



Changes in substrate availability drive carbon cycle response to chronic warming

Grace Pold ^a, A. Stuart Grandy ^b, Jerry M. Melillo ^c, Kristen M. DeAngelis ^{d,*}

^a Graduate Program in Organismic and Evolutionary Biology, 204C French Hall, University of Massachusetts Amherst, 230 Stockbridge Road, Amherst, MA 01003, United States

^b Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, United States

^c The Ecosystems Center, 7 MBL Street, Woods Hole, MA 02543, United States

^d Department of Microbiology, 418 Morrill Science Center IVN, University of Massachusetts Amherst, 639 North Pleasant Street, Amherst, MA 01003, United States

ARTICLE INFO

Article history:

Received 26 September 2016

Received in revised form

25 February 2017

Accepted 8 March 2017

Available online 22 March 2017

Keywords:

Soil carbon

Climate feedbacks

Enzyme activity

Microbial adaptation

ABSTRACT

As earth's climate continues to warm, it is important to understand how the capacity of terrestrial ecosystems to retain carbon (C) will be affected. We combined measurements of microbial activity with the concentration, quality, and physical accessibility of soil carbon to microorganisms to evaluate the mechanisms by which more than two decades of experimental warming has altered the carbon cycle in a Northeast US temperate deciduous forest. We found that concentrations of soil organic matter were reduced in both the organic and mineral soil horizons. The molecular composition of the carbon was altered in the mineral soil with significant reductions in the relative abundance of polysaccharides and lignin, and an increase in lipids. Mineral-associated organic matter was preferentially depleted by warming in the top 3 cm of mineral soil. We found that potential extracellular enzyme activity per gram of soil at a common temperature was generally unaffected by warming treatment. However, by measuring potential extracellular enzyme activities between 4 and 30 °C, we found that activity per unit microbial biomass at *in-situ* temperatures was increased by warming. This was associated with a tendency for microbial biomass to decrease with warming. These results indicate that chronic warming has reduced soil organic matter concentrations, selecting for a smaller but more active microbial community increasingly dependent on mineral-associated organic matter.

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1. Introduction

Soils are dynamic components of land ecosystems, storing and regulating the exchange of carbon with the atmosphere. Biological processes in soils are accelerated by warmer temperatures (Lu et al., 2013; Salwa Hamdi, 2013; German et al., 2012), but the net effect of warming on soil carbon stocks over decades to centuries of climate change is less clear (Todd-Brown et al., 2014). At present, gaps in our understanding of how temperature, microbial communities, and soil carbon stocks interact to drive the global carbon cycle prevents better constraint of models of future carbon cycling and climate (Wieder et al., 2013).

Differences between long- and short-term responses to warming remain a major unknown in predicting how soil carbon stocks will be affected by climate change (Bradford et al., 2008; Knorr et al., 2005; Melillo et al., 2002, 2011). Soil microbes both drive and respond to changes in the soil environment by producing extracellular enzymes (Sinsabaugh, 1994) and organic acids (Keiluweit et al., 2015; Clarholm et al., 2015), and metabolizing small soil carbon compounds. In the short run, elevated temperatures are known to augment both resource supply to (German et al., 2012) and maintenance costs on microbes (Frey et al., 2013; Manzoni et al., 2012). In the long term, warming may also indirectly influence the supply and demand of resources by altering the quantity and quality of carbon available to microbes (Lu et al., 2013). Proposed modulators of the long-term soil carbon response to warming include altered vegetation dynamics (Dukes et al., 2005; Sistla and Schimel, 2013; Zhang et al., 2005), shifts in microbial communities (DeAngelis et al., 2015; Luo et al., 2013),

* Corresponding author.

E-mail addresses: apold@umass.edu (G. Pold), stuart.grandy@unh.edu (A.S. Grandy), jmelillo@mbl.edu (J.M. Melillo), deangelis@microbio.umass.edu (K.M. DeAngelis).

accelerated microbial turnover (Hagerty et al., 2014), and preferential depletion of specific soil carbon pools (Feng et al., 2008; Pisani et al., 2015; Bradford et al., 2008).

An additional regulator of long-term response of the carbon cycle to warming is physical protection (Davidson and Janssens, 2006; Bach and Hofmockel, 2016). As plant litter decomposes, it goes from being primarily protected by complexity of molecular structure (e.g., aromatic rings of lignin compounds), that are difficult for microbial enzymes to attack (Schmidt et al., 2011; Conant et al., 2011), to being primarily physically protected by virtue of tight associations with minerals (Six et al., 2000; Schmidt et al., 2011). During the transition between these two phases, microbes and invertebrates increasingly fragment the litter (particulate organic matter; "POM"), covering it with binding agents such as glomalin proteins (Wright and Upadhyaya, 1998), extracellular polysaccharides (Schimel and Schaeffer, 2012) and mucus (Bossuyt et al., 2005) that attract minerals to its surface and may eventually preclude access by other microbes (Six et al., 2000; Grandy and Robertson, 2007). Experimental warming has been shown to affect both these stages of the physical protection process, accelerating the physical and chemical fragmentation of litter (Pisani et al., 2015; Feng et al., 2008; German et al., 2012) and reducing the extent and stability of soil aggregate formation (Rillig et al., 2002). Sorption to mineral surfaces can also physically-protect byproducts of microbial metabolism such as small molecules, proteins, and lipids from microbial degradation (Schurig et al., 2013; Kleber et al., 2007; Grandy and Neff, 2008). Warming is expected to shift the sorption-desorption balance for the most strongly-bound mineral-associated organic matter (MAOM) toward desorption (Conant et al., 2011), providing a further mechanism for increased microbially-available carbon under climate warming.

Changes in microbial substrate availability in response to chronic warming may also alter metabolic investment in resource acquisition. Microbes produce and secrete extracellular enzymes to depolymerize soil compounds into monomers and oligomers that can be taken up by the cell (Wallenstein et al., 2010). These enzymes are costly to produce (Allison, 2005; Schimel and Weintraub, 2003; Lever et al., 2015), which means extracellular enzyme activity can be the rate-limiting step in the mineralization of soil organic matter (Bengtson and Bengtsson, 2007; Burns et al., 2013), and that enzymes are generally produced proportionate to microbial nutritional requirements (Sinsabaugh et al., 2009). For instance, increased plant litter inputs to soil in response to 8 years of warming in a grassland ecosystem were accompanied by a substantial decrease in lignolytic enzyme activity and expansion of genes for hemicellulose degradation (Zhou et al., 2012).

Soil warming experiments such as the one at the Harvard Forest in Massachusetts provide an opportunity to evaluate how long- and short-term effects of climate warming may interact to drive changes in the forest soil carbon cycle. Established more than 20 years prior to the present study, the Prospect Hill warming experiment (Peterjohn et al., 1994) enables the study of the decadal-cycling soil carbon pools believed to be the most susceptible to climate change (Hopkins et al., 2012). In this experiment, microbial activity has shown a non-linear response to warming in which soil respiration showed the expected instantaneous increase with warming over the first ten and last six years of the experiment (Melillo et al., 2002; unpublished data), but not the intervening period. During the interval in which soil respiration was similar in heated and control plots, soil carbon stocks (Bradford et al., 2008) and microbial biomass (Bradford et al., 2008; Frey et al., 2008) were noted to be depleted in heated plots, while the communities also showed reduced metabolic potential and lower mass-specific respiration at higher temperatures. These characteristics of a long-term response to warming were attributed to a combination

of reduced substrate availability for microbes and adaptation of the microbial community to a lower respiratory state (Bradford et al., 2008). The subsequent secondary increase in soil respiration coincided with a substantial shift in the dominant bacterial community (DeAngelis et al., 2015), and a shift toward classic oligotrophic taxa (Fierer et al., 2007), or microbes suited to slow but steady growth on small, low-quality carbon pools. Meanwhile fungi - considered the major decomposers of fresh litter inputs in forest soils (Boer et al., 2005) - remained less abundant in heated plots (DeAngelis et al., 2015). This may indicate that the microbial communities are accessing carbon pools they did not previously, whether due to novel metabolic capacities within the community (Pold et al., 2015) or due to changes in the substrates available to them.

In this study, we evaluated whether changes in soil carbon due to warming may feed back and alter the ways in which microbes process soil carbon. We studied the chemical composition and physical location of soil organic matter to determine if substrates available to microbes had been enhanced by warming, and assayed extracellular enzyme activity to determine if changes in substrate availability had altered resource allocation to soil organic matter processing. We show that chronic warming has left its mark on the size and chemical composition of soil organic matter pools, and that thermodynamics are central to explaining continued soil carbon loss.

2. Materials and methods

2.1. Experimental design

2.1.1. Study site

Soils collected for this project were taken from the Prospect Hill warming study at the Harvard Forest Long Term Ecological Research Site in Petersham, Massachusetts (42.54°N, 72.18°W). Here, soils have been heated 5 °C above ambient soil temperatures since 1991 using buried resistance cables controlled by a datalogger which adjusts temperature every 10 min (Peterjohn et al., 1994). The experiment is situated in an area of the forest which was abandoned from agriculture in the late-1800's (Peterjohn et al., 1994), and a plow layer is apparent in the top 10 cm of the mineral soil. The secondary forest regrowth is dominated by red oak (*Quercus rubra*), paper birch (*Betula papyrifera* M.), red and striped maple (*Acer rubrum* L., *A. pennsylvanicum* L.), and white ash (*Fraxinus americana* L.). The understory consists of clubmoss (*Lycopodium obscurum*), wintergreen (*Gaultheria procumbens*), Canada mayflower (*Maianthemum canadense*), and starflower (*Trientalis borealis*) (Farnsworth and Bazzaz, 1993).

Soils are sandy loam Typic Dystrudepts of the Gloucester series (Peterjohn et al., 1994), with approximately 2860 g C m⁻² soil in the top 10 cm. Atop this mineral soil sits a readily-distinguished mat of organic matter with approximately 2570 g C m⁻² (DeAngelis et al., 2015). The pH is 3.8 in the organic horizon and 4.4 in the upper mineral soil. Precipitation is distributed approximately evenly throughout the year, with an average of 1180 mm/yr since 1991. Mean monthly temperatures range from -6 °C in January to +20 °C in July (Boose and Gould, 1999; Boose, 2014), with an annual mean of 8 °C. The experimental design consists of eighteen 6 m by 6 m plots in a randomized block design. Each block contains a heated plot, a disturbance control plot where cables have been buried since the beginning of the experiment but not turned on, and a control plot, which has been left undisturbed. We used both organic (O horizon) and upper mineral soil (Ah horizon) samples from all six replicate heated and disturbance control plots unless otherwise noted.

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