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

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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. We have tested the effects on PE of temperature, nutrient availability, biodegradibility of added organic matter (fresh vs. decomposed), soil cover (agricultural vs. forest soil) and interactions.

Our results suggest that the biodegradability of plant debris (wheat straw, fresh or pre-decomposed) is the first determinant of the intensity of PE, far ahead of 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 little 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 soil cover 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.

1. 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 and Reichstein, 2008). Even slight modifications of the C fluxes between soil and atmosphere may have a substantial impact on the future climate (Minasny et al., 2017). Feedbacks between soil and climate have been identified as the main uncertainty in Earth system

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models (ESMs) (Friedlingstein 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 and 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, 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 fertilization 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 soil C sequestration (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 at a lower rate than expected (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 and 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 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 and 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). Based on these observations, it is hypothesized that the energy input induced by the addition of organic matter (OM) stimulates the "mining" of SOM by microbial communities, allowing them to acquire more mineral nutrients from 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). Recent articles (Beghin-Tanneau et al., 2019; Lerch et al., 2019), have suggested that it may be more beneficial to add C to soils in the form of pre-decomposed OM (depleted in energy-rich compounds, *i.e.* with lower biodegradability) in order to minimize PE and therefore the mineralization of old persistent SOC. For example, in the cereal cropping context, this might be achieved 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.

However, although the biodegradability of the added pre-decomposed or fresh organic matter should interact with temperature, the availability of mineral nutrients and the soil cover to determine quantitatively the amount of primed C, 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 (agricultural vs. forest soil). The ultimate objective is to determine whether the effect of a simple change in the management of plant residues (fresh vs. decomposed) on soil C dynamics might interact with temperatures, nutrient levels and soil cover, 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, and (4) lower in the agricultural soil due to the loss of labile carbon induced by agricultural practices.

2. Materials & methods

2.1. Study area and soil description

Soil samples were collected from an agricultural field and an adjacent forest 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 forest site, located within the park of the AgroParisTech domain, is dominated by oak, hornbeam and ash and was established in 1820. The agricultural 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

Table 1
Chemical and physical characteristics of soils (agricultural & forest) and plant residues. The content of C,^{13}C, N and P content was measured with an isotope ratio spectrometer coupled to an elemental analyzer (Delta V plus, Thermo Fischer Scientific).

Properties	Soil		Wheat straw	
	Agric.	Forest	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[a] (%)	39.8	38.2	–	–
Bulk Density (g cm^{-3})	1.25	1.15	–	–
pH	7.5	5.5	–	–

[a] Water holding capacity.

as much C content as the forest soil, but with almost the same C isotopic signature (Table 1).

2.2. Plant material & pre-decomposition

We used ^{13}C-labelled fresh wheat straw ($\delta^{13}C = 5871.51‰$, 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 agricultural soil (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.

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

2.3. Experimental design

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

The temperatures of 15 °C and 20 °C respectively approximate the mean temperature currently observed and that predicted in 50 years during the plant growth period (April–October) in Versailles. The relative amount of carbon added in the forest and agricultural soils was constant on a relative basis, *i.e.* 50 mg of added carbon per g of soil carbon. In treatments with nutrient addition, a mineral nutrient solution (5.2 mg NH_4NO_3 per vial and 0.89 mg KH_2PO_4, dissolved into deionized water) was added in each vial to ensure that soil microbial communities were not nutrient limited, to give final total (soil + added OM) C:N and C:P ratios of at least 10:1 and 80:1, respectively (Fontaine et al., 2004), in all the soil + added OM systems, and to mimic fertilizer stoichiometry. An equivalent volume of distilled water was added in the treatment without nutrients, 4.78 ml for agricultural soil and 4.58 ml for forest soil (*i.e.* 80 % of WHC).

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

2.4. CO2 and δ13C measurements

The concentration of CO2 (ppmv) in the microcosms' headspace and $\delta^{13}C–CO_2$ (‰) were determined on days 1, 3, 7, 14, 24, 44, 71 and 101 of the incubation. The CO_2 concentrations were measured on a 2-mL sample using a micro gas chromatograph (Agilent, 490-PRO Micro GC System). A second 10-mL gas sample was taken and stored in glass vacuum vials for $\delta^{13}C$ measurement using a mass spectrometer (FISONS OPTIMA Isotope Ratio Mass Spectrometer, coupled to an ISOCHROM-GC) at a later date. After each CO_2 sampling, flasks were flushed with moist CO_2-free air, which avoided any significant limitation by oxygen and any reduction of gas volume.

