



Relating the biological stability of soil organic matter to energy availability in deep tropical soil profiles



Madeleine M. Stone, Alain F. Plante*

Department of Earth and Environmental Science, University of Pennsylvania, Hayden Hall, 240 South 33rd Street, Philadelphia, PA 19104-6316, USA

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ABSTRACT

Tropical subsoils contain large reservoirs of carbon (C), most of which is stored in soil organic matter (SOM). Subsoil OM is thought to be particularly stable against microbial decomposition due to various mechanisms and its position in the soil profile, potentially representing a long-term C sink. However, few experiments have explicitly investigated SOM stability and microbial activity across several orders of magnitude of soil C concentrations as a function of soil depth. The objective of this study was to evaluate the biological stability of SOM in the upper 1.4 m of tropical forest soil profiles. We did so by measuring CO₂ evolution during a 90-day laboratory incubation experiment on a sample set that was previously characterized for C and nutrient concentrations and microbial biomass. We concurrently measured the energy content of SOM using differential scanning calorimetry (DSC) as an index of the energy available for microbial metabolism, with the hypothesis that the biological stability of SOM would be inversely related to the energy contained within it. Cumulative CO₂ evolution, mean respiration rates, and the energy density of SOM (energy released during combustion normalized to soil C) all declined with soil depth ($P < 0.01$). Biological indices of C stability were well correlated with measures of SOM energy. There was no change in the mean respiration rate as a function of depth when normalized to soil C, and a trend toward increased respiration per-unit microbial biomass ($P = 0.07$). While reduced microbial respiration in subsoils suggests an increase in the biological stability of SOM, we suggest this is driven principally by concurrent declines in energy availability as measured by DSC and the size of the microbial biomass pool. On a per-unit biomass basis, subsoil OM may be as prone to decomposition and destabilization as surface SOM.

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1. Introduction

Tropical forests are a large terrestrial carbon (C) sink, and their soils contain between one third and half of the total C stored in soil organic matter (SOM) (Jobbágy and Jackson, 2000; IPCC, 2007). Tropical forests also make large contributions to subsoil SOM stocks (Jobbágy and Jackson, 2000; Veldkamp et al., 2003), that is, SOM stored below the upper 20–30 cm of the soil profile (Rumpel and Kogel-Knabner, 2011). Deep SOM is thought to have high potential for long-term sequestration, as indicated by radiocarbon ages on the order of 1000s of years (Trumbore, 2000; Rumpel et al., 2004; Rumpel and Kogel-Knabner, 2011). However, for C to be sequestered over long time scales, it must remain stable against microbial decomposition. Although interest in SOM stability has

increased considerably in recent years (Schmidt et al., 2011), relatively few studies have explicitly investigated stability in tropical forests (Wood et al., 2012; Wieder et al., 2013). Moreover, most studies of tropical soil C cycling have focused exclusively on the upper layers of the mineral soil (but see Trumbore, 2000; Veldkamp et al., 2003; Marin-Spiotta et al., 2011; Kang Min et al., 2013). Understanding how SOM stability changes with depth is critical to predicting the response of deep soil C to land use change or other global change drivers (Veldkamp et al., 2003; Fontaine et al., 2007).

SOM stability is defined as resistance to decomposition, regardless of the mechanism. A wide range of methods are used to infer stabilization (Denef et al., 2009), including biological, chemical and thermal methods, each of which provides information on specific stabilization processes that can produce contrasting results. Generally speaking, SOM stability is thought to increase with soil depth (Rumpel and Kogel-Knabner, 2011), given the general trend of increased SOM radiocarbon age (Trumbore, 2000; Jenkinson

* Corresponding author. Fax: +1 215 898 0964.

E-mail address: aplante@sas.upenn.edu (A.F. Plante).

et al., 2008). One proposed mechanism for the greater stability of deep SOM is increased mineral association (Kaiser et al., 2002; Eusterhues et al., 2003; Rumpel and Kogel-Knabner, 2011), which can reduce the accessibility of SOM to microbial decomposers. However, the importance of mineral stabilization will depend on soil type owing to the effects of texture and mineralogy on surface area and surface charge (Oades, 1984; Trumbore, 2009). For instance, several authors have found Fe-oxides and clay minerals to be the most important stabilizing agents in tropical Oxisols (Eusterhues et al., 2003; Dick et al., 2005; Rumpel et al., 2008), while allophanic minerals stabilize large amounts of C in volcanic soils (Marin-Spiotta et al., 2011). As the mineralogical composition of a soil changes over the course of pedogenesis, the soil's capacity to stabilize OM can also change. These changes can also be observed downward in a soil profile as the most highly weathered materials are typically found at the surface.

In addition, changes in the abundance and activity of microbial decomposers can strongly influence SOM stability. Many studies have observed reduced microbial abundance and activity with soil depth (Blume et al., 2002; Fierer et al., 2003; Stone et al., 2014). Microbial activity can decline in subsoils due to substrate scarcity and nutrient limitation (Fontaine et al., 2007), changes in the spatial distribution of microbes and substrates (Lindahl et al., 2007), and the increased stability of mineral-associated SOM (Rumpel and Kogel-Knabner, 2011). However, specific metabolic activities (normalized to soil C or microbial biomass) sometimes remain high in subsoils (Blume et al., 2002; Gelsomino and Azzellino, 2011; Kramer et al., 2013; Stone et al., 2014), indicating that subsoil microbial communities can retain the metabolic capacity to cycle C in spite of their reduced population size. Subsoil C is often recycled through microbial biomass, resulting in a SOM pool that is chemically labile but old according to its ^{14}C signature (Gleixner et al., 2002; Kaiser and Kalbitz, 2012), a finding which calls into question the notion that radiocarbon-depleted SOM is inherently more stable.

In recent studies, Stone et al. (2014) investigated changes in soil microbial biomass, community structure and extracellular enzyme activities with depth as part of the Luquillo Critical Zone observatory (LCZO), a wet tropical forest in northeastern Puerto Rico. While we found exponential declines in microbial abundance and activity with depth, specific metabolic activity typically did not vary with depth, suggesting that some fraction of the deep SOM pool is available to microbial decomposers. In this study, we investigated changes in the short-term biological stability of SOM along the same tropical soil profiles by measuring CO_2 losses during laboratory incubation to investigate possible implications for deep soil C cycling. We simultaneously used thermal analysis to inform our understanding of SOM stability from an energetic perspective. Thermal analysis by differential scanning calorimetry (DSC) quantifies energy inputs and outputs as a sample is subjected to ramped combustion (Plante et al., 2009). For soils, this technique integrates information about the chemical composition and energy content of SOM with stabilization through interactions with soil minerals. Thermal analysis quantifies the energy as heat required for combustion, as well as the energy stored in the SOM of a sample. SOM that combusts at higher temperatures is considered more thermally stable, and is presumed to have a greater energy barrier to decomposition. This energy barrier is balanced against the energy available to microorganisms upon SOM decomposition, which can be inferred by quantifying the energy released during combustion (Peltre et al., 2013). Since microbial C mineralization depends on the thermodynamic favorability of decomposition, the persistence of organic matter may relate to both the size of the energy barrier and the quantity of energy released.

Our sample set included soils formed from two distinct geologic parent materials weathering to contrasting soils (Oxisols versus Inceptisols), occurring under two climatically distinguished forest types (low-elevation Tabonuco forest versus mid-elevation Palo Colorado forest). This factorial combination of contrasting geologies and forest types allowed us to simultaneously investigate several potential drivers of SOM stability, including soil mineralogy and substrate chemistry. Because of exponential declines in bulk soil C concentrations and microbial biomass with soil depth (Stone et al., 2014), we predicted soil respiration would likewise decline exponentially with depth. We sought to investigate whether soil and forest types mediate the biological stability of SOM, with the prediction that SOM in the higher elevation forest (which has poorer litter quality, Cusack et al. 2011) might exhibit greater biological stability. We also predicted that biological stability of soil C might be greater in the clay-rich Oxisols compared to the sandy Inceptisols. However, because previous reports demonstrated that microbial biomass and soil C stocks were not substantially different across the soil and forest types (Johnson et al., 2015; Stone et al., 2014), we anticipated that any small differences attributable to these landscape-scale factors would be masked by much larger differences attributable to soil depth. To tease apart changes in the biological stability of SOM from changes in the quantities of C and decomposers, we used published datasets of soil C and microbial biomass C concentrations (Stone et al., 2014) to normalize cumulative CO_2 evolution and respiration rates.

The overall goals of this study were to measure changes in SOM stability as a function of soil depth, and to elucidate the possible mechanisms for changes in stability. In addition to unfavorable environmental conditions attributable to position in the soil profile (e.g., lack of oxygen, etc.), and to the conventional mechanisms contributing to SOM stability (e.g., recalcitrance, physical occlusion in aggregates, mineral association through various binding mechanisms), we hypothesize that deep SOM is stable due to low energy contents that are unable to support the metabolic needs of a large microbial population.

2. Methods

2.1. Study site and sample set

This study was conducted using soils collected from the Luquillo Experimental Forest in northeastern Puerto Rico ($18^\circ 18' \text{ N}$, $65^\circ 50' \text{ W}$), which supports both the Luquillo Critical Zone Observatory (LCZO) and a Long Term Ecological Research Program (LTER). The area offers a natural experiment for studying changes in SOM stability with depth in the context of landscape-scale gradients in geology, vegetation and climate. The area is composed of two dominant parent materials of differing age and mineralogy: lower-Cretaceous volcanoclastic (VC) sediments of andesitic composition and an early-Tertiary age quartz-diorite (QD) pluton known as the Rio Blanco stock (Seiders, 1971a,b). The VC parent material weathers to produce Oxisols, which are clay-rich soils containing <10% weatherable minerals. The QD parent material weathers to produce Inceptisols that are sandy and contain up to 40% primary minerals in surface soils, including feldspars and quartz (Scatena, 1989; Silver et al., 1994; Johnson et al., 2015). Soils are moderately to strongly acidic (pH 3–7), and contain substantial kaolinite, as well as iron and aluminum oxyhydroxides in the clay fraction.

The mountainous region is characterized by steep terrain and is highly dissected by slopes $>30^\circ$. The mean annual temperature decreases from approximately 24° C at 300 masl to 21° C at 800 masl and precipitation increases from 3000 mm y^{-1} to 4000 mm y^{-1} across the same elevation gradient (Brown et al., 1983). Most of the vegetation falls into four climate-designated

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