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Soils isolated during incubation underestimate temperature sensitivity of respiration and its response to climate history

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ABSTRACT

Though the positive response of soil organic matter decay rates to temperature is theorized to decline with the bioreactivity (carbon normalized respiration) of organic matter, studies only sometimes support this idea. One potential reason for discrepancies among studies is the isolation of soil horizons in incubation experiments, which may limit the exchange of substrates among horizons that occurs *in situ* and in incubations employing intact, multiple-horizon cores, and thus may limit stimulation of microbial activities. To what degree does the isolation of individual soil horizons influence our ability to predict temperature sensitivity of respiration? Addressing this question is important, because incubation studies are frequently used to parameterize ecosystem process models and to formulate at least qualitative predictions of potential SOC destabilization in future climate scenarios.

To address this question, we conducted three parallel incubation experiments using soil collected from podzolic boreal forest sites in two regions similar in vegetation and soil type, but that differ in climate. The experiments consisted of (1) intact unaltered L, F, H horizons as a whole unit (hereafter called LFH), (2) isolated horizons from the same LFH, and (3) rebuilt LFH of those isolated horizons. The soils were incubated at 5 °C, 10 °C, and 15 °C with greater than 430 days of incubation with soil respiration measured at 6 time points.

Cumulative respiration was greater in the soils collected from the higher latitude region (hereafter cold region) relative to those collected from the lower latitude region (hereafter warm region) regardless of incubation temperature or experiment, suggesting that the warm region soils are less bioavailable. The temperature sensitivity (Q_{10}) of soil respiration, however, was influenced by whether the organic horizons were intact, isolated, or rebuilt. Respiratory responses of the LFH computed from the sum of isolated horizons were not different between the two regions (Q_{10} of 2.84 ± 0.10 and 2.72 ± 0.07 for cold and warm regions, respectively). In contrast, the respiratory responses of the more realistic rebuilt LFH over the entire experiment were significantly higher, and different between regions (3.52 ± 0.12 and 4.68 ± 0.16 for cold and warm regions, respectively). These results are congruent with trends observed in the intact unaltered LFH, and speak to the likely importance of substrate exchange among soil horizons as a driver of aggregated respiratory responses to temperature. The flow of labile substrates across or among horizons may facilitate the decomposition of relatively complex substrates exhibiting higher activation energy of decay. This exchange of labile substrates could promote relatively greater temperature responses of soil respiratory CO_2 losses. Based on these results, we suggest that a full understanding of the temperature sensitivity of SOC transformations requires using soil samples that encompass multiple soil horizons.

1. Introduction

Soil respiration generally increases with temperature at a global scale (Bond-Lamberty and Thomson, 2010), but it is difficult to

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predict the magnitude of the response accurately in diverse soils. Often, investigators invoke laboratory experiments to attempt to unravel the mechanisms that prompt temperature responses of microbial respiration to vary across time and space. For example, different soil organic carbon (SOC) pools exhibit varying temperature sensitivities of decay (Sierra, 2012), often expressed as Q_{10} values for ease of comparison across studies (Kirschbaum, 2006). A warmer climate has the potential to increase the Q_{10} of soil respiration as labile compounds undergo mineralization, leaving an increased relative abundance of relatively complex substrates with higher activation energies (E_a) of decay (Bosatta and Ågren, 1999; Davidson and Janssens, 2006). Such responses are congruent with the carbon quality temperature hypothesis (CQTH), which suggests that enzyme–substrate reactions involving substrates with relatively high E_a will exhibit greater temperature sensitivity of decay (Bosatta and Ågren, 1999; Fierer et al., 2005; van der Meer, 2006). Some studies have provided support for this concept in soils via examination of organic C mineralization rates (Craine et al., 2010), suggesting the importance of soil organic matter (SOM) composition as a driver of the Q_{10} of soil respiration. However, how to best apply this concept to project climate change impacts on C losses from *in situ* soils remains unclear.

The availability of labile soil substrates may also have an important influence on the Q_{10} of SOC mineralization due to its impact on the use of slower-turnover SOM. Labile substrates can be especially plentiful in relatively less degraded horizons or litterfall, and can be transported to other horizons via leaching of dissolved organic matter (DOM) (Kaiser and Kalbitz, 2012) and exploitation by fungal mycelium or bacteria followed by subsequent microbial growth or migration (Gadd, 2006). Labile substrates also are generated via root exudation *in situ* (Zobel and Wright, 2005; Fig. 1a). Both artificially enhanced (glucose, acetate) and natural (root exudates) labile substrates can induce increased mineralization of indigenous, slower-turnover SOM, a phenomenon referred to as a "priming effect" (Bingeman et al., 1953; Fontaine et al., 2004; Blagodatskaya and Kuzyakov, 2008). The prevalence of priming effects in different ecosystems suggests that the use of more complex substrates within soil profiles may be controlled by microbial access to more labile substrates (Sullivan and Hart, 2013; Wild et al., 2014; Nottingham et al., 2015).

