



HAL
open science

Temperature and soil management effects on carbon fluxes and priming effect intensity

Raphaël Guttières, Naoise Nunan, Xavier Raynaud, Gérard Lacroix, Sébastien Barot, Pierre Barré, Cyril Girardin, Bertrand Guenet, Jean-Christophe Lata, Luc Abbadie

► To cite this version:

Raphaël Guttières, Naoise Nunan, Xavier Raynaud, Gérard Lacroix, Sébastien Barot, et al.. Temperature and soil management effects on carbon fluxes and priming effect intensity. *Soil Biology and Biochemistry*, 2021, 153, pp.108103. 10.1016/j.soilbio.2020.108103 . hal-03086435

HAL Id: hal-03086435

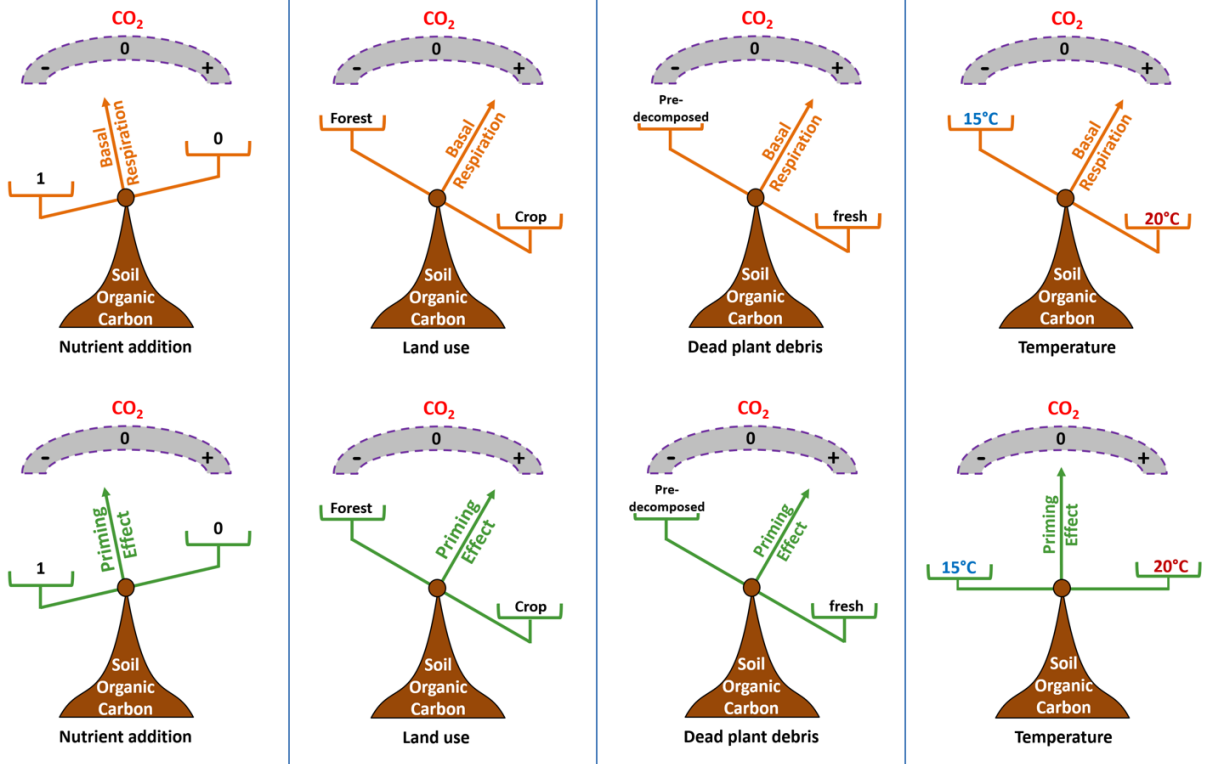
<https://hal.science/hal-03086435>

Submitted on 2 Apr 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Graphical Abstract



Highlight 1:

Degradability of dead plant matter determines the soil priming effect intensity

Highlight 2:

Fresh wheat straw induces 800% more CO₂ emission from soils than pre-decomposed straw

Highlight 3:

Temperature controls degradation of soil organic matter but not the priming effect

Highlight 4:

Management of dead plant matter is a key driver of carbon sequestration in crop soils

Highlight 5:

Land use and plant residue management affect priming effect more than global warming

1 **Temperature and soil management effects on carbon fluxes and priming**
2 **effect intensity**

3
4 Raphaël Guttières¹, Naoise Nunan¹, Xavier Raynaud¹, Gérard Lacroix^{1,6}, Sébastien Barot^{1,4},
5 Pierre Barré³, Cyril Girardin⁵, Bertrand Guenet^{2,3}, Jean-Christophe Lata¹, Luc Abbadie^{1*}

6
7 Affiliations:

8 [1] Sorbonne Université, CNRS, INRA, IRD, University of Paris, UPEC, Institut d'Ecologie et des
9 Sciences de l'Environnement – Paris (iEES-Paris), 7 quai St Bernard, F-75252 Paris, France

10 [2] Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS- UVSQ,
11 Université Paris-Saclay, F-91191 Gif-sur-Yvette, France

12 [3] CNRS, PSL Research University, Laboratoire de Géologie de l'ENS, 24 rue Lhomond, 75231
13 Paris cedex 05, France.

14 [4] IRD, Sorbonne Université, CNRS, INRA, University of Paris, UPEC, Institut d'Ecologie et des
15 Sciences de l'Environnement – Paris (iEES-Paris), 7 quai St Bernard, F-75252 Paris, France.

16 [5] INRAE, UMR Ecosys, Campus AgroParisTech, Bât. EGER, F- 78850 Thiverval-Grignon
17 (France)

18 [6] CNRS, UMS 3194 (ENS, CNRS), CEREEP – Ecotron IleDeFrance, Ecole Normale Supérieure,
19 11 Chemin de Busseau, 77140 St-Pierre-lès-Nemours, France.

20 * Correspondence to: L. Abbadie (lucabbadie@sorbonne-universite.fr)

21

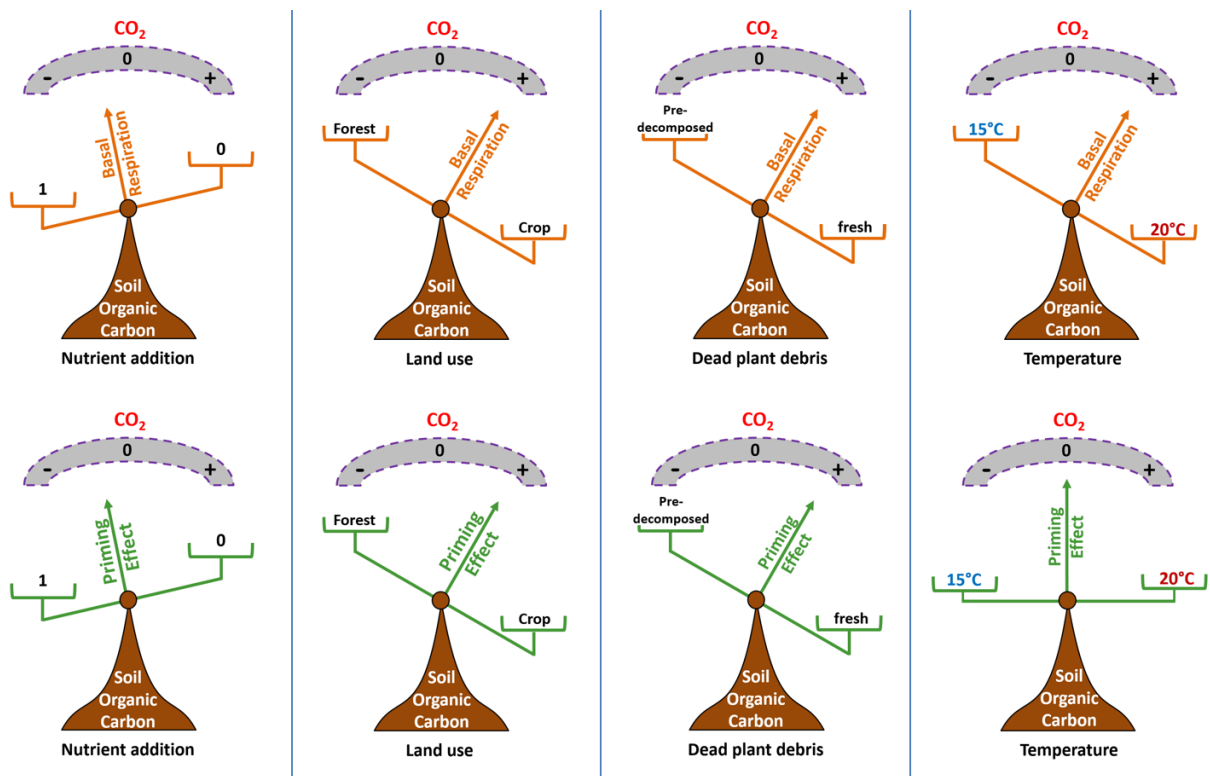
22

23

- Primary Research Article -

24

25 **Graphical abstract**



26

27

28 **Keywords:** global change; priming effect; agricultural practices; organic matter

29 biodegradability; crop vs. forest soils; decomposition; nutrient addition.

30

31 **Abstract**

32 Any change in the intensity and sign of CO₂ flux between soil and atmosphere is expected to
33 have a significant impact on climate. The net emission of CO₂ by soils depends on
34 antagonistic processes: the persistence of dead plant matter and the mineralization of soil
35 organic matter. These two processes are partly interdependent: their interaction is known as
36 the "priming effect" (PE), i.e. the stimulation of the mineralization of stable soil organic
37 matter by more labile fresh organic matter.

38 Documenting the response of PE to global change is needed for predicting long term
39 dynamics of ecosystems and climate change, and for managing carbon cycle in order to slow
40 down the atmospheric CO₂ increase. We have tested the effects on PE of temperature,
41 nutrient availability, energy content of added organic matter, land use and interactions.

