Bronson et al., 2008; Lu et al., 2013; Rustad et al., 2001; Schindlbacher et al., 2012), because of the high labor cost and methodological challenges associated to separating Rh and autotrophic respiration (Ra) (Bond-Lamberty et al., 2011; Kuzyakov, 2006; Subke et al., 2006). A synthesis of 27 field experiments spanning nine biomes and two decades of warming revealed no significant warming effect on the temperature sensitivity of Rs across all biomes except deserts and boreal forests (Carey et al., 2016). However, given the different temperature sensitivities of Rh and Ra, confounding these two variables in Rs can lead to errors in predicted SOM decomposition rates (Wang et al., 2014).

Few field warming experiments have monitored Rh, and very few have reported the Q_{10} of Rh (Wang et al., 2014). The effects of climate warming on the temperature sensitivity of Rh remains uncertain. Some studies report no change in Q_{10} values (D'Orangeville et al., 2013; Noh et al., 2016; Schindlbacher et al., 2015; Vanhala et al., 2011; Vogel et al., 2014), while others report a decrease (Eliasson et al., 2005; Melillo et al., 2002; Zhou et al., 2010) or an increase in Q_{10} (Aguilos et al., 2013; Luan et al., 2014). Changes in the temperature sensitivity of Rh could be driven by depletion of labile carbon (C_{labile}; Bradford et al., 2008; Craine et al., 2010; Eliasson et al., 2005; Kirschbaum, 2004), thermal adaptation of soil microorganisms (Crowther and Bradford, 2013), and/or changes in microbial species composition (Aguilos et al., 2013; Budge et al., 2011; Noh et al., 2016). A major cause of uncertainty in Rh predictions stems from the assumption that its Q_{10} will remain stable at its current level under a warmer climate (Luo et al., 2001). However, if the Q_{10} of Rh does increase with temperature, then model simulations that assume a constant Q_{10} would underestimate both future Rh and CO_2 emissions to the atmosphere.

Predicting the response of Rh to warming is complicated by the high diversity of organic C compounds, for each of which the decomposition rate has its own temperature sensitivity. Complex molecules are characterized by slow Rh and high Q_{10} of Rh (Conant et al., 2011; Craine et al., 2010; Dungait et al., 2012). In addition, environmental factors, like physical and chemical protections of C substrates in the mineral matrix, flooding, drought and freezing, can decrease the Q_{10} of Rh by limiting the substrates' accessibility to enzymes at reaction microsites (Conant et al., 2011; Davidson and Janssens, 2006; Dungait et al., 2012). Finally, each process that contributes to SOM decomposition, such as enzyme production, substrate uptake, and microbial respiration efficiency (CO_2 flux per amount of microbial C biomass), responds differently to changes in temperature and contributes to the overall Q_{10} of Rh (Conant et al., 2011).

In most soils, most C substrates are recalcitrant and largely unavailable to enzymes within the mineral matrix (Davidson and Janssens, 2006). Moreover, in podzols, which are common in upland boreal forest, there is very low vertical mixing of litter materials by soil organisms (Scheu and Parkinson, 1995). Consequently, organic matter remains layered in distinct horizons, corresponding to different decomposition stages. The mean residence time of C in a podzol increases thus clearly with soil depth, from annual cycle to decadal or centennial cycle (Karhu et al., 2010a). Since decadal cycling OM fractions are more temperature-sensitive, Q_{10} of Rh is expected to increase in the next decades for podzols under a warming climate (Hartley and Ineson, 2008; Karhu et al., 2010a).

Buried heating cables are the most common *in situ* soil warming method for forest soils (e.g. Bronson et al., 2008; Eliasson et al., 2005; Schindlbacher et al., 2009). However, their presence can exacerbate root mortality and reduce root number and biomass, which can lead to biased results (Edwards et al., 2004). The alternative method of transferring soils to warmer ecosystems has several advantages: 1) the air and the soil are warmed under natural conditions; 2) the method is powerful and cost-effective, allowing more replications as well as the comparison of many contrasting biomes (Hart, 2006); 3) it allows direct measurement of Rh when soils are confined in 30 cm pipes, as described by Vogel and Valentine (2005). The core transfer method requires control cores, i.e. additional soil cores transplanted close to their original position at the source site, in order to isolate the effect of root trenching from that of warming.

The potential shortcomings of the core transfer method are that microbial respiration may be overestimated because of decomposing excised roots inside the root exclusions, or underestimated because the method neglects annual fine root turnover outside the root exclusions (Vogel and Valentine, 2005). Root exclusion may also block root water uptake, resulting in higher soil water contents compared with controls, thereby confounding differences in microbial activity between treatments (Heinemeyer et al., 2011).

The objective of this study was to test the effect of soil warming on the relationship between heterotrophic respiration and soil temperature for balsam fir (*Abies balsamea* [L.] Mill.) and black spruce (*Picea mariana* [Mill.] B.S.P.) forests. Soil cores were exposed to higher temperatures following their transplantation to a warmer forest site and monitored for 3 years. We hypothesized that soil warming would increase Rh and change the relationship between Rh and soil temperature, altering the temperature sensitivity (Q_{10}) of Rh for both forest types.

2. Material and methods

2.1. Study sites

Twelve study sites (≥1 ha) were selected in 3 different regions of Quebec, Canada, covering a 4–5 °C gradient of air temperature (Table 1). The first 3 boreal sites are balsam fir (BF) stands located in the Forêt Montmorency (balsam fir–white birch bioclimatic domain); the other 3 boreal sites are black spruce (BS) stands near Tirasse Lake (black spruce–moss bioclimatic domain). The 6 southern temperate sites (EH) are eastern hemlock and red spruce stands located at Lotbinière (sugar maple–yellow birch bioclimatic domain). Sites within each region are 5–30 km apart. Compared with the BS and the EH sites, BF sites receive 30% more precipitation and have thinner organic FH layers (fibric and humic material; Soil Classification Working Group, 1998). All soils are well-drained podzols (Soil Classification Working Group, 1998), with a loamy sand to sandy loam texture.

