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The temperature sensitivity of soil organic matter decomposition is constrained by microbial access to substrates

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ABSTRACT

Soils can be sources or sinks of carbon depending on the balance between carbon inputs from plants and losses from the decomposition of soil organic matter (SOM). A good understanding of the temperature sensitivity of SOM decomposition is critical for forecasting whether soils in a warming world will lose or gain carbon, and therefore accelerate or mitigate the rate of increasing atmospheric carbon dioxide (CO_2) concentration.

We provide new evidence to show that the response of SOM decomposition to temperature may be constrained by substrate availability to microbial decomposers. We used laboratory incubations of a grassland soil to compare the temperature sensitivity of SOM decomposition with unmodified substrate availability with that of the same soil in which substrate availability was reduced by adding allophane, a clay-size mineral with a high capacity for binding SOM. In the soil with no added allophane, the decomposition rate increased about 7-fold over the temperature range from 1 to 40 °C. With added allophane, decomposition rate increased only about 3-fold over the same temperature range.

We then used a non-disruptive, natural abundance isotopic technique at our field site to partition total soil respiration into CO_2 efflux from newly released, ^{13}C-depleted SOM (root respiration and rhizosphere decomposition) from CO_2 efflux from older ^{13}C-enriched SOM from the decomposition of more stable SOM. We found no increase in the decomposition rate of the ^{13}C-enriched pool of SOM between 11 and 28 °C. That finding contrasts with most previous studies that have generally reported strong increases in SOM decomposition with temperature. We hypothesised that the large temperature sensitivity observed in laboratory incubations was due to substrate becoming readily available as a result of the disturbance involved in collecting soil samples. In undisturbed field conditions, the limiting step for the decomposition of the more stable SOM pool may be the rate at which decomposable substrate becomes available for decomposition.

Our findings will have important implications for the feedbacks between soil carbon storage and the rate of increase in atmospheric CO_2 concentration mediated by global warming.

1. Introduction

Soils contain three times as much carbon as the atmosphere and 240 times as much as the current annual emissions from burning fossil fuels (Ciais et al., 2014). Small changes in the carbon stored in soils could thus substantially enhance or mitigate the effects of anthropogenic carbon dioxide (CO_2) emissions (Smith et al., 2008; Paustian et al., 2016). Under the influence of climate and land-use change, soils may become sources or sinks of carbon depending on the relative balance between photosynthetic carbon inputs and carbon losses through the decomposition of soil organic matter (SOM) (Filley and Boutton, 2006). In the context of a warming climate, models forecasting the future feedbacks between soil carbon stocks and atmospheric CO_2 concentrations are strongly dependent on functions describing the response of SOM decomposition to temperature. Yet the temperature sensitivity of SOM decomposition remains controversial and continues to be debated (Davidson and Janssens, 2006; Kirschbaum, 2006, 2013; Davidson et al., 2012; Sierra, 2012).

Like most chemical or biochemical reactions, SOM decomposition is likely to be inherently sensitive to temperature and rates may increase

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with increasing temperature in line with Arrhenius kinetics. This describes the temperature sensitivity of enzyme-catalysed reactions, with the hypothesis that reactions with a high activation energy (E_A) should also show a high temperature sensitivity, meaning that turnover of chemically more recalcitrant compounds should be more responsive to changing temperatures (Bosatta and Ågren, 1999; Sierra, 2012). Davidson and Janssens (2006) defined the "intrinsic temperature sensitivity" as solely based on the inherent molecular attribute of the decomposed substrates. However, external factors can limit substrate availability at the enzyme reaction sites and may constrain the intrinsic effect of temperature (Davidson and Janssens, 2006; Kirschbaum, 2006, 2013; Von Lützow and Kögel-Knabner, 2009). Under such conditions, the observed response of decomposition to temperature is defined as the "apparent temperature sensitivity" and should typically be lower than the intrinsic temperature sensitivity (Davidson and Janssens, 2006).

However, only a few studies have empirically assessed the effect of substrate limitation on the temperature sensitivity of SOM decomposition. Gershenson et al. (2009) showed in a laboratory incubation experiment that the temperature sensitivity of SOM decomposition increased when more substrate was made available to decomposition by adding glucose. Gillabel et al. (2010) showed that subsoils incubated in the laboratory presented lower temperature sensitivity than topsoils and attributed this observation to the greater proportion of protected carbon (measured as carbon associated to the silt and clay fraction) in the subsoil samples. But we know of no studies to date that have directly measured the effects of reduced substrate availability on the temperature sensitivity of SOM decomposition.

There are multiple mechanisms that can affect the availability of SOM to decomposition, including chemical reactions regulated by temperature (Conant et al., 2011). Thus, the apparent temperature sensitivity can be defined as the temperature sensitivity of the whole set of reactions needed for decomposition taken collectively, that is, the sum of reactions leading to substrates being available to decomposing enzymes and the enzymatic decomposition *per se* (whose temperature sensitivity is defined as the intrinsic temperature sensitivity). Furthermore, conditions of low substrate availability are likely to be common in the soil environment (Davidson and Janssens, 2006; Dungait et al., 2012; Lehmann and Kleber, 2015). Understanding the apparent temperature sensitivity of SOM decomposition, that is, the temperature sensitivity of the whole chain of reactions leading to SOM being decomposed, is necessary to understand the feedbacks between soils and the warming atmosphere.

Soil organic matter may be unavailable for microbial decomposition when it is physically protected by the formation of aggregates where oxygen and enzyme diffusion is limited, and when it is chemically protected by being adsorbed onto mineral surfaces (Jastrow et al., 1996; Sollins et al., 1996; Six et al., 2002; Conant et al., 2011). In the field, these mechanisms are likely to be interdependent. Furthermore, there is also little doubt that physical disruption of the soil may disturb the dynamics and stability of aggregates in the soil, therefore modifying the physical protection of SOM (Six et al., 2002; Zakharova et al., 2014). Roots may also enmesh aggregates and release compounds binding soil particles together (Bronick and Lal, 2005). Thus, the physical integrity of the soil and the presence of roots are likely to be necessary if we are to measure the apparent temperature sensitivity under realistic conditions.

Nonetheless, most studies to date have employed techniques jeopardizing this integrity. Measuring the SOM decomposition component of soil respiration requires partitioning the two major components of the soil CO_2 efflux (soil respiration, R_S) into a flux representing root and rhizosphere respiration (autotrophic respiration, R_A) and a flux representing the decomposition of SOM (heterotrophic respiration, R_H) (Kuzyakov, 2006). Most studies that have attempted to measure R_H in laboratory incubations of sieved, root-free soils, or partitioned R_S in the field using methods that removed the autotrophic component to deduce R_H (root removal techniques), sometimes involving physical disruption of the soil (reviewed by Kuzyakov, 2006; Subke et al., 2006; Paterson et al., 2009). In other words, estimations of the apparent temperature sensitivity of SOM decomposition are often biased, because they are conducted under conditions where the chain of reactions leading to decomposition is modified.

The present study set out to investigate two interdependent research questions. The first objective was to test directly whether the temperature sensitivity of R_H is modified when substrate availability is limited. To do so, we measured the temperature response of R_H using laboratory incubations of root-free soils from a grassland site in which substrate availability was either left unaltered or reduced by adding allophane, a clay-sized mineral known for its high specific surface area and high capacity for binding organic matter (Parfitt, 2009). The second objective was to provide field estimates of R_H under conditions where substrate limitations were kept at their natural state. R_H was thus measured in the field at the same site, using a natural ^{13}C abundance technique following Millard et al. (2010) and Moinet et al. (2016a, 2016b). This technique allows inference of SOM decomposition rates with minimal disturbance of the soil.

2. Materials and methods

2.1. Site description

The measurements were made at a commercial dairy farm located near Waharoa, in the Waikato region, North Island, New Zealand (lat. 37.77°S, long. 175.8°E, 54 m elevation above sea level). Mean annual temperature and precipitation (1980–2010) at a climate station 13 km to the southwest of the farm were 13.3 °C and 1249 mm, respectively. Soils on the experimental farm were a complex of types formed from rhyolitic and andesitic volcanic ash on rhyolitic alluvium (McLeod, 1992). The soils were yellow-brown loams, classified as a Mottled Orthic Allophanic (Hewitt, 1998).

In June 2013 the field site previously dominated by ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) was converted to establish a diverse mix of legumes, grasses and herbs, hereafter referred to as the diverse pasture, comprising a mixture of Timothy grass (*Phleum pratense* L.) and prairie grass (*Bromus willdenowii* L.), lucerne (or alfalfa; *Medicago sativa* L.), chicory (*Cichorium intybus* L.) and plantain (*Plantago lanceolate* L.), in addition to perennial ryegrass and clover. Four rectangular blocks, each 3 × 10 m, were randomly located and sown with a ryegrass and white clover mix instead of the diverse pasture mix.

The site comprised a mix of weakly gleyed, moderately well-drained soil (Piarere), and moderately gleyed, imperfectly drained soil (Te Puninga) (McLeod, 1992).

2.2. Laboratory incubations to manipulate substrate availability

Three years after pasture renewal, soils were collected to a depth of 200 mm at four locations at our field site (four spatial replicates) in the diverse pasture for a carbon mineralisation experiment following a protocol adapted from Hopkins (2007). The soils were brought back to the laboratory and passed through a 2 mm sieve, and 64 aliquots (16 for each replicate) of approximately 180 g of field-moist samples were stored in air-tight bags (Tedlar® Keika Ventures, Chapel Hill, NC, USA) at 4 °C for 8 days. Preliminary analysis by the phosphate retention method of Saunders (1965) revealed the absence of allophane in the soil at the collection site.

Two aliquots of each spatial replicate were placed in eight insulated polystyrene boxes. The boxes were placed in growth cabinets with an ambient temperature of 1 °C and equipped with heating pads, and controlled to target soil temperatures of 1, 5, 10, 15, 20, 26, 32 and 40 ± 0.5 °C. As our experimental treatments, substrate availability was reduced by mixing allophane into the soil samples. In each box, one aliquot of each spatial replicate was used for the allophane addition