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Factors influencing the calorespirometric ratios of soil microbial metabolism

N. Barros [a, *], L.D. Hansen [b], V. Piñeiro [c], C. Pérez-Cruzado [d], M. Villanueva [a], J. Proupín [a], J.A. Rodríguez-Añón [a]

[a] Department of Applied Physics, University of Santiago de Compostela, Spain
[b] Department of Chemistry and Biochemistry, Brigham Young University, Provo, UT 84602, USA
[c] Elemental Analysis Service, RIAIDT, Lugo, University of Santiago de Compostela, Spain
[d] Forest Inventory and Remote Sensing, Georg-August-University, Göttingen, Germany

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ABSTRACT

Calorespirometric ratio of metabolism connects the metabolic activity with the nature of the substrate and metabolic pathways being used by cells and microorganisms. Calorespirometric ratios have been determined for many living systems including animals, plants, plant and animal cells, and many different microorganisms, but application to soil is very recent. Calorespirometric ratios for soils are obtained by simultaneous calorimetric measurements of heat and CO_2 rates from biodegradation of soil organic matter. The purpose here is to gain a better understanding of the factors influencing the value of the calorespirometric ratio in soil, i.e. changes in the composition of the soil organic matter, soil moisture, soil particle size, and soil management (e.g. conversion of pasture to forest). Results indicate that calorespirometric ratios are sensitive to moisture, soil size fraction, and the source and age of soil organic matter.

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1. Introduction

Direct measurements of CO_2 as an indicator of microbial degradation of soil organic matter (SOM) are important because CO_2 data can be used to evaluate the impact of soil management on atmospheric CO_2. Soil management practices impact the capacity of soil to sequester C, and thus exert a direct effect on future climate change. Soil management needs to be developed on a sustainable basis that minimizes global warming, which requires understanding the mechanisms that favor soil C sequestration. Determination of the properties of SOM and relating those properties with biodegradability is the basis for the concept of SOM stabilization (Field et al., 2007; Conant et al., 2011). This concept has led to many studies about SOM by a wide range of different methodologies providing chemical, physical and biological SOM properties. Among those methods, thermal analysis involves easy and fast procedures that yield data on the physical properties of SOM (Barros et al., 2007; Plante et al., 2009) while calorespirometry provides a means for direct measurements of the rates of microbial processes by combined measurements of the rates of heat and CO_2 production by microbial metabolism (Hansen et al., 2004; Matheson et al., 2004; Battley, 2013).

Soil calorespirometry has the potential to provide a more complete description of microbial processes related to the carbon cycle than do measurements of microbial CO_2 production alone (Herrmann et al., 2014). For example, combining measurements of the heat and CO_2 rates of soil microbial metabolism allows application of thermodynamic models of the efficiency of soil microbial processes for retaining C (Barros and Feijoo, 2003; Harris et al., 2012). The mass-specific heat and CO_2 rates are quantitatively informative about the rates of bioprocesses in soil, but either alone provides little information on the nature of the organic substrate being degraded or on the efficiency of degradation processes. To close this gap, concepts based on the calorespirometric ratio (R_q/R_{CO_2}) in soils have been introduced, but not fully developed. Previous applications to living systems showed R_q/R_{CO_2} ratios inform about the nature of the substrate being degraded by microorganisms and about the efficiency of the metabolism,

* Corresponding author.
E-mail address: nieves.barros@usc.es (N. Barros).

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resulting in an attractive option if applied to soil research that would enrich the knowledge about soil biochemistry. Interpretation of calorespirometric ratios for soils with a stoichiometric model of metabolism is an attractive option to study microbial systems degrading complex substrates (Wadsö et al., 2004). Recent papers (Barros et al., 2010, 2011) showed that calorespirometric ratios measured on different soils differed greatly, but the factors affecting the value of this ratio for soil microbial metabolism could not be clearly identified.

A clear understanding of Thornton's rule, i.e., the enthalpy change for oxidation of any organic material by O_2 is approximately constant when expressed per mole of O_2 (Hansen et al., 2004), is required for interpreting calorespirometric ratios. The value of this approximate constant, the oxycaloric ratio (ΔH_{O_2}), varies from −440 to −470 kJ per mole O_2, depending on conditions and the class of compound being oxidized (Hansen et al., 2004). The average value, −455 kJ mol^{-1} O_2 thus has a range of ±15 kJ mol^{-1} O_2 or ±3.3%.

