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Parent material and conifer biome influence microbial residue accumulation in forest soils

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ABSTRACT

Microbial residues are a significant component of soil organic carbon (C), yet their distribution and function remain understudied. We evaluated changes in microbial residues and their contribution to organic C along a soil development sequence on three contrasting parent materials (granite, basalt and andesite) and three conifer biomes (ponderosa pine (*Pinus ponderosa* Laws.), PP; white fir (*Abies concolor* Lindl.), WF; and red fir (*Abies magnifica* A. Murr.), RF) at different elevations in the Sierra Nevada of California. Soil samples were taken from both A and B horizons and microbial residues were determined by amino sugar analysis. The effect of conifer biome on amino sugars was complex and dependent on parent material and horizon. We found parent material significantly influenced soil amino sugars which exhibited a pattern of andesite > basalt > granite in both A and B horizons. Both correlation and redundancy analyses indicated a significant correlation of amino sugars with the amount of short-range-order materials. This suggests soil mineralogy plays an important role in influencing amino sugar accumulation. This is further supported by larger differences among parent materials than between conifer biomes in ratios of fungal-to bacterial-derived amino sugars. The proportion of amino sugars to soil organic C was significantly influenced by parent material in the B horizon following the pattern of basalt > andesite > granite, but not affected by conifer biome. Our results suggest that mineralogy strongly influences the degree to which soil microbial residues persist in temperate forest soils.

1. Introduction

Stable soil organic carbon (C) influences long-term C sequestration (Swift, 2001) and is a critical soil property influencing the terrestrial C sink (Falloon and Smith, 2000). Microbial residues are regarded as a significant contributor to soil organic C due to their relatively long residence time in soils (Amelung, 2001; Kiem and Kögel-Knabner, 2003; Glaser et al., 2004; Throckmorton et al., 2015). Reports indicate that microbial residues likely play a far greater role in long-term C sequestration and stabilization than traditionally believed (Simpson et al., 2007; Liang and Balser, 2011; Miltner et al., 2012).

Forest biomes play a significant role in global C cycling (Schlesinger, 1997). Investigations about soil organic C storage in forest biomes have focused on the decomposition and transformation of plant-derived C (Liang et al., 2015). A large part of plant litter C and/or nitrogen is transformed into microbial biomass and subsequently into microbial-derived soil organic C (Engelking et al., 2007; Kindler et al., 2009). Microbial residues are likely an important controller of C storage in forest soils (Balser, 2005). Liang et al. (2011) proposed that 80% of soil organic C is composed of unaltered and transformed microbial residues. Given the potential significant contribution of microbial residues to stable soil C, a more detailed characterization of these microbial residues and their contribution to soil organic C is important to improve our predictions of soil C cycling and optimize ecosystem scale C models (Liang and Balser, 2011; Throckmorton et al., 2015).

Amino sugars are key components of microbial cell walls and their presence in soil indicates their contribution to soil organic C (Guggenberger et al., 1999; Amelung, 2001; Glaser et al., 2004). They can serve as a recalcitrant time-integrated biomarker of coarse-scale fungal:bacterial community structure (Amelung, 2001; Nannipieri et al., 1979; Chantigny et al., 1997). Although a

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variety of amino sugars exist in soil, four major ones include glucosamine (GluN), muramic acid (MurA), mannosamine (ManN) and galactosamine (GalN) (Zhang and Amelung, 1996). Glucosamine is predominantly derived from chitin of fungal cell walls, but can also be found in bacteria and soil invertebrates (Parsons, 1981; Chantigny et al., 1997). Muramic acid is uniquely synthesized by bacteria (Parsons, 1981; Appuhn and Joergensen, 2006). Galactosamine is another significant component of the total amino sugar pool (Glaser et al., 2004) and is generally considered to originate in bacteria (Amelung, 2001). The ratios of amino sugars can be used to indicate relative bacterial versus fungal contributions to soil organic C (Guggenberger et al., 1999; Glaser et al., 2004; Joergensen and Wichern, 2008).

The objective of this study was to assess the influence of parent material and forest biome on microbial-derived amino sugars in soil. The study site, which was located on the western slope of the Sierra Nevada, offered an exceptional opportunity for this purpose with soils having contrasting parent materials, different degree of soil development based on altitude and supporting different forest biomes as a function of altitude. We hypothesized that forest biome would be the major driver for changes in amino sugars in the surface soil (A horizon). The conifer litter was distinct for each forest biome along an altitudinal transect (Rasmussen et al., 2006). In subsurface soil (B horizon), however, we predicted that the influence of forest biome on amino sugar concentrations would decline and that parent material would become important.

2. Materials and methods

2.1. Study site

This study was conducted on the western slope of Sierra Nevada in California. The climate of this region is Mediterranean. Variations in air temperature and precipitation along the slope result in altitudinal distribution of different biomes. Previous studies showed that the majority of soil C was stored in the mid-to high-elevation conifer biomes (Rasmussen, 2004). Therefore, we focused our study on three conifer biomes (ponderosa pine (*Pinus ponderosa* Laws.), PP; white fir (*Abies concolor* Lindl.), WF; and red fir (*Abies magnifica* A. Murr.), RF) located on three distinct parent materials (basalt, granite, and andesite). For the PP biome, the dominant vegetation includes *Pinus ponderosa*, *Pinus lambertiana*, *Quercus kelloggii*, and *Calocedrus decurrens*; the elevation limit is between 900 and 1500 m; and the mean annual soil temperature (MAST) and mean annual precipitation (MAP) are 13.6 °C and 103 cm, respectively. For the WF biome, the dominant vegetation includes *Abies concolor* and *Pinus lambertiana*; the elevation limit is between 1500 and 2100 m; and the MAST and MAP are 9.1 °C and 115 cm, respectively. For the RF biome, the dominant vegetation includes *Abies magnifica* and *Pinus jeffreyi*; the elevation limit is between 2100 and 2600 m; and the MAST and MAP are 6.7 °C and 135 cm, respectively. Granite soils were dominated by crystalline minerals such as vermiculite and kaolinite, andesite soils by noncrystalline materials such as allophone and Al-humus complexes, and basalt soils by a mix of crystalline and noncrystalline materials. More detailed information about study site was reported in Rasmussen et al. (2006).

2.2. Soil collection and analysis

Soil samples were taken from three elevational transects within each parent material type. For each transect, three soil pits were sampled from each conifer biome. To minimize micro-climate and landscape variability, sampling sites were constrained to similar aspect, similar slope (<10%), and similar canopy position (outside of tree canopy). Samples were collected by genetic horizon and only the A and B horizons were used in this study. Soil horizon thickness varied from 6–18.7 cm for the A horizon and 17–38 cm for the B horizon. The A horizons were carefully separated from the above organic layers. All visible roots and plant materials were removed manually from soil samples prior to passing through a 2-mm sieve and air-drying for chemical analyses. Soil total C content was determined by dry combustion on an elemental analyzer (Vario EL, Hanau, Germany). Soil clay and short-range-order (SRO) materials content were obtained directly from Rasmussen et al. (2006) and listed in Table S1.

2.3. Amino sugar analysis

Amino sugar content in soils was determined according to Zhang and Amelung (1996). Briefly, finely ground soil samples (containing approximately 0.3 mg N) were mixed with 10 mL of 6 mol L^{-1} HCl. To avoid oxidation of amino sugars during hydrolysis, N_2 gas was bubbled into the mixture during hydrolysis at 105 °C for 8 h. The hydrolysate was filtered through a Whatman 2 filter (125 mm diameter), dried using a rotary evaporator, and redissolved in deionized water. The pH of samples was adjusted to 6.6–6.8 with 1 mol L^{-1} KOH and 0.01 mol L^{-1} HCl. Samples were then centrifuged (1006×*g*, 10 min) in 50-mL glass tubes. The supernatant was freeze-dried, after which amino sugars were recovered in methanol. The recovered amino sugars were transformed into aldononitrile derivatives and extracted with 1.5 mL dichloromethane. Excess anhydride was removed with 1 mol HCl in deionized water. The amino sugar derivatives were redissolved in 300 μL hexane and ethyl acetate solvent (*v*:*v* = 1:1) for final analysis. The amino sugar derivatives were separated on an Agilent 6890A gas chromatography (GC, Agilent Tech. Co. Ltd., USA) equipped with a HP-5 fused silica column (25 m × 0.32 mm × 0.25 μm) and a flame ionization detector. The concentrations of individual amino sugars were quantified based on the internal standard myo-inositol, which was added prior to hydrolyzation. *N*-methyl-D-glucamine was added before derivatization to estimate the derivatization efficiency. The recovery of *N*-methyl-D-glucamine is between 95.3 and 98.6%. The concentration of total amino sugars was calculated as the sum of GluN, GalN, MurA and ManN. Data interpretation is based on the assumption that MurA represents bacterial cell-wall residue and GluN is representative of fungal cell-wall residue in soil (Chantigny et al., 1997; Amelung et al., 2001).

2.4. Statistical analysis

Statistical analyses were performed with R (R Core Team, 2016). To determine the effect of parent material, conifer biome, horizon depth and their interactions on sums and ratios of amino sugars, a linear mixed-effects model was fitted separately for the A and B horizons with the *lme4* package in R. Parent material, conifer biome, and horizon depth were treated as fixed effects and soil pit (field replication) was treated as a random effect nested within parent material × conifer biome. Since soils from A and B horizons are dependent samples, we used the Bonferroni correction to adjust the *P* values. Elevation was not included into the model because its influence was significantly confounded with that of conifer biome. The Tukey's Honestly Significant Difference (HSD) test was run where significant effects were found. Correlations between variables were calculated with the Pearson's correlation coefficient. Figures were plotted using Sigmaplot 10.0 (Systat Software Inc., San Jose, CA).

Redundancy analysis (RDA) was carried out to explore soil amino sugars explained by a linear model of soil properties for the A horizon with the 'rda' function in *vegan* package in R. The