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Both priming and temperature sensitivity of soil organic matter decomposition depend on microbial biomass – An incubation study

Stefany Thiessen*, Gerd Gleixner, Thomas Wutzler, Markus Reichstein

Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany

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ABSTRACT

The effect of temperature and the influence of fresh substrate addition on soil organic matter decomposition are two key factors we need to understand to forecast soil carbon dynamics under climate change and rising CO_2 levels. Here we perform a laboratory incubation experiment to address the following questions: 1) Does the temperature sensitivity differ between freshly added organic matter and bulk soil carbon? 2) Does the addition of fresh organic matter stimulate the decomposition of soil organic matter ("priming effect")? 3) If so, does this priming effect depend on temperature? In our study, we incubated sieved soil samples without and with two labelled plant litters with different ^{13}C signals for 199 days. The incubations were performed with two diurnal temperature treatments (5–15 °C, 15–25 °C) in a flow-through soil incubation system. Soil CO_2 production was continuously monitored with an infrared gas analyser, while the ^{13}C signal was determined from gas samples. Phospholipid fatty acids (PLFA) were used to quantify microbial biomass. We observed that the instantaneous temperature sensitivity initially did not differ between the original and the amended soil. However in the amended treatment the temperature sensitivity slightly but significantly increased during the incubation time, as did the PLFA amount from microbial biomass. Further, we found that addition of fresh plant material increased the rate of decomposition of the original soil organic matter. On a relative basis, this stimulation was similar in the warm and cold treatments (46% and 52%, respectively). Overall our study contrasts the view of a simple physico-chemically derived substrate–temperature sensitivity relationship of decomposition. Our results rather request an explicit consideration of microbial processes such as growth and priming effects.

1. Introduction

Soils contain the largest carbon pool in terrestrial ecosystems which consists of diverse materials with a broad spectrum of different molecular structures. They range from fresh organic matter (FOM), such as plant litter and root exudates, to soil organic matter (SOM) which refers to material no longer recognizable as plant litter. FOM is often referred to be a more easily degradable labile pool due to the more rapid degradation compared the bulk of SOM (Blagodatskaya and Kuzyakov, 2008). On the contrary, soil organic carbon is assumed to consist of more complex or low quality carbon compounds which decompose more slowly and is often referred to as a more recalcitrant carbon pool.

Heterotrophic microorganisms are able to oxidise the carbon in soil and produce CO_2, which diffuses into the atmosphere. This respiration flux is one of the largest fluxes of C from terrestrial ecosystems to the atmosphere (Schlesinger and Andrews, 2000). It is well established that overall soil respiration and soil organic matter decomposition depend on abiotic factors such as temperature and soil moisture (Kirschbaum, 2004) and may be altered by future climate change (IPCC, 2007). The degree to which increasing temperatures cause decomposition to deplete SOM stores and provide a positive feedback to global warming is still a major uncertainty in our ability to predict future CO_2 levels. In most environments the stocks of labile and recalcitrant compounds are not equal, with recalcitrant compounds being much more abundant than easily degradable compounds (Davidson and Janssens, 2006). As prediction from the kinetic theory of Arrhenius the temperature sensitivity increases with increasing activation energy. It is expected from this theory, that if the differences in decomposition rate are entirely due to the activation energy (as a measure of the energy required for decomposers to access the material), the temperature sensitivity should increase with the 'recalcitrance' of the organic material (Davidson and Janssens, 2006; Hartley and Ineson, 2008).

* Corresponding author. Tel.: +49 3641 576267; fax: +49 3641 577200.
E-mail address: sthiessen@bgc-jena.mpg.de (S. Thiessen).

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Slight changes in the turnover of SOM could change the CO_2 concentration in the atmosphere dramatically. However, if the processes slowing decomposition are not related to the molecular nature of organic matter but to a process like sorption, it is unclear what the temperature dependence should be, or if there should be short term temperature dependence at all. Results from past studies are inconsistent and until now no agreement has been reached on temperature sensitivity and its dependence on the complexity of SOM (Conant et al., 2011; Gershenson et al., 2009). Some observations suggest that more resistant SOM decomposition is less (Liski et al., 2000; Luo et al., 2001; Rey and Jarvis, 2006) or more (Conant et al., 2008; Haddix et al., 2011; Hartley and Ineson, 2008) temperature sensitive than the decomposition of more labile substrates. Other studies found equal temperature sensitivity (Fang et al., 2005; Conen et al., 2006; Reichstein et al., 2005) of FOM and SOM.

Not only abiotic effects can influence carbon turnover in soils. Recently biotic effects on decomposition have received increasing attention (e.g. the priming effect, Kuzyakov, 2010). Carbon storage in soils is also driven from aboveground and belowground biomass inputs and losses due to carbon degradation by soil microbial biomass (Pendall et al., 2011). One of the mechanisms linking C input and output in soils is the priming effect (PE) (Guenet et al., 2010b). The real PE has been defined as a change in decomposition rate of SOM as a response to some FOM addition (Bingeman et al., 1953). Real PEs are observed in several studies after the application of different kinds of FOM. The added substrates were varied from easy to more complex degradable carbon sources, e.g. amino acids (Hamer and Marschner, 2005), sugars (Nottingham et al., 2009; Garcia-Pausas and Paterson, 2011), plant litter (Bell et al., 2003; Fontaine et al., 2004, 2007; Nottingham et al., 2009) and biochar (Jones et al., 2011; Zimmerman et al., 2011; Wardle et al., 2008). It could also be shown that rhizodeposition of plant roots influences SOM degradation (Cheng, 2009; Dijkstra et al., 2006; Fu and Cheng, 2002). Up to now the mechanism driving priming is not fully understood (Blagodatskaya and Kuzyakov, 2008) and in the literature positive PE (Garcia-Pausas and Paterson, 2011; Guenet et al., 2012; Nottingham et al., 2009) and negative PE (Guenet et al., 2010a; Zimmerman et al., 2011) were observed. A better knowledge of priming is important because especially real priming can influence turnover times of the large amount of old SOM. A decrease in SOM degradation (negative PE) could increase carbon stocks, while an increase in degradation of SOM (positive PE) might result in a depletion of soil carbon stocks (Kuzyakov et al., 2000). PEs were also observed without influence on SOM decomposition, this was explained by a change in turnover of microbial biomass and is defined as apparent priming (Blagodatskaya and Kuzyakov, 2008).