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 from straw-amended soils, 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).

2.5. Data analyses

All results per gram of soil (gsoil) were normalized per gram of soil carbon (gCsoil) and cumulated over the 101 days of incubation. Statistical analyses were carried out using R version 3.4.1 (R Core Team, 2017). Normality and homogeneity of variance across treatments were tested prior to analyses and no data transformation was necessary. Data are presented as the means of four replicates with standard errors. Mixed-effects analyses of variance (ANOVA) were used to examine the differences among treatments of total CO_2 respired, SOM-derived CO_2, added OM-derived CO_2 and PE at the end of the experiment. In these models, organic matter type, soil, temperature, nutrient addition and all their interactions were set as fixed effects while incubation vials were set as random effects. Tukey's HSD post hoc tests were used to identify statistically significant differences among treatments. For all analyses, we used a $P = 0.05$ significance threshold.

3. Results

3.1. Total mineralization

The total CO_2 respired per g of soil carbon after 101 days of incubation in each treatment are shown in Fig. 1 (a, b). The addition of organic matter was the main factor affecting total mineralization (Table 2). In both soils, C mineralization was the highest in the FOM treatment, followed by the DeOM and control treatments (Fig. 1a and b).

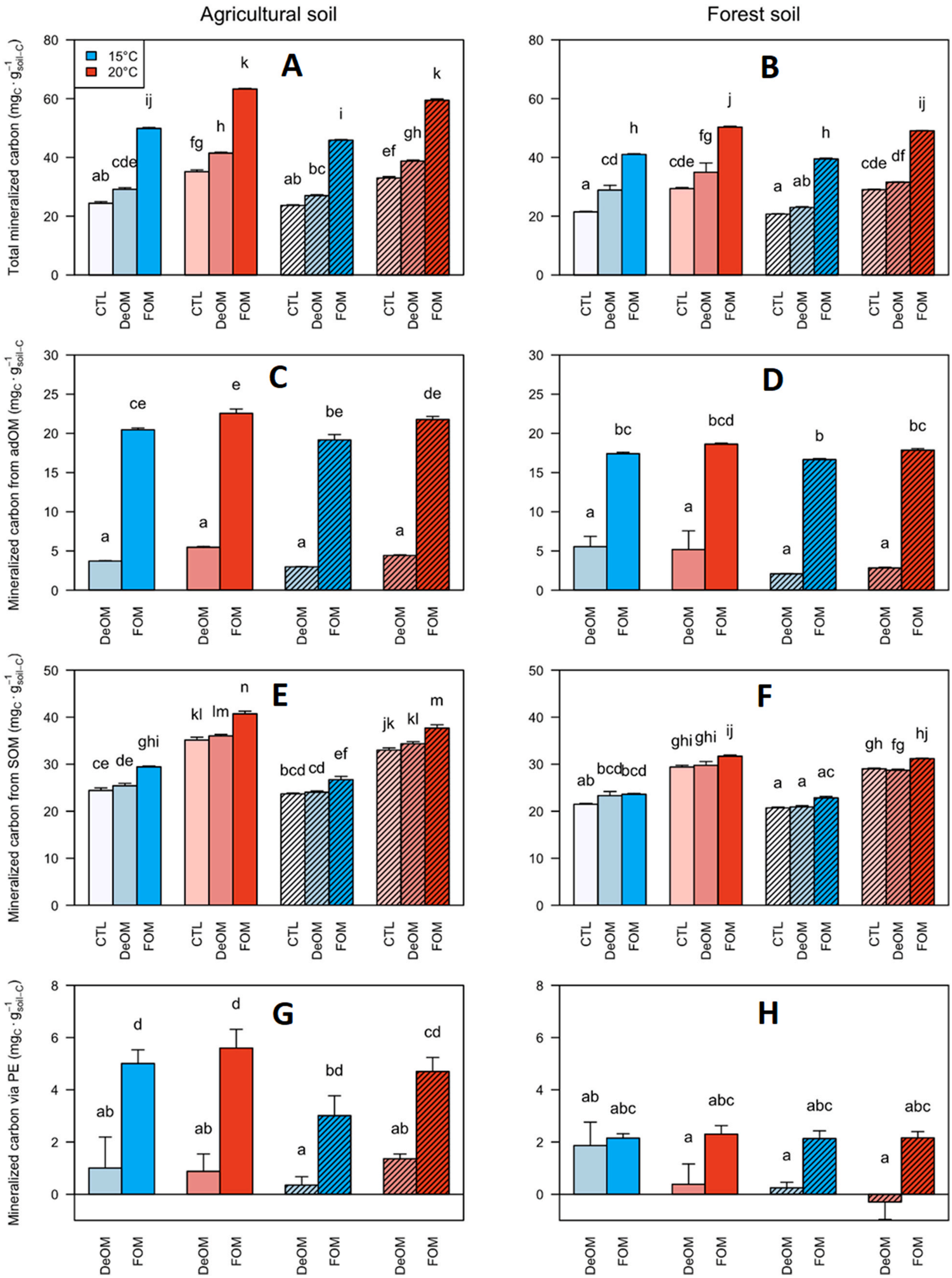

Fig. 1. Carbon emissions and PE per gram of soil carbon. Letters **A** & **B** for Total mineralization, **C** & **D** for adOM-derived mineralization, **E** & **F** for SOM-derived mineralization and **G** & **H** for PE, on agricultural and forest soils, respectively. Data are means of 4 replicates ± SE. Blue & red bars correspond to 15 °C & 20 °C modalities respectively, hatched bars correspond to treatments with mineral nutrients addition. Letter above bars are from Tukey-test: bars with the same letter(s) are not significantly different ($P < 0.05$). Vertical scales are adapted for each C emissions category, but identical between agricultural & forest soil to facilitate the comparison. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Results of ANOVA to evaluate the impact of the quality of added organic matter (adOM), temperature (T°C), nutrient addition (NPK) and soil cover (soil), with F-values and significance stars (NS = Not statistically significant).

