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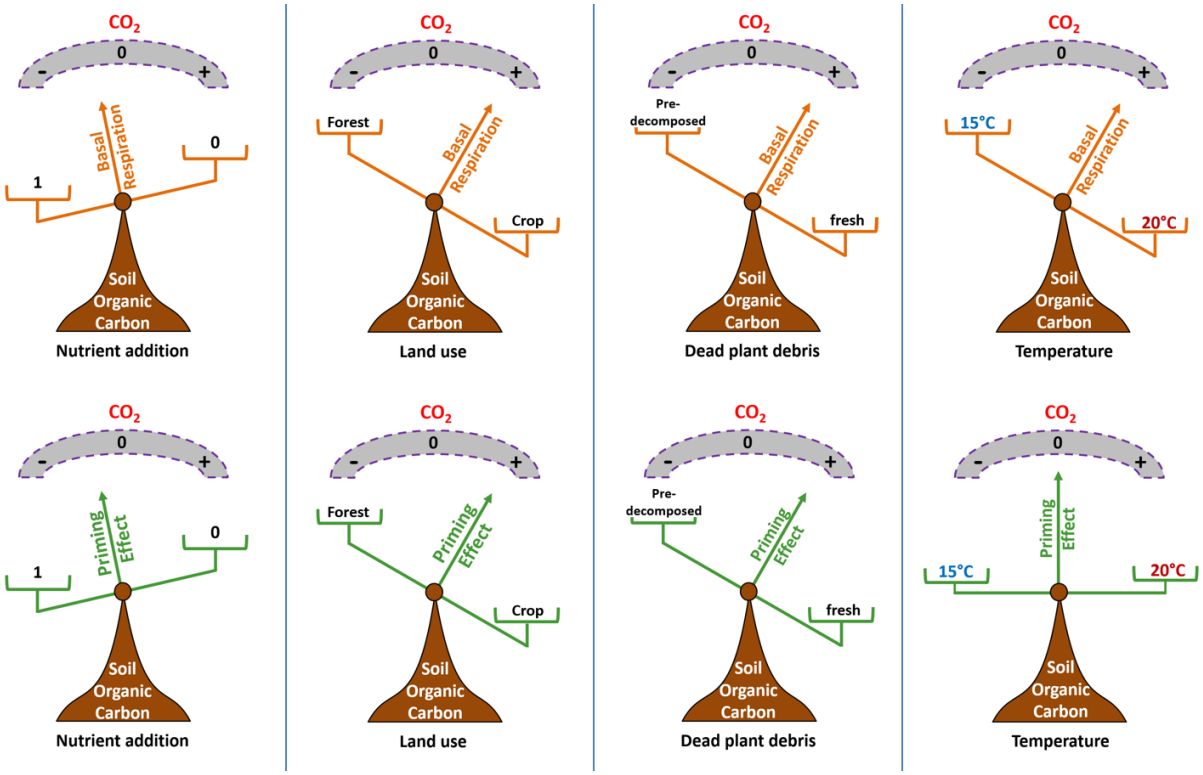
Graphical Abstract (for review)

Graphical Abstract



*Highlights (for review)

Highlight 1:
Degradability of dead plant matter determines the soil priming effect intensity

Highlight 2:
Fresh wheat straw induces 800% more CO_2 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

*Manuscript with continous line numbering
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Temperature and soil management effects on carbon fluxes and priming effect intensity