Up to now the interaction between biotic and abiotic effects has so far not received much attention. Therefore the objective of this study was to investigate the temperature sensitivity of freshly added organic matter and bulk soil carbon to test the kinetic assumption of substrate quality. We applied fresh plant litter with two distinct carbon isotope ratios to a soil from which fresh plant matter was removed. We partitioned between the different carbon sources by using the change in the $^{13}C/^{12}C$ ratio in the different compartments, which is related to the proportion of carbon derived from the new added material (Gleixner et al., 2002). We additionally investigated, if the addition of fresh organic matter accelerated decomposition of soil organic matter ("priming effect") and whether this priming effect was dependent on temperature.

2. Materials and methods

2.1. Soil sampling and preparation

The arable soil used in this experiment was sampled in August 2008 from Großobringen (Thuringia, Germany), a continuous observation plot of the Thuringian regional office for environment and geology (TLUG). The mean annual temperature for this site is 8.4 °C, and average annual precipitation is 556 mm. The dominant soil type found is Chernozem from Loess (pH = 6.6; sand = 16.9%; silt = 54.7%; clay = 28.0%; N_{total} = 0.14%; C_{org} = 1.7% (TLUG, 2012)) with a value of $\delta^{13}C = -26.57 \pm 0.08‰$. Soil was randomly sampled from the first 30 cm of the plough layer. The field moist soil was sieved through a 2 mm mesh sieve and remaining roots and stones were carefully removed at the laboratory. The prepared soil was stored at 4 °C in the dark for 28 months prior to the start of the incubation experiment, to ensure that only more stable carbon was left in the soil.

2.2. Experiment design and addition of fresh plant material

An automated incubation system to perform multiple environmental manipulations of up to 80 constructed soil columns was developed for this experiment (Fig. 1). The homogenised, prepared soil was used to fill closed mesocosm columns (10 cm diameter, 20 cm height) with glass suction plate at the bottom. The connection of the suction plates was achieved by a 1.5 cm slurry soil layer (150 g) and then the column was filled up with 850 g of the same soil. Afterwards the columns were manually moistened with water until

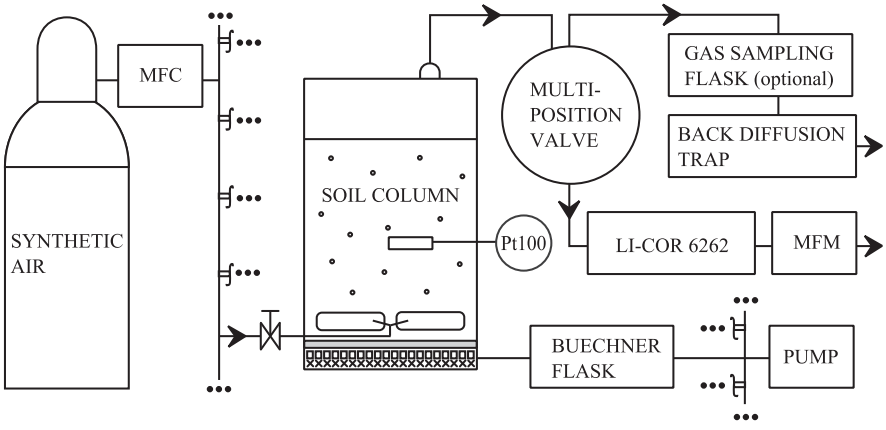

Fig. 1. Schematic diagram of the soil incubation system. Black arrows show the way of the air from gas bottle with mass flow controller (MFC) through the soil column to the LI-COR 6262 or alternatively, the air flow during the non-measuring period, through the gas sampling flasks and then into the atmosphere. The soil column bottom was equipped with suction plate and connected via the Buechner flask to a pump.

the columns were at field capacity using a pump to maintain a pressure of 60 mbar below ambient. Each column was continuously flushed with CO_2 free synthetic air (80%N_2, 20%O_2) from bottom to top by a gas inlet above the suction plate. The air inlet consists of two porous ceramic stones to maximise the air distribution in the soil column. The inlet air flow was held constant at a flow of 30 ± 3 ml/min synthetic air for each soil column. All soil columns were divided into two temperature treatments: a) cold treatment with diurnal temperature cycle that varied between 5 °C and 15 °C (each temperature held for 12 h) and b) warm treatment with a 10 °C diurnal cycle but temperatures varied between 15 °C (12 h) and 25 °C (12 h). Soil temperatures were monitored using 6 temperature sensors (Pt100, RS Components, Germany) per temperature treatment installed in selected soil columns. All prepared columns were pre-incubated at their appropriate temperature cycle for 4 weeks.

As FOM input in the experiment we used the aboveground parts of differently labelled *Echinochloa crus-galli* plant biomass ($\delta^{13}C$: $-5.88 \pm 0.10‰$ (abbreviated in text: $-6‰$) and $\delta^{13}C$: $-27.21 \pm 0.01‰$ (abbreviated in text: $-27‰$)). After the pre-incubation period each temperature treatment was split in three amendment treatments: (1) control, (2) FOM with $\delta^{13}C = -6‰$, (3) FOM with $\delta^{13}C = -27‰$. The litter was shredded and sieved to <360 μm to remove seeds from the plant biomass, which would start to germinate and affect the CO_2 derived from the microbial decomposition. 5.47 ± 0.33 mg_C FOM per gram soil was added to the soil. For this, the soil was removed from each column and FOM was homogenously mixed into the soil and then refilled into the column. Control columns were processed the same way, but did not receive any litter. Afterwards, the whole column was re-attached to the incubation system.

The water content was measured by weighing each soil column, every three days during the first 20 days and after that once per week. Moisture levels were maintained at a constant level throughout the experiment by weighing the columns and adding water to replace what had been evaporated. During the whole incubation the columns were set at a constant low suction of 60 mbar below ambient. Soil column replicates were removed from the incubation system for further analyses: before the litter application at day 0 ($n = 3$; for each temperature treatment), at day 70 and at the incubation end after 199 days ($n_{control} = 2$, $n_{amended} = 4$; for each temperature treatment). A sub sample was taken from the soil, dried at 70 °C, ball milled for elemental analysis (varioMAX CN, Elementar Analsyensysteme GmbH, Hanau, Germany) and $^{13}C/^{12}C$ isotope ratios were determined by isotope ratio mass spectrometry (Delta C, Finnigan MAT, Bremen, Germany). The rest of the soil from these columns was stored in a freezer at −20 °C for determination of microbial biomass by phospholipid fatty acid extraction.

