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ORIGINAL PAPER

Decomposition of added and native organic carbon from physically separated fractions of diverse soils

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Abstract There have been increasing efforts to understand the dynamics of organic carbon (OC) associated with measurable fractions of bulk soil. We compared the decomposition of native OC (native C) with that of an added substrate (glucose) on physically separated fractions of a diverse suite of soils. Five soil orders were selected from four contrasting climate zones (Mollisol from temperate, Ultisol and Oxisol from tropics, Andisol from sub-arctic, and Gelisol from arctic region). Soils from the A horizon were fractionated into particulate OC (POC) and mineral-associated OC (MOC) by a size-based method. Fractions were incubated at 20 °C and 50 % water-holding capacity in the dark after the addition of unlabeled D-glucose (0.4 mg C g^{-1} fraction) and U–^{14}C glucose (296 Bq g^{-1} fraction). Respiration of glucose ^{14}C indicated 64 to 84 % of added glucose ^{14}C which was respired from POC and 62 to 70 % from MOC within 150 days of incubation, with more than half of the cumulative respiration occurring within 4 days. Native C respiration varied widely across fractions: 12 to 46 % of native C was respired from POC and 3 to 10 % was respired from MOC fractions. This suggested that native C was more stabilized on the MOC than on the POC, but respiration from the added glucose was generally similar for MOC and POC fractions. Our study suggests a fundamental difference between the behavior of freshly added C and native C from MOC and POC fractions of soils.

Keywords Native organic carbon · Glucose · Respiration · Particulate organic carbon · Mineral-associated organic carbon

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Introduction

Most soil organic carbon (SOC) compounds are broken down extracellularly by microbial enzymes into simple monomers that can be taken up by microbes. The rate of decomposition can be slowed by inaccessibility of SOC to microorganisms via the physical soil structure and/or through chemical interactions with soil minerals, i.e., physical and chemical protection (Lützow et al. 2006; Oades 1988; Sollins et al. 1996). Physical protection involves the spatial segregation of SOC from microorganisms and enzymes by the pore structure and formation of stabilized soil aggregates (Denef and Six 2006; Jastrow 1996; Six et al. 2002; Tisdall and Oades 1982), where the residence time of SOC is strongly linked to aggregate stability (Besnard et al. 1996). Chemical protection involves specific sorption reactions of dissolved organic C (OC) with soil minerals, which reduce bioavailability by inhibiting enzymatic depolymerization (Jardine et al. 1989; Kaiser and Zech 2000; Kalbitz et al. 2005; Sollins et al. 2009).

Positive relationships between OC content and reactive minerals in soils have been observed across a variety of ecosystems (Burke et al. 1989; Ladd et al. 1996; Mayer 1999; Mayes et al. 2012; Oades 1988), which supports the efficacy of minerals to protect SOC from decomposition.

According to Kalbitz et al. (2005), sorption of dissolved OC on soil minerals reduced SOC mineralization by 70–80 % as compared to that of dissolved OC without sorption. Once a compound becomes sorbed to a mineral surface, the thermodynamics are such that desorption is reduced (Gu et al. 1994, 1995). The chemical bonds formed between OC and mineral surfaces are thought to resist desorption even in the presence of microbial exoenzymes breaking C–C bonds in the OC compound (Quiquampoix et al. 1995). Examples of OC bonds with minerals include cation bridges (Oades 1988), hydrogen bonds, van der Waals forces (Quiquampoix et al. 1995), ion exchange, and ligand exchange (Kaiser and Zech 2000), although there is a large range in bond strength among the types of bonds. The relative importance of these different bond types in a given soil will differ based on the chemistry of OC compounds and on the soil properties, such as pH, clay content and mineralogy, and oxide crystallinity and abundance (Baldock and Skjemstad 2000; Kaiser and Zech 2000; Kleber et al. 2004; Nagarajah et al. 1970; Quiquampoix et al. 1995). Thus, there is a high potential for variability in the strength of mineral protection due to the mineral composition of the soil.