2.2. Experimental design

The experiments at the BF sites and at half of the EH sites were set up in July 2007, while those at the BS sites and at the other half of the EH sites were set up in June 2008. Each site comprised 3 plots (400 m^2 each), placed at least 20 m apart. In each plot, 4 soil cores (8 cm in diameter × 30 cm in length) were extracted with a hammer drill (Fig. 1). Three of these cores (hereafter referred to as EH, BF and BS cores, or site cores) were buried again next to their original position, with their PVC pipe, and used to measure Rh under the original climate and to account for the effect of initial soil disturbance. The fourth core (hereafter referred to as the initial core) was wrapped in cellophane and kept in cool conditions (4 °C) for one week, pending laboratory analysis of initial microbial and chemical conditions. In each plot of the BF and the BS sites, an additional soil core (hereafter referred to as the BF_W and BS_W core, or warmed core) was extracted, wrapped in cellophane and kept in cool conditions for one week until its transport to the EH site.

In each plot, 1 or 2 additional soil cores (hereafter referred to as condition cores) were installed to allow soil core temperature and volumetric water content (VWC) to be measured at the same time as Rh measurements (described below; Fig. 1). In addition, each site core was paired with a collar (8 cm in diameter × 9 cm in length, inserted 7 cm

Table 1
Site characteristics (standard error in parentheses).

	Boreal sites		Temperate sites
Region	Forêt Montmorency	Tirasse Lake	Lotbinière
Bioclimatic domain	balsam fir–white birch	black spruce–moss	sugar maple–yellow birch
Number of sites	3	3	6
Climate			
Latitude N	47°20′	49°12′	46°38′
Elevation (m above sea level)	810	430	100
Mean air temperature (°C yr^{-1})[a]	−0.5 (0.1)	1.0 (0.8)	5.2 (0.5)
Mean precipitations (cm yr^{-1})[a]	128 (11)	95 (9)	94 (2)
Forest			
Type	BF	BS	EH
Main species	balsam fir	black spruce	eastern hemlock, red spruce
Age range (yr) [b]	50–60	75–90	75–180
Mean basal area (m^2 ha^{-1})[c]	49 (1)	47 (5)	57 (3)
Soil			
Thickness of the organic (FH) layers (cm) [d]	8 (1)	15 (1)	17 (3)
Mineral soil texture	Sandy loam	Sandy loam	Loamy sand

[a] From 2007 to 2010 in the Lotbinière region, from 2007 to 2009 in the Forêt Montmorency region, and from 2008 to 2010 in the Tirasse Lake region.
[b] From 8 dominant or codominant trees per site.
[c] From 3 plots per site (radius: 11.28 m).
[d] From 2 perpendicular transects per site (length: 30 m).

into the soil) to measure total soil respiration (Rs) and calculate autotrophic respiration (R_a; Fig. 1). The layer of litter (L, intact litter material; Soil Classification Working Group, 1998) was removed from all buried cores and collars, because L size and CO_2 evolution rate are highly variable during the season (Paré et al., 2006). A silver-coloured metal screen was placed over cores and collars to prevent further L accumulation. The mesh size (2 mm) of the screen permitted precipitations to pass through. The very few mosses re-growing on soil core surface were cut off, if any.

2.3. Field measurements and soil sampling

Soil CO_2 flux was measured with a LI-8100 portable infrared gas analyser (IRGA). The gas chamber was 10 cm in diameter (volume: 835 cm^3) (LI-COR inc., Lincoln, Nebraska, USA), and chamber exposure time was 2 min. Aboveground air volume in each cylinder and collar had been measured previously and was added to the measurement chamber volume. Temperature and VWC were measured in a condition core during Rh measurements, and in free soil during Rs measurements. Temperature of the soil's first 10 cm was measured using an Omega probe (T-handled Type E thermocouple) and VWC, with a Decagon probe (ECH_2O Model EC-5). Moisture probes were calibrated according to forest soil type (EH, BF or BS), by modeling known volumes of added water to the soils and measured probe output (mV) in the laboratory. Meteorological conditions (air temperature, atmospheric pressure, sunny, cloudy or rainy conditions, windy or calm conditions) were also noted. In early October of each year, one Rh core per plot was collected, wrapped in cellophane and brought to the laboratory for microbial and chemical analyses and root biomass measurements. As no soil cores were renewed during the experiment, the resulting number of soil cores per site was 9 the first year, 6 the second year and 3 the third year.

The first efflux measurements were taken 3 weeks after the installation of soil cores and collars to minimize the influence of severed fine root decomposition on soil respiration. CO_2 flux was then measured every 2 weeks during 3 consecutive snow-free seasons (from July to early October in year 1 and from June to early October in years 2 and 3). At each visit of a given site, each core or collar was measured 3 times (morning, noon and afternoon) from 9:30 to 15:30, and each measurement was repeated twice and averaged. Measurements on each site were completed in one day (108 measurements per site), and each region was visited in 3 days (324 measurements per visit). South (EH sites) and north regions (BF and BS sites) were visited in alternation. Each region was visited 8 to 11 times per snow-free season, except in 2007 (5 visits).

2.4. Microbial and chemical analyses

Within a week of core collection, soil cores were separated into organic (FH) and mineral layers, then fresh weighed. Presence of living roots was noted. In spring and autumn 2007 (years 0 and 1 for the EH, BF and BF_w cores), a fraction of soil located at the boundary between FH and B was mistakenly discarded. To overcome this faulty lab manipulation, microbial and chemical characteristics were compared on the basis of concentration or proportion rather than stock base, and root biomass of the EH, BF and BF_w cores was not compared.

The same day of soil core separation, both layers were subsampled (at least 30 g from the FH layers and 80 g of mineral soil), fumigated with chloroform for 24 h or not fumigated (control), and extracted with K_2SO_4 (0.5M) to measure microbial carbon (C_{mic}: C_{tot}) and microbial N (N_{mic}: N_{tot}) (Brookes et al., 1985; Vance et al., 1987). Extracts were kept frozen until determination of total C with a Shimadzu TOC-Vcpn analyser and of total N content with a Shimadzu TNM-1 analyser.