2.3. Soil respiration measurements

During the whole incubation time all columns were flushed with CO_2 free synthetic air. The outgoing gas streams from each soil column were separately connected through an automatic flow-through multiposition valve (Valco multiposition valve SF configuration, Vici Valco Instruments, USA). Sequentially the CO_2 concentration (LI 6262, LI-COR, USA) and the gas flow (MFM, Analyt−MTC, Müllheim, Germany) of the exhaust gas were measured for each column separately in fixed intervals, around nine measurements per treatment group and day. To prevent back diffusion of atmospheric air the exhaust gas of each column passed water filled back diffusion traps before the gas was transferred to the atmosphere.

2.4. Soil air sampling for isotope measurement

By using a bypass in the exhaust gas line, soil gas could be sampled for isotopic measurements. Soil gas samples were taken at day -1, 3, 15, 42, 70, 71, 39, 134, 135, 158 and 199 after the litter amendment ($n_{cold} = 2$ until day 70, afterwards $n_{cold} = 1$; $n_{warm} = 1$). The soil air was continuously flushed through 2.3 l borosilicate glass flasks over 24 h and chemically dried with magnesium perchlorate (Fisher Scientific, Loughborough, UK). At the end of the day cycle the flasks were closed and picked up for analysis. Due to the volume of the sampling flasks and volume flow of the synthetic air the content of a flask represents the average soil air of about 3 h respiration, prior to closing the flasks. We assume that this sample is also representative for the night cycle. The stable carbon isotope ratios were determined by isotope ratio mass spectrometry (Finnigan MAT 252, Bremen, Germany) directly from the sampling flasks.

2.5. Contribution of litter derived carbon

The $\delta^{13}C$ value of the whole sample can be described by the following mixing model for both litter amended soils (Eqs. (1) and (2)) as described by Balesdent and Mariotti (1996):

$$a_1 = f^*c_1 + (1-f)^*b_1 \quad (1)$$

$$a_2 = f^*c_2 + (1-f)^*b_2 \quad (2)$$

where $a_1 = \delta^{13}C_{s6}$ is the $\delta^{13}C$ value of the sample treated with litter addition of $-6‰$ and $a_2 = \delta^{13}C_{s27}$ is the $\delta^{13}C$ value of the corresponding sample with $-27‰$ litter amendment. $c_1 = \delta^{13}C_{p6}$ is the $\delta^{13}C$ from the initial $-6‰$ plant litter and $c_2 = \delta^{13}C_{p27}$ is the $\delta^{13}C$ from the initial $-27‰$ plant litter. f is the proportion of litter derived C in the sample. $b_1 = \delta^{13}C_{soil1}$ is the $\delta^{13}C$ value of the initial soil of the sample treated with litter addition of $-6‰$ and $b_2 = \delta^{13}C_{soil2}$ is the $\delta^{13}C$ value of the initial soil of the sample treated with litter addition of $-27‰$.

As b_1 and b_2 represent $\delta^{13}C$ value of the soil and the soil is the same in all treatments, Eqs. (1) and (2) can be transformed into Eq. (3):

$$a_1 - f^*c_1 = a_2 - f^*c_2 \quad (3)$$

This can be rewritten to:

$$f = \frac{(a_1 - a_2)}{(c_1 - c_2)} = \frac{\delta^{13}C_{s6} - \delta^{13}C_{s27}}{\delta^{13}C_{p6} - \delta^{13}C_{p27}} \quad (4)$$

In both amended treatments *Echinochloa crus-galli* plant biomass was used as litter, which differed only in their $\delta^{13}C$ values. Hence, we could assume equal isotopic fractionation during degradation.

2.6. Quantification of the priming effect

The priming effect (PE) induced by litter was calculated by comparing the amount of ^{12}C in CO_2 with litter to the amount of ^{12}C in control treatments. The PE intensity was calculated according to the following equation (Blagodatsky et al., 2010):

$$PE = {}^*CO_2^{amended} - CO_2^{control} \quad (5)$$

where ${}^*CO_2^{amended}$ is unlabelled CO_2 respired from soil amended with litter, and $CO_2^{control}$ is CO_2 evolved from soil without substrate addition. PE is considered as the difference between SOM degradation with litter and SOM degradation without litter. The relative intensity of priming (PE%) was estimated as a percentage of changes relative to the unlabelled CO_2 production with and without litter addition by:

$$PE\% = \frac{{}^{*}CO_2^{amended} - CO_2^{control}}{CO_2^{control}} \times 100 \quad (6)$$

2.7. Determination of microbial biomass

Phospholipid fatty acids (PLFA) are good indicators for living organisms, since they are not synthesized in storage compounds and are rapidly degraded after cell death and lysis (Zelles et al., 1992). Studies have shown that the analysis of PLFA can be used to estimate microbial biomass (Zelles et al., 1995). Remaining plant litter was removed from the thawed soil samples by shaking the sample in distilled water for 1 h and sieving the soil through a 63 μm mesh. Wash water was removed from the soil by centrifuging (3500 rpm) until the water was crystal clear.

The lipid extractions from soil (50 g dry weight) were performed as described by Bligh and Dyer (1959). Lipids were extracted with a mixture of chloroform, methanol and 0.05 M phosphate buffer (pH 7.4) and fractionated into neutral-, glycol- and phospholipids using silica gel columns conditioned with chloroform, eluted with chloroform, acetone and methanol. The collected phospholipid fractions were then converted to fatty methyl esters (FAMEs) through mild alkaline methanolysis. These FAMEs were separated into saturated, monosaturated and polyunsaturated FAMEs with a silver impregnated SCX column. The FAMEs were dried in a N_2 stream and redissolved in isooctane combined with methyl nonadecanoate (C19:0) as an internal standard for all samples.

The Fames were identified and quantified by GC–FID (Agilent, Böblingen, Germany) and GC/MS (Thermo Electron, Dreieich, Germany). PLFA peaks were quantified by the comparison with known standards and mass spectral data from an in house database (Thoms et al., 2010).

For further analyses only PLFAs with an abundance greater than 1 mol% of total PLFA (represent 89 ± 1% of the total PLFA concentration) were chosen. To represent the bacterial biomass the used PLFA biomarkers were: 15:0i, 15:0a, 16:0i, 16:1ω7c, 17:0a, 17:0cyc, 17:0(10Me), 18:1ω7c, 18:0(10Me), 19:0cyc and 19:0(10Me) (Frostegård and Bååth, 1996; Zelles, 1999). The PLFA biomarker 18:2ω6,9 was chosen as indicator for fungi, as plant material was removed from soil prior analysis (Frostegård et al., 1993). PLFAs which do not belong to a specifically fungal or bacterial group were assigned to unspecified biomarkers: 16:0, 16:1, 16:1ω11, 17:0br, 17:1ω8c, 17:1ω8t, 18:0, 18:1ω9c, 18:3 and 23:0br. The sum of all PLFAs was included in the total PLFA amount (nmol g_{soil}^{-1}) and used as an index of microbial biomass. The ratio of fungal to bacterial PLFA was calculated from fungal PLFA marker divided by the sum of bacterial PLFA biomarkers (Frostegård and Bååth, 1996).

