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Fast labile carbon and litter exhaustion under no-tillage after 5-year soil warming

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ABSTRACT

No-tillage continuously contribute organic matter and increase carbon sequestration in the soil. However, global warming may stimulate microbial activity and accelerate soil organic matter (SOM) decomposition, also especially in the topsoil. Understanding the responses of microbial utilization of SOM accumulated under no-tillage to higher temperatures is necessary to develop management strategies to sustain soil fertility. Determine the response of microbial extracellular enzyme activities and SOM decomposition to long-term warming by incorporation of ^{14}C-labelled maize litter to *in situ* warmed soil from no-tillage and till systems. We compared decomposability of litter and SOM in soils from a 5-year *in situ* experiment with two tillage systems (Till and No-till) and under two temperature levels: ambient temperature and continuous soil warming (+1.6 °C at 5 cm soil depth). We hypothesized that decomposition of crop litter (^{14}C-labeled maize) at increasing temperature (15, 21, and 27 °C for 59 days) will be more intensive in warmed soil vs. ambient and the effects should be stronger under No-till vs. Till system. As expected, soil from field warming had always higher total CO_2 efflux (from 5.5 to 12%) than the non-warmed counterpart in Till and No-till systems. Five-year warming increased temperature sensitivity (Q_{10}) of CO_2 efflux for 2-folds under No-tillage vs. Till. Litter decomposition (measured as $^{14}CO_2$) in No-till with warming was 7.9% greater than in No-tillage without warming. Three extracellular enzymes (β-glucosidase, chitinase, and sulfatase) had higher activities under warming in No-till but not under Till system. Our results demonstrated that the 5-year *in situ* warming accelerated preferential microbial utilization of labile SOM fractions in No-till notably, and from stable SOM in Till system. Consequently, warming will accelerate SOM decomposition in future and this acceleration will be especially pronounced on the labile SOM under No-tillage systems.

1. Introduction

Conservation tillage is an important practice to decrease greenhouse gas emissions by increasing soil carbon (C) sequestration, which in turn plays a substantial role to maintain and increase soil fertility and crop yield (Lal, 2004; Sun et al., 2019). Compared to conventional tillage, conservation agriculture involving no-tillage can contribute more soil organic matter (SOM) and sequester more soil organic C via retention of crop litter on the surface and physical protection within the soil matrix by the absence of disturbance and aggregate disruption by ploughing (Chen et al., 2009; Su et al., 2021).

The contribution of SOM is linked to the increase in the biodiversity of organisms present in it, as there is greater availability of food (Oldfield et al., 2019; Torres et al., 2021). Climate warming increases the soil temperature, which strongly affects SOM decomposition and stability (Hartley et al., 2007; Moinet et al., 2020). Most of the studies on

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temperature sensitivity of SOM decomposition were conducted in short- to medium-term experiments and the microbial adaptation to temperature in the long-term is not fully clear. Therefore, there is a strong need for long-term studies on the effects of warming on microbial utilization of organic matter in no-tillage systems.

Responses of SOM decomposition to warming vary depending on the quality of the C pools (Kirschbaum, 2004; Wen et al., 2019). Long-term warming causes the labile SOM to decline over years (Lavallee et al., 2020), which leads to slower decomposition of remaining stable SOM (Parton et al., 1987). Microbial decomposers may adapt to elevated temperatures and use stable SOM to obtain energy (Blagodatskaya et al., 2016; Razavi et al., 2016; Streit et al., 2014). This shift of microbial resource use may lead to a decreased temperature sensitivity (Q10) of SOM decomposition (Moinet et al., 2018).

Often higher Q10 could be measured from the beginning of incubation, when ample of easily decomposable SOM pools are available (Hou et al., 2016; Malik et al., 2020). Annual retention of crop litter supplies labile organic substances for microbial utilization (Chen et al., 2019). Thus, higher Q10 was well described for agricultural soils (Zang et al., 2020). In conventional tillage, lower crop litter input, long-term warming stimulate microorganisms to use stable SOM fractions (Feng et al., 2017). However, soils with no-tillage usually have greater labile organic C and microbial biomass than conventional tillage, especially in the surface layer (Baker et al., 2007; Li et al., 2021).

SOM decomposition is primarily regulated by microbial physiology and the production of extracellular enzymes, which catalyze decomposition of complex organic polymers into digestible monomers (Chen and Sinsabaugh, 2021; Dijkstra et al., 2011). Microbial extracellular enzyme activities (EEAs) is adapted to seasonal fluctuations of soil temperature (Razavi et al., 2015; Wallenstein et al., 2010). However, the fundamental role of temperature in regulating enzyme activity in long-term is still not fully understood, and pronounced temperature effects (Bradford et al., 2010) as well as no effects (Rousk et al., 2012; Schindlbacher et al., 2015) were observed under warming.

Long-term warming has lasting effects on Q_{10} of SOM decomposition via changing microbial EEAs. However, it is still unclear how no-tillage under elevated temperatures might have affected the SOM decomposition by changing the quality of the C pools and microbial EEAs. Thus, the aims of the present study were: 1) to determine the lasting effects of warming on Q_{10} of CO_2 production under a five years warming field experiment; 2) to determine the response of the preferential substrate decomposition (labile vs. stable) and microbial EEAs to long-term warming by incorporation of ^{14}C-labelled maize litter to *in situ* warmed soil from no-tillage and conventional tillage systems.