	Total C emission		adOM derived C		SOM derived C		PE	
	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
adOM	**1850.4**	***	**1792.4**	***	**128.4**	***	**98.5**	***
T°C	**982.7**	***	**13.9**	***	**2554.2**	***	0.4	NS
NPK	**55.9**	***	**15.1**	***	**65.3**	***	**6.7**	*
Soil	**350.4**	***	**24.5**	***	**705.5**	***	**26.2**	***
adOM: T°C	**5.0**	**	1.5	NS	2.1	NS	2.8	NS
adOM: NPK	**5.3**	**	1.9	NS	1.7	NS	0.1	NS
adOM: Soil	**32.3**	***	**18.7**	***	**16.9**	***	**14.6**	***
T°C: NPK	0.1	NS	0.2	NS	0.0	NS	2.0	NS
T°C: Soil	**30.7**	***	3.1	NS	**55.5**	***	**5.5**	*
NPK: Soil	0.4	NS	1.4	NS	**7.1**	**	0.1	NS
adOM: T°C: NPK	0.4	NS	0.01	NS	0.7	NS	0.3	NS
adOM: T°C: Soil	1.8	NS	0.03	NS	1.4	NS	0.1	NS
adOM: NPK: Soil	**4.7**	*	2.5	NS	**3.7**	*	**5.1**	*
T°C: NPK: Soil	1.7	NS	0.1	NS	3.4	NS	0.4	NS

The addition of straw always induced a higher mineralization compared to control (+51% on average), but changes were only +18% with DeOM *vs.* +84% with the FOM (Fig. 1 a, b). Temperature was the second factor affecting total mineralization (Table 2). Compared to the incubation at 15 °C, the highest temperature (*i.e.* 20 °C) increased by 32% on average the amount of released CO_2, and the addition of mineral nutrients decreased it by ca. −6% (Fig. 1 a, b). Soil cover (cropland or forest) was the third factor explaining the variability of the amount of released CO_2 (Table 2). On average, the total mineralization was higher by 18% in the agricultural soil compared to the forest one (Fig. 1 a, b). Last, the addition of mineral nutrients decreased the amount of released CO_2 by *ca.* −6% (Fig. 1 a, b). Statistical analysis (Table 2) revealed strong ($p < 0.001$) interactions only between soil and OM addition on the one hand, and between soil and temperature on the other hand. While the responses to OM addition and to temperature increase were similar in both soils, the differences were less marked in the forest soil compared to the agricultural soil. The other significant interaction effect (3-factor interaction) only explained a negligible fraction of the observed variability in the amount of released CO_2 (Table 2).