In steady-state aerobic systems with no significant net growth of microorganisms, the calorespirometric ratio is given by Hansen et al. (2004):

$$R_q/R_{CO_2} = -\Delta H_{O_2}[1-(\gamma_s/4)] = (455\pm15)[1-(\gamma_s/4)] \quad (1)$$

$-\Delta H_{O_2}$ is Thornton's constant (455 kJ mol^{-1} O_2) and γ_s is the oxidation state of the substrate carbon. Under these conditions, R_q/R_{CO_2} depends solely on the oxidation state of the substrate. However, note that γ_s is the oxidation state of the substrate carbon being oxidized to CO_2, not the average oxidation state of the SOM. Therefore, if the ratio is measured at steady state microbial metabolism with no microbial growth, comparison of R_q/R_{CO_2} values obtained experimentally to those expected from the main substrates constituting the SOM, provide information on the substrate being degraded by soil microorganisms. The presence of microbial growth is typically apparent from an exponentially increasing heat rate during a measurement while steady state conditions are shown by a nearly constant heat rate along the measurement. Table 1 summarizes approximate expected values of R_q/R_{CO_2} for substances commonly found in soil organic matter.

This work is focused on measuring R_q/R_{CO_2} of soil microbial metabolism under metabolic steady-state conditions, i.e., with no significant net gain in microbial activity, to determine how these ratios vary in soil under more controlled experimental procedures than those reported previously (Barros et al., 2011). SOM physical properties are determined by thermal analyses and ^{13}C CPMAS to understand the effect of SOM properties on R_q/R_{CO_2} values and R_q/R_{CO_2} values are determined under common soil treatments to see how conditions affect the ratio. The goal is to improve knowledge about the factors influencing these ratios in soil for further application in soil microbial metabolism responsible for SOM biodegradation.

2. Material and methods

2.1. Soil samples

Soil samples used in this study represent an alumiumbric regosol with inclusions of alumi-humic cambisols, alumi-humic umbrisols and district cambisols (IUSS Working Group WRB, 2006) collected in Borreiros–Viveiro (43° 37′ 51.94″ N 7° 37′ 22.63″) and Castro del Rey (43° 12′ 31″ N 7° 24′ 1″ W) Lugo, Spain. These samples were under different managements and vegetation (pasture, *Pinus radiata* and *Eucalyptus nitens*).

The evolution of SOM properties and calorespirometric ratios with depth was determined with samples of aluminiumbric regosol from Borreiros collected from 0 to 10 cm, 10 to 20 cm and 20 to 30 cm from the soil surface. The sampling procedure was developed under standard statistical criteria to obtain representative samples of the sampling area avoiding edge effects (Núñez-Regueira et al., 2006; Rodríguez-Añón et al., 2007). Two plots were selected in the sampling area. In each of these, a 50 × 50 cm^2 area was marked with 4 metal pegs graduated from 0 to 50 cm. Four soil sub-samples in each of the selected areas were extracted from 0 to 10 cm, 10 to 20 cm and 20 to 30 cm from the surface, avoiding contamination among samples. In the laboratory, a total of 8 subsamples were pooled by depth to one sample and sieved to 2 mm. A portion of each soil sample from different depths was dried at 105 °C in an oven during 24 h for elemental and thermal analysis. Samples for calorespirometric measurements under different moisture percentages were air dried at 21 °C for 3 days. These were stored in polyethylene bags at 4 °C during one month before the calorespirometric measurements to allow soils to stabilize after this treatment.

The influence of moisture on soil biodegradation and calorespirometric ratios was determined with soil samples from different depths stored at 4 °C. The water holding capacity (WHC) was determined prior to storage using a glass tube fitted with a fritted glass disc in the bottom being immersed in water. The water content of the samples was measured by weight loss after drying at 105 °C in an oven for about 24 h. Biodegradation rates were measured after bringing the samples stored at 4 °C to 13, 25, 38, 50, 63, 88 and 112% of WHC. For each calorespirometric measurement, 7 subsamples (10 g) of the soil from each depth stored at 4 °C for one month were first equilibrated at 25 °C during 24 h inside polyethylene bags. After this equilibration, subsamples from each depth were rewetted to the different moisture percentages and incubated inside polyethylene bags at 25 °C during 4 days before the calorespirometric measurements. The incubation is done with a water container inside the polyethylene bags to prevent drying. The incubation period permits soil to stabilize after rewetting, avoiding measurement of the initial flux of CO_2 and heat caused by the treatment. This behavior of the soil was previously tested by calorimetry to check that after 4 days of incubation the heat rate was at a steady state.

Table 1
Expected values of R_q/R_{CO_2} for microbial oxidation reactions by O_2 of common compounds constituting soil organic matter.

Reaction	Oxidation number/γ_s	R_q/R_{CO_2}/kJ mol^{-1}
Cellulose, starch oxidation by O_2	0	455
Lignin oxidation by O_2	−0.60 ± 0.06[a]	523
Protein oxidation by O_2	−1.0	543
Lipid oxidation by O_2	−1.4	611
Humates oxidation by O_2	−0.1 to +0.9[b]	470–350
Oxidative decarboxylation of organic compounds	+2	228

[a] http://terra.rice.edu/department/faculty/masiello/RIGG/html/research/cox.html accessed April 2015.
[b] Hunt et al. (2000).

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