2. Materials and methods

2.1. Site description

A long-term tillage experiment (since 2003) with a double-cropped system winter wheat (*Triticum aestivum* L.) and summer maize (*Zea mays* L.) common on the North China Plain was located at the Yucheng Comprehensive Experiment Station of the Chinese Academy of Science (36°50′ N, 116°34′ E). The site is located in a temperate semi-arid climate, with mean annual temperature of 13.1 °C, and mean annual precipitation of 560 mm with 70% precipitation from June to September (Fig. S1). The soil is classified as a Calcaric Fluvisol (FAO-UNESCO system), and the soil texture is silty loam (sand, 12%; silt, 66%; clay, 22%) with a pH of 7.1.

2.2. Experimental design

The warming was started from Feb. 2010 on the background of no-tillage (No-till) and conventional tillage (Till) treatments. Randomized block design was used with tillage practices as the main factor and warming as secondary factor. There were four treatments: Till with and without warming (Till-Warm or Till-NoWarm), and No-till with and without warming (NoTill-Warm or NoTill-NoWarm). Each treatment had four field replications. The size of each treatment subplot was 2 m × 2 m.

For the Till, a rotary tiller was used with a tillage depth of approximately 10–15 cm after summer maize harvest; No-till was done between winter wheat harvest and summer maize seeding. The details of fertilisation, irrigation, residue return, and other management practices followed have been previously described (Hou et al., 2012; Wang et al., 2022).

The warming plots were continuously heated (about 1.6 °C increase at 5 cm depth) using an MSR-2420 infrared heater (Kalglo Electronics, Inc., Bethlehem, PA, USA) which were placed 3 m above ground. Soil temperature (5 cm depth) and moisture (0–10 cm) were continuously measured by PT-100 thermocouples and FDS100 soil moisture sensors (Unism Technologies Incorporated, Beijing), respectively.

2.3. Soil sampling and analyses

Five soil samples were randomly collected in May 2015 from each subplot from 0 to 5 cm depth using a 3.7 cm diameter soil auger. The soil samples from each subplot were carefully mixed and 10 g was used to measure soil moisture. The rest of the fresh soil samples were sieved by 2 mm mesh, then separated into three groups and 30 g of each group were stored in air-tight containers (120 ml) for 15, 21, and 27 °C incubation temperature, respectively. Three incubation temperatures were used to obtain the Q_{10} values.

^{14}C-labelled maize litter (200 mg, the specific ^{14}C activity was 3560 disintegration per minute, DPM mg^{-1}C) was ground with a ball mill and thoroughly mixed with the soil samples prior to incubation. Soils from warmed and non-warmed plots were subsequently incubated at the three temperatures for 59 days in four replicates.

Soil moisture was maintained with deionized water at 70% of water-holding capacity. Soil CO_2 was trapped using 3 ml of 1.0 M NaOH in small vials, which were placed in each of incubation jars. The trapped CO_2 amount was estimated by titration with 0.1 M HCl using phenolphthalein as an indicator. The ^{14}C activity in $^{14}CO_2$ was measured by adding 2 ml scintillation cocktail Rothiscint-22x (Roth Company, Germany) to 1 ml aliquot of NaOH after the decay of chemiluminescence.

The ^{14}C counting efficiency was about 87% and the ^{14}C activity measurement error was<2%. The CO_2 concentration was measured 8 times during incubation at the 1st, 3rd, and 6th day during the first week, then every week for the next two weeks, and thereafter every 10–13 days till the end of the incubation period.

To calculate the temperature sensitivity (Q_{10} value), CO_2 efflux of each incubation temperature was fitted with an exponential model:

$$Rs = ae^{bT} \quad (1)$$

$$Q_{10} = e^{10b} \quad (2)$$

where *Rs* is soil CO_2 efflux, *T* is incubation temperature, and *a* and *b* are two regression coefficients (Luo et al., 2001).

The contents of soil organic carbon (SOC) and total nitrogen (TN) were determined with a LECO CN2000 analyzer (Elementar Analysensysteme GmbH, Germany). Soil microbial biomass carbon (MBC) and K_2SO_4-extracted carbon – dissolved organic carbon (DOC) were determined by the fumigation-extraction method (Vance et al., 1987) and were measured before and after the incubation. A K_C value of 0.45 was used to calculate the C content of the MBC.

To analyze the response of microorganisms to warming, the activities of the three hydrolytic enzymes were examined: β-glucosidase, chitinase, and sulfatase responsible for holocellulose, chitin, and organic S decomposition, respectively (Arcand et al., 2016; Haynes and Knight, 1989).

Extracellular enzyme activities (EEAs) were measured by

fluorogenically labelled substrates according to a modified technique described in Stemmer (2004). In brief, three fluorogenic enzyme substrates based on 4-methylumbelliferone (MUF) were used: MUF-b-D-glucopyranoside (MUF-G; EC 3.2.1.21) for the detection of β-glucosidase, MUF-N-acetyl-b-D-glucosaminide dehydrate (MUF-NAG; EC 3.2.1.14) for chitinase, and MUF-sulfate potassium salt (MUF-S; EC 3.1.6) for sulfatase activity. 2 ml of 2-methoxyethanol was used to dissolve the MUF-substrates.