3.2. Added OM derived-CO_2

The quality of added OM was by far the first factor explaining its degradability in soils. All other factors only explained a rather small fraction of the amount of CO_2 released by added OM. The mineralization of added FOM was 4.8 times higher than that of DeOM (Fig. 1 c, d). On average, 92% of DeOM-carbon was still present in the soils at the end of the incubation, whereas only 61% of FOM-carbon remained in soil (Fig. 1 c, d). Soil cover (cropland or forest) was the second factor explaining the variability of the amount of released CO_2 (Table 2). On average, the mineralization of added OM was higher by 17% in the agricultural soil compared to the forest one (Fig. 1 c, d). Moreover, a significant interaction effect between soil cover and the biodegradability of added OM was observed: while the amount of CO_2 released by added DeOM did not differ significantly between agricultural and forest soils, the amount of CO_2 released by added FOM was significantly higher in the agricultural soil compared to the forest one (see letters from Tukey test on Fig. 1 c, d). The increase in temperature significantly increased (12%) the amount of CO_2 derived from added OM (Table 2, Fig. 1 c, d). Nutrient addition significantly decreased the mineralization of added OM in both soils by *ca.* −11%. Statistical analysis revealed that the other interaction effects were not significant (Table 2).

3.3. SOM derived-CO_2 respiration

In contrast to the mineralization of the straw residues, the main factor affecting SOM-derived CO_2 emissions was temperature (Table 2). On average, there was a 38% increase in SOM mineralization at 20 °C compared to 15 °C (Fig. 1 e, f). Soil cover was the second factor explaining the variability of the amount CO_2 released by SOM (Table 2). On average, the amount of SOM-derived CO_2 released per gram of soil carbon was higher by 19% in the agricultural soil compared to the forest one. Moreover, a highly significant interaction effect between soil cover and temperature was observed (Table 2), with a higher increase of SOM-derived CO_2 released in the agricultural soil compared to the forest one (Fig. 1 e, f). The third main factor affecting SOM-derived CO_2 emissions was the added OM (Table 2). The effect of added OM was strongly dependent upon its biodegradability. The addition of DeOM had no significant effect on the basal respiration (*i.e.* SOM derived-CO_2 in control soils, without any straw addition). In contrast, a statistically significant increase in basal SOM-derived respiration (+12% relative to controls) was found in FOM treatments. A highly significant interaction effect between soil cover and OM addition on SOM-derived CO_2 emissions was also observed (Table 2): The increase of SOM mineralization in presence of FOM was strong in the agricultural soil but rather low in the forest one (see letters from Tukey test on Fig. 1 e, f). The addition of mineral nutrients had a highly significant (Table 2), but low (decrease by *ca.* −5%), negative effect on SOM-derived respiration (Fig. 1 e, f). Statistical analysis revealed that the other interaction effects were either weak or not significant (Table 2).

3.4. SOM derived–CO_2–priming effect

The PE depended mainly on the quality of OM addition (Table 2): the maximum PE was induced by the addition of Fresh organic matter (FOM), which induced on average + 467% higher mineralization of SOM compared to the addition of more recalcitrant compounds (DeOM) (Fig. 1 g, h). Land use was the second factor determining PE effect intensity, which was 2 fold higher in the agricultural soil compared to the forest one. A highly significant interaction effect between soil cover and added OM was also observed (Table 2). This interaction effect was associated to a stronger increase of PE intensity in presence of FOM in the agricultural soil compared to the forest one. Mineral nutrient addition significantly decreased the PE by *ca.* −29% (Table 2; Fig. 1 g, h). Globally, we did not observe any significant effect of temperature on PE intensity. However, the statistical analysis revealed a significant interaction effect between soil cover and temperature: while there was no clear effect of temperature on PE in the forest soil, PE increased with temperature in the agricultural one (Fig. 1 g, h). The last significant effect (3-factor interaction) only explained a small fraction of the total variance in PE intensity (Table 2).