42 Our results suggest that the biodegradability of the dead plant debris (wheat straw, fresh or
43 pre-decomposed) is the first determinant of the intensity of PE, far ahead temperature and
44 nutrients: fresh wheat straw addition induced up to 800% more CO₂ emission than pre-
45 decomposed one. The raise of temperature from 15 to 20°C, increased basal soil organic
46 matter mineralization by 38%, but had no effect on PE. Interactions between
47 biodegradability of straw and the other factors showed that the agricultural soil was more
48 responsive to all factors than the forest soil.

49 We have shown in our study that the intensity of PE could be more dependent on land use
50 and plant residue management than on other drivers of global change, particularly
51 temperature and nutrients. There is an urgent need to assess the genericity of our results by

52 testing other soil types and plant debris for a better integration of PE in models, and for
53 identifying alternative land carbon management strategies for climate change mitigation.

54

55 **Introduction**

56 One of today's major scientific challenges is to better understand the biological mechanisms
57 regulating carbon (C) fluxes between the soil and the atmosphere and to determine how
58 these fluxes impact climate change through climate-ecosystem feedback loops ([Bardgett et](#)
59 [al., 2008](#); [Heimann & Reichstein, 2008](#)). Soils are the largest reservoir of terrestrial organic C
60 (OC): it has been estimated to 615 Gt C in the top 0.2 m soil layer and to 2,344 Gt C in the
61 first 3 meters ([Jobbágy & Jackson, 2000](#)). The annual flux of C-CO₂ from the soil to the
62 atmosphere is approximately 60 Gt, more than 6 times the 9 Gt C emitted anthropogenically
63 ([Stockmann et al., 2013](#)). Therefore, even slight modifications of the C fluxes between soil
64 and atmosphere may have a substantial impact on the future climate ([Minasny et al., 2017](#)).
65 A better understanding of the mechanisms and interactions underlying these fluxes is
66 therefore essential.

67 Feedbacks between soil and climate have been identified as the main uncertainty in Earth
68 system models (ESMs) ([Friedlínstein et al., 2006](#); [He et al., 2016](#)). ESMs simulate the
69 removal of CO₂ from the atmosphere by the land surface *via* the photosynthesis, and the
70 increases in atmospheric CO₂ concentrations *via* the respiratory activity of living organisms
71 including plants and soil. Nevertheless, several feedbacks between these two fluxes are not
72 represented in ESMs ([Heimann & Reichstein, 2008](#)), whereas it is now widely acknowledged
73 that these two processes are intimately linked and that their interactions can have

74 significant consequences for the C cycle (Schmidt et al., 2011; Luo et al., 2016; Guenet et al.,
75 2018). One of the most significant potential mechanisms leading to such interaction is the
76 stimulation of soil organic matter (SOM) mineralization by microorganisms after the addition
77 of fresh organic matter (FOM), known as the priming effect (PE) (Löhnis, 1926; Bingeman,
78 1953).

79 Even though the addition of FOM does not always result in a PE (see the concept of
80 “negative priming effect”, Kuzyakov et al., 2000), the most frequently reported response is
81 the acceleration of SOM mineralization, sometimes with a rate up to 400% (Fontaine et al.,
82 2004; Fontaine et al., 2011; Shahzad et al., 2012; Tian et al., 2016; Sun et al., 2019). The
83 priming effect is likely a universal phenomenon that could affect significantly the C
84 accumulation ability of soils in very different contexts (Perveen et al., 2019). The CO₂
85 fertilisation effect (*i.e.* the increase in photosynthesis due to the increase in atmospheric CO₂
86 concentration), for example, could lead to a weaker gain of soil C than expected or even to a
87 net loss of soil organic C (SOC) stocks (Chemidlin Prévost-Bouré et al., 2010; Dijkstra et al.,
88 2013). Much recent interest has also been shown in stabilizing atmospheric CO₂ levels
89 through C sequestration, with particular attention being paid to C sequestration in soil, as
90 illustrated by the international 4 per 1000 initiative (Minasny et al., 2017). As the
91 management practices designed to increase SOC stocks are generally based on an increase
92 of C inputs to the soil, the PE may reduce the impact of such practices and make the yearly
93 SOC stock increase targeted by the 4 per 1000 difficult to achieve (Baveye et al., 2018).
94 Indeed, global scale models in which PE is represented diverge considerably in their
95 predictions of soil C stocks from those that do not include PE (Guenet et al., 2018).

96 The PE has been studied for many years, but its underlying mechanisms are still not fully
97 understood (Blagodatskaya & Kuzyakov, 2008; Liu et al., 2018; Mason-Jones et al., 2018).
98 This lack of a clear mechanistic understanding means that it is difficult to predict the
99 occurrence or the extent to which the PE may affect soil C dynamics under different
100 conditions, particularly those expected in the context of global change or changes in soil
101 management or agricultural practices. For example, the effect of the expected rising
102 temperatures on the PE is still unclear, as both positive (Thiessen et al., 2013; Li et al., 2017;
103 Yanni et al., 2017), neutral (Ghee et al., 2013) or negative (Frøseth & Bleken, 2015; Yanni et
104 al., 2017) PE responses have been found. The stoichiometry of the plant-soil-microorganism
105 system is also known to be an important determinant of the occurrence and the extent of
106 the PE (Chen et al., 2014; Fang et al., 2018): generally, the higher the stoichiometric
107 imbalance between the availability of mineral nutrients and the microbial requirements in
108 mineral nutrients, the higher the PE (Kuzyakov et al., 2000; Fontaine et al., 2011; Chen et al.,
109 2014). It is hypothesized that the energy input induced by the addition of organic matter
110 (OM) stimulates the SOM “mining” activity of microbial communities, allowing them to
111 acquire more mineral nutrients by the consumption of SOM when their availability in the soil
112 solution is low (Fontaine et al., 2004).

113 The energy status of the added OM can also affect the occurrence and the intensity of the
114 PE. OM in which the energy is readily available to soil microbial communities tends to
115 stimulate the PE to a greater extent than OM in which energy is less available (Wang et al.,
116 2015; Lonardo et al., 2017; Chen et al., 2019). We therefore suggest that it may be more
117 beneficial to add C to soils through pre-decomposed (depleted in energy-rich compounds,
118 i.e. with lower biodegradability) OM in which there is an adequate mineral nutrient supply,

119 in order to minimize PE and therefore the decay of old persistent SOC. In the cereal cropping
120 context, this might be achievable by simply allowing straw to decompose at the soil surface,
121 post-harvest, before its incorporation into the soil, rather than incorporating it fresh through
122 tillage (Liu et al., 2014; Chen et al., 2015) or exporting it. This, however, has yet to be
123 verified. Furthermore, the biodegradability of the added pre-decomposed or fresh organic
124 matter should interact with temperature and the availability of mineral nutrients to
125 determine quantitatively the amount of primed C. However, virtually nothing is known about
126 such interactions.

127 In this study, we aim at quantifying the PE after the addition of pre-decomposed or fresh
128 OM, at two temperatures and two nutrient levels in two soils with different native organic
129 matter contents to assess the robustness of the results. The ultimate objective is to
130 determine whether a simple change in management practices could substantially alter soil C
131 dynamics in crop lands and how such a putative change might interact with different
132 temperatures and nutrient levels, in a global change context. We predict that the intensity of
133 the PE would be higher (1) in the soils that receive fresh OM, (2) at higher temperatures, (3)
134 without the addition of mineral nutrients.

135

136

137 **Materials & methods**

138

139 *Study area and soil description*

140 Soil samples were collected from an agricultural field (A) and an adjacent forest (F) in
141 Thiverval-Grignon (48°84'29081 N, 1°93'46532 E, AgroParisTech domain, France). The site
142 was chosen because the two land managements (cropland and forest) were on the same soil
143 type and only distant from each other by *ca.* 50 m. This was done in order to minimize
144 confounding effects such as soil texture and climate, and to better focus on the effects of the
145 quality and quantity of the soil organic matter (SOM). The soil was a silty loam (clay:silt:sand
146 ratio was 0.22:0.70:0.08) and classified as Luvisol ([Barré et al., 2017](#)). The F site, located
147 within the park of the AgroParisTech domain, is dominated by oak, hornbeam and ash and
148 was established in 1820. The A site, located in the same domain, has been under
149 conventional management for several decades and had been used for cropping for at least
150 two centuries. Cropland management was characterized by rotations based on cereals, an
151 annual tillage to 30 cm depth, mineral fertilization and exports of cereal straw ([Barré et al.,](#)
152 [2017](#)). The mean annual temperature was 10.7°C and the mean annual rainfall was 649 mm.

153 Soils samples from the two sites were taken to a depth of 15 cm after removal of the litter
154 layer. Fresh soils were immediately transported to the laboratory and the remaining organic
155 residues and stones were carefully removed by hand. Samples were then dried at room
156 temperature, sieved through a 2-mm mesh sieve and stored at ambient temperature, in the
157 dark ([Lauber et al., 2010](#)). Their chemical and physical properties are given in [Table 1](#).

158 Although both soils were of the same type, they differed in several aspects: the pH of the
159 agricultural soil was close to neutral, whereas the forest soil was acidic ([Table 1](#)). The
160 agricultural soil also contained half as much C content as the forest soil, but with almost the
161 same C isotopic signature ([Table 1](#)).

163

164 **Table 1.** Chemical and physical characteristics of soils (A for agricultural, F for forest) and plant
 165 residues.