In further, pre-dissolved MUF-substrates were diluted with sterile distilled water to give the desired concentrations. Soil samples (1 g) were suspended in water (20 ml) and shaken on an overhead shaker for 15 min at room temperature at maximum speed to ensure thorough mixing. A subsample of the soil suspension (50 µL) was added to the 100 µL MUF-substrate solution and 50 µL MES-buffer, pre-pipetted in deep well microplates (96-wells, 0.5 ml, HJ-Bioanalytik GmbH, Monchengladbach, Germany).

Fluorescence was measured at an excitation wavelength of 360 nm and an emission wavelength of 460 nm at 0, 30 and 60 min after amendment using a Victor^3 1420–050 Multilabel Counter (PerkinElmer, Waltham, MA, USA). Calibration curves with pure MUF of increasing concentration (from 0 till 200 µM) were included in every series of enzyme assay. Enzyme activities were expressed as MUF release in nanomoles per gram bulk soil dry weight per hour (nmol $g^{-1}h^{-1}$).

2.4. Statistical analyses

Two-way ANOVAs were used to examine the effects of tillage and warming on MBC, DOC, and β-glucosidase, chitinase and sulfatase activities before and after incubation. Means of main effects were compared using the least significant difference (LSD) test after a two-way ANOVA test. All differences were considered significant at $p < 0.05$. All statistical analyses were conducted with SPSS software (SPSS for Windows, version 11.5, SPSS Inc., Champaign, IL).

3. Results

3.1. Effects of temperature and tillage on soil CO_2 efflux and maize litter decomposition

Total CO_2 efflux from all incubated soil samples increased with the warming. CO_2 efflux under NoTill-NoWarm was 4.8% higher than Till-NoWarm and 10.0% higher under NW than Till-Warm on average of the three temperatures. The cumulative CO_2 efflux in warmed soil was by 5.5% and 11.9% higher than non-warmed soil in Till and No-till, respectively (Fig. 1a). The temperature sensitivity of CO_2 efflux (Q_{10}) was higher in warmed soils than in non-warmed soils under both tillage systems, by 0.04 units for till and 0.09 for No-till (Fig. 1a).

Depending on the tillage, the $^{14}CO_2$ release was similar to the cumulative CO_2 during the two months of incubation (Fig. 1b). The ^{14}C labelled CO_2 production ranged from 85.5 mg (Till-NoWarm at 15 °C) to 123 mg (NoTill-Warm at 27 °C), accounting for 40–60% of the total initial ^{14}C input by maize litter (Fig. 1b). The decomposition of maize litter was much higher under NoTill-Warm than NoTill-NoWarm. However, the $^{14}CO_2$ efflux was similar between Till-Warm and Till-NoWarm.

MBC content (microbial biomass carbon) before incubation was highest under NoTill-NoWarm (302 mg kg^{-1} soil) than under Till-NoWarm (207 mg kg^{-1}) ($p < 0.05$). Long-term warming decreased MBC for both Till (14%) and No-till (4.3%) soils. After incubation, MBC content decreased with increasing incubation temperature. The highest MBC content was at 15 °C for all four treatments. NoTill-NoWarm had higher MBC than Till-NoWarm at each incubation temperature ($p < 0.05$) and similar results were observed between NoTill-Warm and Till-Warm (Fig. 2, top).

Dissolved organic matter (DOC) content declined by 10% because of warming in the initial soils (55 and 49 mg kg^{-1} soil for Till-NoWarm and NoTill-Warm, respectively) and 12% (67 and 59 mg kg^{-1} soil for NoTill-NoWarm and NoTill-Warm, respectively) (Fig. 2, bottom). DOC decreased with increase temperature after the incubation, similar to MBC.

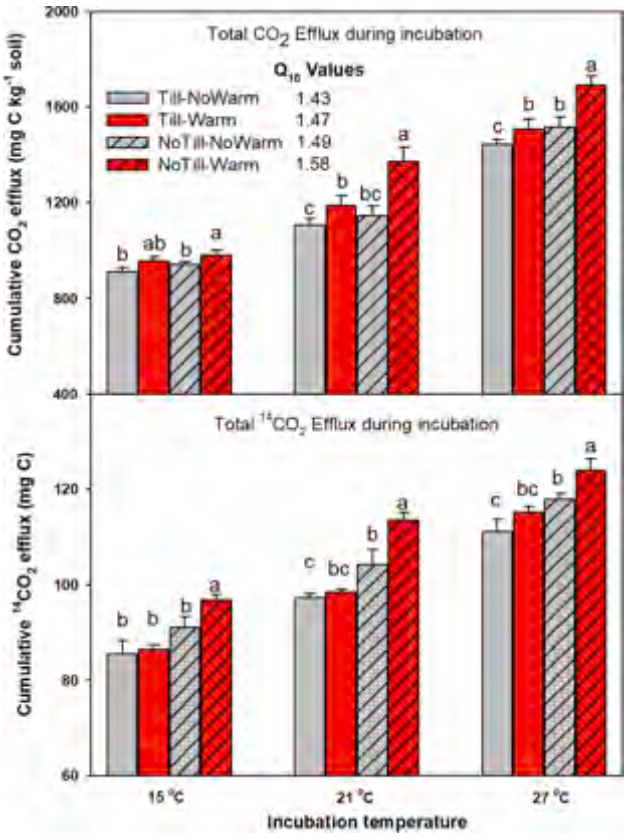

Fig. 1. Cumulative CO_2 efflux after 59 days of incubation (a), and recovery of initial ^{14}C activity (as % of ^{14}C input) added as maize litter in $^{14}CO_2$ efflux (b) (±standard errors) from soil under Till-NoWarm, Till-Warm, NoTill-NoWarm and NoTill-Warm treatments at three incubation temperatures: 15, 21 and 27 °C. Q_{10} reflects the changes of CO_2 efflux by 10 °C temperature increase. Letters indicate significant differences among the four treatments at the same incubation temperature ($p < 0.05$).

