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Short Communication

Cellular and non-cellular mineralization of organic carbon in soils with contrasted physicochemical properties

Benoit Kéraval[a,b,*], Sébastien Fontaine[b], Audrey Lallement[b], Sandrine Revaillot[b], Hermine Billard[a], Gaël Alvarez[b,c], Fernando Maestre[d], Christian Amblard[a], Anne-Catherine Lehours[a]

[a] Université Clermont Auvergne, CNRS, Laboratoire Microorganismes: Génome et Environnement, F-63000 Clermont-Ferrand, France
[b] INRA, UR874 (Unité de Recherche sur l'Ecosystème Prairial), 5 Chemin de Beaulieu, 63039, Clermont-Ferrand, France
[c] Clermont Université, VetAgro Sup, BP 10448, F-6300, Clermont-Ferrand, France
[d] Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Calle Tulipán Sin Número, 28933, Móstoles, Spain

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ABSTRACT

It has been recently demonstrated that soil organic carbon (SOC) mineralization is supported by intracellular respiration of heterotrophic microorganisms and by non-cellular oxidative processes. However, little is known about the prevalence and drivers of non-cellular SOC mineralization among soils. In this study, untreated and gamma-irradiated soils sampled along a latitudinal gradient and exhibiting contrasted physicochemical properties were incubated in order to quantify potential non-cellular SOC mineralization and to identify its sensibility to soil properties. In sterilized and unsterilized soils, CO_2 emission mirrored O_2 consumption signifying the presence of several coupled redox reactions transferring electrons from organic C to intermediate acceptors and to O_2. This supports the idea that non-cellular mineralization results from extracellular oxidative metabolisms catalyzed by soil enzymes and/or abiotic catalysts. Our findings also show that non-cellular SOC mineralization is ubiquitous and contributes to 24% of soil respiration on average. Cellular and non-cellular SOC mineralization are positively linked but the contribution of non-cellular processes to soil CO_2 emissions increases with dissolved organic carbon concentration.

Representing one of the largest terrestrial source of CO_2 flux, soil organic carbon (SOC) mineralization significantly impacts atmospheric CO_2 concentration and climate (Lal and Kimble, 2000; Paterson and Sim, 2013). SOC mineralization is traditionally viewed as a two-step process. First, microorganisms secrete extracellular enzymes to convert insoluble SOC polymers into compounds assimilable by microbial cells. In the second step, during which carbon (C) is released as CO_2, assimilated compounds are carried out by an oxidative metabolism including many coupled reactions, enzymes and cofactors as well as required redox and pH conditions. Given this complexity, it is taught that respiration (second step of the C mineralization process) is strictly an intracellular process. However, recurrent observations of persistent substantial CO_2 emissions in soil microcosms where sterilization treatments reduced microbial activities to undetectable levels challenged this paradigm (*e.g.*, Peterson, 1962; Lensi et al., 1991; Maire et al., 2013; Blankinship et al., 2014; Kéraval et al., 2016). Different non-cellular processes (Fig. S1) have been proposed as potential contributors to these CO_2 emissions such as (i) the partial degradation of aromatic compounds induced by reactive oxygenated species and/or metals (Fe^{3+}, Mn^{4+}) (Majcher et al., 2000; Wang et al., 2017), (ii) the extracellular decarboxylation of the metabolites of the Krebs cycle supported by some decarboxylases released during cell lysis and retaining their activities in soil (Maire et al., 2013; Blankinship et al., 2014) and (iii) the complete mineralization of organic compounds supported by an extracellular oxidative metabolism (EXOMET) (Maire et al., 2013; Kéraval et al., 2016). EXOMET differs from the two other processes in its complexity. Whereas (i) and (ii) involve single catalytic reactions, EXOMET implies numerous coupled redox reactions capable of complete conversion of organic C into CO_2 with an electron transfer to O_2.