2.8. Temperature response

To describe the relationship between temperature and respiration rate we used the Arrhenius function and the Q_{10} model.

We calculated the activation energy using the exponential Arrhenius function:

$$y = A \cdot e^{\frac{-E_A}{R \cdot T}} \quad (7)$$

where y = is the respiration rate (change in quantity of substrate or product per unit time), A = constant, E_A = the activation energy in J mol^{-1}, R = the universal gas constant (8.314 J mol^{-1} K^{-1}) and T is the absolute temperature (K). In chemical kinetics, E_A is defined as the necessary energy for reacting molecules to break and form new bonds after a collision. The E_A was calculated from the daily relation between day and night carbon respirations in soil columns. We used only the respiration rates of the hours where the temperature was constant in the soil columns after the temperature shift. It was assumed that the small substrate concentration changes within one day can be neglected. For the daily E_A calculation we made a maximum likelihood estimate of the slope of the linear regression of the natural logarithms of day and night respiration rates against the reciprocal of absolute incubation temperature. Activation energy estimates were calculated by multiplying the slope values by the gas constant R.

An alternative analysis uses the Q_{10} model with the following equation

$$Q_{10} = \left(\frac{y_{high}}{y_{low}}\right)^{\frac{10}{T_{high} - T_{low}}} \quad (8)$$

where y_{high} = respiration rate at the higher (T_{high}) temperature and y_{low} = respiration rate at the and lower (T_{low}) temperatures. Q_{10} is an empirically fitted parameter and a measure for the sensitivity of the respiration rate to temperature variations. The same data was used as for calculating the activation energy.

2.9. Statistical analysis

The data were statistically analysed using R for Windows (version 2.13.0). Differences within PLFA microbial biomass were tested with the Mann–Whitney U test. A multiple generalized mixed effect linear regression model was used to test for differences in temperature sensitivity on soil temperature, amendment and incubation time. We used a generalized model because the variance of the residuals decreased with time. A mixed model was applied because of systematic differences between columns, i.e. replicates, within one treatment. Initially we included amendment, temperature, incubation time and interactions between those predictors in the model. However, predictors and interactions that did not significantly improve the model (tested by Log-Likelihood ratio test) were dropped from the model. Especially, removing all effects of temperature did not hamper the model fit.

3. Results

3.1. Microbial biomass

The warm treated soils contained a significantly ($p = 0.05$) greater microbial PLFA amount (+39 ± 14%) compared to the cold treatments before the litter addition, after soil preparation and the pre-incubation period of 30 days (Table 1). Within the two temperature treatments the initial fungal:bacterial ratio did not differ significantly (Table 1).

Generally, the microbial biomass in the litter amended treatments tended to increase over the whole measurement period. After the incubation period the soil microbial PLFA amount was still higher in cold (+80 ± 47%) and warm (+7 ± 28%) litter amended soils, while the control treatments tended to lose microbial biomass (cold: 0 ± 19%, warm: −38 ± 15%) compared to the initial PLFA biomass at the end of the experiment. Furthermore, the microbial PLFA amount of litter amended soils was higher in cold (+80 ± 39%) and warm (74 ± 55%) amended soils in comparison to their control soils at the end of the incubation.

The fungal:bacterial ratio did not shift significantly for both control soils during the experiment. Contrarily to that, the fungal:bacterial ratio in amended soils tended to increase in cold ($p = 0.08$) and warm ($p = 0.05$) treatments towards the incubation end.

Table 1
Microbial biomass a) total PLFA amount nmol g_{soil}^{-1} and the b) fungal:bacterial ratio. Incubation start mean of $n = 3 \pm$ sd for warm and cold. Afterwards amend mean of $n = 4 \pm$ sd, control mean of $n = 2 \pm$ sd.

		a) Amount (nmol g_{soil}^{-1})			b) Fungal:bacterial ratio		
		Day 0	Day 70	Day 199	Day 0	Day 70	Day 199
Amended	Cold	29.5 ± 4.9	64.8 ± 9.8	52.8 ± 10.6	0.017 ± 0.002	0.044 ± 0.011	0.062 ± 0.002
	Warm	41.0 ± 4.4	39.3 ± 7.8	43.6 ± 10.3	0.022 ± 0.005	0.043 ± 0.005	0.046 ± 0.012
Control	Cold	29.5 ± 4.9	39.1 ± 12.7	29.3 ± 2.4	0.017 ± 0.002	0.015 ± 0.003	0.022 ± 0.006
	Warm	41.0 ± 4.4	34.5 ± 2.8	25.1 ± 5.4	0.022 ± 0.005	0.017 ± 0.000	0.021 ± 0.008

3.2. Litter addition

The application of differently labelled litter allowed the partitioning of the total respired CO_2 into C derived from fresh plant litter and SOM. The addition of ^{13}C labelled litter was clearly reflected in the ^{13}C signature of the respired CO_2, indicating that litter decomposition contributed significantly to soil CO_2 efflux. In our study 90 ± 9% of the litter amendment were recovered at the end of the incubation. This was determined by comparing the cumulative respiration (Fig. 2) with the C content measured from soil samples (data not shown) at the end of the incubation.

A marked peak of CO_2 efflux was observed in all amended treatments shortly after the litter application. Subsequently, the respiration rates declined rapidly during the first 30 days and then slowed down continuously until the end of the incubation (Fig. 3A). The respiration rates for the control columns had a smaller magnitude and decreased monotonously throughout the experiment (Fig. 3B).

The maximal contribution of fresh litter to total heterotrophic respiration was already measured during the first day after the litter application (Fig. 4A). The proportion of CO_2 evolved from the added litter declined more rapidly in the warm treatment compared to the cold treatment. At the end of the experiment 31% and 44% of the respired C originated from the litter pool in the warm and cold soils, respectively. However, total respiration rates were lower in the cold treated soils. After the incubation of 199 days, the amount of litter respired C was nearly the same in both temperature treatments, 61 ± 5% in the warm and 57 ± 4% in the cold treatments (Fig. 4B).

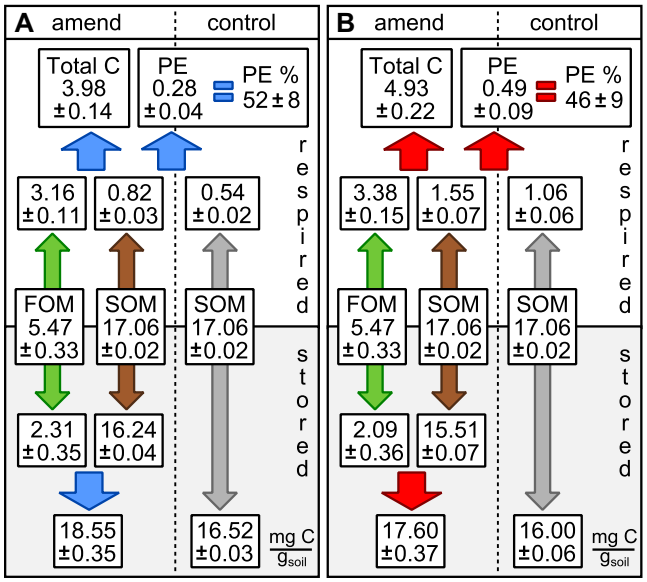

Fig. 2. Soil carbon balance for the A) cold and B) warm treatments at the end of incubation. Mean summed error calculated from cumulated respiration rate data.

3.3. Soil carbon dynamics

The litter addition increased the total soil C content from 17.06 ± 0.02 mg C g_{soil}^{-1} to 22.53 ± 0.33 mg C g_{soil}^{-1}. Over the entire experiment more total carbon was degraded in the warm treated soils in comparison to the cold treatments, this result could be observed in amended and control soils (+24 ± 7% +96 ± 13%, respectively) (Fig. 2). Subtracting the C originating from litter from total respired C allows us to quantify the contribution originating from the soil. In the amended treatments more soil carbon was degraded compared to the control treatments. Hence, overall a positive priming effect was identified in both temperature treatments at the end of incubation.

The soil of the cold treatment started with a negative priming phase which turned into positive priming after four days (Fig. 3C). The soils from warm treatments started with a positive priming effect from the first day. The maximal amount of primed carbon per time unit was reached after three days in the warm, after nine days in the cold treatment and declined rapidly afterwards. The priming effect was higher in the warm treatment (0.49 ± 0.09 mg C g_{soil}^{-1}) than in the cold treatment (0.28 ± 0.04 mg C g_{soil}^{-1}) in absolute terms (Eq. 5). However, amounts of primed carbon were similar in both temperature treatments relative to the respired soil C from the respective control soils (cold: +52 ± 8%, warm: +46 ± 9%) (Eq. 6). The amount of primed carbon which could be degraded per nmol PLFA microbial biomass was calculated based on the initial microbial biomass. The primed C amount was similar in cold (9.6 ± 2.1 μg C $nmol^{-1}$ PLFA) and warm (12.1 ± 2.6 μg C $nmol^{-1}$ PLFA) treated soils.

3.4. Temperature sensitivity

The initial activation energy (E_A) calculated from litter amended soils did not differ from the control soils in the beginning (Table 2). With increasing incubation time the temperature sensitivity rises for the amended soils ($p < 0.01$, Table 2). There were no differences in temperature sensitivity between respective warm and cold treatments. The activation energy averaged at 70.0 ± 5 kJ mol^{-1} and 63.0 ± 3 kJ mol^{-1} for the cold amended and cold control soil and at 68.4 ± 3 kJ mol^{-1} and 65.1 ± 3 kJ mol^{-1} for the warm amended and warm control soil (Fig. 5A and B). The Q_{10}, an alternative measure of temperature sensitivity, showed the same pattern and averaged at 2.86 ± 0.23 and 2.57 ± 0.10 for the cold amended and cold control columns and at 2.61 ± 0.12 and 2.49 ± 0.09 for the warm amended and warm control columns, respectively (Fig. 5C and D). The increase of temperature sensitivity with time is proportional to carbon loss from soil in the amended treatments (Fig. 6A and B). On the contrary, the activation energy did not change significantly for control treatments over time (Fig. 6C and D). We note that the first 10 days were excluded from the statistical test (Table 2) because of transient behaviour after the initial disturbance: Initial temperature sensitivity was likely influenced by fast degradable SOC that was previously protected but made available by disrupting the soil structure during litter incorporation and refilling the soil in the columns.

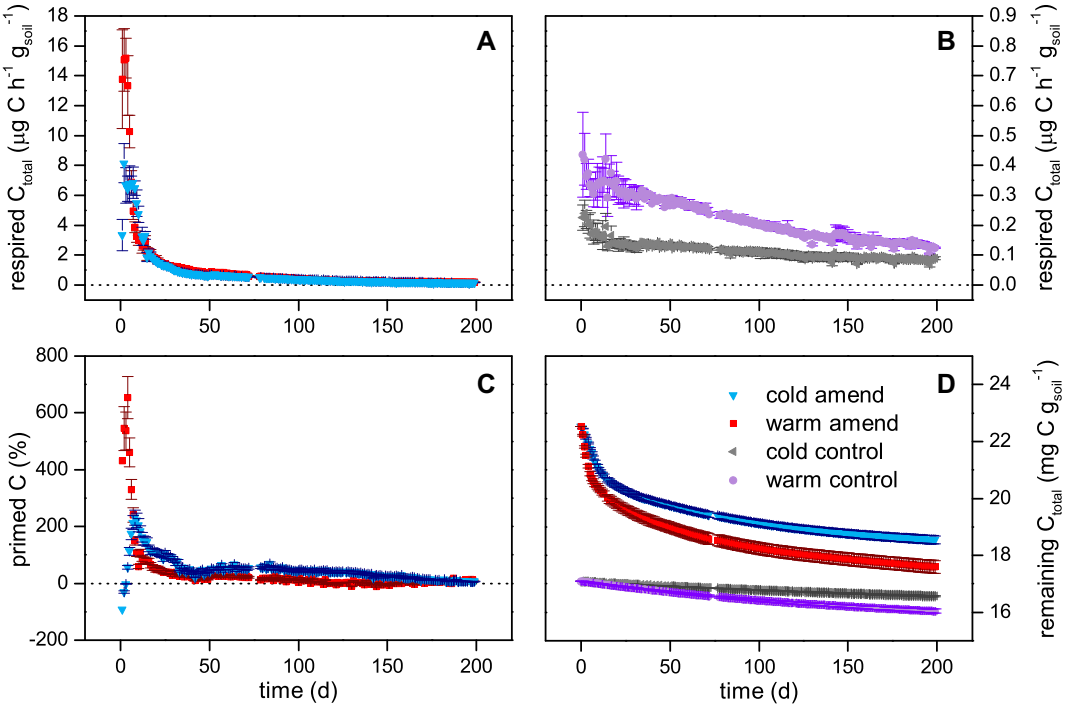

Fig. 3. The decomposition rate over time A) for amend treatments (triangle down = cold, square = warm) and B) for control (triangle left = cold, circle = warm) during incubation. C) Primed carbon from soil. D) Development of the total C content in soil calculated by cumulated respiration for all treatments. For amendment mean of $n = 8 \pm$ sd until day 70, afterwards $n = 4$. For control mean of $n = 4 \pm$ sd until day 70, afterwards $n = 2$.

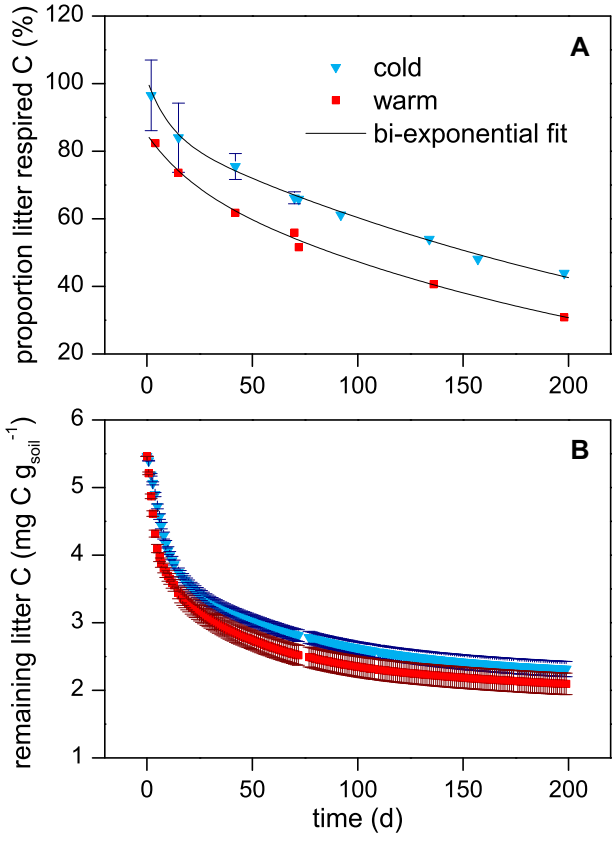

Fig. 4. Litter pool behaviour. A) Relative contribution of litter derived carbon from respired CO_2 during 199 days of incubation for cold (triangle) and warm (square) treatments. Mean of 2 columns until day 70, afterwards $n = 1$ for cold treatments. For warm treatments $n = 1$. B) Development of the litter content in soil calculated by cumulated respiration for cold (triangle) and warm (square) treatments. For amendment mean of $n = 8 \pm$ sd until day 70, afterwards $n = 4$. For control mean of $n = 4 \pm$ sd until day 70, afterwards $n = 2$.

4. Discussion

Our study design allowed examining the short-term temperature response of the decomposition via analysing 24 h cycles and the longer-term response via warm and cold treatments. Combined with the isotopic labelling we could study the effect of fresh litter amendment on temperature sensitivity of respiration and the effect of temperature on priming. Our results reveal distinct temperature effects on overall respiration in the amended and control soil samples. Furthermore a strong priming effect was detected in our study which itself exhibited the same temperature sensitivity as the

Table 2
Multiple generalized mixed effect linear regression model of activation energy, i.e. temperature sensitivity, as a function of treatments and time. $E_A = \beta_0 + \beta_{amendment} + b_{column} + (\beta_{day} + b_{column*day} + \beta_{amendment*day}) * day + \varepsilon$ with $\varepsilon \sim N(0, \sigma)$, $b_{column} \sim N(0, \sigma_{column})$, and $b_{column*day} \sim N(0, \sigma_{column*day})$. Where β_i are fixed effects and b_i are random effects of differences among columns, i.e. replicates, of one treatment. The variance of residuals decreased with time: $Var(\sigma) = \sigma_0^2 + day^{2\delta}$. The first 10 days were excluded from the model fit.

Coefficient	Value	p-Value	Description
β_0	62.751 ± 1.440	<0.001***	Mean initial activity of control
$\beta_{amendment}$	0.009 ± 0.006	<0.2	Initial activity offset with amendment
β_{day}	2.426 ± 1.777	<0.2	Slope with time
$\beta_{amendment*day}$	0.020 ± 0.007	<0.01**	Offset in slope with amendment
σ_0	13.394		Residual standard deviation at day 0
δ	−0.444		Increase of residual variance with time
σ_{column}	3.937		sd of initial activity among columns
$\sigma_{column*day}$	0.014		sd of slope among columns