The extent of OC protected by mineral interactions can be studied by fractionating the bulk soil and isolating the fine fraction (<53 μm) from the course fraction (>53 μm). The fine fraction consists of silt and clay-sized particles which is referred as mineral-associated OC (MOC), and the coarse fraction consists of sand and un-decomposed plant residues, which is referred as particulate OC (POC). Respiration of native C may be unequal between the two fractions because POC may contain a higher proportion of original detritus, while MOC may contain a higher proportion of partially degraded material. So far, studies comparing the C mineralization rate of isolated fractions are limited. Among soil C models, there is a general agreement that POC decomposes faster than MOC (Coleman and Jenkinson 1999; Parton et al. 1987; Trumbore 1997). Progressive oxidation of fresh inputs (e.g., POC) is assumed to lead to increasingly recalcitrant forms of C stabilized in "passive" pools associated with mineral surfaces (e.g., MOC). However, through laboratory incubation of isolated fractions, Swanston et al. (2002) and Crow et al. (2006) reported that cumulative respiration is not always higher from POC as compared to MOC fraction. Soils from a deciduous forest site exhibited higher respiration from POC fraction, while soils from a coniferous site exhibited higher respiration from the MOC fraction (Crow et al. 2006). As recently noted by Schmidt et al. (2011), older C may be extensively recycled between and within these pools through incorporation into microbial biomass and adsorption–desorption reactions. The fate of new C in the different fractions is uncertain as various factors may act to stabilize new inputs into the MOC fraction.

The purpose of this study was to determine the rate and extent of decomposition of native C compared to added substrate in size-separated MOC versus POC fractions of soils. We hypothesized that respiration of native C would be lower in the MOC fraction compared to the POC fraction due to chemical protective associations and that respiration of C from the added substrate would be similar between the fractions because glucose reported to exhibit poor sorption on soil minerals. We used glucose as a model substrate to understand the dynamics of freshly added C from fractions because glucose is one of the primary C compounds released into the soil by rhizodeposition and by the decomposition of cellulose and hemicellulose which are the most abundant constituents of plant C inputs and microbial cell walls (Paul and Clark 1996; Larionova et al. 2007). Glucose has been used widely as a marker in C decomposition experiments (Van Veen et al. 1985; Paul and Clark 1989).

Materials and methods

Soils and fractionation

Soils were selected from four contrasting climatic zones—temperate, tropical, sub-arctic, and arctic. The selected soils are from major soil orders of the respective climatic regions: Mollisols of temperate, Ultisol and Oxisol of tropics, Andisol of sub-arctic, and Gelisol of arctic regions (Table 1). From each location, five soil cores were collected to a depth of 15 cm, composited, air-dried, and sieved to <2 mm.

The POC fraction (plant residue+sand particles) was separated from the MOC fraction (clay and silt-sized particles) by size-based fractionation (modified from Allison and Jastrow 2006). Soil (25 g) was combined with 125 ml of deionized water and 25 glass beads (4 mm diameter) in a 250-ml polyethylene bottle and shaken on a reciprocal shaker (200 strokes per minute) for 16 h. The number of beads and time and speed of shaking were optimized in preliminary tests to ensure satisfactory disruption of aggregates with minimal fragmentation of plant residues. The efficacy of the separation was assessed in a preliminary test by adding sodium polytungstate solution (density 1.6 g cm^{-3}) to a subsample of MOC fraction and observed minimal floated POC materials. Mechanical dispersion of soil with glass beads does introduce osmotic and physical stress to the microorganisms, but we chose this method over chemical dispersion using sodium hexametaphosphate because ionic solutions can denature enzymes and alter microbial activity (Allison and Jastrow 2006). We also did not select density-based separation as most density liquids (e.g., sodium polytungstate) reduce the population of viable microbial population and hence tend to reduce microbial activities (Compton and Boone 2002; Crow et al. 2007; Magid et al. 1996).

The dispersed soil solution was wet-sieved through a 53-μm sieve. The silt- and clay-sized fraction (MOC) passed

Table 1 Soil locations and taxonomy

Soil	Ecoregion	Location	Soil taxonomy
Mollisol	Temperate	Batavia, IL, USA	Typic endoaquolls
Ultisol	Tropical	Lavras, Minas Gerais, Brazil	Typic hapludult
Oxisol	Tropical	Peje Annex, La Selva, Costa Rica	Haplic haploperox
Andisol	Sub-arctic	Krýsuvíkurheiði, Reykjanes, Iceland	Haplic andosol[a]
Gelisol	Arctic	Fairbanks, AK, USA	Typic aquiturbels