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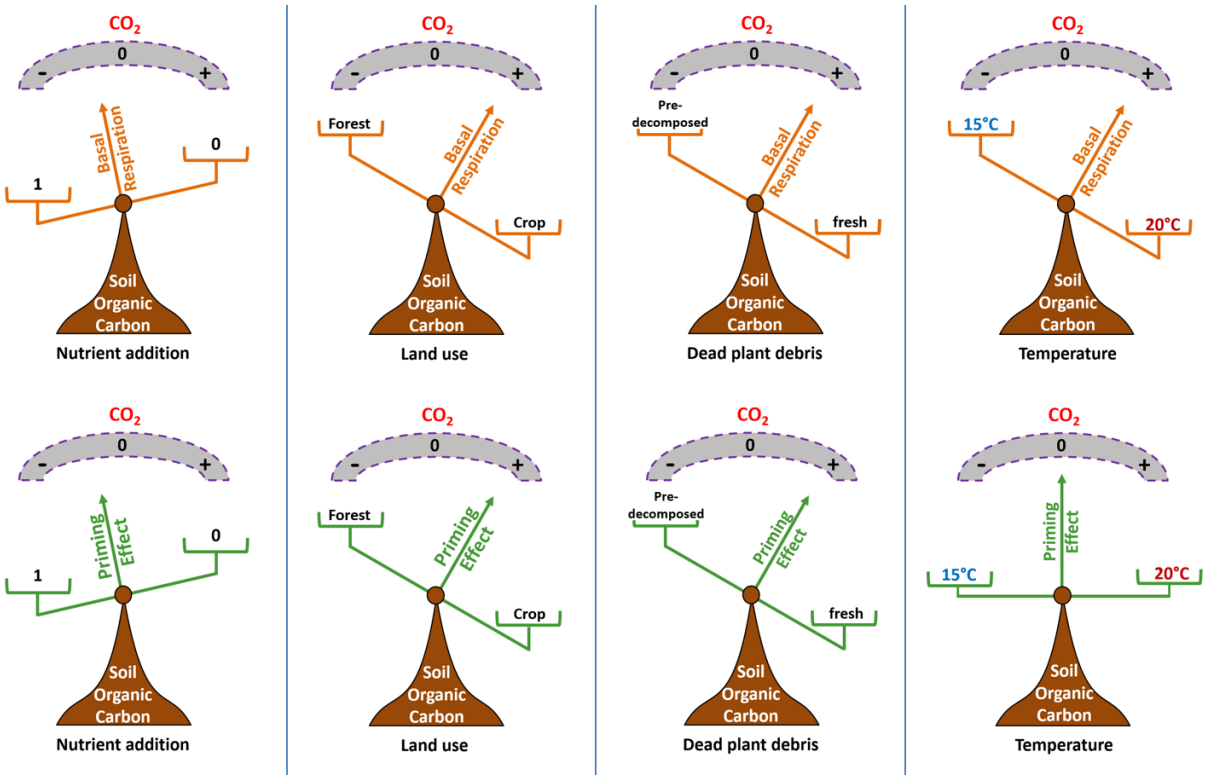
- Primary Research Article -

Graphical abstract



Keywords: global change; priming effect; agricultural practices; organic matter biodegradibility; crop *vs.* forest soils; decomposition; nutrient addition.

Abstract

Any change in the intensity and sign of CO_2 flux between soil and atmosphere is expected to have a significant impact on climate. The net emission of CO_2 by soils depends on antagonistic processes: the persistence of dead plant matter and the mineralization of soil organic matter. These two processes are partly interdependent: their interaction is known as the "priming effect" (PE), i.e. the stimulation of the mineralization of stable soil organic matter by more labile fresh organic matter.

Documenting the response of PE to global change is needed for predicting long term dynamics of ecosystems and climate change, and for managing carbon cycle in order to slow down the atmospheric CO_2 increase. We have tested the effects on PE of temperature, nutrient availability, energy content of added organic matter, land use and interactions.

Our results suggest that the biodegradability of the dead plant debris (wheat straw, fresh or pre-decomposed) is the first determinant of the intensity of PE, far ahead temperature and nutrients: fresh wheat straw addition induced up to 800% more CO_2 emission than pre-decomposed one. The raise of temperature from 15 to 20°C, increased basal soil organic matter mineralization by 38%, but had no effect on PE. Interactions between biodegradability of straw and the other factors showed that the agricultural soil was more responsive to all factors than the forest soil.