** $p < 0.01$, *** $p < 0.001$.

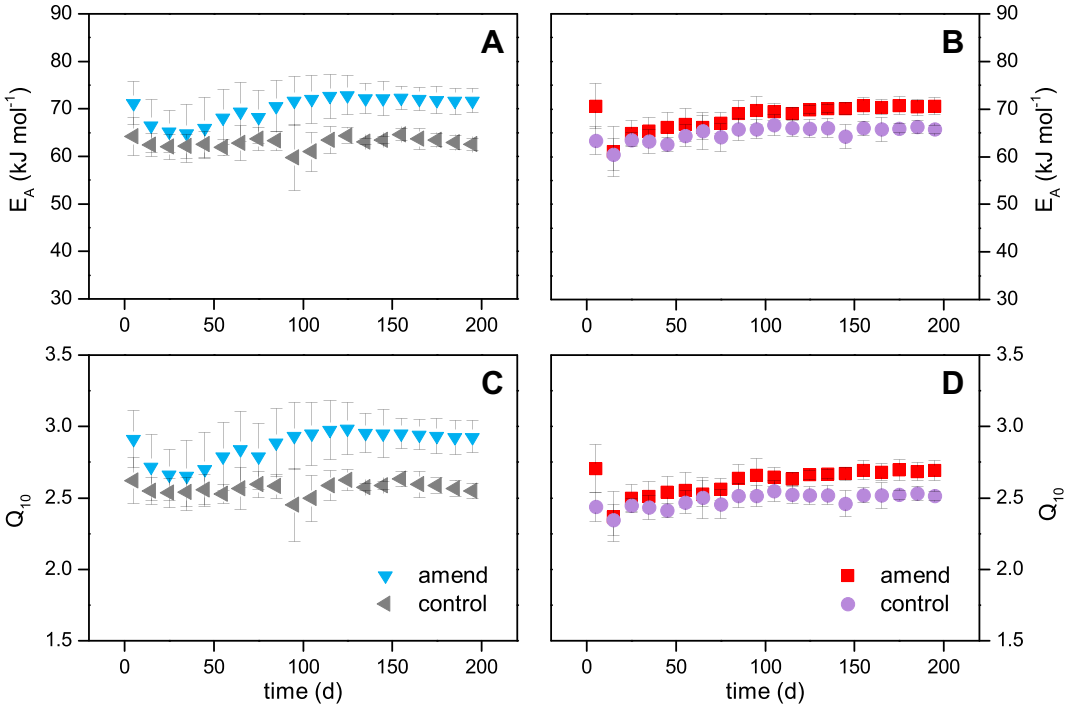

Fig. 5. The development of E_A over time A) for cold treatments (triangle down = amend, triangle left = control) and B) warm treatments (square = amend, circle = control) over during incubation time. The analogous Q_{10} values are shown for the cold treatments in C) and for the warm treatments in D). Mean over 10 d ± sd. For amendment mean of $n = 8 * 10 \pm$ sd until day 70, afterwards $n = 4 * 10$. For control mean of $n = 4 * 10 \pm$ sd until day 70, afterwards $n = 2 * 10$.

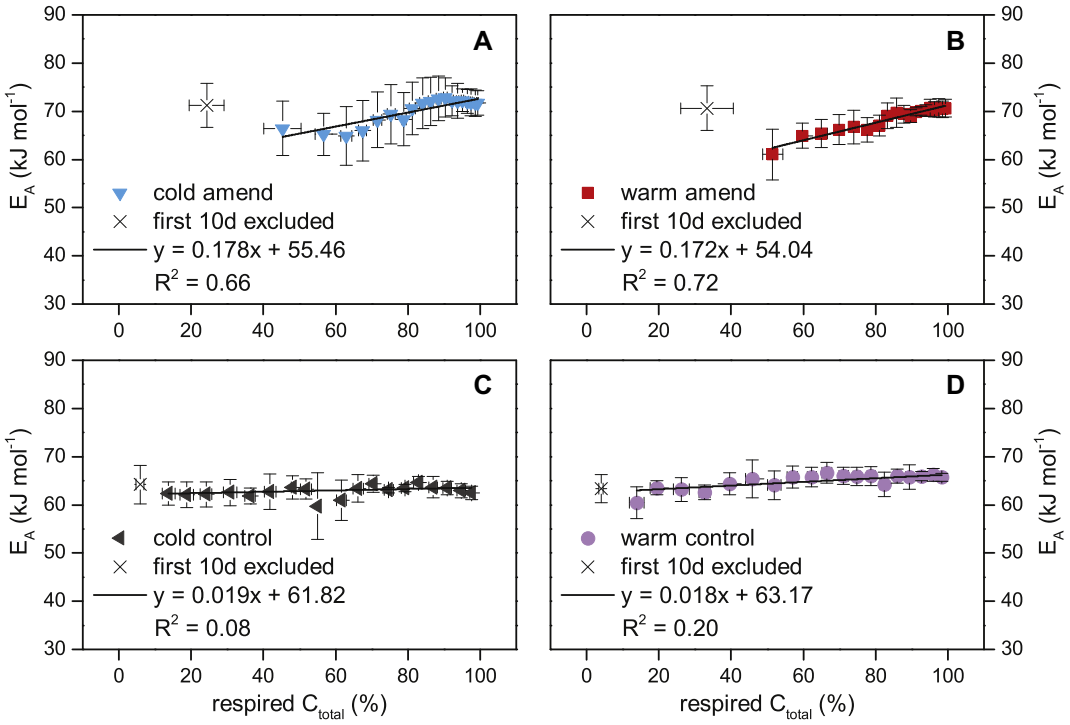

Fig. 6. Temperature sensitivity over accumulated respired soil C %. A) cold amend (triangle down), B) warm amend (square), C) cold control (triangle left), D) warm control (circle). Mean over 10 d ± sd. For amendment mean of $n = 8 * 10 \pm$ sd until day 70, afterwards $n = 4 * 10$. For control mean of $n = 4 * 10 \pm$ sd until day 70, afterwards $n = 2 * 10$. Linear regression displayed calculated from daily values.

respiration in the control soil, so that the relative priming effect (Fig. 2) remains unchanged between the warm and cold treatment.

4.1. Temperature sensitivity

Based on chemical kinetics it is often assumed that temperature sensitivity depends on substrate quality. Arrhenius kinetics predicts that recalcitrant SOC should be more sensitive to temperature compared to labile fresh organic matter. This is because the SOC is said to consist of old, complex organic molecules which require higher activation energies for decomposition. An increase in temperature will therefore more strongly affect the dynamics of this fraction (Yuste et al., 2007).

However, in our study we did not observe higher temperature sensitivities (expressed as E_A or as Q_{10}) in the more recalcitrant control than in soils where more labile litter was added. The inconsistency of measured temperature sensitivities of labile and recalcitrant substrates from past studies may stem from the common practice of omitting the role of substrate availability, which influences temperature sensitivity (Gershenson et al., 2009). By analysing the short-term temperature sensitivity using diurnal cycles we could avoid a confounding effect of changing substrate availability (e.g. Reichstein et al., 2000). A similar strategy was used in previous studies (Fang et al., 2005; Reichstein et al., 2005) where no changes in the temperature sensitivity were found in natural samples over time.

In this study a small but significant increase of the temperature sensitivity with time (and hence an increase in cumulatively respired carbon) was found in the amended samples, both in the cold and warm treatments. These results agree with the observation of Fierer et al. (2005), where temperature sensitivity of litter and substrates added to soil seems to be inversely related to their quality. At first glance this might support the substrate quality – temperature sensitivity theory, assuming that labile carbon (with low activation energy for decomposition) was respired and depleted first, while the more complex and stable carbon with higher E_A dominated the respiration at later times.

According to this theory however, the amended soil should first have a lower temperature sensitivity, which should converge towards the value of the control soils because the amended soil loses the fresh carbon over time. At the end, the carbon should more and more resemble the quality of the control soil. Yet, the opposite was observed. At the start of the experiment the control and amended soil had similar temperature sensitivities. The temperature sensitivity of the amended soil increased, whereas that of the control soil remained constant over time. Our results suggest that the chemical structure of the respired substrate is not the most important determinant of temperature sensitivity. This is in accordance to observations with other studies which showed that the age of soil C is often not related to molecular structure or thermodynamic stability (Gleixner et al., 2002; Kleber et al., 2011) and that molecular structure alone does not control SOM stability (Schmidt et al., 2011). In the following we put forward hypotheses of the reasons of this observation, which was not expected by the substrate complexity based hypothesis.