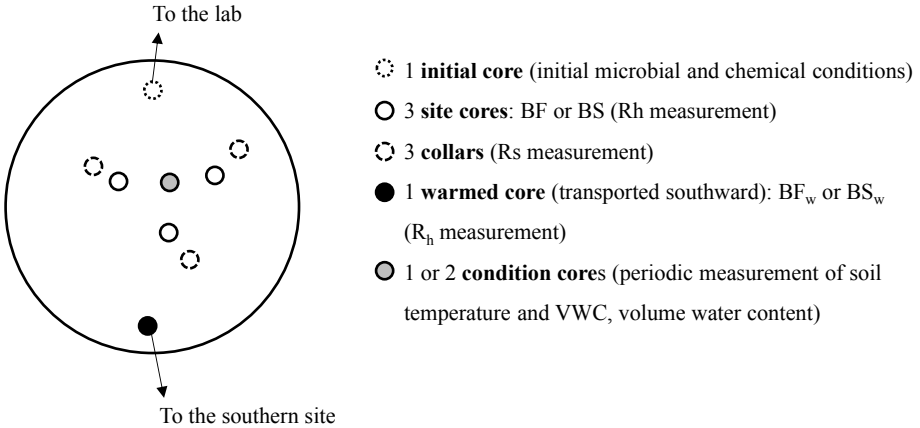

Fig. 1. Sampling design within a plot on a boreal (balsam fir, BF, or black spruce, BS) site.

Incomplete extraction was corrected with a compensation factor of 0.41 for C (K_{EC}; Martikainen and Palojärvi, 1990), and of 0.54 for N (K_{EN}; Joergensen and Mueller, 1996). The rest of original soil in cores were stored in a freezer (−5 °C) until they could be processed for further measurements.

Once the rest of original soil in cores were thawed (3–12 h), roots were removed, washed, fresh weighed and oven-dried (60 °C, ≥ 48–72 h) to determine dry weight. Soil samples were air-dried (48–72 h) and sieved through a 2 mm mesh screen. Volumetric samples of mineral soils were weighed before and after sieving to calculate bulk density, as described by Federer et al. (1993). Sieved subsamples were measured for C and N content. NH_4^+, NO_3^-, and NO_2^- (N_{min}) ions were extracted with KCl 2M and quantified by flow injection analysis (FIA). Total C and total N contents (C_{tot} and N_{tot}) were determined using a LECO TRUMAC CN analyser, on previously ground subsamples (500 µm mesh). Total C content was assumed to equal to organic C content, since the sampled soils were acid podzols containing no calcareous minerals. The proportions of chemically labile C (C_{labile}: C_{tot}) and N (N_{labile}: N_{tot}) were calculated as the difference between the total C and total N contents of the original sample and the total C and total N contents of the non-hydrolysed (recalcitrant) residue after hydrolysis with HCl 6M (adapted from Rovira and Vallejo, 2007). Proportions of chemically labile C and N were only determined for the FH layers because of lab operating limits. All nutrients are reported on the basis of oven-dried mass (105 °C).

2.5. Statistical analyses

Prior to analyses, aberrant respiration observations were discarded in the following situations: 1) heavy rain, 2) flux greater than 8µmoles CO_2 m^{-2} s^{-1}, and 3) variation coefficient > 5% during flux measurements. Flux greater than 8µmoles was rejected because very uncommon: a manipulation error of the Li-8100 was more probable. Daily soil core or collar measurements were averaged to remove diurnal variations.

The analyses were performed using the SAS *MIXED* procedure (SAS Institute, 2012; version 9.3). To take into account the hierarchical structure of the data and the repeated measures, random effects were included in the model. Sites, plots, and cores or collars were considered as random effects. Since many measurements were taken on the same unit, a time-continuous autoregressive covariance structure was used. Normality and variance homogeneity assumptions were verified graphically. If assumptions were not met, data was normalized and variance was stabilized by log- or square-root transformation. In cases where data was transformed for analysis, means were computed on the transformed scale and back-transformed using bias correction (Land, 1971).

2.5.1. ANOVA analyses

Three ANOVAs were carried out. First, we analysed the cylinder effect (site cores versus collars) on soil respiration (Rh and Rs), temperature and VWC according to years. Second, we analysed the warming effect (warmed [BF_w and BS_w] versus site cores [BF and BS]) on Rh, temperature and VWC according to the date of visit within years. For this ANOVA, we tested the BF and BS cores separately because they were installed with a 1-year lag, and, for each subset, the warmed and the site cores were compared on the nearest dates of visit (usually a lag of 3–7 days). Finally, a third analysis was done to measure the warming effect on soil core properties across years (warmed [BF_w and BS_w] versus site cores [BF and BS]). Means were compared with a bilateral test (H_o: $mean_1 = mean_2$). Significance levels for multiple comparisons were adjusted with a simulation method in SAS (Westfall et al., 1999).

2.5.2. Regression analysis

We developed a model to quantify the relationship between Rh and soil temperature for all site cores and warmed cores (BS, BF, EH, BS_w and BF_w). We also compared the temperature sensitivity of Rh for BF versus BF_w cores, BS versus BS_w cores, and BF_W versus BS_W cores (regression coefficient b; comparison level: 0.05/3 = 0.02). In addition to soil temperature, we tested core type, soil moisture and meteorological conditions. We chose an empirical Gaussian model, which Tuomi et al. (2008) demonstrated to be the best fit for various soil types, including podzols:

$$R_h = R_{h_0}\, e^{bT+cT^2}$$

Where R_h = heterotrophic respiration.