166

Properties	Soil		Wheat straw	
	A	F	Fresh	Decomposed
TOC (g kg ⁻¹)	12.94	28.34	398.2	388.5
Total N (g kg ⁻¹)	1.42	2.5	11.0	34.9
C:N ratio	9.13	11.33	36.44	11.15
Total P (g kg ⁻¹)	0.062	0.01	1.45	6.99
$\delta^{13}\text{C}$ (‰)	-25.2	-26.4	5871.5	5343.6
WHC* (%)	39.8	38.2	—	—
Bulk Density (g cm ⁻³)	1.25	1.15	—	—
pH	7.5	5.5	—	—

*Water holding capacity

167

168 *Plant material & pre-decomposition*

169 We used ¹³C-labelled fresh wheat straw ($\delta^{13}\text{C} = 5871.51\text{‰}$, CEA of Cadarache). The chemical
 170 properties of this fresh organic matter (FOM) are given in [Table 1](#). Wheats were cultivated
 171 on an inert substrate in order to avoid uncontrolled CO₂ input from the soil, and they were
 172 therefore supplied with a non-limiting nutrient solution throughout the culture. Half of the
 173 FOM was pre-decomposed in the laboratory. The straw was first dried at 30°C for 10 days,
 174 and then finely milled (2 mm, Waring commercial® blender). The milled plant material was
 175 distributed in 12 litterbags (mesh size 35 µm), which were then placed on top of 600 g of soil
 176 A (dry weight equivalent) at 80% of the water holding capacity (WHC), itself in 4
 177 polyethylene containers. The containers were covered with Parafilm to minimize
 178 evaporation without affecting other gas exchanges ([Wang et al., 2015](#)) (and thus prevent
 179 CO₂ accumulation) and placed in incubation chambers at 25°C for 3 months. The location of
 180 the containers in the incubation chambers was randomised weekly.

181 The small mesh size of the litterbags allowed the colonisation of bacterial and fungal
182 decomposer communities (Johnson et al., 2002) and prevented the uncontrolled mixing of
183 the plant material with the soil for an easy recovery at the end of the pre-decomposition
184 step. All litterbags were weighed before and at the end of the incubation in order to
185 determine mass loss. At the end of this pre-decomposition step, the pre-decomposed wheat
186 straw (thereafter called DeOM) had lost 71.7% of its initial mass, 72.4% of initial C and had
187 reached a $\delta^{13}\text{C}$ of 5343.62‰ (Table 1). The DeOM C:N ratio had also decreased 3 fold
188 compared to FOM C:N.

189

190 *Experimental design*

191 The experimental design was fully factorial with four factors, three of which had two levels
192 and one of which had three levels. There were two temperature treatments (15 or 20°C),
193 two soils (A or F), 2 levels of nutrient addition (with or without) and 3 types of OM addition
194 (fresh (FOM) or pre-decomposed (DeOM) wheat straw and a control treatment (CTL)
195 without straw). The experimental units consisted of 15 g (dry weight equivalent) of soil A or
196 F in 120 ml hermetically sealed glass vials at 80% water holding capacity. Each treatment
197 combination was replicated 4 times. This led to 24 different treatments and 96 vials.

198 In treatments with nutrient addition, a mineral nutrient solution (NH_4NO_3 , KH_2PO_4 , dissolved
199 into deionized water) was added to ensure that soil microbial communities were not
200 nutrient limited, to give final total (soil + added OM) C:N and C:P ratios of at least 10:1 and
201 80:1, respectively (Fontaine et al., 2004) in all the soil + added OM systems, and to mimic

202 fertilizer stoichiometry. An equivalent volume of distilled water was added in the treatment
203 without nutrients.

204 Prior to the experiment, the soils were pre-incubated for 9 days at 15°C and 80% of WHC in
205 order to avoid the flush of mineralization (Birch effect) that is known to occur when a dried
206 soil is rewetted (Birch, 1958). Subsequently, 50 mgC.gC_{soil}⁻¹ of ¹³C-labelled organic matter
207 (FOM or DeOM) was added and thoroughly mixed in order to distribute the plant material
208 homogeneously within the soil. Control soils without OM addition were also mixed to apply
209 the same physical disturbance. The head-space of each microcosm was flushed with CO₂-
210 free air and immediately sealed with hermetic septum (Butyl/PTFE, Joint Pharma-Fix). The
211 microcosms were then placed at either 15 or 20°C and incubated in the dark for 101 days.
212 Throughout the incubation, samples were regularly weighed to control for water losses and
213 water content was readjusted when necessary.

214

215 *CO₂ and δ¹³C measurements*

216 The concentration of CO₂ (ppmv) in the microcosms' headspace and δ¹³C-CO₂ (‰) were
217 determined on days 1, 3, 7, 14, 24, 44, 71 and 101 of the incubation. The CO₂ concentrations
218 were measured using a micro gas chromatograph (Agilent, 490-PRO Micro GC System). A
219 second gas sample was taken and stored in 12 ml glass vacuum vials for δ¹³C measurement
220 using a mass spectrometer (FISONS OPTIMA Isotope Ratio Mass Spectrometer, coupled to an
221 ISOCHROM-GC) at a later date. After each CO₂ sampling, flasks were flushed with C CO₂-free
222 air. This air was led through a bottle of distilled water to moisten it and to prevent soil
223 drying. The septum was renewed each time to prevent the risks of air leakage.

224

225 *Partitioning of CO₂-C from added OM and SOM sources and PE calculation*

226 The origin of the CO₂ measured in the headspace of the microcosms was assessed using the
227 following equations (Mary et al., 1992):

228

$$229 \quad C_{SOM} = C_{Total} \times (\delta_{Total} - \delta_{adOM}) / (\delta_{CTL} - \delta_{adOM})$$

$$230 \quad C_{adOM} = C_{Total} - C_{SOM}$$

231

232 where C_{Total} is the total CO₂-C emission measured from incubation vials under different
233 treatments, C_{SOM} is the SOM-derived CO₂-C emissions, C_{adOM} is the added OM-derived CO₂-C
234 emissions, and δ correspond to the measured $\delta^{13}C$ in the respective compartment (where
235 CTL correspond to control treatment). We assumed that fractionation during the
236 biodegradation processes was negligible (Mary et al., 1992).

237 PE was calculated as follows:

238

$$239 \quad PE = C_{SOM} - C_{CTL}$$

240

241 where C_{CTL} is the SOM-derived CO₂-C emission in the control treatment (which is equal to
242 total CO₂-C emission in CTL treatment).

243

244 *Data analyses*

245 Raw results per gram of soil (g_{soil}) were normalized per gram of soil carbon (gC_{soil}) and
246 cumulated over the 101 days of incubation.

247 Statistical analyses were carried out using R version 3.4.1 (R Core Team 2017). Normality and
248 homogeneity of variance across treatments were tested prior to analyses and no data
249 transformation was necessary. Data are presented as the means of four replicates with
250 standard errors. Analyses of variance (ANOVA) were used to examine differences in
251 cumulative CO_2 respiration (including total CO_2 , SOM-derived CO_2 and added OM-derived
252 CO_2) and PE (including relative PE and cumulative PE) at the end of experimentation, among
253 treatments. Tukey's HSD post hoc tests were used to identify statistically significant
254 differences among treatments.

255

256

257 **Results**

258

259 *Total mineralization*

260 The total CO_2 produced in each treatment during the 101 days of the incubation are shown
261 in [Figure 1 \(a, b\)](#). In both soils, Tukey's test ([Figure 1a, b](#)) showed that C mineralization was
262 the highest in the FOM treatment, followed by the DeOM and control treatments. The input

263 of straw always induced a higher mineralization compared to control (+51% on average)
 264 (Table 2) for both pre-decomposed and fresh modalities, but only +18% with DeOM vs. +85%
 265 with the FOM (Figure 1 a, b). The highest temperature (*i.e.* 20°C) increased by 34% on
 266 average the amount of released CO₂, and the addition of mineral nutrients decreased it by
 267 *ca.* -8% (Figure 1 a, b). The patterns were similar in both soils, though the differences were
 268 less marked in the forest soil: there were significant differences among nearly all (11/12)
 269 treatment combinations in soil A, but only half the treatment combinations showed
 270 significant differences in soil F (See letters from Tukey test on the figure 1 a, b).

271

272 **Table 2.** Results of ANOVA to evaluate the impact of the quality of added organic matter
 273 (adOM), mineral nutrients addition (NPK) and temperature rise on 5°C (T°C) with F-values
 274 and significance stars for the two land-uses considered together. (NS = Not statistically
 275 Significant).

276

	Total C emission		adOM derived C		SOM derived C		PE	
	A-soil	F-soil	A-soil	F-soil	A-soil	F-soil	A-soil	F-soil
adOM	4547.1 ***	394.6 ***	151.3 ***	144.8 ***	2740.9 ***	2287.2 ***	69.1 ***	28.1 ***
NPK	125.3 ***	188.2 ***	4271.7 ***	959.8 ***	2477.3 ***	462.1 ***	3.1 .	2.2
T°C	2611.8 ***	13.3 ***	5658.9 ***	764.3 ***	100.9 ***	2206.5 ***	3.0 .	4.0 .
adOM : T°C	19.1 ***	1.0	4878.1 ***	943.8 ***	1813.7 ***	1897.8 ***	0.6	3.2 .
adOM : NPK	9.7 ***	4.2 *	4671.3 ***	990.5 ***	2029.5 ***	1906.4 ***	2.4	3.0 .
T°C : NPK	1.7	0.8	4685.6 ***	881.9 ***	1806.7 ***	2034.0 ***	1.6	0.8
adOM : T°C : NPK	1.0	0.4	4610.6 ***	925.9 ***	1922.3 ***	1922.1 ***	0.0	0.4

277

278 *Added OM derived-CO₂*

279 The mineralization of added FOM was 2 to 7 times higher than that of DeOM, depending on
 280 the treatment combination (Figure 1 c, d). Up to 95% of DeOM-carbon was still present in