[a] Based on World Reference Base system; all others are based on USDA-NRCS system

through the sieve and was oven dried at 60 ° C. The POC fraction, consisting of sand-sized (>53 μm) mineral and organic particles, was recovered from the sieve and dried at 40 ° C. The MOC fraction was dried at an elevated temperature compared to the POC fraction because water was more strongly retained by clay in MOC fraction after the fractionation process. Although we used a modest method of fractionation and minimal temperature for drying the POC and MOC fractions, we expect some alterations in microbial community size and composition in the isolated fractions compared to fresh soils. Other studies also fractionated bulk soils and dried the fractions at similar temperatures and subsequently used those fractions for incubation experiments (Mutuo et al. 2006; Swanston et al. 2002). The particle-size distribution after the size fractionation method was comparable to the standard textural analysis by the bouyoucos hydrometer method (±5 %) (Gee and Or 2004). Major physicochemical properties of the fractions varied widely across the soil orders (Table 2).

Incubation experiments

Six replicates of POC and MOC fractions from each soil type were incubated at room temperature (20 °C) for 150 days in the dark in a temperature- and humidity-controlled room. For each sample, 5 g POC or 25 g MOC fractions were pre-incubated at 40 % water-holding capacity (WHC) for 1 week to avoid the respiration response of the microbial community to rewetting (Haddix et al. 2011; Paul et al. 2001). The MOC fractions were mixed with 25 g of acid-washed sand particles (Ottawa White Frac Sand, size 20/40 from US silica) in order to improve aerobic conditions during the incubation (Crow et al. 2007; Swanston et al. 2002). Since POC fraction is a mixture of plant residues and sand grains of size >53 μm, we did not add artificial sand to this fraction.

Three of the six total replicates were amended with 1 ml unlabeled D-glucose at the concentration of 0.4 mg C g^{-1} fraction and with U–^{14}C glucose at an activity of 296-Bq g^{-1} fraction. The final moisture content of the fractions was adjusted to 50 % WHC with MilliQ (MQ) water, and of the six glucose addition replicates, three were monitored throughout the duration of the incubation for respiration of $^{14}C–CO_2$ and native $C–CO_2$. The three remaining replicates were designated as "control" samples, which received only MQ water and incurred no glucose addition. These three control samples were also incubated for the duration of the experiment to measure the native C respiration. All samples, contained in specimen cups, were placed in 1-L glass jars along with a glass vial containing 17 ml of 0.5 N NaOH solution to trap the evolved CO_2. The jars were tightly closed and incubated in the dark at 20 °C. The NaOH solution was exchanged 13 times within the 150 days of incubation using daily to weekly intervals in the first 2 months and monthly intervals thereafter. Diluted NaOH (0.1 N) was used after 60 days of incubation in order to increase the sensitivity of assay when CO_2 production

Table 2 Physicochemical characteristics of the MOC and POC fractions of soils

Soil	Organic C (g kg^{-1})	Organic N (g kg^{-1})	pH	Clay[a] (g kg^{-1})	Fe_d (g kg^{-1})
MOC					
Mollisol	30.37	3.62	7.13	380	17.41
Ultisol	28.48	3.53	4.70	726	32.98
Oxisol	24.19	3.81	3.93	700	84.91
Andisol	93.95	9.53	5.04	176	72.37
Gelisol	11.97	1.28	5.86	141	16.49
POC					
Mollisol	351.9	14.12			
Ultisol	325.9				
Oxisol	386.2	16.73			
Andisol	314.1	14.78			
Gelisol	371.5	15.55			

Fe_d dithionate–citrate–bicarbonate extraction

[a] This was derived considering clay+silt in MOC as 1,000 g kg^{-1}

was reduced (Hopkins et al. 2008). Moisture content was kept constant by weighing the samples periodically and adding MQ water as needed.