The temporal evolution of the cumulative PE is illustrated in Fig. 2. The PE profile over time depended on the biodegradability of OM addition and the soil. There was little or no PE following the addition of

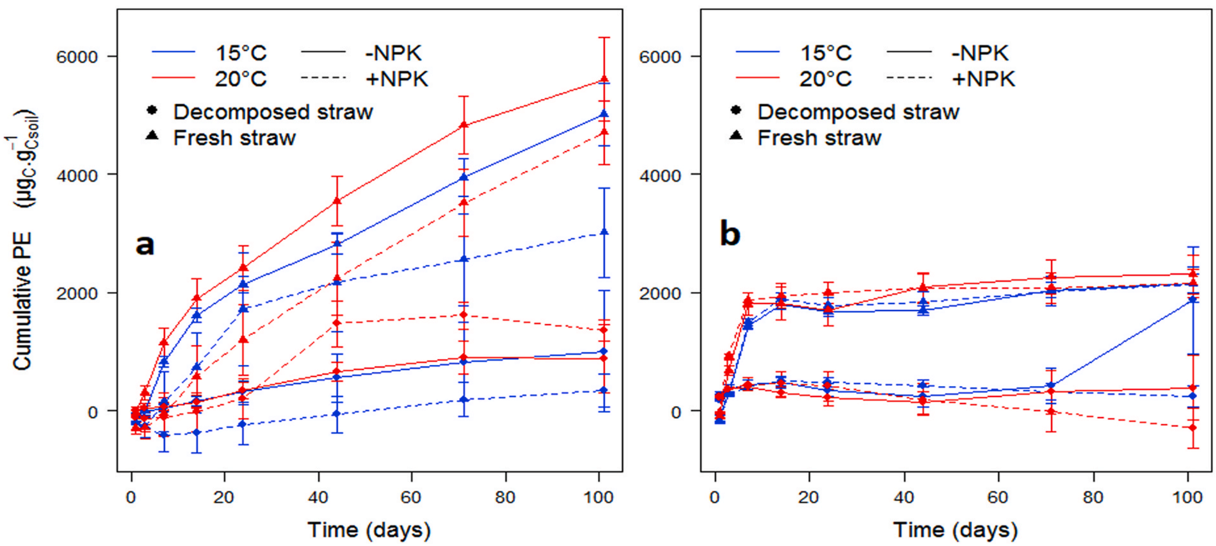

Fig. 2. Changes of cumulative priming effect (PE) for different straw residues (fresh or decomposed), temperature and nutrient treatments with the incubation time. Means ± 1SD (n = 4) are shown. Letter **a** is for agricultural soil, and **b** for forest soil.

DeOM, regardless of the soil. In agricultural soil, the PE after the addition of FOM was relatively high and persisted throughout the duration of the incubation, whilst it was lower and reached a plateau after 7 days in forest soil (Fig. 2).

4. Discussion

4.1. 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 (Fig. 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. However, > 70% of the straw C was lost during its pre-decomposition stage, which might negatively impact the overall C balance. In addition, a part of the added carbon might be transferred to the soil organic stable carbon pool. 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 (i) 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 and Sinsabaugh, 2006; Chen et al., 2014), and (ii) that the addition of FOM provides the energy necessary to make such an investment (Kuzyakov et al., 2000; Fontaine et al., 2003; Blagodatskaya and 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 (respiration in the controls), which is higher per unit organic C in the agricultural soil compared to the forest one (Fig. 1). Assuming a fixed carbon use efficiency, the respiration per unit organic C is considered to be an indicator of the decomposability of the OM (Lomander et al., 1998; Manzoni et al., 2012). 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 and 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).

4.2. Soil cover effect

Agricultural and forest soils differ by several aspects such as OM type, microbial & fungal communities, dynamics of OM inputs and outputs, exposition to climatic & anthropic disturbances (Guo and Gifford, 2002; Foley et al., 2005). This led to three main differences noticed here between soil responses: 1) all effects observed on the forest soil were very limited compared to the agricultural one; 2) the forest soil C concentration was 2 times higher than the agricultural soil while it was the reverse for the PE by g of soil C; 3) the kinetics of PE induced by FOM addition had very different shapes (Fig. 2), with an early threshold reached after 7 days on forest soil whereas PE stayed relatively high and persisted throughout the duration of the incubation on agricultural soil.

With the support of literature, we could hypothesize that the difference of behaviour between agricultural and forest soils is the result of a combination of factors such as pH (Hung and Trappe, 1983; Bottner et al., 1998; Walse et al., 1998; Leifeld, 2005), tannin content of SOM (Kraus et al., 2003), total organic C content (Zimmerman et al., 2011; Paterson and Sim, 2013), C contents in microbial biomass (Blagodatskaya and Kuzyakov, 2008), evolution (by different selection pressures between soils), quality of SOM and bacteria/fungi ratio (Fontaine et al., 2011; Terrer et al., 2016; Lonardo et al., 2017). Among all these possibilities, the most influential could be related to the differences in C contained in the microbial biomass (C_{mic}) of the two soils. According to Blagodatskaya and Kuzyakov (2008), if our FOM-C input was greater than the C_{mic} of agricultural soil but less than or equal to C C_{mic} of forest soil, then this abrupt cessation of PE after 7 days on forest soil could be the result of a simple apparent PE. In this case, the supplied FOM-C would only have served to renew the C_{mic}. This C_{mic} having the isotopic signature of the soil, the CO_2 resulting from its mineralization would be read as PE, but without being derived from the over-mineralization of the SOM.