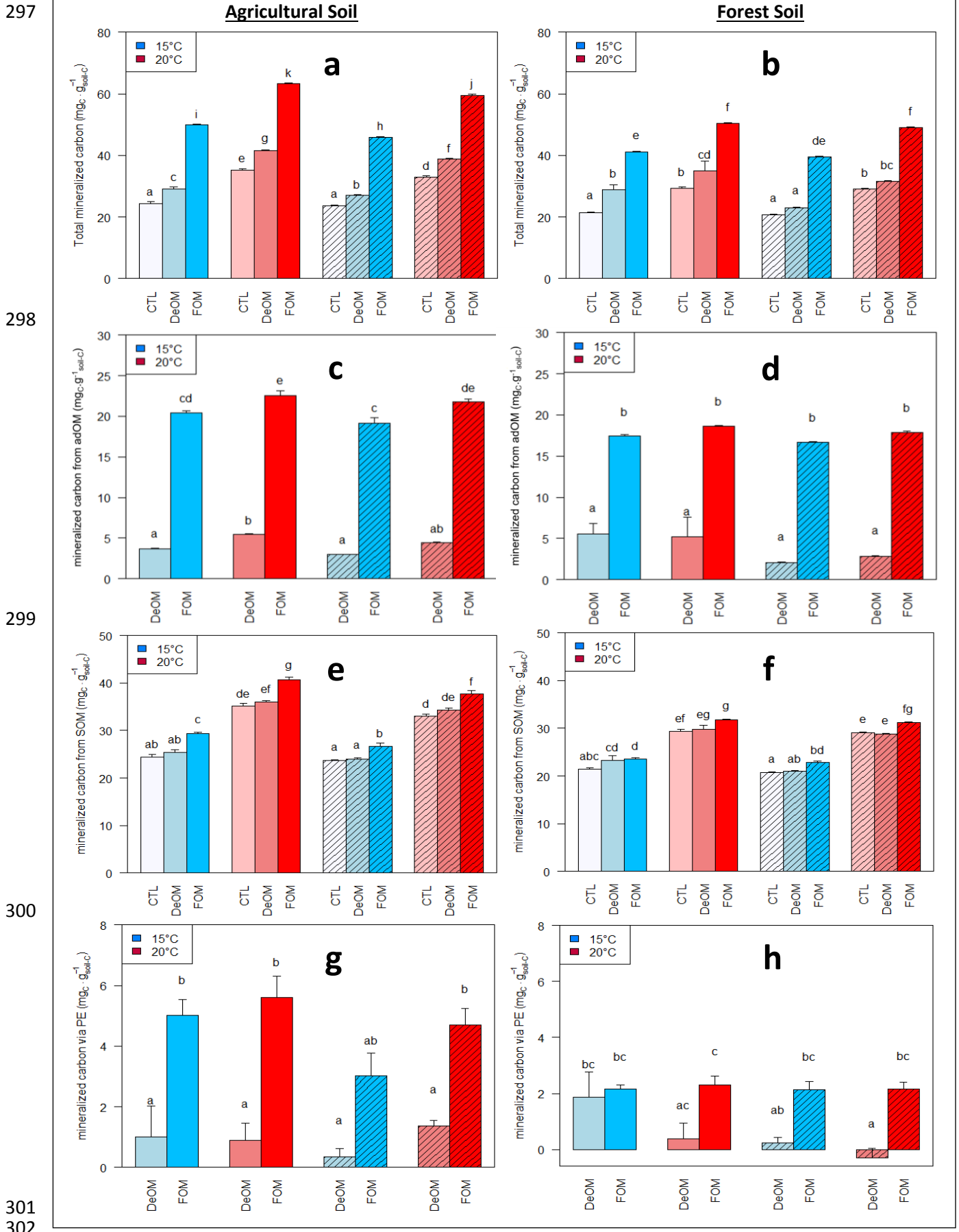
281 the soils at the end of the incubation, whereas less than 55% of FOM-carbon remained in soil
282 (Figure 1 c, d). There was a significant temperature effect on the mineralization rates of
283 added OM but also a significant interaction between soil and temperature (Table 2). Indeed,
284 post-hoc tests suggest that added OM mineralization was quite sensitive to temperature
285 when added to soil A, but less to soil F (Figure 1 c, d). Nutrient addition did not affect the
286 mineralization of added OM in either soil.

287

288 *SOM derived-CO₂-basal respiration*

289 In contrast to the mineralization of the straw residues, the main factor affecting basal SOM derived
290 CO₂ emissions was temperature (Figure 1 e, f). On average, there was a 38% increase in basal SOM-
291 mineralization at 20°C compared to 15°C (Figure 1 e, f). Furthermore, the addition of DeOM had no
292 significant effect on the basal respiration (*i.e.* SOM derived- CO₂), indicating that there was no PE in
293 this case. In contrast, a statistically significant increase in basal SOM-derived respiration (+12%
294 relative to controls) was found in FOM treatments. The addition of mineral nutrients had no
295 significant effect (Figure 1 e, f).

296



301
302

303 **Figure 1.** Carbon emissions and PE, normalized from grams of soil to grams of soil-C. Letters
304 **a & b** for Total mineralization, **c & d** for adOM-derived mineralization, **e & f** for SOM-derived
305 mineralization and **g & h** for PE, on soil A and F, respectively. Data are means of 4 replicates
306 \pm SE. **Blue & red** bars correspond to **15°C & 20°C** treatment respectively, hatched bars
307 correspond to treatment with mineral nutrients addition. Letter above bars are from Tukey-
308 test: bars with the same letter(s) are not significantly different ($P < 0.05$). Vertical scales are
309 adapted for each C emissions category, but identical between soil A & F to facilitate the
310 comparison (but letters from Tukey are not comparable between soils).

311

312 *SOM derived-CO₂-priming effect*

313 The PE depended mainly on both the quality of OM addition and the land use ([Figure 1 g, h](#)).
314 The maximum PE was induced by the addition of easily mineralizable compounds (FOM),
315 which induced up to +834% higher mineralization of SOM compared to the addition of more
316 recalcitrant compounds (DeOM) ([Figure 1 g, h](#)). There was no effect of the +5°C increase in
317 temperature on PE intensity. Mineral nutrient addition weakly negatively impacted the PE
318 (but significantly) on both soils ([Figure 1 g, h](#)) when we considered both soils together in the
319 ANOVA ([Table 2 and Figure 1 g, h](#)).

320 The temporal evolution of the cumulative PE is illustrated in [Figure 2](#). The PE profile over
321 time depended on the quality of OM addition and the soil. There was little or no PE following
322 the addition of DeOM, regardless of the soil. In soil A, the PE after the addition of FOM was
323 relatively high and persisted throughout the duration of the incubation, whilst it was lower
324 and reached a plateau after 7 days in soil F ([Figure 2](#)).

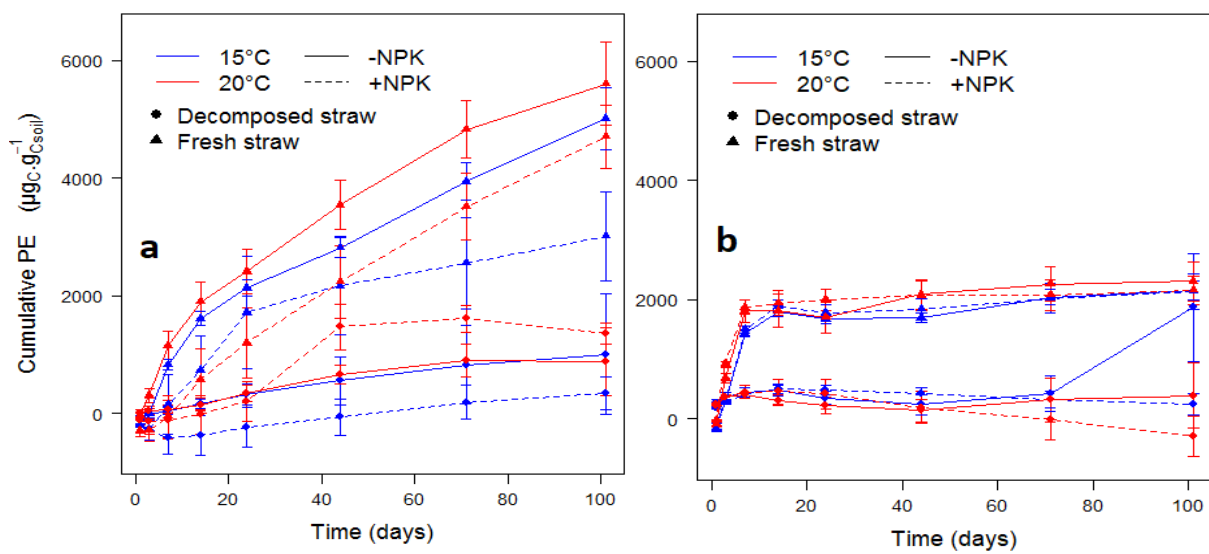
325

326 *Interactions between treatments*

327 Statistical analysis performed on the entire dataset (Table 2) revealed strong ($p < 0.001$)
 328 interactions, only between soil and other factors, as discussed below.

329

330



331

332 **Figure 2.** Changes of cumulative priming effect (PE) for different straw residues (fresh or
 333 decomposed), temperature and nutrient treatments with the incubation time. Means \pm 1SD
 334 ($n = 4$) are shown. Letter **a** is for agricultural soil, and **b** for forest soil.