R_{h_0} = heterotrophic respiration at a soil temperature of 0 °C
T = soil temperature (°C)

This model describes 3 consecutive respiration phases: first, an increase at lower temperatures, then a maximum, and finally, a decrease at higher temperatures. Using the form $\ln(R_h) = a + bT + cT^2$, R_{h0} becomes e^a. Coefficient a determines the baseline value of Rh at 0 °C; coefficient b determines the rate at which Rh increases with temperature (i.e., its temperature sensitivity) before reaching its maximum; and coefficient c determines the rate at which Rh decreases at temperatures above the optimum. The temperature sensitivity of Rh was calculated as $Q_{10} = Rh_{(T+10)}/Rh_{(T)}$.

3. Results

3.1. Soil core respiration under original climate

Core respiration (Rh) represented 90%–99% of collar respiration (Rs), according to years (ln scale, $P < 0.01$; not shown). For VWC and soil temperature, the difference between cores and free-soil varied among years and forest types ($P < 0.01$). Soil cores were 3%–8% wetter and up to 0.6 °C colder than free soil. The largest differences were observed during the third snow-free season ($P < 0.05$ for VWC; $P < 0.0001$ for soil temperature). Daily respiration rates of soil cores and collars ranged from 0.2 to 8.0µmoles CO_2 m^{-2} s^{-1}; soil core temperatures, from 1 to 22 °C; core VWC, from 10% to 42% (not shown). Three quarters of the measurement days were sunny or cloudy, without rain.

The fitted Rh models revealed significant effects of soil temperature between regions for site cores (BF, BS and EH cores, $P < 0.0001$, ln scale). As differences in Rh across regions were found to vary significantly with soil temperature ($P < 0.0001$; Fig. 2a and c), the effects of region on Rh were compared at low (10 °C), intermediate (13 °C) and high (16 °C) soil temperatures. Compared to EH cores, BF cores showed higher Rh rates in all temperature ranges (+20%, $P < 0.05$; not shown). Squared correlation between back-transformed predicted values and observed values (r^2) was 57% for EH cores, 43% for BF cores and 37% for BS cores (Table 2).

3.2. Soil core properties under original climate

Compared to the FH layers of BS cores, BF cores showed higher chemically labile C (+52%, $P < 0.001$), labile N (+16% to +21%, $P < 0.05$), as well as a lower C: N ratio (−45% to −50%, $P < 0.0001$; Table 3). BF cores showed also higher N_{min} concentration relative to BS cores, both in the FH (6–10 times in years 0 and 1, $P < 0.0001$) and the mineral layers (2–5 times, $P < 0.0001$; Table 3). In years 0, 1 and 2, BF cores showed higher C_{mic} (FH: 1.5 to 5 times, $P < 0.05$; mineral: 2 to 3 times, $P < 0.01$) and N_{mic} concentrations (FH: 2 to 3 times, $P < 0.0001$; mineral: 2 to 3 times, $P < 0.0001$) than BS cores (Table 3).

At the end of the third snow-free season, C_{mic} concentration of the FH layers decreased by 54%–63% ($P < 0.0001$), relative to initial values, for the three forest types (Table 3). Moreover, in the BF cores only,

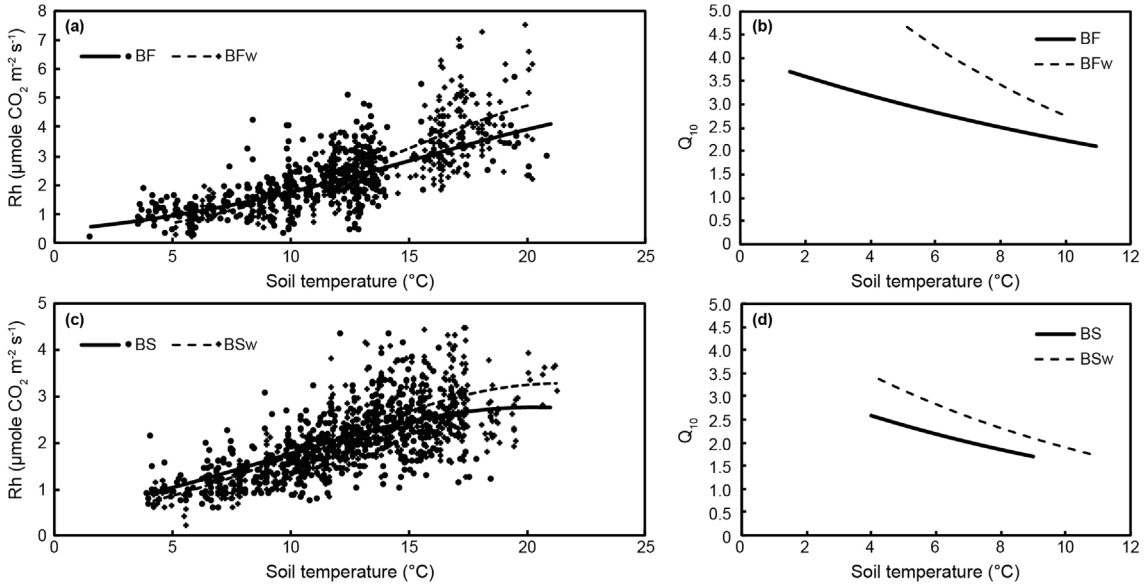

Fig. 2. Changes in soil core heterotrophic respiration (Rh: a, c) and temperature sensitivity of core Rh (Q_{10}: b, d) as a function of soil temperature, for boreal site cores (balsam fir, BF, and black spruce, BS) and warmed cores (BF_w and BS_w). The BF and BS sites are described in Table 1.

Table 2
Estimated parameters of soil core respiration (*Rh*) models (ln *(Rh)* = $a+bT+cT^2$) according soil temperature (*T*), for site cores (eastern hemlock, EH, balsam fir, BF, and black spruce, BS) and warmed cores (BF_w and BS_w). Standard errors are in parentheses. The EH, BF and BS sites are described in Table 1.