Measurement of CO_2 respiration

We determined the amount of CO_2 efflux from both native C and added ^{14}C glucose. The amount of total C mineralized to CO_2, i.e., native C and glucose ^{14}C, was analyzed by titrating an aliquot of NaOH collected at each sampling time with 0.5 N HCl by an automatic titrator (Metrohm USA). Before the titration, the CO_2 trapped in NaOH was precipitated as $BaCO_3$ by adding 2 ml of 10 % $BaCl_2$. The volume of acid needed to neutralize the remaining NaOH (unreacted with CO_2) was determined by the titration, which was used to calculate the concentration of CO_2 trapped in the NaOH solution (Zibilske 1994). Respiration of the ^{14}C-labeled glucose was determined by measuring the activity of ^{14}C–CO_2 trapped in NaOH solution with a Packard Tri-Carb Liquid Scintillation Counter (LSC) after mixing 5 ml of the NaOH solution with 10 ml of the scintillation cocktail Ultima Gold XR (PerkinElmer). We assumed that the signature of the ^{14}C spike was fully representative of the stable glucose added to the soil, which enabled us to distinguish the respiration of glucose C from that of native C. The CO_2 derived from native C was calculated from the difference between total CO_2 and glucose-derived $^{14}CO_2$.

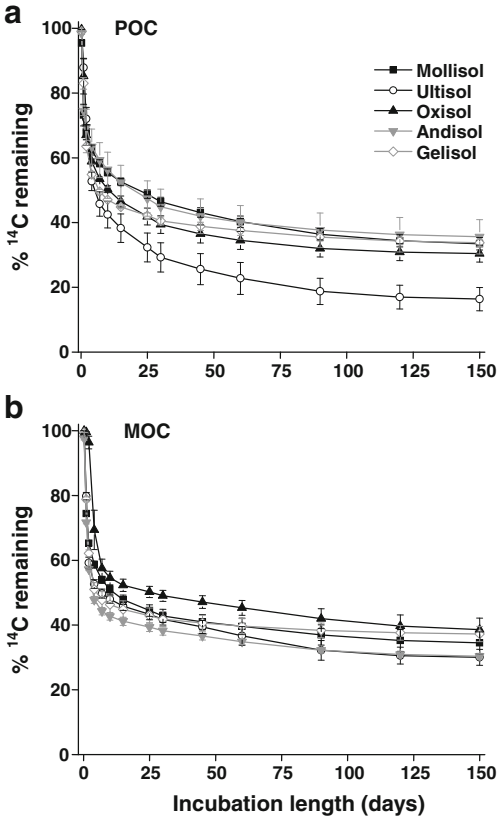

Fig. 1 Mineralization of glucose ^{14}C from **a** particulate organic C (*POC*) and **b** mineral-associated organic C (*MOC*) fractions of soils. *Symbols* represent the average percentage of ^{14}C remaining in the soil over time along with standard error bars, $n=3$

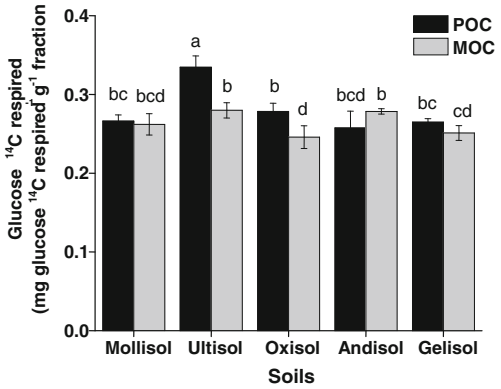

Fig. 2 Cumulative respiration of glucose ^{14}C after 150 days, normalized to the mass of each fraction. Particulate organic C (*POC*) and mineral-associated organic C (*MOC*) *fraction bars* represent the average respiration, $n=3$. *Different letters* indicate significant differences in respiration between soil types and fractions determined by ANOVA

Statistical analysis

Statistical analyses were conducted using SAS software (SAS Institute 2002). The analyses of variance (ANOVA) for testing the difference between POC and MOC fractions of measured parameters used the PROC GLM procedure (fixed effects model). Statistical significance was evaluated at $P \leq 0.05$, and the mean effects were separated using the F-protected least significant difference (LSD) test. PROC REG of SAS was used to perform the simple linear regression between CO_2 respired and initial SOC concentration ($P \leq 0.05$).