335

336 **Discussion**

337

338 *Effect of the biodegradability of added OM*

339 Consistently with our hypothesis about the PE theory, the quality of the organic material
340 brought has strongly impacted the mineralization of the different types of organic matter.
341 First, once incorporated into the soil, the straw itself was mineralized 3 to 8 times more
342 when it was fresh rather than pre-decomposed ([Figure 1 c, d](#)), which reflects a higher
343 availability to microbial decomposers, *i.e.* a better biodegradability. In other words, this
344 confirms that the pre-decomposition stage decreased the biodegradability of the original
345 plant material compounds. Obviously, this large difference in degradability affected total
346 mineralization. It also affected the mineralization of SOM, *i.e.* PE. Indeed, by providing
347 substrates more easily accessible to soil microorganisms, fresh straw induced a higher
348 mineralization of the SOM compared to that induced by pre-decomposed straw and control
349 without input, particularly on the agricultural soil. The first hypothesis of this study – namely
350 that the addition of fresh wheat straw would stimulate PE to a greater extent than the
351 addition of pre-decomposed wheat straw – was validated, regardless of the treatment
352 combination. Our results are in total accordance with those of [Beghin-Tanneau et al. \(2019\)](#)
353 and [Lerch et al. \(2019\)](#), who observed, in a 6-month and a 3-year experiment respectively,
354 that a positive PE on SOM mineralization was only observed when adding undigested plant
355 residues. This underpins that an avenue for increasing soil C stocks in cultivated soils might
356 be to add decomposed straw residues rather than incorporating them fresh. We
357 acknowledge that > 70% of the straw C was lost during its pre-decomposition stage, which
358 might negatively impact the overall C balance. However, for a given land use, this loss is
359 compensated in field conditions by the CO₂ fixation during growth. It is also important to
360 note that the C lost during the pre-decomposition process is recently fixed in the contrary of
361 the C primed, which is older and stabilized for years ([Fontaine et al., 2007](#)).

362 The higher PE following the FOM input relative to the DeOM input is most likely associated
363 with the stimulation of microbial activity due to higher biodegradability, i.e. to more readily
364 available C and energy source in the FOM (Fang et al., 2018). It has been suggested that
365 microbial activity in soil is often constrained by the large investment in enzymes that
366 microbial communities must make in order to acquire nutrients and energy from
367 heterogeneous soil organic matter (Fontaine et al., 2003; Moorhead & Sinsabaugh, 2006;
368 Chen et al., 2014) and that the addition of FOM provides the energy necessary to make such
369 an investment (Kuzyakov et al., 2000; Fontaine et al., 2003; Blagodatskaya & Kuzyakov,
370 2008). It should be noted that the PE was much lower in the forest soil, suggesting that
371 microbial communities were less energy/C limited in this soil. This is at odds with the basal
372 respiration data from both soils, which is higher per unit organic C in the agricultural soil
373 (Figure 1). Generally, the respiration per unit organic C is considered to be an indicator of the
374 decomposability of the OM (Lomander et al., 1998). This suggests that the energy
375 perspective alone cannot explain the differences in PEs observed.

376 The OM content of the forest soil was higher than that of the agricultural soil and several
377 other studies have found that the PE is negatively related to the OM content of soil
378 (Paterson & Sim, 2013; Zimmerman et al., 2011). The reason for such relation is not clear
379 but, as contact between decomposers, or their enzymes, and OM is a requirement for
380 decomposition (Dignac et al., 2017), one possible explanation is that the average distance
381 between OM and decomposers is higher in soils with low OM contents, and that the energy
382 provided by the addition of FOM allows microbial communities to explore (e.g. through
383 fungal growth) the soil volume to a greater extent, which increases their access to OM and
384 the subsequent PE (Salomé et al., 2010).

385

386 *Temperature effect*

387 The temperature is known to be one of the principal controllers of decomposition process
388 (Yuste et al., 2007; Gregorich et al., 2016). Here, the increase of 5°C led to a strong increase
389 in the total carbon (SOM + added OM) mineralization rate. More specifically, the isotopic
390 labelling clearly showed that the mineralization of the C contained in the SOM increased
391 with the increase in temperature. We noted a tremendous average increase of 40% in
392 carbon emissions from SOM between 15 and 20°C during these 101 days. This is consistent
393 with the Arrhenius law (Arrhenius, 1889) that implies that the temperature sensitivity of
394 decomposition increases with the stability of organic compounds (Lefèvre et al., 2014), due
395 to higher activation energies for stabilised substrates than for labile ones (Lützwow & Kögel-
396 Knabner, 2009). This result is in accordance with many other incubation studies (Kirschbaum,
397 1995, 2006; Davidson & Janssens, 2006; Conant et al., 2008, 2011; Lützwow & Kögel-Knabner,
398 2009; Craine et al., 2010; Lefèvre et al., 2014). It confirms that a positive feedback to global
399 warming could occur through this mechanism. This feedback could be compensated by the
400 effect of the increase in T°C and CO₂ on primary production, but probably only in a partial
401 way (Lloyd & Taylor, 1994; Schimel et al., 1994; Fierer et al., 2005; Davidson & Janssens,
402 2006; Kirschbaum, 2006; Heimann & Reichstein, 2008; Vestergård et al., 2016).

403 Notwithstanding this high temperature sensitivity of SOM mineralization, the magnitude of
404 the PE here remained relatively unaffected by the increase in temperature. This result is in
405 contrast to what was found in some studies (increase in PE with temperature, see Thiessen
406 et al., 2013; Li et al., 2017; Yanni et al., 2017; decrease in PE with temperature, see Frøseth &
407 Bleken, 2015; Yanni et al., 2017; decrease and increase, see Lenka et al., 2019). However,

408 others have also found that temperature does not affect PE (Ghee et al., 2013) even during a
409 long-term warming experiment (Vestergård et al., 2016), but without deep mechanistic
410 explanation. As PE is a stimulation of the decomposition of SOM that is relatively stable, an
411 increase in PE with temperature could indeed be expected, but it was not the case here. This
412 could be probably due to the fact that the decomposition of the added OM was only slightly
413 affected by temperature whereas the decomposition of SOM was highly affected (Figure 1 c,
414 d, e, f). Indeed, still in accordance with Arrhenius equation, this increase of temperature
415 from 15 to 20°C affected the mineralization of wheat straw residues (added OM, Figure1 c,
416 d) but in a very lesser extent, and the DeOM seemed to be 3.3 times more sensitive than the
417 fresh one. This result further tends to confirm the idea that our pre-decomposing phase
418 made straw residues more biochemically recalcitrant. Indeed, the temperature sensitivity of
419 mineralization was quite similar for the DeOM and for the SOM (+44% & +38% respectively,
420 between 15 and 20°C), while for the FOM it was *ca.* 4 times lower with only a +9.5%
421 increase. However, although this difference in sensitivity of the two types of residues is very
422 clear, this corresponds to a quantitatively similar increase in C emitted - but which remains
423 very small compared to the effect on SOM. As a result, the release of energy from the two
424 quality types of added OM was similar at both temperatures and was quantitatively very
425 small relative to the mineralization of SOM, which could lead to the absence of effect of
426 temperature on PE in controlled conditions. Yet, temperature could have indirect impacts
427 through the effect on soil water content (Miller & Johnson, 1964; Cassman & Munns, 1980;
428 Linn & Doran, 1984; Skopp et al., 1990; Weier et al., 1993; Cambardella, 2005; Rey et al.,
429 2005; Sun et al., 2016) and become therefore, most likely, ecologically significant.

431 *Nutrient-addition effect*

432 For the mineralization of all types of OM, the addition of mineral nutrients had significant
433 effect but much lower than the effect of temperature and type of OM added. When it was
434 statistically significant, it decreased PE in this study, as often found ([Kuzyakov et al., 2000](#);
435 [Chen et al., 2014](#); [Dimassi et al., 2014](#)). The PE response to the availability of mineral
436 nutrients could be explained by a reduction in the need of mineral nutrient mining within
437 SOM for microbial communities. Here however, the addition of mineral nutrients also
438 decreased the total mineralization, the mineralization of SOM and of the added OM,
439 particularly in the agricultural soil ([Figure 1](#)). As suggested by [Spohn et al. \(2016\)](#), this may be
440 due to changes in the intracellular partitioning of C within the microbial communities, with
441 an increased C allocation to biomass and a decreased allocation to respiration when
442 nutrients are readily available.

443

444 *Interactions*

445 This fully cross-factorial design with four factors allowed us to test simple effects as we
446 previously discussed, but also and mostly the interactions between them. Surprisingly, from
447 the ecological point of view, the land use was the only factor (*i.e.* soil) with which
448 interactions have been established, no other significant interactions were found among
449 factors. By the same, except for land use (discussed at the end of discussion), the impacts of
450 the various global change factors tested here appear to simply add up, with no particular
451 amplification or attenuation effect.

452

453 *Soil effects & interactions*

454 Agricultural and forest soils differ by several aspects such as OM type, microbial & fungal
455 communities, dynamics of OM inputs and outputs, exposition to climatic & anthropic
456 disturbances (Guo & Gifford, 2002; Foley et al., 2005). This led to three main differences
457 noticed here between soil responses: 1) all effects observed on the forest soil were very
458 limited compared to the agricultural one; 2) the forest soil C concentration was 2 times
459 higher than the agricultural soil while it was the reverse for the PE by g of soil C. In fact, we
460 found that the PE was realized more efficiently on soil A than F: to over-mineralize 1 C unit
461 from SOM via PE, 5.4 C units were needed to be mineralized from the added OM (FOM and
462 DeOM) in soil A while 8.1 C units were needed in soil F. 3) Finally, the kinetics of PE induced
463 by FOM addition had very different shapes (Figure 2), with an early threshold reached after 7
464 days on soil F whereas PE stayed relatively high and persisted throughout the duration of the
465 incubation on soil A.

466 With the support of literature, we could hypothesize that the difference of behaviour
467 between soil A and soil F is the result of a combination of factors such as pH (Hung & Trappe,
468 1983; Bottner et al., 1998; Walse et al., 1998; Leifeld, 2005), tannin content of SOM (Kraus et
469 al., 2003), total organic C content (Zimmerman et al., 2011; Paterson & Sim, 2013), C
470 contents in microbial biomass (Blagodatskaya & Kuzyakov, 2008), evolution (by different
471 selection pressures between soils), quality of SOM and bacteria/fungi ratio (Fontaine et al.,
472 2011; Terrer et al., 2016; Lonardo et al., 2017). Among all these possibilities, the most
473 influential could be related to the differences in C contained in the microbial biomass (C_{mic})
474 of the two soils. According to Blagodatskaya & Kuzyakov (2008), if our FOM-C input was
475 greater than the C_{mic} of soil A but less than or equal to C_{mic} of soil F, then this abrupt

476 cessation of PE after 7 days on soil F could be the result of a simple apparent PE. In this case,
477 the supplied FOM-C would only have served to renew the C_{mic} . This C_{mic} having the isotopic
478 signature of the soil, the CO_2 resulting from its mineralization would be read as PE, but
479 without being derived from the over-mineralization of the SOM.