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

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

Introduction

One of today's major scientific challenges is to better understand the biological mechanisms regulating carbon (C) fluxes between the soil and the atmosphere and to determine how these fluxes impact climate change through climate-ecosystem feedback loops (Bardgett et al., 2008; Heimann & Reichstein, 2008). Soils are the largest reservoir of terrestrial organic C (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 first 3 meters (Jobbágy & Jackson, 2000). The annual flux of C-CO_2 from the soil to the atmosphere is approximately 60 Gt, more than 6 times the 9 Gt C emitted anthropogenically (Stockmann et al., 2013). Therefore, even slight modifications of the C fluxes between soil and atmosphere may have a substantial impact on the future climate (Minasny et al., 2017). A better understanding of the mechanisms and interactions underlying these fluxes is therefore essential.

Feedbacks between soil and climate have been identified as the main uncertainty in Earth system models (ESMs) (Friedlinfstein et al., 2006; He et al., 2016). ESMs simulate the removal of CO_2 from the atmosphere by the land surface *via* the photosynthesis, and the increases in atmospheric CO_2 concentrations *via* the respiratory activity of living organisms including plants and soil. Nevertheless, several feedbacks between these two fluxes are not represented in ESMs (Heimann & Reichstein, 2008), whereas it is now widely acknowledged that these two processes are intimately linked and that their interactions can have

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

Even though the addition of FOM does not always result in a PE (see the concept of "negative priming effect", Kuzyakov et al., 2000), the most frequently reported response is the acceleration of SOM mineralization, sometimes with a rate up to 400% (Fontaine et al., 2004; Fontaine et al., 2011; Shahzad et al., 2012; Tian et al., 2016; Sun et al., 2019). The priming effect is likely a universal phenomenon that could affect significantly the C accumulation ability of soils in very different contexts (Perveen et al., 2019). The CO_2 fertilisation effect (*i.e*. the increase in photosynthesis due to the increase in atmospheric CO_2 concentration), for example, could lead to a weaker gain of soil C than expected or even to a net loss of soil organic C (SOC) stocks (Chemidlin Prévost-Bouré et al., 2010; Dijkstra et al., 2013). Much recent interest has also been shown in stabilizing atmospheric CO_2 levels through C sequestration, with particular attention being paid to C sequestration in soil, as illustrated by the international 4 per 1000 initiative (Minasny et al., 2017). As the management practices designed to increase SOC stocks are generally based on an increase of C inputs to the soil, the PE may reduce the impact of such practices and make the yearly SOC stock increase targeted by the 4 per 1000 difficult to achieve (Baveye et al., 2018). Indeed, global scale models in which PE is represented diverge considerably in their predictions of soil C stocks from those that do not include PE (Guenet et al., 2018).

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

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

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

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

Materials & methods

Study area and soil description

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

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

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

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

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
δ^{13}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

Plant material & pre-decomposition

We used ^{13}C-labelled fresh wheat straw (δ^{13}C = 5871.51‰, CEA of Cadarache). The chemical properties of this fresh organic matter (FOM) are given in Table 1. Wheats were cultivated on an inert substrate in order to avoid uncontrolled CO_2 input from the soil, and they were therefore supplied with a non-limiting nutrient solution throughout the culture. Half of the FOM was pre-decomposed in the laboratory. The straw was first dried at 30°C for 10 days, and then finely milled (2 mm, Waring commercial® blender). The milled plant material was distributed in 12 litterbags (mesh size 35 µm), which were then placed on top of 600 g of soil A (dry weight equivalent) at 80% of the water holding capacity (WHC), itself in 4 polyethylene containers. The containers were covered with Parafilm to minimize evaporation without affecting other gas exchanges (Wang et al., 2015) (and thus prevent CO_2 accumulation) and placed in incubation chambers at 25°C for 3 months. The location of 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 $\delta^{13}C$ 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 ^{13}C -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 CO_2-
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 where regularly weighed to control for water losses and
213 water content was readjusted when necessary.