The ^{14}C recovery in microbial biomass after incubation ranged from 1.3% (NW, at 27 °C) to 3.9% (Till-NoWarm, at 15 °C) of the initial ^{14}C in maize residues (Fig. 3). Less ^{14}C was incorporated into MBC and DOC of warmed soils relative to non-warmed soils at all incubation temperatures (Fig. 3, bottom). The ^{14}C recovery in MBC was on average 5.1% lower in Till-Warm than Till-NoWarm, while it was 8.8% lower in NoTill-Warm than NoTill-NoWarm. The differences in DOC were much higher: up to 10% and 26% for till and No-till, respectively.

3.2. Extracellular enzyme activities

The extracellular enzyme activities (EEAs) of all three enzymes (β-glucosidase, Chitinase and Sulphatase) were higher ($p < 0.05$) in NoTill-Warm comparing with NoTill-NoWarm before incubation (Fig. 4). However, EEAs in warmed soil were similar to those in non-warmed tilled soil. No-till had higher ($p < 0.05$) EEAs than Till (Fig. 4).

After incubation, higher EEAs for warmed compared to non-warmed soils were only in No-till soils. The NoTill-Warm soil had higher β-glucosidase activity than NoTill-NoWarm at 15 and 27 °C. Similarly, Chitinase activity was higher for NoTill-Warm compared to NoTill-NoWarm for all incubation temperatures (Fig. 4). Sulphatase activities were higher for NoTill-Warm than NoTill-NoWarm at 21 °C ($p < 0.05$). EEAs were higher for No-till compared to till, both before and after

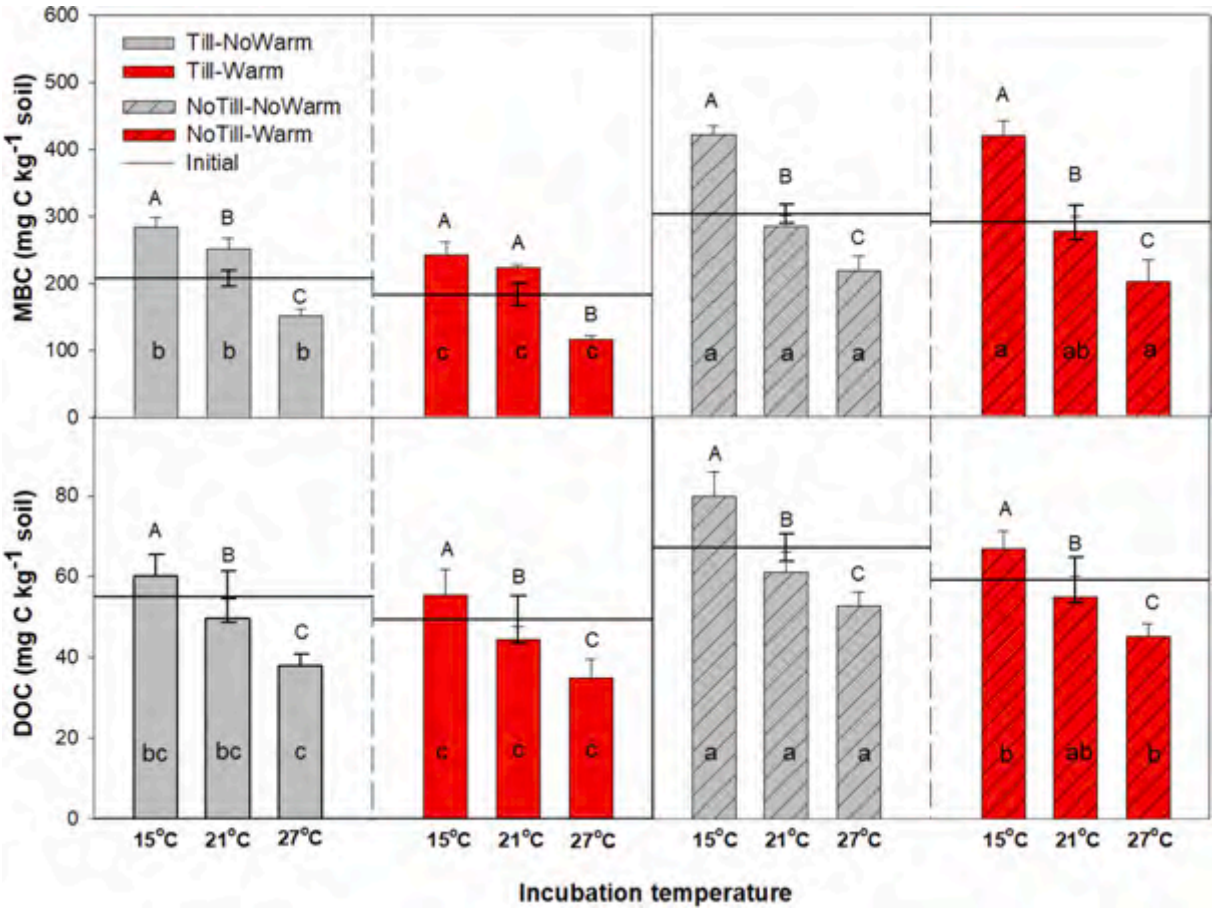

Fig. 2. Microbial biomass carbon (MBC) and dissolved organic matter (DOC) in soil (Initial, horizontal lines; after 59 days incubation, bars) under Till-NoWarm, Till-Warm, NoTill-NoWarm and NoTill-Warm treatments at three incubation temperatures (15, 21 and 27 °C) (±standard errors). Lowercase letters show significant differences within the same incubation temperature among the four treatments. Uppercase letters show significant differences within the same treatment between the three incubation temperatures.

incubation (Fig. 4).

The EEA ratios (No-till/till) of the three enzymes were about 2 for initial temperatures (Fig. 5). Warmed soils had higher ($p < 0.05$) ratios of all three EEAs than non-warmed at 15 °C. While, significant increase in the ratio was found for chitinase and β-glucosidase only for 21 and 27 °C, respectively (Fig. 5).

4. Discussion

4.1. Temperature sensitivity of CO_2 efflux under two tillage systems

The cumulative CO_2 efflux was higher in soils warmed over 5 years under field conditions at all three incubation temperatures than in the non-warmed control. Averaging across the three incubation temperatures, CO_2 efflux was 17% higher in warmed compared to soils under ambient temperature (Fig. 1a). This demonstrates that warming has a lasting and positive effect on SOM decomposition via increasing microbial activity mainly by the synthesis of extracellular enzymes (Ma et al., 2017).

Similar to our findings, a field experiment by (Hartley et al., 2007) reported higher microbial respiration under warmed plots than in control plots after warming was stopped. Another study with soils from a 12-year field warming, also found higher respiration from warmed soils during a 3-year incubation experiment (Feng et al., 2017). Thus, long-term warming under field conditions lead to microbial adaptations which have lasting effects even after warming is stopped.

Some studies reported that No-till accelerated the decomposition of SOM (Silveira et al., 2021; Torres et al., 2019). Compared to Till, No-till systems reduce the soil disturbance and increase in physical protection, resulting in increasing soil available water. The higher soil moisture contents might enhance the decomposition or cycling of nutrients from organic matter by increasing microbial activity under suitable temperature circumstances (Six et al., 2002). In temperate regions, the lower temperature might cause that the microbial C assimilation efficiency faster than the decomposition rates of SOM, resulting in higher organic matter accumulation (Six et al., 1999).

Temperature sensitivity (Q_{10}) of SOM decomposition is an index to reveal the respiratory response to temperature change. Q_{10} was 1.5 on average of the four treatments and increased by 0.04 and 0.09 units under Till and No-till systems, respectively due to warming (Fig. 1). Similarly, Q_{10} of SOM decomposition increased by 0.08 units per 1 °C under a 3–4 years continuous warming experiment in a temperate forest (Rousk et al., 2012). Thus, there are the lasting effects of warming on Q_{10} of CO_2 efflux under a five years warming field experiment.

However, the warming-induced Q_{10} increase was contrary to many previous experiments that observe a decline of Q_{10} in warmed soils, caused by easily available substrate depletion (Eliasson et al., 2005; Luo et al., 2001). In the current experiment, the added maize litter provided ample substrate which led to an increase in Q_{10} (Fig. 1). The Q_{10} was higher in the beginning of incubation and declined with substrate depletion (Hou et al., 2016; Nie et al., 2013; Piva et al., 2012). Thus, warming induced a lasting effect on higher CO2 efflux and Q10 in warmed soils compared to non-warmed soils, indicating a microbial physiology change due to microbial thermal adaptation to 5-year field