Irrespective of the mechanism, nothing is known about the prevalence and drivers of non-cellular SOC mineralization ($R_{NON\text{-}CELLULAR}$) in soils with contrasting physicochemical properties. The objectives of this study were to (i) generalize non-cellular SOC mineralization to

* Corresponding author. LMGE, UMR CNRS 6023, Université Blaise Pascal, 1 impasse Amélie Murat, CS 60026, 63178, Aubière Cedex, France.
E-mail address: benoit.keraval@gmail.com (B. Kéraval).

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Table 1
Main physicochemical properties of the twenty two soils sampled. (S1 to B6, see Table S1 for correspondence). OC: organic carbon, IC: inorganic carbon, DOC: dissolved organic carbon.

Soil references	OC	IC	DOC	pH	Sand	Clay	Silt
	$mg.g^{-1}$		$\mu g\ g^{-1}$		%		
B1	1.0	0.5	9.6	6.5	96.6	2.2	1.1
B2	1.4	0.9	13.8	6.2	95.6	3.3	1.1
B3	2.2	0.5	17.8	6.2	95.7	1.1	3.2
B4	2.1	0.7	11.3	6.2	96.6	0.0	3.4
B5	2.9	0,0	13.0	6.3	96.7	1.1	2.2
B6	1.6	0.7	9.7	6.0	92.3	2.2	5.5
S1	31.7	62.4	58.7	8.1	59.2	6.0	34.8
S2	20.4	79.2	62.1	8.2	44.4	6.2	49.4
S3	31.1	64.4	81.3	8.0	49.0	7.2	43.8
S4	43.2	67.8	63.4	7.7	48.9	6.2	44.9
S5	31.8	76.8	68.9	8.0	54.4	6.8	38.8
S6	20.3	83.1	49.4	8.1	49.4	3.9	46.8
S7	25.9	49.5	54.4	7.6	52.4	4.1	43.5
S8	17.8	94.7	48.1	8.1	49.8	9.2	41.0
S9	44.9	25.5	115.3	8.0	60.4	2.2	37.4
S10	28.3	66.5	63.8	8.1	59.4	5.8	34.8
S11	29.6	27.4	114.7	7.6	74.3	6.6	19.1
F1	21.9	0.0	84.3	6.4	70,0	6.8	23.3
F2	15.2	6.7	23.4	8.1	42.2	10.0	47.8
F3	21.5	0.6	26.9	6.0	32.2	3.3	64.4
F4	17.4	6.2	21.2	7.6	42.2	16.7	41.1
F5	34.8	0.0	41.9	6.0	55.6	13.3	31.1

many soils, (ii) quantify $R_{NON\text{-}CELLULAR}$ and its contribution to total SOC mineralization and (iii) identify soil properties that most influence $R_{NON\text{-}CELLULAR}$.

Twenty two soils (Table S1) with various physicochemical properties (Table 1, Fig. S2, Table S2) were collected in permanent grasslands along a latitudinal gradient from Europe to Southern Africa. Untreated and sterilized soils (*gamma*-irradiations) were incubated to measure potential $R_{NON\text{-}CELLULAR}$ and total SOC mineralization (R_{SOIL}), respectively (see Supplementary information). Soils were incubated at 20 °C and at a water potential of −100 kPa. We used γ-irradiations at 45 kGy to sterilize soil samples because previous investigations combining various molecular, microscopic and biochemical techniques showed that such procedure reduce microbial biomass to undetectable levels, prevent any microbial re-colonization (McNamara et al., 2003; Berns et al., 2008; Maire et al., 2013) and limit the impact of sterilization treatment on the physicochemical soil properties compared to the use of fumigants or thermal sterilization treatments (McNamara et al., 2003). All manipulations were done under sterile conditions and sterility of soils was checked, at the end of incubation, using culture approach and propidium iodide staining coupled to flow cytometry (see Supplementary information).