Core type	n	*a*	*b*	*c*	r^{2a}	R_0[b] (µmole CO_2 m^{-2} s^{-1})
EH	1129	−0.83 (0.07)	0.13 (0.01)	−0.001 (0.0004)	0.57	0.44 (0.03)
BF	373	−0.90 (0.11)	0.17 (0.02)	−0.003 (0.0008)	0.43	0.41 (0.05)
BF_w	449	−1.62 (0.16)	0.26 (0.03)	−0.005 (0.0010)	0.62	0.20 (0.03)
BS	474	−0.78 (0.16)	0.17 (0.03)	−0.004 (0.0013)	0.37	0.46 (0.07)
BS_w	612	−1.16 (0.12)	0.21 (0.02)	−0.005 (0.0007)	0.61	0.31 (0.04)

[a] r^2: squared correlation between back-transformed predicted values and observed values.
[b] $R_0 = e^a$, the respiration level at 0 °C.

we observed a decrease in N_{min} (−64%, $P < 0.0001$) and N_{mic} concentration (−50%, $P < 0.0001$) in the FH layer, and a decrease in C_{mic} concentration (−31%, $P < 0.0001$) and C: N ratio (−23%, $P < 0.0001$) in the mineral layer (Table 3). Neither chemically C labile of the FH layers, nor total root biomass in soil cores (BS cores) changed significantly over three years (Table 3).

3.3. Responses to soil warming

Differences between warmed and control soils were observed repeatedly for temperature (on 78% and 71% of visits for the BF_w and BS_w soil cores, respectively), for Rh (on 48% and 32% of the visits), and for VWC (22% and 18% of the visits, Fig. 3). Compared to their corresponding site cores, the warmed cores showed an increase in mean temperature (+3.2 ± 0.4 °C for BF_w cores and +2.3 ± 0.4 °C for BS_w cores; Fig. 3 a, d), Rh (+60% ± 14% for BF_w cores and +27% ± 5% for BS_W cores, Fig. 3 b, e), and VWC (+%1 ± 1% for BF_w cores and +3% ± 1% for BS_w cores; Fig. 3 c, f).

Significant increases in Rh of warmed cores relative to their corresponding site cores were detected only during the second and third snow-free seasons. For the BF_w cores, the warming effect was +4.2 ± 0.3 °C and +3.5 ± 0.6 °C, leading to mean increases of Rh by +107% ± 25% and +44% ± 15%; (Fig. 3a and b). For the BS_w cores, the warming effect was +2.0 ± 0.8 °C and +2.2 ± 0.8 °C, leading to mean increases of Rh by +39% ± 9% and +19% ± 8% (Fig. 3d and e).

The greater increases in Rh observed in BF_w relative to BS_w cores were accompanied by changes in baseline respiration rates and temperature sensitivity of Rh. According to the Rh model, the respiration rate at 0 °C (R_0) was 50% less in the warmed BF_w cores than in the control BF cores (*a* coefficients, $P < 0.001$, ln scale; R_0 = 0.20 ± 0.03µmole CO_2 m^{-2} s^{-1} for BF_W cores and 0.41 ± 0.03µmole CO_2 m^{-2} s^{-1} for BF cores, Table 2). At the same time, the *b* coefficient was 53% greater in BF_w cores than in BF cores ($P < 0.01$, ln scale, Table 2). By contrast, model coefficients *a* and *b* did not differ significantly for BS_w and BS cores. The Q_{10} of Rh was calculated up to 10–12 °C to stay within the range of observed temperatures for each core types, i.e. from 2 to 22 °C. At 16 °C, Rh in the BF_w cores was 26% greater than in BS_w cores (3.49 versus 2.78 µmol CO_2 m^{-2} s^{-1}, $P < 0.01$, Fig. 2a and c). Squared correlation between back-transformed predicted values and observed values (r^2) was 62% for BF_w cores and 61% for BS_w cores (Table 2). Calculating annual Q_{10} leaded to the same conclusions concerning the warming effect on BF_w cores relative to BS_w during the second and third snow-free seasons (not shown).

During the 3 years of testing, we observed no significant changes in soil properties between warmed and control cores (Table 3). Comparisons of soil properties between BF_w and BS_w cores were consistent with those between BF and BS cores. As in control cores, the C_{mic} concentration of warmed soils had significantly decreased in the FH layers by the end of the third growing season, relative to initial values (−73% for BF_w, $P < 0.0001$ and −64% for BS_w, $P < 0.0001$; Table 3). Moreover, in the BF_w cores only, a decrease in N_{min} (−50%, $P < 0.05$) and N_{mic} (−31%, $P < 0.0001$) was observed in the FH layers, and a decrease in C_{mic} (−50%, $P < 0.0001$) and C: N ratio (−27%, $P < 0.0001$) was observed in the mineral layer (Table 3). Neither chemically labile C of the FH layers, nor total root biomass in soil core (BS_w cores) changed significantly over three years (Table 3).

Table 3
Soil properties of the FH and mineral layers and root biomass by year, for site cores (eastern hemlock, EH, balsam fir, BF, and black spruce, BS) and warmed cores (BF_w and BS_w). Standard errors are in parentheses. The EH, BF and BS sites are described in Table 1. For all mean values, small cap letters (left) indicate significant differences between years for a given core type (vertical comparisons), while different capital letters (right) indicate significant differences between core types within a given year (horizontal comparisons).