If access to labile substrates regulates the mineralization of more complex SOM compounds, it may represent an important factor controlling the Q_{10} of bulk SOM mineralization (Fissore et al., 2013). Across global biomes, Q_{10} of soil respiration is generally observed to be lower in laboratory settings (mean 2.6 ± 1.2; Hamdi et al., 2013) relative to *in situ* settings (3.0 ± 1.1; Bond-Lamberty and Thomson, 2010). This holds true when comparing laboratory and *in situ* studies that have been conducted on the same forest soils, further emphasizing how laboratory values for Q_{10} of soil respiration tend to be lower compared to *in situ* settings (Table 1). Part of this discrepancy may be due to root respiration exhibiting a greater positive response to temperature than microbial respiration (Boone et al., 1998). However, *in situ* soils receive labile root and litterfall inputs, and are subjected to DOM fluxes transporting soluble substrates from surface horizons to deeper SOM pools, which also may help explain the typically higher Q_{10} of *in situ* soil respiration values (Fig. 1a). In contrast, laboratory incubation studies are conducted under conditions in which labile substrate inputs have been significantly reduced or eliminated and *in situ* soil properties modified (ie bulk density, porosity) (Fig. 1b–d). As such, incubation studies do not incorporate potential priming effects that ultimately may influence the temperature sensitivity of soil CO_2 losses. Organic soil horizons are ideal for testing these influences, as they provide SOM pools with clearly varying degradative states (Li et al., 2012), and minimal SOM protection associated with organo-mineral complexes (Kogel-Knabner et al., 2008).

In this study, we explored the role of soil composition and soil horizons in regulating respiratory responses to temperature in organic soil horizons collected from boreal forests sites. At these sites, soils exhibit predictable declines with depth in bioreactivity as revealed using multiple indices: carbon normalized cumulative respiration at a given temperature (Laganière et al., 2015); C:N ratios (Li et al., 2012); fungal:bacterial (F:B) ratios (Kohl et al., 2015); and increases with depth in alkyl-C to O-alkyl-C proportions, suggesting more degraded SOM in deeper horizons (Ziegler et al., 2015). Furthermore, the higher latitude (hereafter cold region)

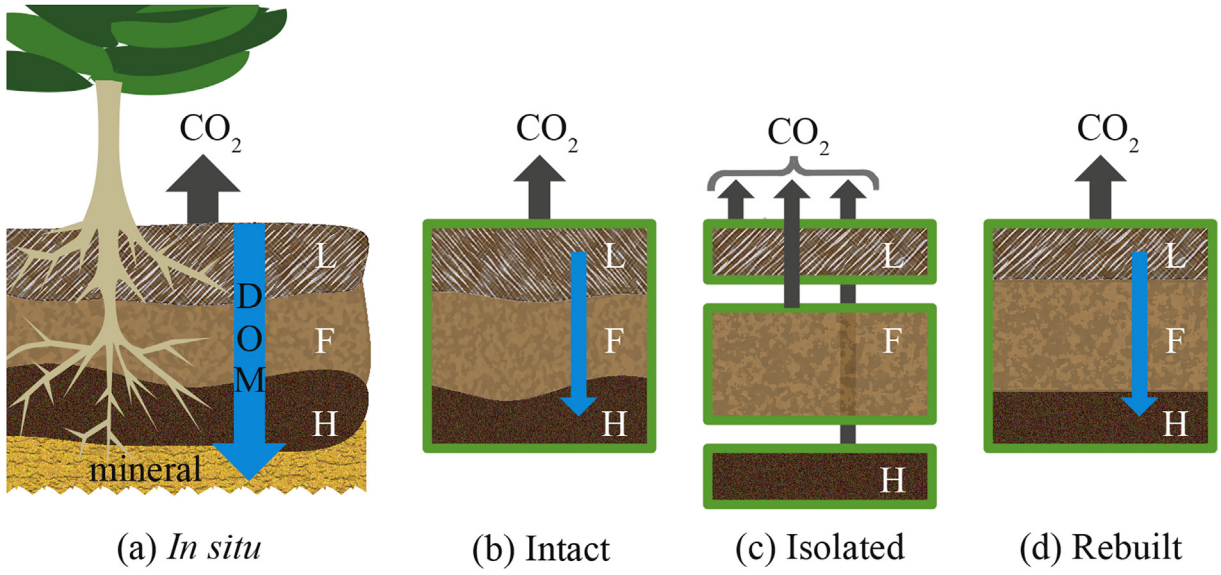

Fig. 1. Conceptual figure depicting *in situ* and experimental incubations: (a) *In situ* profiles include root exudates, dissolved organic matter (DOM) fluxes, and microbial substrate exploitation across horizons; (b) Intact unaltered LFH should maintain the greatest level of substrate exchange among the incubation experiments, albeit reduced from *in situ* conditions; (c) Individual L, F, and H horizons incubated in isolation permit no exchange among horizons, and; (d) rebuilt LFH from the homogenized horizons consist of soils disturbed to a greater extent than intact cores, but where exchange of substrates between horizons is maintained.