We recorded O_2 consumption and CO_2 production over a 16-day incubation period in γ-irradiated and untreated soil microcosms (Fig. 1a and b, Table S3). As none viable cells were detected in irradiated soil microcosms (Supplementary information, Table S4), we assumed that γ-irradiations allowed quantifying potential $R_{NON\text{-}CELLULAR}$ in sterilized

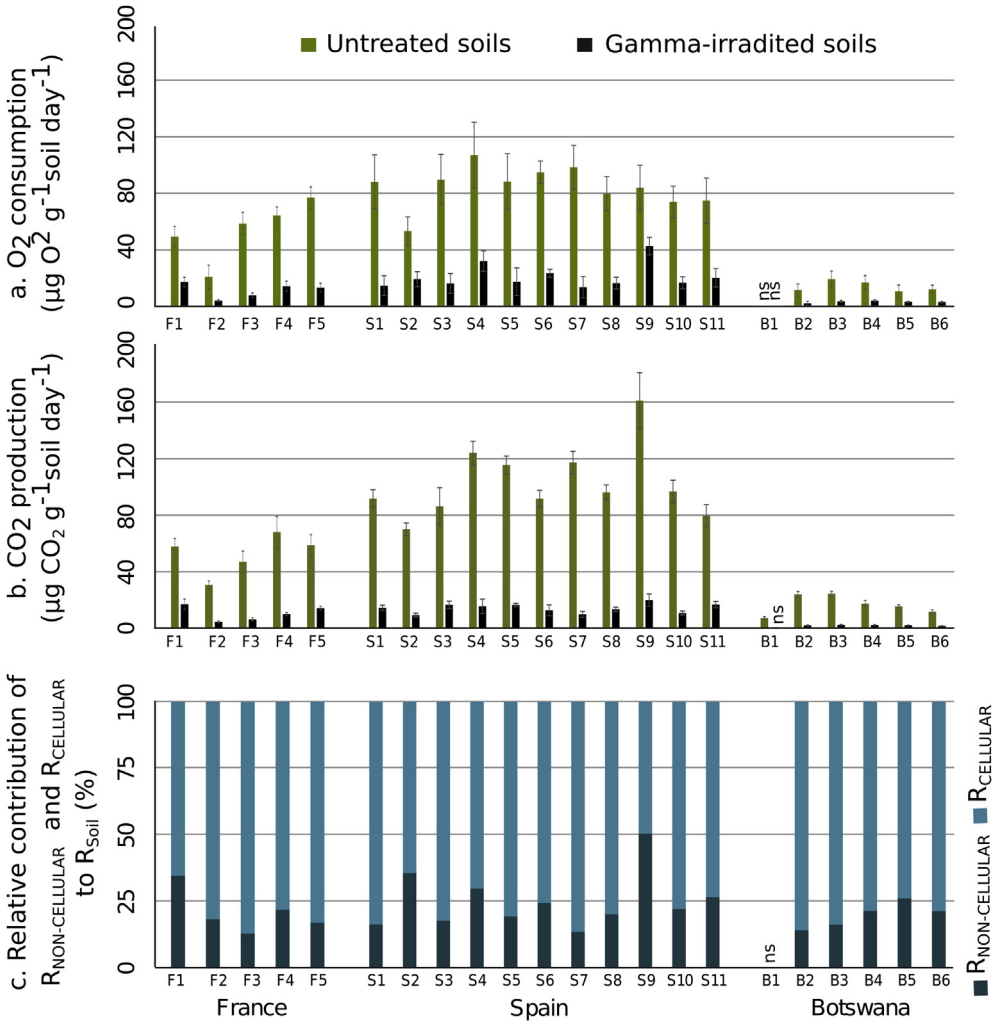

Fig. 1. (A) O_2 consumption and (b) CO_2 production by γ-irradiated and untreated soil microcosms. Twenty two soils sampled along a latitudinal gradient were incubated (From S1 to B6 in x axis, see Table S1 for correspondence). (c) Contribution (in %) of $R_{NONCELLULAR}$ and $R_{CELLULAR}$ to R_{SOIL} see SI). ns indicates that measured fluxes were not significantly different from 0 ($p < 0.05$).