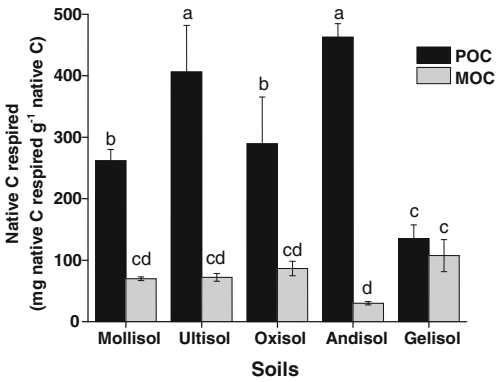

Fig. 3 Cumulative respiration of native C after 150 days, normalized to the amount of native C in each fraction. Particulate organic C (*POC*) and mineral-associated organic C (*MOC*) *fraction bars* represent the average respiration, $n=3$. *Different letters* indicate significant differences in respiration between soil types and fractions determined by ANOVA

Results

Glucose ^{14}C mineralization

Respiration of added glucose ^{14}C was faster in the beginning of the incubation experiment for both POC and MOC fractions (Fig. 1a, b). After 150 days, 64 to 84 % of added glucose ^{14}C was mineralized from POC fraction of all soils, and 62–70 % was mineralized from MOC fractions. Irrespective of the fractions, more than 50 % of the total respiration occurred within the first 4 days of incubation and slowed considerably thereafter. Accordingly, the mineralization rate was 0.12 to 1.2 % of added C per hour for the first 4 days and was reduced by an order of magnitude from day 4 to day 30 and by two to three orders of magnitude after 30 days. Glucose ^{14}C mineralization from the MOC fraction varied within a narrow range across different soils (Fig. 1b). However, in the POC fraction, more added glucose ^{14}C was degraded from the tropical Ultisol than from other soils (Fig. 1a). When cumulative glucose ^{14}C respiration after 150 days was normalized by the mass of fractions, the highest respiration was observed from Ultisol POC and the lowest was from Oxisol MOC (Fig. 2). The glucose C respiration between POC and MOC fractions was statistically similar for all the soils except for tropical Ultisol and Oxisol.

Native C mineralization

The amount of respiration from native C was calculated as the difference between total CO_2 evolution and glucose $^{14}CO_2$ evolution. The POC fraction respired more native C over 150 days than the MOC fraction when data was normalized to the amount of native C incubated (Fig. 3) and to the mass of fraction incubated (data not shown) except in the Gelisol. Native C mineralization from POC fractions varied from 135 to 463 mg C g^{-1} C_{native}, and the native C respiration from MOC fractions ranged from 30 to 107 mg C g^{-1} C_{native}. Native C respiration from control MOC and POC fractions was statistically similar to the glucose-amended fractions throughout the incubation experiment (Fig. 4). There was an inverse relationship between the concentration of native C and the percentage of native C lost