214

215 *CO_2 and $\delta_{13}C$ measurements*

216 The concentration of CO_2 (ppmv) in the microcosms' headspace and $\delta^{13}C$-CO_2 (‰) were
217 determined on days 1, 3, 7, 14, 24, 44, 71 and 101 of the incubation. The CO_2 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 $\delta^{13}C$ measurement
220 using a mass spectrometer (FISONS OPTIMA Isotope Ratio Mass Spectrometer, coupled to an
221 ISOCHROM-GC) at a later date. After each CO_2 sampling, flasks were flushed with C CO_2-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.

Partitioning of CO_2-C from added OM and SOM sources and PE calculation

The origin of the CO_2 measured in the headspace of the microcosms was assessed using the following equations (Mary et al., 1992):

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

$$C_{adOM} = C_{Total} - C_{SOM}$$

where C_{Total} is the total CO_2-C emission measured from incubation vials under different treatments, C_{SOM} is the SOM-derived CO_2-C emissions, C_{adOM} is the added OM-derived CO_2-C emissions, and δ correspond to the measured $\delta^{13}C$ in the respective compartment (where CTL correspond to control treatment). We assumed that fractionation during the biodegradation processes was negligible (Mary et al., 1992).

PE was calculated as follows:

$$PE = C_{SOM} - C_{CTL}$$

where C_{CTL} is the SOM-derived CO_2-C emission in the control treatment (which is equal to total CO_2-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 CO_2, 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-CO_2*

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

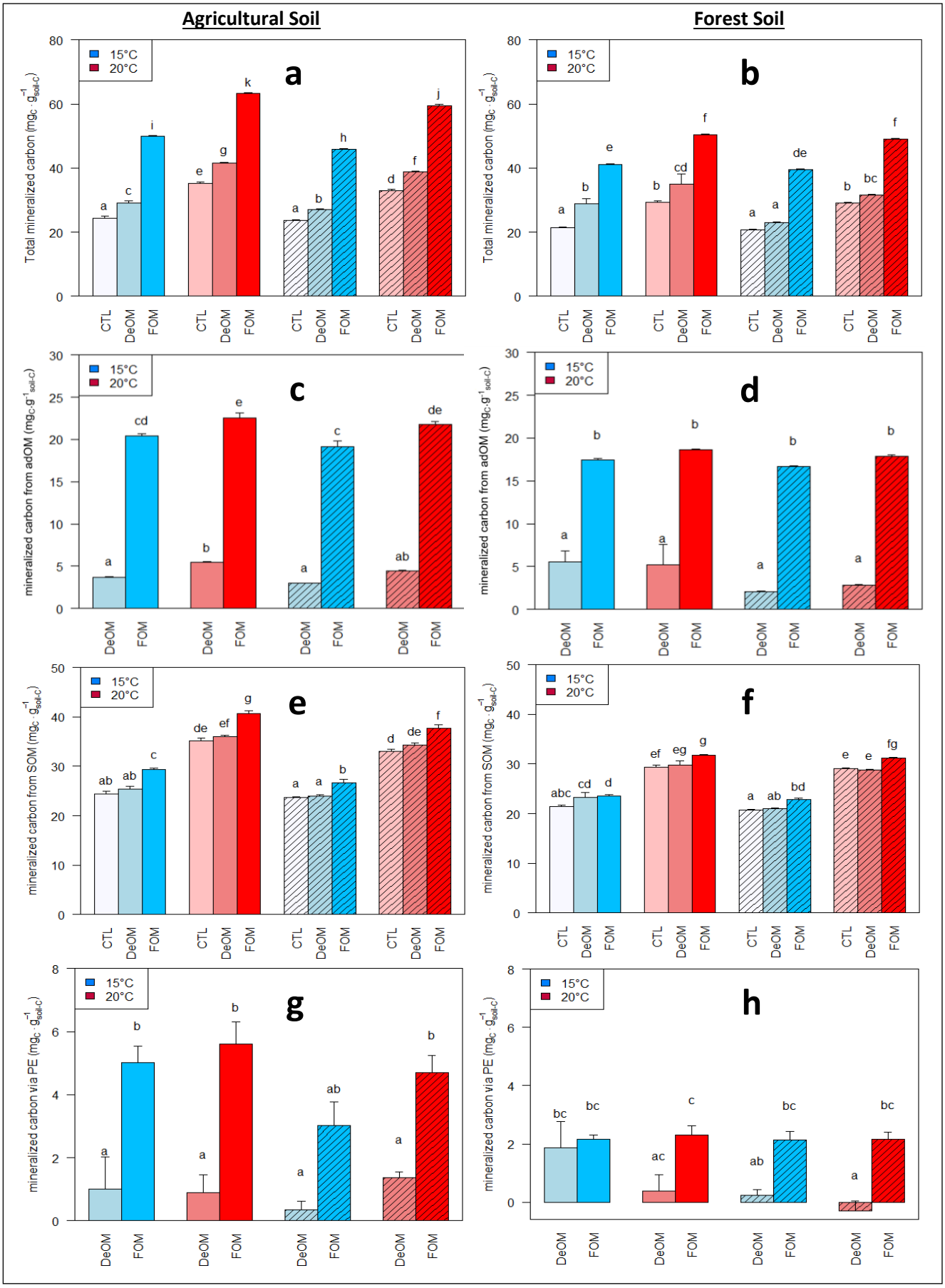
281 the soils at the end of the incubation, whereas less than 55% of FOM-carbon remained in soil
282 (Figure 1 c, d). There was a significant temperature effect on the mineralization rates of
283 added OM but also a significant interaction between soil and temperature (Table 2). Indeed,
284 post-hoc 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-CO_2-basal respiration*