Despite all the differences noticed between results obtained on these two soils, general mineralization patterns were similar for the two soils and underpin a certain robustness of our results. Particularly, our main hypothesis was validated on both soils: the quality of the organic matter brought in the form of fresh or pre-decomposed straw residues led to very significant differences in the intensity of the induced PE. This further supports that the biodegradability of added OM inducing the PE process is a major factor to take into account for SOC dynamics. In addition, these 2 soils are both luvisols with *ca.* the same clay/silt/sand ratio, and initially only differ by their land-use, established about two centuries ago. This particularity allows us to notice that, at the end of these past 200 years, the agricultural soil has a 2.19-times lower SOC content than the forest soil, which could be considered here as the reference system. In other words, this means that, depending of the land-use (such as deforestation for farmland establishment) and agricultural practices (as input of highly degradable FOM), soils can become a significant source of CO2 through the mineralization of large amount of stable C (Guenet et al., 2012; Chen et al., 2015). Yet, it also means that with better understanding and practices, this agricultural soil has the potential to store – at least – 2.19 times more C (Chenu et al., 2018), as its forest counterpart and neighbour.

4.3. Temperature effect

The temperature is known to be one of the main drivers 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, assuming that recycling of labelled material is negligible as classically done in priming experiments (Chen et al., 2014; Fontaine et al., 2004, 2007; Guenet et al., 2012), 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 38% in carbon emissions from SOM between 15 and 20 °C after 101 days. This is consistent with the Arrhenius law (Arrhenius, 1889), which implies that the temperature sensitivity of decomposition increases with the stability of organic compounds (Lefèvre et al., 2014), due to higher activation energies for stabilized substrates than for labile ones (Lützow and Kögel-Knabner, 2009). This result is in accordance with many other incubation studies (Kirschbaum, 1995, 2006; Davidson and Janssens, 2006; Conant et al., 2008, 2011; Lützow and 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 and Taylor, 1994; Schimel et al., 1994; Fierer et al., 2007; Davidson and Janssens, 2006; Kirschbaum, 2006; Heimann and 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 and 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. There was no significant interaction effect between added OM and temperature on PE. However, the response trends of SOM, FOM and DeOM to temperature were consistent with this hypothesis (Fig. 1 c, d, e, f). Indeed, still in accordance with Arrhenius equation, 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. The significant interaction between temperature and soil cover on PE supports the hypothesis of a differential response to temperature according to OM recalcitrance. Indeed, we observed a positive response in the agricultural soil, contrasting with a weakly negative or neutral response in the forest one. This might explain the contradictory results of literature.

4.4. Nutrient-addition effect

For the mineralization of all types of OM, the addition of mineral nutrients had significant effect but much lower than the effect of temperature and type of OM added. It decreased significantly the PE intensity by *ca.* 29% on average, as often found (Kuzyakov et al., 2000; Chen et al., 2014; Dimassi et al., 2014). The PE response to the availability of mineral nutrients could be explained by a reduction in the need of mineral nutrient mining within SOM for microbial communities. Here however, the addition of mineral nutrients also decreased the total mineralization, the mineralization of SOM and of the added OM, particularly in the agricultural soil (Fig. 1). As suggested by Spohn et al. (2016), this may be due to changes in the intracellular partitioning of C within the microbial communities, with an increased C allocation to biomass and a decreased allocation to respiration when nutrients are readily available.

To summarise, in the conditions of the present study, we were able to test the impacts of several factors and their combinations on the mineralization of different pools of organic matter and PE. The soil cover appeared to have strong interactions with all other factors, but surprisingly, only a few relevant interactions were noticed between the other factors. 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 soil cover and plant residues management are, among the factors we tested here, the most influential ones 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. 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 and through the significant interaction effect between soil cover and temperature.

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

Declaration of competing interest

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.

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