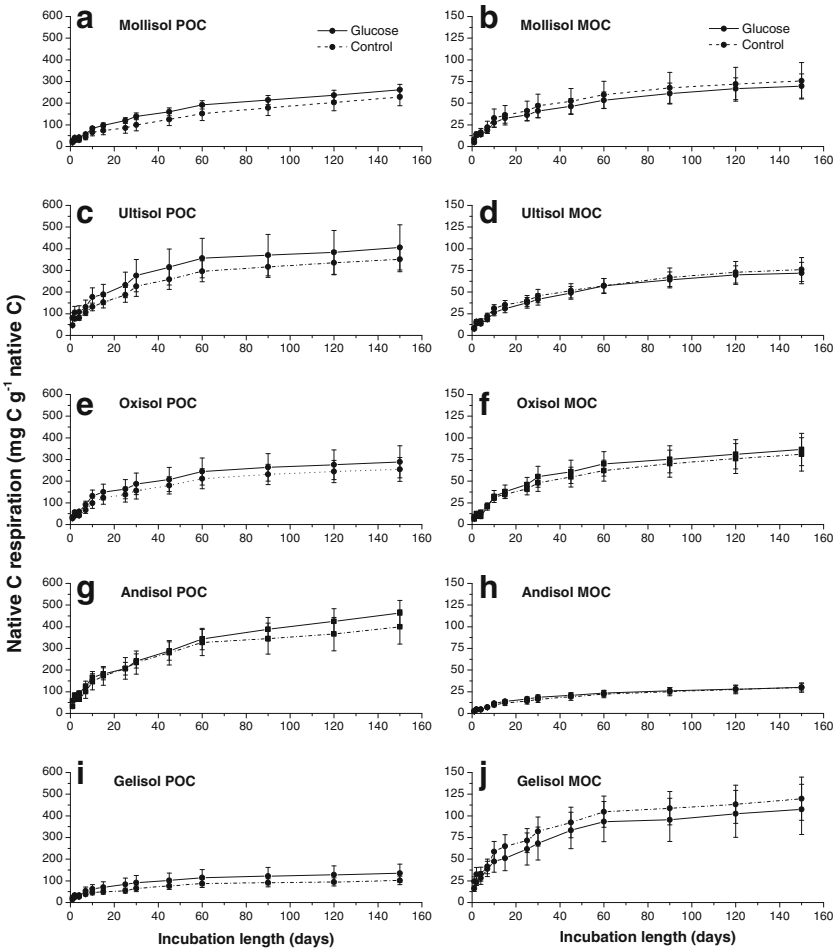

Fig. 4 Respiration of native C from glucose-amended (*solid lines*) and glucose-unamended (*dotted lines*) POC (**a**, **c**, **e**, **g**, **i**) and MOC (**b**, **d**, **f**, **h**, **j**) fractions. Note that the upper limit of *y*-axis is different for POC (600) and MOC (100) fractions

through respiration in both glucose-amended and control samples (Fig. 5). The relationship between C mineralization and native C content was stronger in the MOC fraction (R^2=0.89 for glucose-amended and 0.85 for unamended fractions) than the POC fraction (R^2=0.64 for glucose-amended and 0.60 for unamended fractions). Among the POC fractions, 12 to 46 % of native C was lost and among the MOC fractions and 3 to 11 % of native C was lost over 150 days.

Discussion

In this study, the respiration of added ^{14}C glucose and native C was evaluated in POC and MOC fractions of five soils (temperate Mollisols, tropical Ultisols and Oxisols, arctic Gelisols, and sub-arctic Andisols) for 150 days. The highest mineralization rate from added ^{14}C glucose occurred in the first few days of incubation and decreased thereafter, which was similar to previous results in bulk soils (Bremer and Kuikman 1994; Bremer and van Kessel 1990; Chotte et al. 1998; Nguyen and Guckert 2001; Nguyen and Henry 2002; Schneckenberger et al. 2008; Van Veen et al. 1985). Here, similar glucose ^{14}C respiration was observed for the POC and MOC fractions of most soils. Small but statistically significant differences were observed for the tropical soils, but overall, glucose availability was similar for both fractions. The decomposition of native C proceeded at a slower rate in the MOC versus the POC fractions, and considerably greater respiration of native C was observed from the POC fractions than the MOC fractions except the Gelisol (Figs. 3 and 4).

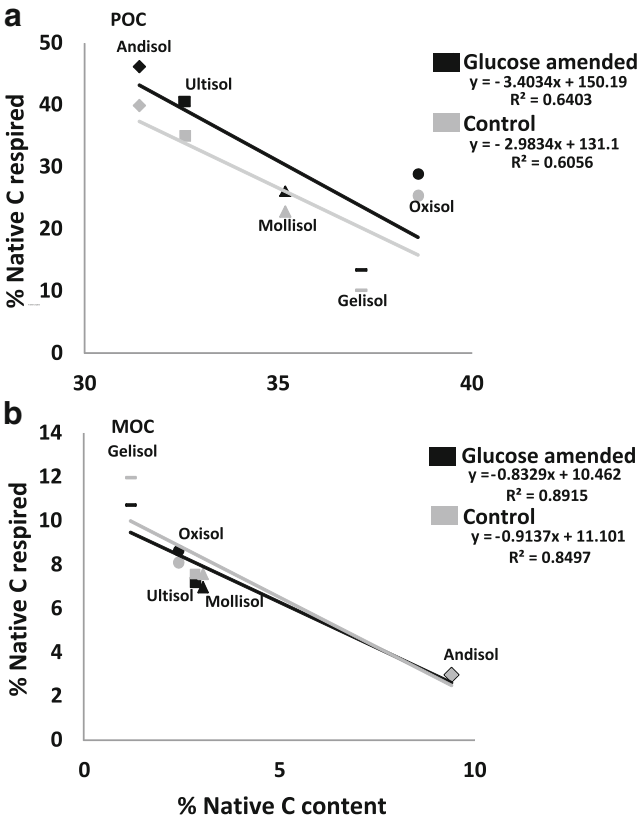

Fig. 5 Relationship between cumulative native C mineralization at 150 days versus the amount of native C content in **a** particulate organic C (*POC*) fraction, both glucose amended (*black*) and control (*gray*) and **b** mineral-associated organic C (*MOC*) fraction, both glucose amended (*black*) and control (*gray*)