480 Despite all the differences noticed between results obtained on these two soils, general
481 mineralization patterns were similar for the two soils and underpin a certain robustness of
482 our results. Particularly, our main hypothesis was validated on both soils: the quality of the
483 organic matter brought in the form of fresh or pre-decomposed straw residues led to very
484 significant differences in the intensity of the induced PE. This further supports that the
485 quality of added OM inducing the PE process is a major factor to take into account for SOC
486 dynamics. In addition, these 2 soils are both luvisols with *ca.* the same clay/silt/sand ratio,
487 and initially only differ by their land-use, established about two centuries ago. This
488 particularity allows us to notice that, at the end of these past 200 years, the agricultural soil
489 has a 2.19 times lower SOC content than the forest soil - which could be considered here as
490 the reference system. In other words, this means that, depending of the land-use (such as
491 deforestation for farmland establishment) and agricultural practices (as input of highly
492 degradable FOM), soils can become a significant source of CO_2 by the mineralization of large
493 amount of stable C ([Guenet et al., 2012](#); [Chen et al., 2015](#)). Yet it also means that with better
494 understandings and practices, this agricultural soil has the potential to store – at least – 2.19
495 times more C ([Chenu et al., 2018](#)), as its forest counterpart and neighbour.

496 To summarise, in the conditions of the present study, we were able to test the impacts of
497 several factors and their combinations on the mineralization of different pools of organic
498 matter and PE. The land use appeared to have strong interactions with all other factors, but

499 surprisingly, no relevant interactions were noticed between the other factors, and this for
500 the mineralization of all OM pools (total, SOM, added OM and PE). Obviously, as only two
501 soils were used in this study, these results could not be neither generalized nor considered
502 as representative of all agricultural and forest soils functioning. Nonetheless, they suggest
503 that the land use – and their associated plant residues management – is, among the factors
504 we tested here, the most influential factor for SOM mineralization. Indeed, the addition of
505 fresh OM induced a large PE whereas the addition of pre-decomposed OM led to no
506 significant effect, *i.e.* the biodegradability of added OM was the most determinant factor far
507 ahead the temperature and nutrients availability. Consistent with the concept of PE, this
508 suggests that the biodegradability of the OM provided is a key element to consider with
509 regard to the storage-loss dynamics of SOC, and so, of SOM. Furthermore, as suggested by
510 its stability in time within each soil, PE seemed to be very dependent on the bio-available C.
511 While the increase in temperature strongly impacted the basal mineralization of the soils –
512 which confirms the worrisome positive feedback on global warming, no significant effect was
513 detected on PE itself. However, an indirect sensitivity of PE to temperature was observed
514 through the temperature sensitivity of the added OM mineralization. In addition, the
515 comparison of the two land-uses from 200 years allows us to imagine the potential of C re-
516 stocking or de-stocking, depending on practices, for instance through initiative such as 4 per
517 1000, and by taking the PE into account, in addition to other direct practice impacts such as
518 tillage ([Six et al., 2002](#); [Haddaway et al., 2017](#)), OM export ([Wang et al., 2020](#)), or both ([Virto](#)
519 [et al., 2012](#); [Zang et al., 2019](#); [Dhaliwal et al., 2020](#)).

520 Finally, in our study, the effect of land use through the management of crop residues
521 appeared to induce the greatest impact on the PE, to the point of rendering the expected

522 responses to the stoichiometry and temperature negligible. The level of easily available
523 energy contained in amendments (*i.e.* OM biodegradability) have to be highly monitored for
524 the sustainability and crop production, in order to prevent C losses and optimise ecosystemic
525 soil services, as long-term C storage and fertility. Further studies are needed to assess the
526 importance of the factors tested here under more realistic conditions – up to *in situ* field
527 experiment, and also to test the response of PE with plant residues from other crop species
528 and other pre-decomposition and composting methods. These results show the importance
529 of paying particular attention to these issues in our critical context of global change and lack
530 of sustainability of agricultural practices.

531

532 **Acknowledgments:**

533 We are grateful to Valérie Pouteau for her contribution to the analyses, to Thomas Lerch for
534 his contribution to the experimental protocol, and to Pauline Pierret for her contribution to
535 figures. RG received financial support from the Sustainable Development Research Network
536 of the Region-Ile-de-France (grant R2DS 2014-03). All authors designed the experimental
537 protocol and contributed substantially to the paper. RG performed the experiment, helped
538 by CG, and RG wrote the first full draft of the paper. XR, NN, BG and RG performed statistical
539 analyses and created figures. Authors declare no competing interests. Correspondence and
540 requests for materials should be addressed to LA.

541

542 **Bibliography**

543 Arrhenius, S., 1896. On the influence of carbonic acid in the air upon the temperature of the
544 ground. The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science
545 41, 237–276.

546 Bardgett, R. D., Freeman, C., & Ostle, N. J., 2008. Microbial contributions to climate change
547 through carbon cycle feedbacks. *The ISME Journal* 2, 805–814.

548 Barré, P., Durand, H., Chenu, C., Meunier, P., Montagne, D., Castel, G., Billiou, D.,
549 Soucémarianadin, L., & Cécillon, L., 2017. Geological control of soil organic carbon and
550 nitrogen stocks at the landscape scale. *Geoderma* 285, 50–56.

551 Baveye, P. C., Berthelin, J., Tessier, D., & Lemaire, G. 2018. The "4 per 1000" initiative: A
552 credibility issue for the soil science community? *Geoderma* 309, 118–123.

553 Beghin-Tanneau, R., Guerin, F., Guiresse, M., Kleiber, D., & Scheiner, J. D., 2019. Carbon
554 sequestration in soil amended with anaerobic digested matter. *Soil & Tillage Research* 192,
555 87-94.

556 Bingeman, C. W., 1953. The effect of the addition of organic materials on the decomposition
557 of an organic soil. *Soil Science Society of America Proceedings* 29, 692–696.

558 Birch, H. F., 1958. The effect of soil drying on humus decomposition and nitrogen availability.
559 *Plant and Soil* 10, 9-31.

560 Blagodatskaya, E., & Kuzyakov, Y., 2008. Mechanisms of real and apparent priming effects
561 and their dependence on soil microbial biomass and community structure: Critical review.
562 *Biology and Fertility of Soils* 45, 115–131.

- 563 Bottner, P., Austrui, F., Cortez, J., Billès, G., & Coûteaux, M. M., 1998. Decomposition of ¹⁴C-
564 and ¹⁵N-labelled plant material, under controlled conditions, in coniferous forest soils from a
565 north-south climatic sequence in western Europe. *Soil Biology & Biochemistry* 30, 597–610.
- 566 Cambardella, C. A., 2005. Formation and Decomposition. In: Hillel, D. (Ed), *Encyclopedia of*
567 *Soils in the Environment*, Academic Press 170–175.
- 568 Cassman, K. G., & Munns, D. N., 1980. Nitrogen mineralization as affected by soil moisture,
569 temperature and depth. *Soil Science Society of America Journal* 44, 1233–1237.
- 570 Chemidlin Prévost-Bouré, N., Soudani, K., Damesin, C., Berveiller, D., Lata, J. C., & Dufrêne,
571 E., 2010. Increase in aboveground fresh litter quantity over-stimulates soil respiration in a
572 temperate deciduous forest. *Applied Soil Ecology* 46, 26–34.
- 573 Chen, L., Liu, L., Qin, S., Yang, G., Fang, K., Zhu, B., Kuzyakov, Y., Chen, P., Xu, Y., & Yang, Y.,
574 2019. Regulation of priming effect by soil organic matter stability over a broad geographic
575 scale. *Nature Communications* 10, 5112.
- 576 Chen, R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X., Blagodatskaya, E.,
577 & Kuzyakov, Y., 2014. Soil C and N availability determine the priming effect: Microbial N
578 mining and stoichiometric decomposition theories. *Global Change Biology* 20, 2356–2367.
- 579 Chen, S., Wang, Y., Hu, Z., & Gao, H., 2015. CO₂ emissions from a forest soil as influenced by
580 amendments of different crop straws: Implications for priming effects. *Catena* 131, 56–63.
- 581 Chenu, C., Angers, D. A., Barré, P., Derrien, D., Arrouays, D., & Balesdent, J., 2018. Increasing
582 organic stocks in agricultural soils: Knowledge gaps and potential innovations. *Soil & Tillage*
583 *Research* 188, 41-52.

584 Conant, R. T., Ryan, M. G., Ågren, G. I., Birge, H. E., Davidson, E. A., Eliasson, P. E., Evans, S.
585 E., Frey, S. D., Giardina, C. P., Hopkins, F. M., Hyvönen, R., Kirschbaum, M. U. F., Lavelle, J.
586 M., Leifeld, J., Parton, W. J., Megan Steinweg, J., Wallenstein, M. D., Martin Wetterstedt, J.
587 Å., & Bradford, M. A., 2011. Temperature and soil organic matter decomposition rates –
588 synthesis of current knowledge and a way forward. *Global Change Biology* 17, 3392–3404.

589 Conant, R. T., Steinweg, J. M., Haddix, M. L., Paul, E. A., Plante, A. F. and Six, J., 2008.
590 Experimental warming shows that decomposition temperature sensitivity increases with soil
591 organic matter recalcitrance. *Ecology* 89, 2384–2391.

592 Craine, J. M., Fierer, N., & Mclauchlan, K. K., 2010. Widespread coupling between the rate
593 and temperature sensitivity of organic matter decay. *Nature Geoscience* 3, 854–857.

594 Davidson, E. A., & Janssens, I. A., 2006. Temperature sensitivity of soil carbon decomposition
595 and feedbacks to climate change. *Nature* 440, 165-173.

