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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