The difference in respiration between POC and MOC was much larger for native C than for glucose ^{14}C. Native C is therefore effectively retained on soil minerals in the MOC fraction. Bulk native C, in both POC and MOC fractions, contains a wide variety of organic C compounds that decompose at different rates due to variations in chemical structure, molecular weight, hydrophobicity, and degree of polymerization (Baldock et al. 1997; Gleixner et al. 2002). Further, high molecular weight and/or hydrophobic compounds tend to form stronger chemical bonds with soil minerals compared to those with low molecular weight and/or more hydrophilicity (Chenu et al. 2006; Gu et al. 1994; Jardine et al. 1989; Kaiser and Zech 1997; Kaiser et al. 2001). Setia and Marschner (2013) reported higher native C respiration from soils amended with pea residues containing a higher amount of low molecular weight compounds as compared to wheat residues. The finding of greater degradation of native POC versus MOC suggests that mineral protection of native C is important for the range of complex compounds in soils. The finding of generally similar degradation of glucose ^{14}C between MOC and POC fractions suggests that mineral protection was not a common mechanism of protection of glucose-like compounds in soils. Sugars do not necessarily form strong chemical bonds with soil minerals (Jones and Edwards 1998; Kuzyakov and Jones 2006), which could explain the greater degradation compared to native C. For example, we found that the affinity of soils for several OC compounds (L-alanine, salicylic acid, sinapyl alcohol, oxalic acid, starch, cinnamic acid, and stearic acid) was always greater than for glucose (Jagadamma et al. 2012, 2014).

The inverse linear relationships between initial native C content of the fractions and the cumulative C mineralization (Fig. 5) suggest that native C concentration was a good indicator of the extent of respiration in POC and MOC fractions. Proportionally less C was respired from soils having higher native C contents. As we only studied five soils from diverse climate zones, more soils will need to be tested to validate the relationship between native C content and respiration rate. Mineralization of native C from glucose ^{14}C-amended and control fractions remained statistically similar throughout the experiment for most soils, suggesting no priming effect (Fig. 4). Past studies reported either positive, negative, or no priming effects with the addition of labile C substrates (Blagodatskaya et al. 2007; De Nobili et al. 2001;

Hamer and Marschner 2005; Kuzyakov and Bol 2006; Kuzyakov et al. 2007). de Graaff et al. (2010) reported positive priming with the addition of 0.7 mg C g^{-1} soil labile C, negative priming with the addition of >7.2 mg C g^{-1} soil, and no priming with intermediate amount (1.4 to 3.6 mg C g^{-1} soil). Our results indicated that the addition of 0.4 mg C g^{-1} fraction did not cause a priming effect.

Conclusion

We wanted to know if the decomposition of native C and applied C was different for MOC and POC fractions in a variety of soils. We hypothesized that mineralization of native C would be lower from the MOC versus the POC fraction because of stronger chemical bonding in the MOC fraction. We also hypothesized that added labile C might be respired equally from MOC and POC fractions because the added substrate would not readily form strong bonds with either fraction. Indeed, the mineralization of native C was higher from POC than MOC, and the mineralization of glucose ^{14}C was similar for both fractions. More information is therefore needed regarding the stability of various types of C associated with the mineral fraction using, for example, novel isotope labeling techniques. We also suggest that studies be conducted on bulk soil and on soil fractions to better understand the long residence times observed for soil C in the mineral fraction. In our work, further studies are underway to investigate the distribution of added glucose in various soil pools (e.g., microbial biomass and soil solution) by extracting and determining the residual glucose at different time points during the incubation. Future studies could also include position-specific labeling approach to determine if the added glucose was used mostly for energy production or biosynthesis, as described by Dijkstra et al. (2011). We are also considering the use of new technologies to understand in situ oxidation of organic C sources including glucose by investigating the newly emerging gene expression techniques (Rice et al. 2012).

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