596 Dhaliwal, S. S., Naresh, R. K., Gupta, R. K., Panwar, A. S., Mahajan, N. C., Singh, R., & Mandal,
597 A., 2020. Effect of tillage and straw return on carbon footprints, soil organic carbon fractions
598 and soil microbial community in different textured soils under rice–wheat rotation: a review.
599 *Reviews in Environmental Science and Biotechnology* 19, 103-115.

600 Dignac, M. F., Derrien, D., Barré, P., Barot, S., Cécillon, L., Chenu, C., Chevallier, T., Freschet,
601 G. T., Garnier, P., Guenet, B., Hedde, M., Klumpp, K., Lashermes, G., Maron, P. A., Nunan, N.,
602 Roumet, C. & Basile-Doelsch, I., 2017. Increasing soil carbon storage: mechanisms, effects of
603 agricultural practices and proxies. A review. *Agronomy for Sustainable Development* 37(2),
604 14.

- 605 Dijkstra, F. A., Carrillo, Y., Pendall, E., & Morgan, J. A., 2013. Rhizosphere priming: a nutrient
606 perspective. *Frontiers in Microbiology* 4, 216.
- 607 Dimassi, B., Mary, B., Fontaine, F., Perveen, N., Revaillet, S., & Cohan, J. P., 2014. Effect of
608 nutrients availability and long-term tillage on priming effect and soil C mineralization. *Soil*
609 *Biology and Biochemistry* 78, 332–339.
- 610 Fang, Y., Nazaries, L., Singh, B. K., & Singh, B. P., 2018. Microbial mechanisms of carbon
611 priming effects revealed during the interaction of crop residue and nutrient inputs in
612 contrasting soils. *Global Change Biology* 24, 2775–2790.
- 613 Fierer, N., Bradford, M. A., & Jackson, R. B., 2007. Toward an ecological classification of soil
614 bacteria. *Ecology* 88, 1354–1364.
- 615 Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Stuart Chapin, F.,
616 Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C.
617 J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K., 2005. Global
618 consequences of land use. *Science* 309, 570–575.
- 619 Fontaine, S., Mariotti, A., & Abbadie, L., 2003. The priming effect of organic matter: a
620 question of microbial competition? *Soil Biology and Biochemistry* 35, 837-843.
- 621 Fontaine, S., Bardoux, G., Abbadie L., & Mariotti, A., 2004. Carbon input to soil may decrease
622 soil carbon content. *Ecology Letters* 7, 314-320.
- 623 Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel., C., 2007. Stability of organic
624 carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450, 277-280.

625 Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J. M. G., Maire, V., Mary, B., Revallot,
626 S., & Maron, P. A., 2011. Fungi mediate long term sequestration of carbon and nitrogen in
627 soil through their priming effect. *Soil Biology and Biochemistry* 43, 86–96.

628 Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S.,
629 Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W.,
630 Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.,
631 Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., & Zeng, N., 2006. Climate–carbon
632 cycle feedback analysis: results from the C4MIP model intercomparison. *Journal of climate*
633 19, 3337–3353.

634 Frøseth, R. B., & Bleken, M. A., 2015. Effect of low temperature and soil type on the
635 decomposition rate of soil organic carbon and clover leaves, and related priming effect. *Soil*
636 *Biology and Biochemistry* 80, 156–166.

637 Ghee, C., Neilson, R., Hallett, P. D., Robinson, D., & Paterson, E., 2013. Priming of soil organic
638 matter mineralisation is intrinsically insensitive to temperature. *Soil Biology and*
639 *Biochemistry* 66, 20–28.

640 Gregorich, E. G., Janzen, H., Ellert, B. H., Helgason, B. L., Qian, B., Zebarth, B. J., Angers, D. A.,
641 Beyaert, R. P., Drury, C. F., Duguid, S. D., May, W. E., McConkey, B. G. and Dyck, M. F., 2017.
642 Litter decay controlled by temperature, not soil properties, affecting future soil carbon.
643 *Global Change Biology* 23, 1725-1734.

644 Guenet, B., Juarez, S., Bardoux, G., Abbadie, L., & Chenu, C., 2012. Evidence that stable C is
645 as vulnerable to priming effect as is more labile C in soil. *Soil Biology and Biochemistry* 52,
646 43-48.

- 647 Guenet, B., Camino-Serrano, M., Ciais, P., Tifafi, M., Maignan, F., Soong, J. L., & Janssens, I.
648 A., 2018. Impact of priming on global soil carbon stocks. *Global Change Biology* 24, 1873-
649 1883.
- 650 Guo, L. B., & Gifford, R. M., 2002. Soil carbon stocks and land use change: a meta-analysis.
651 *Global Change Biology* 8, 345–360.
- 652 Haddaway, N. R., Hedlund, K., Jackson, L. E., Kätterer, T., Lugarto, E., Thomsen, I. K.,
653 Jorgensen, H. B., & Isberg, P. E., 2017. How does tillage intensity affect soil organic carbon? A
654 systematic review. *Environmental Evidence* 6, 30.
- 655 He, Y., Trumbore, S. E., Torn, M. S., Harden, J. W., Vaughn, L. J. S., Allison, S. D., & Randerson,
656 J. T., 2016. Radiocarbon constraints imply reduced carbon uptake by soils during the 21st
657 century. *Science* 1419–1424.
- 658 Heimann, M., & Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate
659 feedbacks. *Nature* 451, 289–292.
- 660 Hung, L., & Trappe, J. M., 1983. Growth variation between and within species of
661 ectomycorrhizal fungi in response to pH in vitro. *Mycologia* 75, 234-241.
- 662 Jobbágy, E. G., & Jackson, R. B., 2000. The vertical distribution of soil organic carbon and its
663 relation to climate and vegetation. *Ecological Applications* 10(2), 423–436.
- 664 Johnson, D., Leake, J. R., Ostle, N., Ineson, P., & Read, D. J., 2002. In situ ¹³CO₂ pulse-labelling
665 of upland grassland demonstrates a rapid pathway of carbon flux from arbuscular
666 mycorrhizal mycelia to the soil. *New Phytologist* 153, 327–334.

667 Kirschbaum, M. U. F., 1995. The temperature dependence of organic-matter decomposition
668 and the effect of global warming on soil organic C storage. *Soil Biology & Biochemistry* 27,
669 753–760.

670 Kirschbaum, M. U. F., 2006. The temperature dependence of organic-matter decomposition
671 — still a topic of debate. *Soil Biology & Biochemistry* 38, 2510–2518.

672 Kraus, T. E. C., Dahlgren, R. A., & Zasoski, R. J., 2003. Tannins in nutrient dynamics of forest
673 ecosystems - a review. *Plant and Soil* 256, 41–66.

674 Kuzyakov, Y., Friedel, J. K., & Stahr, K., 2000. Review of mechanisms and quantification of
675 priming effects. *Soil Biology & Biochemistry* 32, 1485–1498.

676 Kuzyakov, Y., 2010. Priming effects: Interactions between living and dead organic matter.
677 *Soil Biology and Biochemistry* 42, 1363–1371.

678 Lauber, C. L., Zhou, N., Gordon, J. I., Knight, R., & Fierer, N., 2010. Effect of storage
679 conditions on the assessment of bacterial community structure in soil and human-associated
680 samples. *FEMS Microbiology Letters* 307, 80–86.

681 Lefèvre, R., Barré, P., Moyano, F. E., Christensen, B. T., Bardoux, G., Eglin, T., Girardin, C.,
682 Houot, S., Kätterer, T., van Oort, F., & Chenu, C., 2014. Higher temperature sensitivity for
683 stable than for labile soil organic carbon – Evidence from incubations of long-term bare
684 fallow soils. *Global Change Biology* 20, 633–640.

685 Leifeld, J., 2005. Interactive comment on “On the available evidence for the temperature
686 dependence of soil organic carbon” by W. Knorr et al. *Biogeosciences Discussions* 2, 348–
687 352.

- 688 Lenka, S., Trivedi, P., Singh, B., Pendall, E., Bass, A., & Lenka, N.K., 2019. Effect of crop
689 residue addition on soil organic carbon priming as influenced by temperature and soil
690 properties. *Geoderma* 347, 70-79.
- 691 Lerch, T. Z., Dignac, M. F., Thevenot, M., Mchergui, C., & Houot, S., 2019. Chemical changes
692 during composting of plant residues reduce their mineralisation in soil and cancel the
693 priming effect. *Soil Biology and Biochemistry* 136, 107525.
- 694 Li, Q., Tian, Y., Zhang, X., Xu, X., Wang, H., & Kuzyakov, Y., 2017. Labile carbon and nitrogen
695 additions affect soil organic matter decomposition more strongly than temperature. *Applied*
696 *Soil Ecology* 114, 152–160.
- 697 Linn, D. M., & Doran, J. W., 1984. Effect of water-filled pore space on carbon dioxide and
698 nitrous oxide production in tilled and nontilled soils. *Soil Science Society America Journal* 48,
699 1267–1272.
- 700 Liu, C., Lu, M., Cui, J., Li, B., & Fang, C., 2014. Effects of straw carbon input on carbon
701 dynamics in agricultural soils: a meta-analysis. *Global Change Biology* 20, 1366–1381.
- 702 Liu, W., Qiao, C., Yang, S., Bai, W., & Liu, L., 2018. Microbial carbon use efficiency and
703 priming effect regulate soil carbon storage under nitrogen deposition by slowing soil organic
704 matter decomposition. *Geoderma* 332, 37-44.
- 705 Lloyd, J., & Taylor, J. A., 1994. On the temperature dependence of soil respiration. *Functional*
706 *Ecology* 8, 315–323.
- 707 Löhnis, F., 1926. Nitrogen availability of green manures. *Soil Science* 22, 253-290.

708 Lomander, A., Kätterer, T., & Andren, O., 1998. Carbon dioxide evolution from top- and
709 subsoil as affected by moisture and constant and fluctuating temperature. *Soil Biology &*
710 *Biochemistry* 30, 2017–2022.