The observed temperature response may have been much lower than that of the kinetics based solely on molecular structure of the substrate (Davidson and Janssens, 2006) due to substrate limitations. It is generally accepted that low quality SOC limits the amount of available energy for the soil community. The sieved soil used for our incubation was stored several months in a refrigerator at 4 °C to suppress microbial activity. However, respiration and SOM degradation during this time will still have been going on at a low rate. Hence, the soil microbial biomass became more and more C depleted. It was shown by Fontaine et al. (2007), that C limited microbes cannot decompose recalcitrant materials without an addition of an easy to metabolize energy source. Soil microorganisms are not capable of directly metabolizing structurally complex and recalcitrant substrates without the help of energy costly extracellular enzymes (Gershenson et al., 2009). A gradual relief of this substrate limitation could explain the increasing temperature sensitivity of the amended treatment.

Moreover, substrate availability is directly affected by stabilisation of organic compounds (e.g. carbon which is associated with minerals, bound in aggregates) or directly by external factors (e.g. water, oxygen and pH) that limit decomposition (von Lützow and Kögel-Knabner, 2009). Enzymes may have been excluded from these degradable carbon sources due to this physical and chemical stabilization process. We hypothesize that the processes that stabilize the soil organic matter, which drive the kinetics in the control, are less temperature sensitive than those processes driven by the substrate quality based on the Arrhenius kinetic assumption.

The condition of soil microbial biomass itself is another factor that can affect the temperature sensitivity. The application of litter strongly increased the decomposition rate, and therefore increased microbial activity in all litter treated soils. This corresponds to the observations that in soils with litter addition the amount of microbial biomass determined by PLFA estimation increased during the incubation period. In contrast, the determined amount of microbial biomass remained constant in the reference soils. This observation supports the hypothesis that the soil community was previously energy limited and the hypothesis that this energy limited community is responsible for the lower temperature sensitivity. Larionova et al. (2007) showed that the temperature response of non-substrate limited respiration depends on the portion of growing microbial biomass in the total microbial C pool: the larger the portion of the growing biomass is, the higher is the detected temperature sensitivity of microbial respiration. The relatively low fungal:bacterial ratio in amended and control soils suggests that the microbial community and degradation processes were dominated by bacteria. Nevertheless the microbial distribution in the litter amended soil slightly changed during incubation, as the fungal:bacterial ratio increased with time. The role of fungi on degradation processes was expected to increase as the easily degradable substances from litter material decreased and more complex molecules remained with increasing incubation time (van der Heijden et al., 2008; Strickland and Rousk, 2010). Fungi are the dominant decomposers for cellulose and lignin under aerobic conditions (de Boer et al., 2005). In contrast, the fungal:bacterial ratio of the control soils remained constant.

4.2. Soil C dynamics and priming

As expected, the litter amended soil communities degraded more total carbon at higher temperatures than soils at lower temperatures. This also was the case in the control columns without litter addition. The litter amended soil microbial community further had the ability to degrade additional SOM from the original soil, corresponding to a positive priming effect in both temperature treatments. Priming effects were detected immediately after the litter addition for both temperature treatments, but the priming rate did not follow the same dynamics. This finding must be seen with caution, because the soils were also influenced by the soil disruption due to the litter application in the beginning of the experiment. During the first three days negative priming was detected for the cold treatment. This might indicate a preferential substrate utilization that induces a temporary decrease in SOM degradation (Kuzyakov and Bol, 2006). In contrast, in warm treated soils the response of the system was much faster and we could not detect initial negative priming. The input of labile C stimulates the decomposition of the recalcitrant SOM fraction (Kuzyakov et al.,

2000) by providing the energy which is required to mineralize SOM and mobilise nutrients limiting microbial activity and growth (Paterson et al., 2009; Garcia-Pausas and Paterson, 2011). These changes can be explained by changes in the microbial activity as a response availability of labile C (Blagodatskaya and Kuzyakov, 2008). A series of enzymes act as a cascade, so an increase in enzyme production triggered by labile litter would also stimulate decomposition of recalcitrant SOM (von Lützow and Kögel-Knabner, 2009).

Although we observed larger absolute priming in the warm treatments than in cold treated soils, the relative priming, i.e. divided by the respiration of the respective controls, was nearly the same at both temperatures at the end of the incubation period. Relative terms were similar because there was also lower respiration at colder temperatures in the control treatment. This observation can be explained with a basic mind model of the priming effect, in which the addition of fresh organic substrates increases microbial activity which in turn increases decomposition of SOC (Wutzler and Reichstein, 2008; Blagodatsky et al., 2010). The absolute effect is larger in the warm treatment compared to the cold treatment, because microbial activity can reach a higher peak. However, the effect also more rapidly diminishes with time because the amended fresh carbon is consumed more rapidly. In the cold treatment the effect is smaller but lasts longer. According to the model we see initially lower priming in the cold treatment, but it catches up after a sufficiently long time.

After the pre-incubation period, initially the amount of microbial biomass was higher in the warm treated soil. This corresponds to observations of (e.g. Joergensen et al., 1990; Nicolardot et al., 1994). Nevertheless, the composition of the microbial community was not influenced by this effects, as no significant difference between the fungal:bacterial ratio of cold and warm soils was detectable. The higher amount of microbial biomass in the warm treatments implies a potentially higher initial activity in the warm treated soils than in the cold treated soils. Thus, the amount of primed carbon per nmol PLFA microbial biomass was estimated from respiration and measured initial biomass. Hereby, it was assumed, that only negligible changes in the relative difference of microbial biomass between warm and cold treated soils occur within the first 14 days. Then, one nmol of microbial biomass primed the same amount of SOM in the warm and the cold treatment. This corresponds to the observations of more absolute priming in the warm treatment, but similar relative priming in both temperature treatments. In particular this finding suggests that the PE depends on the size of the active microbial community and therefore the PE is only indirectly related to temperature.

5. Conclusion

This incubation study showed that litter application favours microbial growth and leads to a slight but significant increase in temperature sensitivity with incubation time. Furthermore, the addition of readily available C substrate increased decomposition of soil derived carbon, especially in soils treated at higher temperature levels; whereas the relative stimulation was similar for both temperature treatments. Overall we conclude that substrate complexity alone cannot account for observed temperature sensitivity of soil respiration. The emergent temperature sensitivity is based on more complex interactions like stabilization processes, community structure and amount of active microbial biomass.

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