289 In contrast to the mineralization of the straw residues, the main factor affecting basal SOM derived
290 CO_2 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- CO_2), 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


Agricultural Soil
Forest Soil
15°C
20°C
a
b
c
d
e
f
g
h
Total mineralized carbon (mgC · gsoil-C-1)
mineralized carbon from adOM (mgC·gsoil-C-1)
mineralized carbon from SOM (mgC · gsoil-C-1)
mineralized carbon via PE (mgC · gsoil-C-1)
CTL
DeOM
FOM

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 ± 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-CO_2-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

Interactions between treatments

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

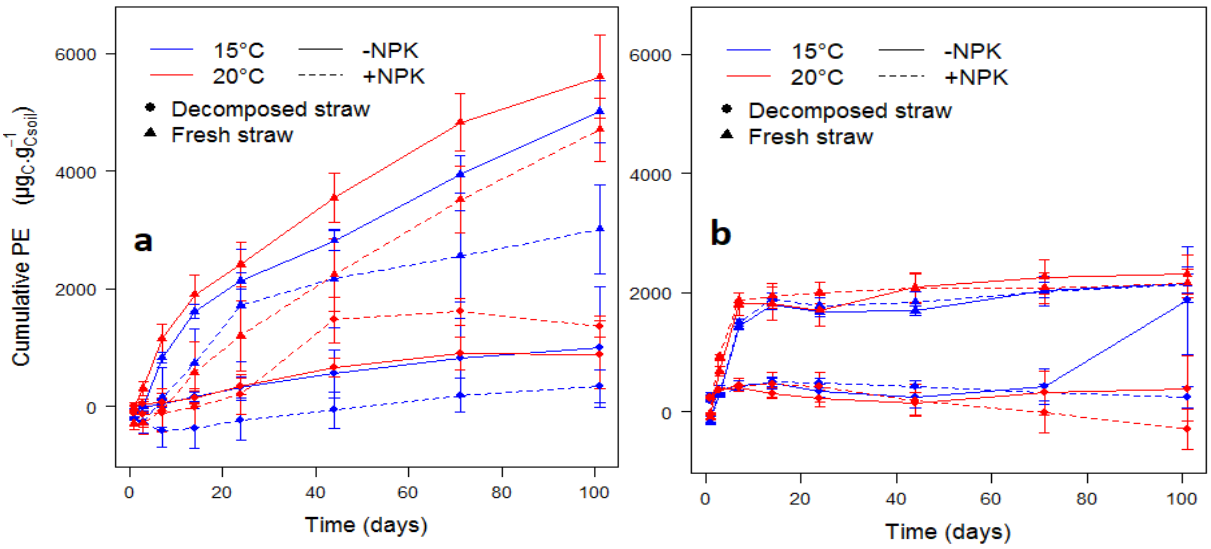


Figure 2. Changes of cumulative priming effect (PE) for different straw residues (fresh or decomposed), temperature and nutrient treatments with the incubation time. Means ± 1SD (n = 4) are shown. Letter **a** is for agricultural soil, and **b** for forest soil.

Discussion

Effect of the biodegradability of added OM

Consistently with our hypothesis about the PE theory, the quality of the organic material brought has strongly impacted the mineralization of the different types of organic matter. First, once incorporated into the soil, the straw itself was mineralized 3 to 8 times more when it was fresh rather than pre-decomposed (Figure 1 c, d), which reflects a higher availability to microbial decomposers, *i.e.* a better biodegradability. In other words, this confirms that the pre-decomposition stage decreased the biodegradability of the original plant material compounds. Obviously, this large difference in degradability affected total mineralization. It also affected the mineralization of SOM, *i.e.* PE. Indeed, by providing substrates more easily accessible to soil microorganisms, fresh straw induced a higher mineralization of the SOM compared to that induced by pre-decomposed straw and control without input, particularly on the agricultural soil. The first hypothesis of this study – namely that the addition of fresh wheat straw would stimulate PE to a greater extent than the addition of pre-decomposed wheat straw – was validated, regardless of the treatment combination. Our results are in total accordance with those of Beghin-Tanneau et al. (2019) and Lerch et al. (2019), who observed, in a 6-month and a 3-year experiment respectively, that a positive PE on SOM mineralization was only observed when adding undigested plant residues. This underpins that an avenue for increasing