711 Lonardo Di, D. P., De Boer, W., Klein Gunnewiek, P. J. A., Hannula, S. E., & Van der Wall, A.,
712 2017. Priming of soil organic matter: Chemical structure of added compounds is more
713 important than the energy content. *Soil Biology and Biochemistry* 108, 41–54.

714 Luo, Z., Wang, E., & Sun, O. J., 2016. A meta-analysis of the temporal dynamics of priming
715 soil carbon decomposition by fresh carbon inputs across ecosystems. *Soil Biology and*
716 *Biochemistry* 101, 96-103.

717 Lützow, M. Von, & Kögel-knabner, I., 2009. Temperature sensitivity of soil organic matter
718 decomposition — what do we know? *Biology and Fertility of Soils* 46, 1-15.

719 Mary, B., Mariotti, A., & Morel, J. L., 1992. Use of ¹³C variations at natural abundance for
720 studying the biodegradation of root mucilage, roots and glucose in soil. *Soil Biology &*
721 *Biochemistry* 24, 1065–1072.

722 Mason-Jones, K., Schmöcker, N., & Kuzyakov, Y., 2018. Contrasting effects of organic and
723 mineral nitrogen challenge the N-Mining Hypothesis for soil organic matter priming. *Soil*
724 *Biology and Biochemistry* 12, .38–46.

725 Miller, R. D., & Johnson, D. D., 1964. The effect of soil moisture tension on carbon dioxide
726 evolution, nitrification, and nitrogen mineralization. *Soil Science Society of America Journal*
727 28, 644-647.

- 728 Minasny, B., Malone, B. P., McBratney, A. B., Angers, D. A., Arrouays, D., Chambers, A.,
729 Chaplot, V., Chen Z. S., Cheng, K., Das, B. S., Field, D. J., Gimona, A., Hedley, C. B., Hong, S. Y.,
730 Mandal, B., Marchant, B. P., Martin, M., McConkey, B. G., Mulder, V. L., O'Rourke, S., Richer-
731 de-Forges, A. C., Odeh, I., Padarian, J., Paustian, K., Pan, G., Poggio, L., Savin, I., Stolbovoy, V.,
732 Stockmann, U., Sulaeman, Y., Tsui, C. C., Vågen, T. G., van Wesemael, B., & Winowiecki, L.,
733 2017. Soil carbon 4 per mille. *Geoderma* 292, 59–86.
- 734 Moorhead, D. L., & Sinsabaugh, R. L., 2006. A Theoretical model of litter decay & microbial
735 interaction. *Ecological Monographs* 76, 151–174.
- 736 Paterson, E., & Sim, A., 2013. Soil-specific response functions of organic matter
737 mineralization to the availability of labile carbon. *Global change biology* 19, 1562–71.
- 738 Perveen, N., Barot, S., Maire, V., Cotrufo, M. F., Shahzad, T., Blagodatskaya, E. R., Stewart, C.
739 E., Ding, W., Siddiq, M. R., Dimassi, B., Mary, B. & Fontaine, S., 2019. Universality of priming
740 effect: An analysis using thirty-five soils with contrasted properties sampled from five
741 continents. *Soil Biology and Biochemistry* 134, 162-171.
- 742 Rey, A., Petsikos, C., Jarvis, P. G. & Grace, J., 2005. Effect of temperature and moisture on
743 rates of carbon mineralization in a Mediterranean oak forest soil under controlled and field
744 conditions. *European Journal of Soil Science* 56, 589–599.
- 745 Salomé, C., Nunan, N., Pouteau, V., Lerch, T. Z. & Chenu, C., 2010. Carbon dynamics in topsoil
746 and in subsoil may be controlled by different regulatory mechanisms. *Global Change Biology*
747 16, 416–426.

- 748 Schimel, D. S., Braswell, B. H., Holland, E. A., McKeown, R., Ojima, D. S., Painter, T. H., Parton,
749 W. J., & Townsend, A. R., 1994. Climatic, edaphic, and biotic controls over storage and
750 turnover in soils. *Global Biogeochemical Cycles* 8, 279–293.
- 751 Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A.,
752 Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P.,
753 Weiner, S., & Trumbore, S. E., 2011. Persistence of soil organic matter as an ecosystem
754 property. *Nature* 478, 49–56.
- 755 Shahzad, T., Chenu, C., Repinçay, C., Mougin, C., Ollier, J. L., & Fontaine, S., 2012. Plant
756 clipping decelerates the mineralization of recalcitrant soil organic matter under multiple
757 grassland species. *Soil Biology and Biochemistry* 51, 3–80.
- 758 Six, J., Feller, C., Denef, K., Ogie, S. M., De Moraes Sa, J. C., & Albrecht, A., 2002. Soil organic
759 matter, biota and aggregation in temperate and tropical soils - Effects of no-tillage.
760 *Agronomie* 22, 755-775.
- 761 Skopp, J., Jawson, M. D., & Doran, J. W., 1990. Steady-State Aerobic Microbial Activity as a
762 Function of Soil Water Content. *Soil Science Society of America Journal* 54, 1619–1625.
- 763 Spohn, M., Klaus, K., Wanek, W., & Richter, A., 2016. Soil microbial carbon use efficiency and
764 biomass turnover in a long-term fertilization experiment in a temperate grassland. *Soil*
765 *Biology and Biochemistry* 97, 168–175.
- 766 Stockmann, U., Adams, M. A., Crawford, J. W., Field, D. J., Henakaarchchi, N., Jenkins, M.,
767 Minasny, B., McBratney, A. B., de Remy de Courcelles, V., Singh, K., Wheeler, I., Abbott, L.,
768 Angers, D. A., Baldock, J., Bird, M., Brookes, P. C., Chenu, C., Jastrow, J. D., Lal, R., Lehmann,

- 769 J., O'Donnell, O. G., Parton, W. J., Whitehead D., & Zimmermann, M., 2013. The knowns,
770 known unknowns and unknowns of sequestration of soil organic carbon. *Agriculture,*
771 *Ecosystems and Environment* 164, 80–99.
- 772 Sun, J., He, F., Zhang, Z., Shao, H., & Xu, G., 2016. Temperature and moisture responses to
773 carbon mineralization in the biochar-amended saline soil. *Science of the Total Environment*
774 569–570.
- 775 Sun, Z. L., Liu, S. G., Zhang, T. A., Zhao, X. C., Chen, S., & Wang, Q. K., 2019. Priming of soil
776 organic carbon decomposition induced by exogenous organic carbon input: a meta-analysis.
777 *Plant and soil* 443, 463-471.
- 778 Terrer, C., Vicca, S., Hungate, B. A., Philipps, R. P., & Prentice, I. C., 2016. Mycorrhizal
779 association as a primary control of the fertilization effect. *Science* 353, 72–74.
- 780 Thiessen, S., Gleixner, G., Wutzler, T., & Reichstein, M., 2013. Both priming and temperature
781 sensitivity of soil organic matter decomposition depend on microbial biomass - An
782 incubation study. *Soil Biology and Biochemistry* 57, 739–748.
- 783 Tian, J., Pausch, J., Yu, G., Blagodatskaya, E. & Kuzyakov, Y., 2016. Aggregate size and glucose
784 level affect priming sources: A three- source-partitioning study. *Soil Biology and*
785 *Biochemistry* 97, 199–210.
- 786 Vestergård, M., Reinsch, S., Bengston, P., Ambus, P., & Christensen, S., 2016. Enhanced
787 priming of old, not new soil carbon at elevated atmospheric CO₂. *Soil Biology & Biochemistry*
788 100, 140–148.

789 Virto, I., Barré, P., Burlot, A., & Chenu, C., 2012. Carbon input differences as the main factor
790 explaining the variability in soil organic C storage in no-tilled compared to inversion tilled
791 agrosystems. *Biogeochemistry* 108, 17–26.

792 Walse, C., Berg, B., & Sverdrup, H., 1998. Review and synthesis of experimental data on
793 organic matter decomposition with respect to the effect of temperature, moisture, and
794 acidity. *Environmental Reviews* 6, 25-40.

795 Wang, H., Boutton, T., Xu, W., Hu, G., Jiang, P., & Bai, E., 2015. Quality of fresh organic
796 matter affects priming of soil organic matter and substrate utilization patterns of microbes.
797 *Scientific Reports* 5, 10102.

798 Wang, X., He, C., Liu, B., Zhao, X., Liu, Y., Wang, Q., & Zhang, H., 2020. Effects of residue
799 returning on soil organic carbon storage and sequestration rate in China's croplands: a meta-
800 analysis. *Agronomy* 10, 691.

801 Weier, K. L., Doran, J. W., Power, J. F. & Walters, D. T., 1993. Denitrification and the
802 dinitrogen / nitrous oxide ratio as affected by soil water, available carbon, and nitrate. *Soil*
803 *Science Society America Journal* 57, 66–72.

804 Yanni, S. F., Diochon, A., Helgason, B. L., Ellert, B. H., & Gregorich, E. G., 2017. Temperature
805 response of plant residue and soil organic matter decomposition in soil from different
806 depths. *European Journal of Soil Science* 69, 325-335.

807 Yuste, J. C., Baldocchi, D. D., Gershenson, A., Goldstein, A., Misson, L., & Wong, S., 2007.
808 Microbial soil respiration and its dependency on carbon inputs, soil temperature and
809 moisture. *Global Change Biology* 13, 2018-2035.

- 810 Zhang, Y., Li, X., Gregorich, E. G., McLaughlin, N. B., Zhang, X., Guo, Y., Gao, Y., & Liang, A.,
811 2019. Evaluating storage and pool size of soil organic carbon in degraded soils: Tillage effects
812 when crop residue is returned. *Soil and Tillage Research* 192, 215-221.
- 813 Zimmerman, A. R., Gao, B., & Ahn, M., 2011. Positive and negative carbon mineralization
814 priming effects among a variety of biochar-amended soils. *Soil Biology and Biochemistry* 43,
815 1169–1179.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: