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Short-term effects of labile organic C addition on soil microbial response to temperature in a temperate steppe

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ABSTRACT

It remains unclear how soil microbes respond to labile organic carbon (LOC) inputs and how temperature sensitivity (*Q*10) of soil organic matter (SOM) decomposition is affected by LOC inputs in a short-term. In this study, ¹³C-labeled glucose was added to a pristine grassland soil at four temperatures (10, 15, 20, and 25 °C), and the immediate utilization of LOC and native SOM by microbes was measured minutely in a short-term. We found that the LOC addition stimulated the native SOM decomposition, and elevated temperature enhanced the intensity of microbial response to LOC addition. The ratio between microbial respiration derived from LOC and native SOM increased with higher temperature, and more LOC for respiration. Additionally, LOC addition increased the *Q*10 of SOM decomposition, and the *Q*10 of LOC decomposition is higher than that of native SOM. Overall, these findings emphasize the important role of temperature and LOC inputs in soil C cycles.

Pulsed or continuous labile organic carbon (LOC) inputs into the soil is prevalent and generally induce priming effect on the native SOM (Kuzyakov, 2010; Li et al., 2021), With global change, temperature will increase and LOC input into the soil will increase due to higher plant productivity increases (Wu et al., 2011; Xu et al., 2012). Numerous studies have investigated how temperature affects the priming effect but so far, no clear pattern has emerged (Ghee et al., 2013). In particular, the short-term processes involved in the microbial response to LOC inputs and how this process is affected by temperature are still unclear.

The temperature sensitivity of SOM decomposition is often quantified using *Q*10, which is defined as the proportional increased in CO2 emission rate for a 10 °C increase in temperature (Davidson and Janssens, 2006). The *Q*10 is often considered as an intrinsic property of a given pool independent from the environmental conditions and this how this is classically represented in models (Davidson and Janssens, 2006). Nevertheless, recent studies showed that the *Q*10 value is influenced by multiple environmental factors (Delgado-Baquerizo et al., 2017; Li et al., 2017; Liu et al., 2017), but also by the input of organic matter (Fissore et al., 2013; Liu et al., 2021). We therefore assume that the inconsistent results on priming effect response to temperature might be due to a

significant modification of the *Q*10 of SOM when LOC is added compared to control without LOC. Moreover, the C quality-temperature (CQT) hypothesis suggest that more biochemically complex and recalcitrant substrates have a higher *Q*10 (Craine et al., 2010). We therefore assume that the *Q*10 of LOC decomposition is lower than that of native SOM decomposition.

In this study, we sampled soils from a temperate steppe and conducted a laboratory incubation experiment. Specifically, ¹³C-labeled glucose was added to the soils incubated at four temperature treatments (10, 15, 20, and 25 ◦C), and a fully automated soil microbial respiration sampling measurement system was used to measure the microbial respiration rate derived from LOC and SOM at a minute scale during a 53-h period. Detailed information on soil sampling, incubation experiment, and data analysis was described in Supplementary materials.

The soil microbe response to LOC addition was rapid (Fig. 1A), higher temperatures enhanced the response intensity (Fig. S3) and increased $CO₂$ emissions from both LOC and native SOM (Fig. 1D–F). This observation confirmed our hypothesis and was in line with theoretical consideration. Generally, microbes are mainly limited by the availability of C substrates (Blagodatskaya and Kuzyakov, 2013), a large

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proportion of microbes are inactive without an addition of labile substrates, but maintain 'physiological alertness' and are ready in case of occasional input of substrate (De Nobili et al., 2001; Blagodatskaya and Kuzyakov, 2013). Thus, LOC addition promoted the decomposition of native SOM (Fig. 1B), due to the enhanced microbial activity (De Nobili et al., 2001). There is also a potential reason that could be that the LOC increases the availability of C substrate to microbes, microbial growth and metabolism will be limited by N (Dilly, 1999). Therefore, microbes need to decompose more native SOM to obtain nutrients to meet growth requirements, thus promoting the decomposition of native SOM (Craine et al., 2007; Chen et al., 2014). The temperature-promoting effects on LOC and native SOM decomposition are consistent, because of higher temperatures can provide a more suitable environment for microbes to accelerate chemical reaction rates, enzyme activity, and result in the promotion of microbial utilization for different C sources (Fang and

Moncrieff, 2001). However, this challenging the previous studies which suggested that the glucose catabolism by microorganisms is insensitive to temperature (Frey et al., 2013; Hagerty et al., 2014), and attributed this to the different enzymatic requirements of different substrate catabolic processes. Differences in microbial community structure may be responsible for the different results, the reasons for which need further investigation.

The ratio between LOC and native SOM respired increased with higher temperature and more LOC was mineralized (Fig. 2, Fig. S4). Higher temperature accelerates microbial activity and biochemical reactions, but elevated temperature also affects carbon use efficiency and the respiration increase observed when temperature increase might be also partially due to a modification of microbial physiology (Manzoni et al., 2008). Furthermore, according to the microbial stoichiometry theory, microorganisms have a relatively stable stoichiometric requirement, and resources in excess of their requirements would be wasted in the form of respiration (Chen et al., 2014; Buchkowski et al., 2015). The findings indicated that the elevated temperature not only promotes the decomposition of SOM, but also is detrimental to the stabilization of LOC input to the soil through multiple pathways.

*Q*10-SOM was significantly larger than *Q*10-ck at phases I and II (Fig. 3D and E), and gradually decreased with the prolongation of incubation time (Fig. 3B), confirming our first assumption suggesting *Q*10 of SOM when LOC is added is scaled with *Q*10 of LOC. It is mainly because the addition of LOC increased the availability of labile substrates (Fissore et al., 2013; Liu et al., 2021). Theoretically, the Michaelis-Menten kinetics $(R_s = V_{max} \times C/(K_m + C))$ provides a more appropriate model to interpret this phenomenon—increasing the SOM availability to microorganisms after LOC additions may increase the difference between C and K_m . Therefore, the relative importance of K_m in the calculation of R_s reduced when LOC is added. It has been shown that both *V*max and *K*^m increase when temperature increase leading to some cancelling effect of

Fig. 1. Changes in soil microbial respiration rates and cumulative CO2 emissions under different temperature treatments after LOC addition. **A–C**: soil microbial respiration rates derived from LOC, native SOM, and the total respiration rate, respectively, under different temperature treatments; **D–F**: the cumulative CO2 emissions derived from LOC, native SOM, and the total, respectively, over 53-h. *P* values and different letters indicate significant differences among the different temperature treatments ($n = 4$, mean \pm SE). Black lines indicate the fitted curves of the corresponding parameters versus temperature. R^2 and $*$ denote the goodness of fit and significance level, respectively. The level of significant was set at *P <* 0.05.

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Fig. 2. Changes in the ratio of microbial respiration derived from LOC and SOM at different temperatures. (**A**) Trends in the proportion of LOC and SOM used by microbial respiration $(R_{\text{LOC}}/R_{\text{SOM}})$ over 53h; (**B**–**C**) comparison of $R_{\text{LOC}}/R_{\text{SOM}}$ at phases I and II under different temperatures. (**D**) Comparison of the percentage of LOC and SOM mineralized by microorganisms at different temperatures during 53h. In the box-whisker plot, horizontal line inside each box represents the mean values, top and bottom of the box represent the first and third quartiles, respectively, and vertical lines represent 1.5 times the interquartile range. Hollow dots represent outliers. The *, **, and *** in the figures indicate statistical difference levels of *P <* 0.05, *P <* 0.01, and *P <* 0.001, respectively, and *NS* indicates no significant

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Fig. 3. Temperature sensitivity changes of LOC and native SOM decomposition over time. A–C: the comparison of *Q*10-LOC, *Q*10-SOM, and *Q*10-Total at three different stages, respectively; **D–F:** the comparison of $Q_{10\text{-}c\text{-}k}$, $Q_{10\text{-}10\text{-}G\text{-}k}$, $Q_{10\text{-}50\text{-}M}$, and $Q_{10\text{-}Total}$ at three identical stages, respectively. Significant differences were detected using Wilcoxon test. The $*, **$, and $***$ in the figures indicate statistical difference levels of $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively, and *NS* indicates no significant difference.

temperature increase but V_{max} seems more sensitive than K_{m} (Razavi et al., 2015). Thus, the reduced relative importance of K_m with LOC addition induce a higher $Q_{10\text{-SOM}}$ compared to $Q_{10\text{-ck}}$. Nevertheless, we found that $Q_{10\textrm{-}I,OC}$ was significantly higher than $Q_{10\textrm{-}SOM}$ in phases I and II (Fig. 3D and E), contrary to our hypothesis and to the CQT theory. An alternative explanation might be due a differential effect of temperature on the carbon use efficiency of the glucose compared to the SOM. Indeed, carbon use efficiency is controlled by different factors including temperature and substrate quality (Manzoni et al., 2012) but to our knowledge an interaction between both drivers has not been reported yet in the literature. Nevertheless, substrate supply capacity is also an important factor that affects *Q*10 (Fissore et al., 2013; Liu et al., 2021). Hence, prolongation of incubation time gradually depleted glucose, which leads to a decrease in $Q_{10\text{-LOC}}$ and is lower than $Q_{10\text{-SOM}}$ in phase III. Currently, there are only a few studies on the *Q*10 of LOC decomposition, which should be emphasized in future studies, especially in the context of climate change that will lead to more plant-C input to the soil (Wu et al., 2011; Xu et al., 2012).

In summary, we found that soil microorganisms responded rapidly to LOC addition and that the addition of LOC stimulated the native SOM decomposition. Additionally, elevated temperature enhanced the intensity of microbial response to added LOC and resulted in more LOC for respiration. More importantly, the input of LOC increased the Q_{10} of native SOM decomposition. These results highlight the importance of temperature on microbial utilization of LOC and native SOM for soil C formation and stabilization under conditions of climate change and increased C inputs.

Author contributions

N. He. and C. Xiao. designed this study; C. Li. conducted the study and drafted the manuscript; C. Xiao., N. He., B. Guenet., M. Li., and L. Xu. reviewed and revised the manuscript; all authors contributed to revisions.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at [https://doi.](https://doi.org/10.1016/j.soilbio.2022.108589) [org/10.1016/j.soilbio.2022.108589.](https://doi.org/10.1016/j.soilbio.2022.108589)

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