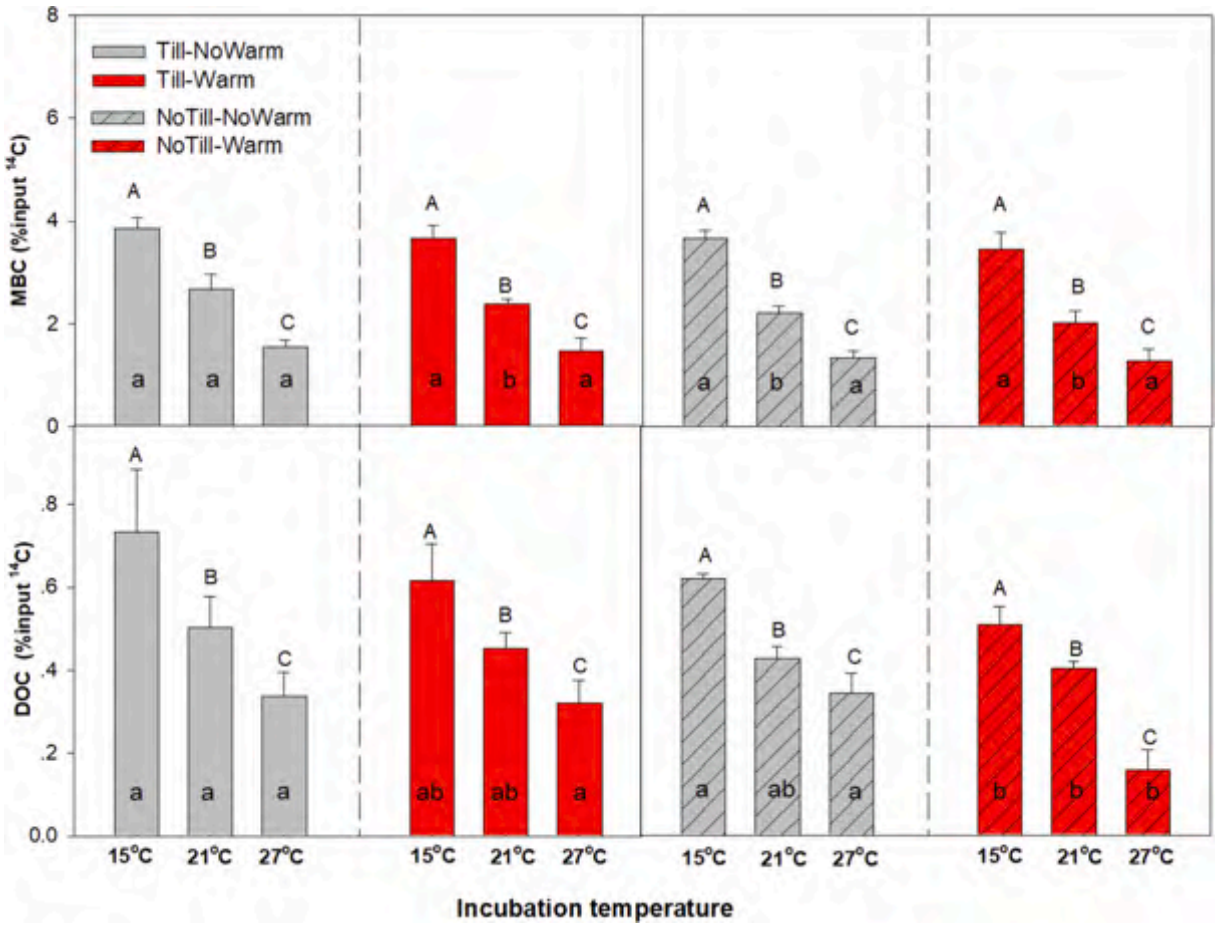

Fig. 3. Incorporation of ^{14}C (as % of input, ± standard errors) from maize litter into MBC and DOC under Till-NoWarm, Till-Warm, NoTill-NoWarm and NoTill-Warm treatments at three incubation temperatures: 15, 21 and 27 °C. Lowercase letters show significant differences within the same incubation temperature among the four treatments. Uppercase letters show significant differences within the same treatment between the three incubation temperatures.

warming (Bradford, 2013).

4.2. Microbial utilization of litter and SOM under two tillage systems

The effects of warming on the labelled litter decomposition depended on the tillage system. Warmed soils under No-till had higher ^{14}C-CO_2 effluxes than non-warmed at each incubation temperature, while there was no difference among incubation temperatures in tilled soils (Fig. 1a). The preferred substrate for Till and No-till soils was labelled litter and SOM, respectively, indicating that preferential substrate (labile vs. stable) decomposition in warmed soils depends on the tillage system.

A *meta*-analysis suggested that long-term warming enhanced lignase activity but had no effect on cellulase activity (Chen et al., 2018). This result showed preferential utilization of the recalcitrant C pools by soil microbes under elevated temperature (Zhang et al., 2022) and long-term limited substrate supply to microorganisms thereby leading to the degradation of relatively resistant SOC (Guo et al., 2021). These results support our findings in tilled soils that relatively low input of crop residues resulted in microorganisms' adaptation to decomposition of stable C and that warming enhanced their preference for decomposition of stable substrates.

In contrast, the yearly crop litter retention maintained the balance between warming-induced greater labile SOC decomposition and litter-C input for the No-tillage system. Microorganisms did not need to shift the utilization from labile SOM to stable SOM when substrates are ample (Streit et al., 2014) under No-till. As a result, the sequestration of SOM under long-term warming will depend on availability of easily decomposable substrate.

Compared to Till-NoWarm, NoTill-NoWarm had greater CO_2 efflux during incubation. Similar results were also found between Till-Warm and NW. These results could be explained by the higher SOM, MBC and DOC contents (Table. S1, Fig. 2) under No-till as compared to Till system. This implies that the warming probably decreased the microbial carbon use efficiency (Frey et al., 2013; Tucker et al., 2013). At same time, 14C abundance in both MBC and DOC were relatively lower comparing with non-warmed soils (Fig. 3), indicating less ^{14}C was allocated to microbial biomass but higher metabolisms in warmed soils.

5. Effects of long-term warming on extracellular enzyme activities

NoTill-NoWarm had higher EEAs than Till-NoWarm for all three enzymes. The same results were also found between NoTill-Warm and Till-Warm (Figs. 4 and 5). However, 5-year warming had no significant effects on any of the three EEAs for the tilled systems. Thus, tillage systems had stronger effects on the EEAs than climate warming. Crop litter retention increased the activities of β-glucosidase, chitinase and sulfatase under conservation tillage as compared to conventional tillage as the microbial response to increased substrate resource availability (Arcand et al., 2016; Mbuthia et al., 2015).

The EEAs were higher under NoTill-Warm than NoTill-NoWarm, but there was no difference between Till-Warm and Till-NoWarm before incubation (Fig. 4). In contrast to the pronounced increases of EEAs in No-till soils, Jing et al. (2014) did not find effects of 4-years steppe soil warming on EEAs and attributed the absence to the sharp decline (by

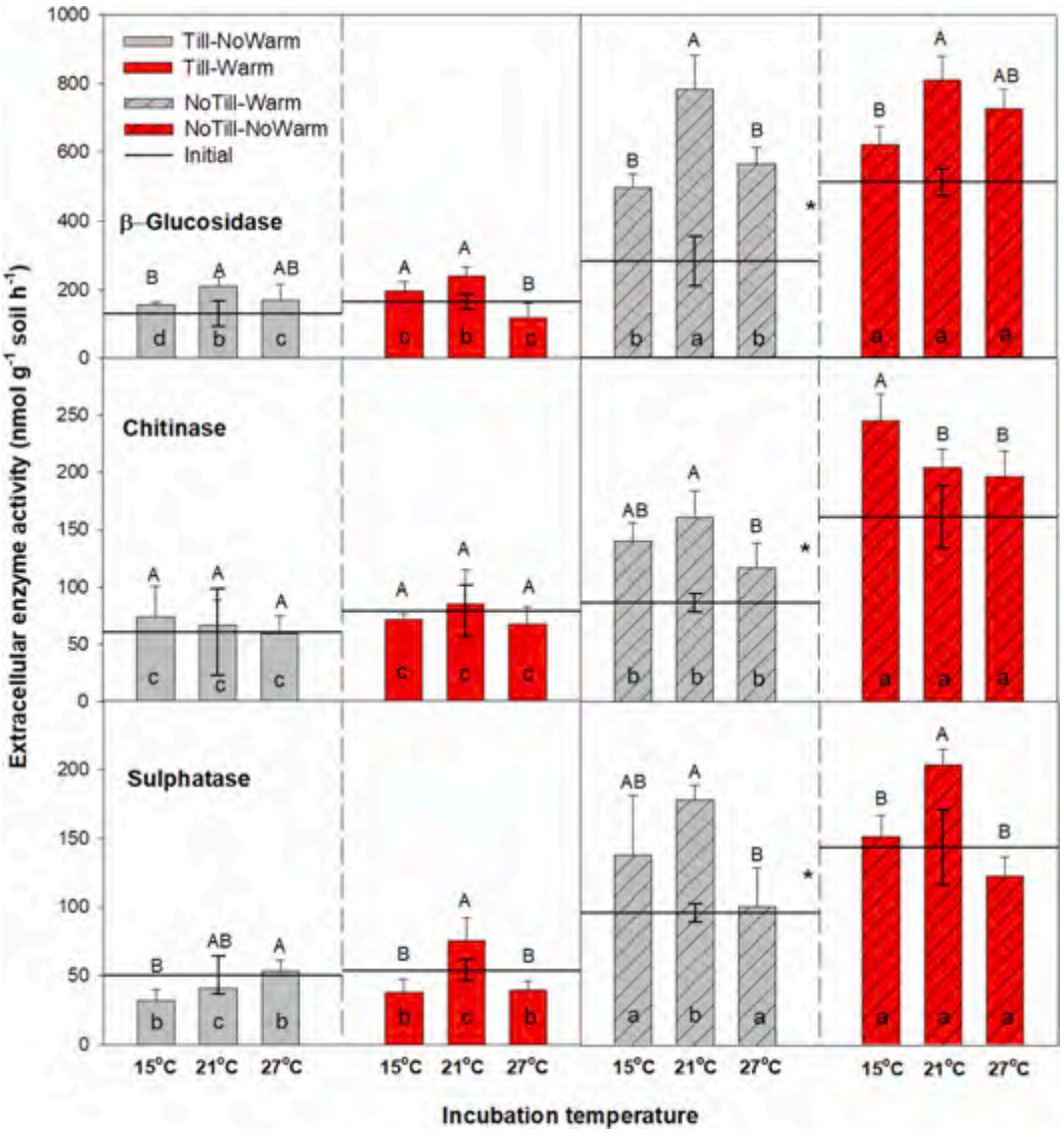

Fig. 4. Activities of three enzymes: β-glucosidase, chitinase, and sulfatase before and after incubation of non-warmed and warmed soils under till- and No-till systems (±standard errors). Horizontal lines represent the initial enzyme potential activities (Vmax) before incubation. The asterisks (*) represent significant differences of enzyme activity of initial soils between treatments. Lower letters represent significant differences among treatments of activity at same temperature after incubation; Uppercase letters represent significant differences of activity among three incubation temperatures of each treatment ($p < 0.05$).

32%) in soil moisture caused by warming. However, increasing precipitation (Gu et al., 2020) or irrigation in cropland (Thiery et al., 2020) might offset the warming-inducing decrease in soil moisture, which cause uncertainty about the effects of warming on soil EEAs. In this study, the warming-induced decline in soil moisture was only 14% in Till systems (Table. S1). This result was explained by the routine irrigation in this cropland. Thus, such a decline in soil moisture did not cause negative effects on EEAs.

Warming also increased No-till/till ratios of the three EEAs in initial soils and the soils incubated under 15 and 21 °C (Fig. 5). The increase in No-till/till ratio corroborates with more complete microbial utilization of labile SOM under warming under no-tillage relative to till. This indicated that the original preferential substrate utilization of labile C would be invoked by microorganisms under higher temperatures (Suseela et al., 2013; Wen et al., 2019). As a result, warming would strongly affect labile or stable SOC pools depending on tillage management.

Overall, the lasting effect of warming on Q_{10} and SOM decomposition, enabled microbial adaptation to warming that lead to greater CO_2 production but not back to the pre-warming level in cropland soil. Clearly, warming-induced higher EEAs will increase the labile SOM turnover rates, ultimately leading to weaken the role of litter in C sequestration under No-till systems (Fig. 6). This study explored the microbial preferential substrates of labile C after long-term warming under Till and No-till systems. Consideration of Q_{10} and microbial substrate utilization can significantly improve the C cycling prediction in cropland system models with tillage practices.

This study confirms microbial thermal adaptation with higher Q_{10} and EEAs in No-till compared to tilled soil. However, this thermal adaptation may not well explain the fate of SOM in this study since the organic matter accumulation has not been determined. Meanwhile, whether warming-inducing more root exudates and litter inputted to the soil offset a part of the C loss associated with the enhancement in microbial decomposition. To determine the microbial effect of climate warming on SOM, further studies are required to prove whether this acclimatization is associated with a shift of the microbial community structure depending on tillage systems.

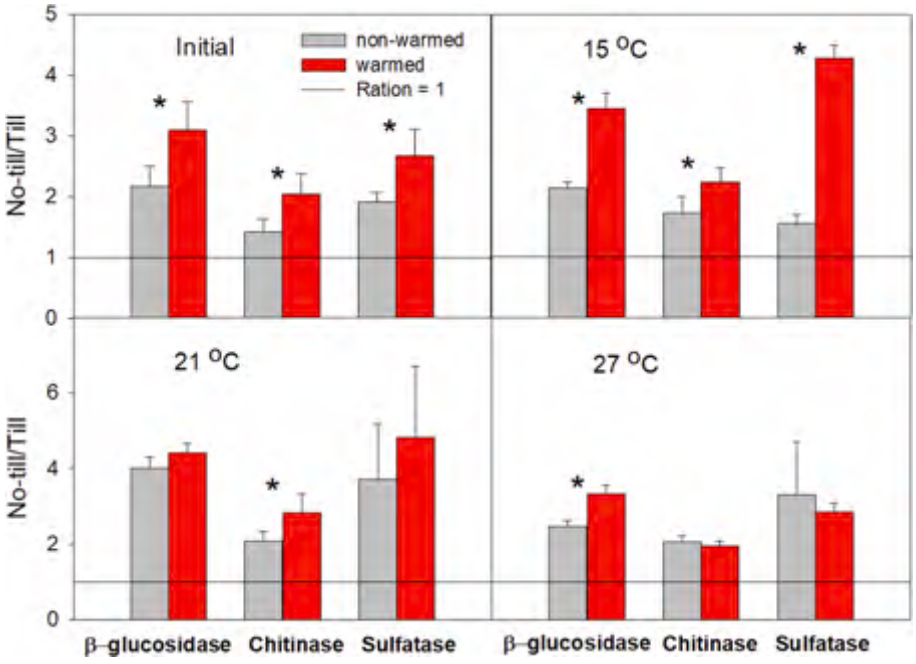

Fig. 5. No-till/till ratios of the activities of each enzyme, including initial soils before incubation and after incubation at three temperatures. Grey and red columns indicated non-warmed and warmed soils, respectively. The asterisks (*) represent significant difference ($p < 0.05$) between non-warmed and warmed soils. Horizontal black line shows the ration = 1.0 to reflect the intensity of the No-till effects.

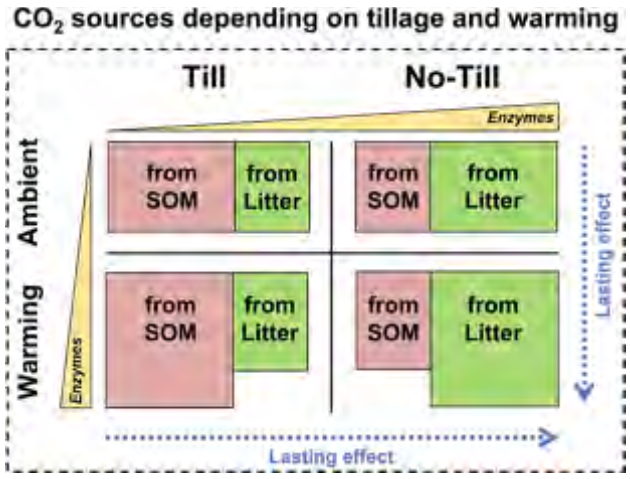

Fig. 6. Effects of warming on amounts and sources of CO_2 efflux from soil by microbial decomposition of litter and soil organic matter (SOM) under tillage and No-tillage systems. After four years of continuous warming (+2 °C), microorganisms preferred litter-C under No-till as reflected by the higher extracellular enzyme activities. Under tillage, SOM was a preferential C source. The blue dashed lines show the intensity of lasting effect.

6. Conclusions

Long-term soil warming has a prolonged and invoked effect and so, the soil organic matter (SOM) decomposition was still intensive in warmed soils than in non-warmed soils during two months of incubation after the warming was stopped. Based on the Q_{10} and ^{14}C-CO_2 production, we concluded that the long-term warming increases SOM decomposition from stable and labile SOM fractions for Till and No-till soils, respectively. The increased microbial extracellular enzyme activities in warmed soils was especially pronounced in No-till system and was caused by thermal adaptation of microorganisms.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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