Layer	Soil properties[a]	Year[b]	Core type[c]														
			EH			BF			BF_w			BS			BS_w		
FH	Mass (g cylinder^{-1})	all		151 (11)			63 (2)			56 (4)			83 (9)			84 (7)	
	C_{labile}: C_{tot} (%)	all		25 (1)	B		32 (1)	A		32 (1)	A		21 (1)	BC		19 (1)	C
	N_{labile}: N_{tot} (%)	0	a	83	B	ab	87	A	a	87	A	a	72	C	a	72	C
		1	a	83	B	b	87	A	a	87	A	a	75	BC	a	72	C
		2	a	83	B	ab	87	A	a	88	A	a	75	BC	a	70	C
		3	a	83	B	a	88	A	a	87	A	a	75	B	a	73	B
	C_{tot} (g kg^{-1})	0	b	439	A	a	475	A	a	475	A	b	397	A	b	397	A
		1	a	493	A	ab	472	A	a	492	A	ab	450	A	ab	430	A
		2	ab	459	A	ab	460	A	a	439	A	ab	456	A	ab	432	A
		3	ab	460	A	b	401	A	a	433	A	a	482	A	a	478	A
	N_{min} (mg kg^{-1})	0	b	115	B	ab	300	A	a	300	A	b	29	C	b	29	C
		1	a	265	A	a	371	A	a	454	A	a	57	B	a	63	B
		2	b	92	A	c	107	A	b	84	A	a	87	A	a	79	A
		3	b	121	AB	bc	154	A	b	141	A	a	72	AB	ab	57	B
	C: N	0	a	31	B	a	27	B	a	27	B	a	50	A	a	50	A
		1	a	35	BC	a	28	C	a	27	C	a	51	A	a	45	AB
		2	a	33	B	a	27	B	a	27	B	a	52	A	a	47	A
		3	a	32	B	a	24	C	a	25	BC	a	48	A	a	54	A
	C_{mic} (mg kg^{-1})	0	a	3540	B	a	6948	A	a	6948	A	a	4750	B	a	4750	B
		1	ab	2701	C	a	7467	A	ab	5611	AB	a	3634	BC	b	2982	C
		2	ab	2543	B	b	5021	A	b	4794	A	b	1046	B	c	991	B
		3	b	1646	A	c	2570	A	c	1853	A	b	1911	A	bc	1721	A
	N_{mic} (mg kg^{-1})	0	a	566	B	a	1107	A	a	1107	A	a	327	B	a	327	B
		1	a	479	B	a	1201	A	ab	927	A	a	504	B	a	401	B
		2	a	501	BC	b	852	A	b	736	AB	a	315	C	a	366	C
		3	a	428	B	c	557	AB	b	769	A	a	332	B	a	341	B
Mineral	Mass (g cylinder^{-1})	all		1275 (40)			1276 (41)			1278 (53)			1397 (46)			1389 (13)	
	C_{tot} (g kg^{-1})	all		24 (4)	B		63 (6)	A		59 (6)	A		25 (6)	B		25 (6)	B
	N_{min} (mg kg^{-1})	0	b	6	B	b	16	A	b	16	A	a	3	C	b	3	C
		1	a	9	B	a	28	A	a	31	A	a	5	C	a	7	BC
		2	c	4	B	c	9	A	c	9	A	a	4	B	b	4	B
		3	bc	5	B	bc	13	A	b	18	A	a	5	B	ab	4	B
	C: N	0	a	32	A	a	26	A	a	26	A	a	27	A	a	27	A
		1	a	32	A	a	26	A	a	25	A	a	27	A	a	28	A
		2	a	32	A	a	25	A	a	25	A	a	26	A	a	28	A
		3	a	29	A	b	20	BC	b	19	C	a	26	AB	a	28	A
	C_{mic} (mg kg^{-1})	0	a	204	B	b	424	A	a	424	A	a	245	B	a	245	B
		1	a	179	C	a	560	A	a	407	B	a	264	C	a	181	C
		2	a	139	B	bc	391	A	a	406	A	b	112	B	a	122	B
		3	a	124	B	c	291	A	b	203	AB	ab	197	AB	a	172	AB
	N_{mic} (mg kg^{-1})	0	a	24	B	ab	63	A	a	63	A	a	22	B	a	22	B
		1	a	19	C	a	76	A	a	54	B	a	31	C	a	27	C
		2	a	20	B	ab	61	A	a	57	A	a	21	B	a	19	B
		3	a	17	B	b	57	A	a	65	A	a	22	B	a	23	B
Total root biomass (g cylinder^{-1})[d]		0		n.d.			n.d.			n.d.		a	8.8		a	8.8	
		1		n.d.			n.d.			n.d.		a	7.4		a	9.6	
		2		11.5			9.7			7.7		a	5.5		a	9.5	
		3		8.0			6.0			5.5		a	3.5		a	5.7	

[a] C_{labile}: C_{tot}: chemically labile C percentage; N_{labile}: N_{tot}: chemically labile N percentage; C_{tot}: total C concentration; N_{min}: mineral N concentration; C: N: C-N ratio; C_{mic}: microbial C concentration and N_{mic}: microbial N concentration.
[b] 0 = first spring, 3 = third autumn.
[c] For each year, n = 18 observations for EH cores and n = 9 for all other core types.

[d] Total root biomass was not compared for EH, BF and BF_w cores because of incomplete mass measurements in spring and autumn 2007 (years 0 and 1 for the EH, BF and BF_w cores).

4. Discussion

4.1. Soil core respiration under original climate

The proportions of soil core Rh reported here (90%–99% of Rs) were higher than or comparable to previous reports from studies using coring in mature coniferous forests (Lalonde and Prescott, 2007: 65% with a 2–3 cm collar insertion; Laganière et al., 2012: 86%–96% with a 5 cm-collar insertion; Vogel and Valentine, 2005; 40%–80% with a 2–3 cm collar insertion). Because of the deeper insertion (7 cm) of our collars, they may have severed the superficial root system, reducing the levels of autotrophic and total respirations (Heinemeyer et al., 2011). As a result, the measured soil core CO_2 flux would be heterotrophic respiration, but at a level that is overestimated relative to total soil respiration because of the depth of collar insertion. This hypothesis is supported by the fact that northern forests harbor high concentration of roots and hyphae in their soils' organic and upper mineral layers (Brassard et al., 2009). Stabilizing collars with small brackets could avoid collar insertion in the soil.

The small differences in temperature (0.3 ± 0.1 °C) and VWC (5% ± 1%) observed between cores and free soil suggest that root disturbances and 3 years of containment did not substantially modify soil core microclimate. Moreover, during the first weeks of measurements, we did not observe the initial CO_2 flush that would have resulted from the death of fine roots and mycelia in the soil cores, providing a significant short-term input to decomposers. The influence of severed fine root decomposition on soil respiration may have been buffered by the 3 weeks lag between soil core installation and first CO_2 measurements. This last result suggests that our soil coring method did not overestimate Rh during the first weeks of measurements.

Both the significant exponential relationship between Rh and soil temperature and the lack of relationship between Rh and VWC support the hypothesis that SOM decomposition in these forest soils is limited by temperature rather than water, at least for the study period and the range of VWC observed. Soil temperature has been identified as the main factor driving Rh in other boreal soils of the region (Laganière et al., 2012).

The range of daily CO_2 fluxes measured in the boreal soils that we studied (from 0.2 to 8.0μmoles CO_2 m^{-2} s^{-1}) compares to previous observations in similar boreal black spruce stands (Laganière et al., 2012). For a given temperature, Rh observed at BF sites was 20% greater than at the more temperate EH site. This difference can be explained by the greater proportion (+28%) of chemically labile C in the BF soils, since most microbial processes are limited by C availability (Kaye and Hart, 1997).

4.2. Soil core properties under original climate

In the FH layers of EH, BF and BS cores, the overall 54%–63% decrease of C_{mic} relative to initial values (Table 3) suggests a decrease in microbial biomass. Mycorrhizal fungi biomass certainly dropped as the activity of roots was stopped by soil coring. The resulting microbial population in soil cores probably became saprophytic fungi. Despite soil cores were deprived of C-input in this study, the possibility of lack of available C substrates was rejected, since no decrease in chemically labile C was detected in the FH layers of EH, BF and BS cores during the

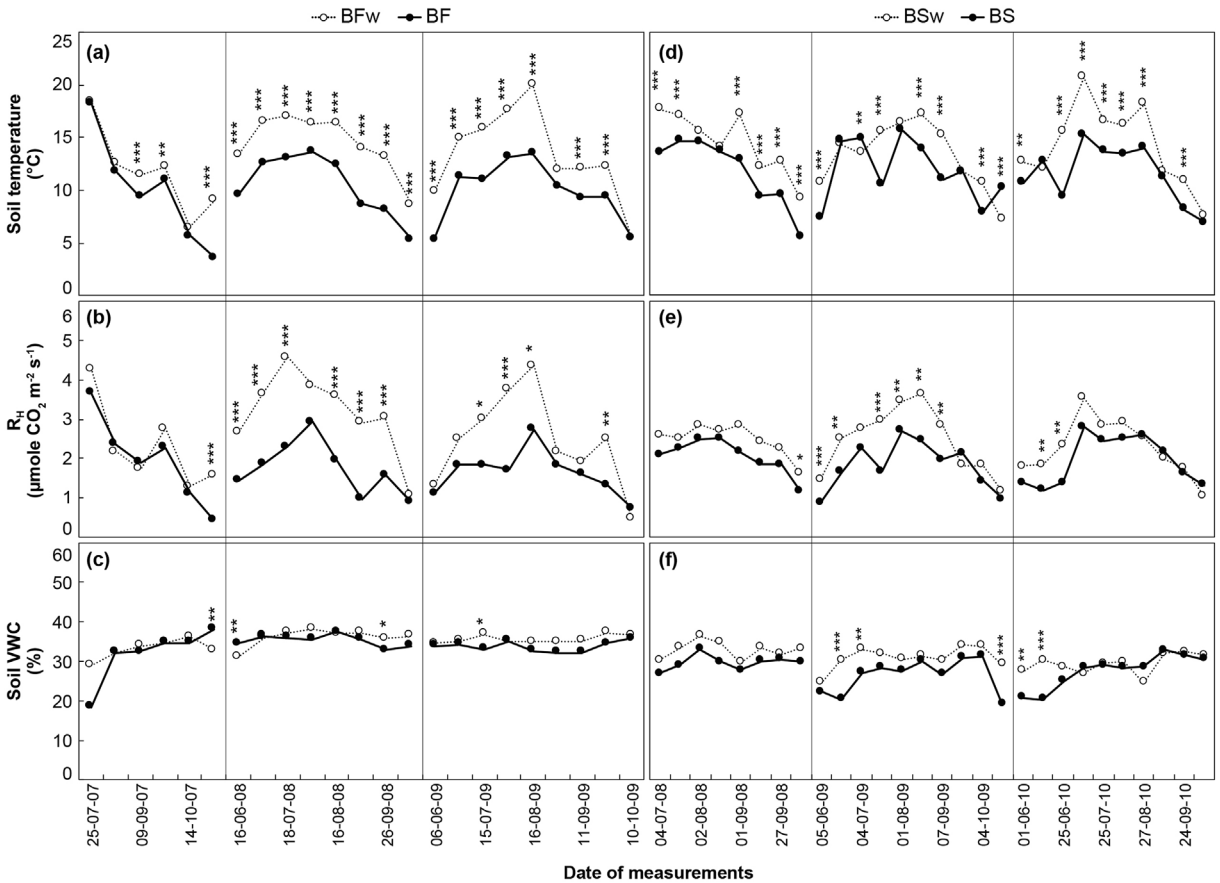

Fig. 3. Soil core temperature (a, d), heterotrophic respiration (Rh: b, e) and volumetric water content (VWC: c, f) according to date of visit and core type. Asterisks above the symbols of a given date indicate significant differences between the site cores (BF or BS) and the warmed (BF_w or BS_w) cores (* = $P < 0.05$; ** = $P < 0.01$; ***: $P < 0.001$).

experiment. The migration of microorganisms from organic to deeper mineral horizons also appears unlikely since C_{mic} concentration decreased also in the mineral layer of the BF cores at the end of the third snow-free season. Regardless of the reasons, the decrease of the C_{mic} concentration in the FH layers suggests a possible underestimation of Rh rate, at least during season 3. On the other hand, the decrease in root biomass of the BS and BS_w cores over three years (Table 3), although non-significant, suggests a possible overestimation of Rh due to decomposition of roots into soil cores during the experiment.

4.3. Responses to soil warming

The mean +2 °C to +3 °C soil warming obtained by transplanting soil cores to the southern site corresponds to the anticipated warming of the region's boreal soils over the next century (Houle et al., 2012). The small difference in mean VWC between warmed and control cores (less than 5%) suggests that transferring soil cores to a warmer region didn't cause significant soil drying, even for the BF_w cores that received 34 cm less annual precipitations after their transfer to the southern site (Table 1). The high precipitation regime within the studied sites (94–128 cm yr^{-1}) and adequate drainage of water in podzols probably contributed to reduce VWC differences between warmed and control cores.

The 27%–60% increase in Rh reported here is consistent with earlier warming studies (2–5 °C increase in soil temperature) in coniferous stands, which reported Rh increases of 40%–45% (Schindlbacher et al., 2009), 31% (Vogel et al., 2014) and 20%–35% (Wang et al., 2014). Other studies have reported even larger Rh increases (82%, Aguilos et al., 2013; 120%, Hart, 2006; 67%–81%, Vanhala et al., 2011). Our results thus support the hypothesis that soil warming increases heterotrophic respiration in balsam fir and black spruce forest soils during the first years of warming.

The warming effect on Rh was detected only from the second snow-free season on, perhaps because the experiment began late in the first year (July). During the second and third snow-free seasons, significant mean increases of Rh were observed for the BF_w and the BS_w cores. The larger increase in Rh for the BF_w cores relative to the BS_w cores could be correlated with the larger mean warming effects of these seasons (+4.2 °C and +3.5 °C for BF_w cores versus +2.0 °C and +2.2 °C for BS_w cores; Fig. 3a and d). Other explanations could be the higher chemically labile C (+52%), C_{mic} (1.5–5 times in years 0, 1 and 2), and N_{min} concentrations (6–10 times in years 0 and 1) of the FH layers of the BF_w cores relative to the BS_w cores (Table 3).

Variations in the mean warming effect during the experiment resulted from different weather conditions during the visits to boreal and southern sites. In fact, the boreal and southern sites were distant enough to meet different weather conditions, and were visited in alternation (usually a lag of 3–7 days). Our results suggest that a mean warming effect of at least 3 °C is necessary over a snow-free season to increase Rh of BF and BS soils. This temperature difference was not always reached during the measurements, especially for BS_w cores.

Warming increased the Q_{10} of Rh for the BF soils. At 10 °C – the mean temperature of the FH layers of BF soils during the snow-free season – a 10 °C soil warming would roughly triple soil respiration (Q_{10} of Rh = 2.8 for BF_w cores), rather than doubling it (Q_{10} of Rh = 2.2 for BF cores; Fig. 2b). Under a more realistic +5 °C soil warming (from 10 °C to 15 °C), mean predicted Rh of BF soils would increase by 83% (from 1.8 μmoles CO_2 m^{-2} s^{-1} to 3.3 μmoles CO_2 m^{-2} s^{-1}) rather than by 56% (from 1.8 μmoles CO_2 m^{-2} s^{-1} to 2.8 μmoles CO_2 m^{-2} s^{-1}; Fig. 2a). In other words, considering the increased temperature sensitivity of Rh of BF soils under a 5°C-soil warming during three snow-free seasons can lead to a 30% higher Rh prediction.

Soil moisture didn't seem a determinant factor for Q_{10} of Rh at soil temperature higher than 20 °C since 1) soils at 20–22 °C represented 2% of the data and didn't show problematic volumetric water content (VWC; 13–44%) for Rh, and 2) there was no significant correlation between VWC and log (Rh) for soils warmer than 20 °C.

Warming increased the Q_{10} of Rh for the BF soils, but not the BS soils. As mentioned earlier for the larger Rh of the BF_w cores, larger mean warming effects and higher chemically labile C are possible causes. Other possible causes could be different changes in microbial community composition (Karhu et al., 2014) and/or in microbial respiration efficiency (CO_2 flux per amount of microbial C biomass; Luan et al., 2014) between BF_w and BS_w cores. The decrease in microbial biomass of the FH layer for BF_w cores (by 60% from the 2nd to 3rd year) and BS_w cores (by 70% from the 1st to 2nd year) suggests a half to two-thirds reduction in microbial respiration efficiency, assuming no significant change in mean seasonal Rh level. Inter-seasonal temporal variation appears unlikely since the samples for microbial biomass were all collected in early October.

Scaled-up to the bioclimatic domain level, the mean seasonal C release induced by our soil warming experiment would represent 18 MT C per snow-free season in the balsam fir–white birch domain (area of 14 Mha in Quebec) and 24 MT C per snow-free season in the black spruce–moss domain (area of 41 Mha in Quebec). This adds up to a potential release of 154 MT CO_2 per snow-free season from the soil of these two domains to the atmosphere in response to a 2–3 °C soil warming. This seasonal amount represents almost twice the annual anthropogenic emissions for the province of Québec in 2014 (83 MT CO_2, Environment and Climate Change Canada, 2016); it also compares to the annual CO_2 emissions from fossil fuel combustion of the New York state in 2014 (170 MT CO_2; U.S. Energy Information Administration, 2016). These Rh projections however bears some uncertainties since 1) our results are limited to three years of warming, 2) a 3°C-warming was not always met during the warmed and control cores visits, especially for BS soils, and 3) the microbial C decrease in the FH layers of warmed and control cores suggests an underestimation of Rh. Also, in the longer term, the adaptation of soil microorganisms to new conditions may level the warming effect.

5. Conclusions

Transplanting boreal soils to a warmer region increased heterotrophic respiration in balsam fir (+60%) and black spruce forest soils (+27%) without significant changes in soil properties between warmed and control cores. Soil warming also increased the temperature sensitivity of Rh of balsam fir soils. Considering this increase in temperature sensitivity can lead to a 30% higher Rh prediction for BF soils, if warmed by 5 °C during three sow-free seasons. Compared to black spruce soils, the larger increase in Rh and the increase in Q_{10} of Rh of balsam fir soils can be partly explained by higher chemically labile C of the FH layers and a larger warming effect observed during the visits of warmed and control soils. However, longer-term studies are needed to see if this increase in Q_{10} of Rh for BF soils would be maintained for longer periods.

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