soil C stocks in cultivated soils might be to add decomposed straw residues rather than incorporating them fresh. We acknowledge that > 70% of the straw C was lost during its pre-decomposition stage, which might negatively impact the overall C balance. However, for a given land use, this loss is compensated in field conditions by the CO_2 fixation during growth. It is also important to note that the C lost during the pre-decomposition process is recently fixed in the contrary of the C primed, which is older and stabilized for years (Fontaine et al., 2007).

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

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

Temperature effect

The temperature is known to be one of the principal controllers of decomposition process (Yuste et al., 2007; Gregorich et al., 2016). Here, the increase of 5°C led to a strong increase in the total carbon (SOM + added OM) mineralization rate. More specifically, the isotopic labelling clearly showed that the mineralization of the C contained in the SOM increased with the increase in temperature. We noted a tremendous average increase of 40% in carbon emissions from SOM between 15 and 20°C during these 101 days. This is consistent with the Arrhenius law (Arrhenius, 1889) that implies that the temperature sensitivity of decomposition increases with the stability of organic compounds (Lefèvre et al., 2014), due to higher activation energies for stabilised substrates than for labile ones (Lützow & Kögel-Knabner, 2009). This result is in accordance with many other incubation studies (Kirschbaum, 1995, 2006; Davidson & Janssens, 2006; Conant et al., 2008, 2011; Lützow & Kögel-Knabner, 2009; Craine et al., 2010; Lefèvre et al., 2014). It confirms that a positive feedback to global warming could occur through this mechanism. This feedback could be compensated by the effect of the increase in T°C and CO_2 on primary production, but probably only in a partial way (Lloyd & Taylor, 1994; Schimel et al., 1994; Fierer et al., 2005; Davidson & Janssens, 2006; Kirschbaum, 2006; Heimann & Reichstein, 2008; Vestergård et al., 2016).

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

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

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

Finally, in our study, the effect of land use through the management of crop residues 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

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*Declaration of Interest Statement

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: