Soil Biology and Biochemistry 150 (2020) 107985

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: http://www.elsevier.com/locate/soilbio

Short-term temperature history affects mineralization of fresh litter and extant soil organic matter, irrespective of agricultural management

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ARTICLE INFO

Keywords:
Mineralization dynamics
Temperature sensitivity
Soil carbon
Priming effect

ABSTRACT

The influence of temperature on mineralization of plant litter and pre-existing soil organic matter (SOM) involves not only the prevailing temperature, but also how it has changed through time. However, little is known about how temperature variability through time influences mineralization processes. Here, we investigated how short-term temperature history affects the mineralization of SOM and plant litter in soils from different agricultural management systems. We used soils from a long-term experiment with conventional and organic management treatments to set up microcosms. The microcosms were exposed to eight days of contrasting temperature regimes (different mean temperatures and constant versus fluctuating temperatures). Microcosms were then returned to a common temperature of 16 °C, ^{13}C-labelled plant litter was added to half of them, and CO_2 efflux was measured over the following week. We found that SOM and litter mineralization were both sensitive to the temperature history, with lower mean temperatures during preliminary treatment associated with higher mineralization during the subsequent common-temperature incubation. This effect persisted through the week after temperature differences were removed. Different patterns of temperature fluctuation and agricultural management did not significantly affect mineralization during common-temperature incubation. The history sensitivity of litter mineralization, despite litter being added after temperature differences had ended, indicates that the temperature history effects may be driven by short-term microbial acclimation. We conclude that organic matter and litter mineralization, which are key processes in the carbon cycle, are sensitive to short-term temperature history. This suggests that future investigations of soil CO_2 efflux may need to take recent weather effects into account.

1. Introduction

Plant litter and older soil organic matter (SOM) are crucial inputs to soil food webs (Wardle, 2002). Soil organisms decompose and mineralize these inputs to CO_2, which is a central process for microbial ecosystems and soil carbon cycling (Jackson et al., 2017), and can impact atmospheric carbon concentrations and global warming (Cavicchioli et al., 2019; Schlesinger and Andrews, 2000; Zhou et al., 2012). Temperature has been acknowledged as a major driver of microbial activity and a principal determinant of SOM and litter mineralization (Curiel Yuste et al., 2007) with higher temperatures in general causing greater CO_2 production (Dieleman et al., 2012). On a timescale of months to years, higher temperatures increase SOM mineralization rates (Bradford et al., 2016), deplete pools of easily degraded SOM (Kirschbaum, 2006), and alter microbial communities (Frey et al., 2008). The long-term temperature history of a soil thus has an important influence on SOM and litter mineralization (Carrera et al., 2015). Responses to short-term temperature fluctuations as occur through diurnal cycles or weather are, however, poorly understood, despite these fluctuations being characteristic of virtually all soil habitats.

Previously reported dynamic effects of temperature change indicate that SOM mineralization can be affected by past temperatures. SOM mineralization at the same prevailing temperature can be enhanced by lower temperatures experienced in the past, demonstrated for contrasting temperature histories over seven days (Koepf, 1953) or 72 days (Wei et al., 2014). Mineralization responses to a given temperature depend on the period of time that the soil has experienced that temperature (Conant et al., 2011). Moreover, hysteresis in SOM mineralization has been reported during cycling between two temperatures, where mineralization is higher at a given temperature during the

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https://doi.org/10.1016/j.soilbio.2020.107985
Received 14 June 2020; Received in revised form 26 August 2020; Accepted 29 August 2020
Available online 1 September 2020

heating phase than during subsequent cooling (J. Li et al., 2017; Liu et al., 2018; Vargas and Allen, 2008). In hysteresis, higher mineralization during warming could be interpreted as a response to the preceding 'history' of lower temperatures, and vice-versa for cooling. Temperature history effects are often attributed to the depletion of labile SOM at higher temperatures (Bai et al., 2017; Kirschbaum, 2006; von Lützow and Kögel-Knabner, 2009), leaving more resistant material for mineralization during subsequent periods. Alternatively, soil microbial communities can acclimate to different temperatures (Bai et al., 2017; Bárcenas-Moreno et al., 2009; Bradford, 2013; Karhu et al., 2014; Wei et al., 2014), through mechanisms that include increased exoenzyme synthesis at lower temperatures to counteract reduced reaction rates (Burns et al., 2013), expression of isoenzymes with altered kinetics (Razavi et al., 2016; Stone et al., 2012), or changing community composition (Bai et al., 2017). It can be postulated, for example, that a low-temperature microbial community might acclimate by increasing exoenzyme synthesis. A temperature increase will then stimulate higher mineralization (as a result of the higher enzyme abundance) than occurs in a soil that has already experienced the higher temperature for a long period of time.

Prevailing temperature not only controls the mineralization of SOM, but also of plant litter, with higher temperatures typically increasing litter mineralization rates (Fierer et al., 2005; Lenka et al., 2019; Stewart et al., 2015; Thiessen et al., 2013). Wetterstedt et al. (2010) demonstrated, in the absence of soil, that litter decomposition is also sensitive to temperature history, with lower temperatures over several months leading to higher mineralization in subsequent periods. Moreover, the mineralization of litter and SOM can interact, as addition of litter often also accelerates the mineralization of pre-existing SOM, a phenomenon termed priming (Kuzyakov, 2010). Some studies report no or inconsistent effects of prevailing temperature on priming (Lenka et al., 2019; Luo et al., 2016; Thiessen et al., 2013), suggesting that temperature may have comparable effects on SOM and litter decomposition. However, how litter mineralization and priming depend on temperatures in the recent past has not been tested.

Litter and SOM mineralization are affected not only by abiotic factors such as temperature, but also by land management. In agricultural ecosystems, soils under organic management are known to host different microbial communities (Hartmann et al., 2015; Lupatini et al., 2019; Martínez-García et al., 2018), with higher microbial abundance and soil enzyme activities (Birkhofer et al., 2008; Flieβbach et al., 2007; García-Ruiz et al., 2008; Lori et al., 2017) than soils under conventional management. In addition, the quantity or quality of SOM can differ between organic and conventional management systems (Gattinger et al., 2012; Martínez-García et al., 2018). These outcomes of management can be attributed to higher inputs of organic fertilizer, and lower inputs of pesticides and herbicides in organic than in conventional agricultural systems (Flieβbach et al., 2007; F. Li et al., 2017). Changes in microbial composition and functioning and the quality of SOM may have consequences for how mineralization responds to temperature and temperature history (Conant et al., 2011; Fierer et al., 2005), but these effects are not yet well understood.

Here, we studied how short-term temperature history affects the mineralization of SOM and litter in conventionally and organically managed soils. Whereas most previous studies have added litter to soil before applying temperature treatments, and therefore could not unambiguously separate the effects of acclimation from differences in the depletion of labile litter compounds, we excluded depletion effects by adding litter only after re-establishing a standard temperature for all treatments (Carrera et al., 2015). We tested the hypotheses (i) that short-term differences in temperature history, here tested over eight days, would influence SOM mineralization after temperature differences were removed. In particular, we expected a history of lower temperature to elicit higher mineralization. We also hypothesized (ii) that this recent temperature history would similarly influence the mineralization of litter, with litter added after temperature differences were removed. Because all temperature treatments received the same litter composition at the start of mineralization measurements, this would indicate microbial acclimation rather than labile C depletion as the underlying mechanism. We further postulated that short-term acclimation would be reversible in the short term, and therefore hypothesized (iii) that history effects would subside within a week after temperature differences were removed. Finally, we explored how the responses to temperature history differed between organic and conventionally managed soils from a long-term agricultural experiment.

2. Materials and methods

2.1. Soil and site

Soil samples were collected from the Soil Health Treatment experiment at the Vredepeel agricultural experimental station of Wageningen University in May 2019 (51°32′27.6″N 5°50′55.7″E). The soil is a cultivated Gleyic Podzol with 1.1% clay, 3.7% silt and 94.9% fine sand (Boesten and van der Pas, 2000; Korthals et al., 2014). The field experiment has been running since 2006 and includes organic and conventional management plots (6 m × 6 m, 4 replicates) that differ in fertilization and pest and weed management, but receive the same cropping and tillage (Korthals et al., 2014). At the time of sampling, the plots were under a barley (*Hordeum vulgare*) cover crop, sown at the end of March following a winter fallow. A composite sample of five soil cores was collected from each plot (3 cm diameter, 20 cm deep) and kept cool during transport to the laboratory. Samples were sieved (4 mm), visible roots removed, and stored at 4 °C prior to the start of the experiment. Soil (25 g dry weight equivalent) was weighed into plastic centrifuge tubes for the preliminary (Stage 1) temperature treatments (12 tubes per plot).

2.2. Preliminary temperature treatments (stage 1)

Soil subsamples from each plot were randomly assigned to six different temperature regimes for eight days of preliminary incubation (Stage 1). The temperature treatments were as follows (Fig. 1): Temp4 was held constant at 4 °C, corresponding to the temperature at which soils are conventionally stored between field sampling and experimentation. Temp16 was constant at 16 °C, the mean daily maximum for the site in June, the month following sampling. Temp25 was constant at 25 °C, reflecting the higher end of daily maxima typically experienced at the site in June. Variable temperature treatments were Temp4_25 and Temp25_4, each including a step change after four days from one temperature to another, to test for path dependency; and TempDN, which simulated diurnal temperature oscillations between 10.4 and 21.1 °C (12 h each), the average daily minimum and maximum temperatures at the site in June. Open trays of water were placed inside incubation cabinets to maintain air humidity, and soil moisture was kept constant gravimetrically.

2.3. Main incubation and CO_2 measurement (stage 2)

Following Stage 1, all soil samples were equilibrated to a temperature of 16 °C for six hours and then transferred from the centrifuge tubes into airtight 500 mL plastic tubes with rubber septa fitted in their lids. Half of the tubes contained 15 mg of freeze-dried isotopically-labelled ryegrass litter (*Lolium perenne*; uniformly labelled 15.8 atom% ^{13}C, IsoLife, Wageningen, the Netherlands). All tubes were gently shaken to mix the transferred soil, closed, and the headspace flushed with air. Blank tubes were included to correct for atmospheric CO_2. The tubes were then randomly placed into the same incubator at 16 °C.

Twenty-four hours after litter addition, headspace gas was sampled with a syringe into pre-evacuated Exetainer vials (Labco, Lampeter, UK). Tubes were immediately returned to the incubator with lids slightly ajar to allow for gas exchange. The flushing, 24 h incubation, and sampling

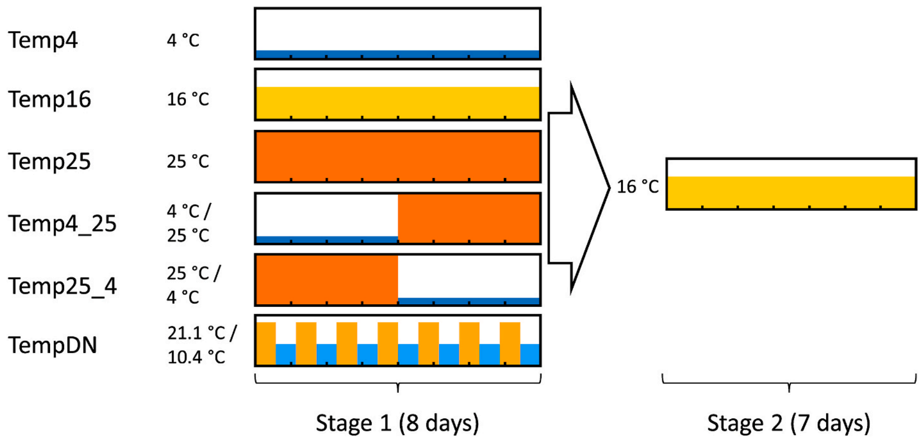

Fig. 1. Temperature pre-treatments over 8 days (Stage 1) after which all samples were returned to 16 °C for the main incubation (Stage 2).

process was repeated on day 4, and again on day 7. CO_2 concentrations were determined by gas chromatography with flame ionization detection on a Trace GC Ultra (Thermo Fischer Scientific, Waltham, USA). Isotopic abundance of $^{13}CO_2$ was determined by gas chromatography-isotope ratio mass spectrometry using a Trace GC Ultra coupled to a Delta V Advantage MS (Thermo Fischer Scientific, Waltham, USA).

2.4. Calculations and statistical analysis

Mineralization rates were calculated from headspace CO_2 concentrations by comparison with the soil-free blank microcosms, taking into account the soil mass, headspace volume, and time of incubation. Litter mineralization was calculated from total CO_2 efflux and CO_2 isotopic composition using a two-pool mixing model (Glaser et al., 2012). Four data points were removed as outliers, which were more than four standard deviations from the corresponding replicates and all single timepoints of different microcosms. Priming effects were calculated as the difference in mean SOM-derived CO_2 efflux with and without litter addition, with other factors the same. Cumulative mineralization was estimated by interpolating between CO_2 efflux measurements over time.

SOM-derived CO_2 efflux data from microcosms that did not receive litter was used to fit a linear mixed model with agricultural management, time, and Stage 1 temperature treatment as fixed factors, and field plot of origin as a random factor. Models were fitted using the lme4 package in R (Bates et al., 2015). Litter-derived CO_2 and priming effects were tested using a similar model, including data from microcosms that received litter in Stage 2. Homogeneity of variance was assessed by Levene's test in the car package (Fox and Weisberg, 2019). No evidence of non-normality of residuals was detected for SOM-derived CO_2 (Shapiro-Wilk test on residuals and inspection of QQ-plots). However, litter-derived CO_2 demonstrated tailing and was therefore log-transformed prior to fitting an analogous model. Cumulative CO_2 values for both SOM and litter were modelled separately without time as a factor and without transformation. Model parameter significance was tested with Satterthwaite's method and Type III sums of squares. Where effects were significant, pairwise post-hoc comparison of marginal means between the different temperature treatments was performed by Tukey HSD tests using the multcomp package (Hothorn et al., 2008). Statistical analysis was performed in R version 4.0.0 (R Core Team, 2020).

3. Results

The different temperature history treatments in Stage 1 altered CO_2 efflux in the subsequent common temperature incubation in Stage 2 (Fig. 2). Temperature treatment and the time of measurement affected SOM-derived CO_2 efflux from microcosms without litter addition ($F_{(5,101)} = 8.7$ and $F_{(2,101)} = 14$, respectively; both $p < 0.001$). Estimated effects of temperature treatments were all negative relative to Temp4, with Temp25 the strongest. For the constant temperature treatments (Temp4, Temp16 and Temp25), higher Stage 1 temperature tended to lower SOM-derived CO_2 efflux in Stage 2, although in post-hoc tests this was only statistically evident between Temp4 and Temp25 ($p < 0.001$), with a modelled effect size of 0.08 ± 0.06 μg $C.g^{-1}$. h^{-1} (family-wise 95% confidence interval). We did not find an effect of agricultural management ($F_{(1,6)} = 0.28$, $p = 0.61$) or interactions between temperature treatment, time or management. Temperature treatment also significantly affected cumulative SOM-derived CO_2 efflux ($F_{(5,29)} = 3.4$; $p = 0.015$), following the same pattern as the individual timepoints.

Stage 1 temperature treatments affected the mineralization of the litter added at the start of Stage 2 ($F_{(5,99)} = 4.8$, $p < 0.001$), although post-hoc tests could not distinguish significant pairwise differences. Litter-derived CO_2 efflux declined over the seven-day incubation (Fig. 3). We did not find interactions between Stage 1 temperature and management or between Stage 1 temperature and time ($F_{(5,99)} = 2.1$, $p = 0.068$ and $F_{(10,99)} = 0.58$, $p = 0.82$, respectively). An interaction between management and time was observed ($F_{(2,99)} = 3.4$, $p = 0.037$), but there were no significant post-hoc comparisons between management practices at any single timepoint. None of the treatments significantly affected cumulative litter mineralization ($F_{(5,27)} = 2.1$, $p = 0.10$ and $F_{(1,6)} = 1.9$, $p = 0.21$ for temperature and management, respectively).

Litter addition resulted in priming effects (Fig. 4), which shifted over time from strongly negative on the first day to neutral on day 4 and positive by the end of the week (main effect of time $F_{(2,98)} = 359$, $p < 0.001$). No significant effects of Stage 1 temperature or management were found for priming ($F_{(5,98)} = 0.50$, $p = 0.78$ and $F_{(1,6)} = 0.86$, $p = 0.39$, respectively), although an interaction between temperature treatment and management was found ($F_{(5,98)} = 359$, $p = 0.049$).

4. Discussion

Temperature is a principal determinant of SOM and litter mineralization, and all soils experience variations in temperature over time. Here we have shown that differences in short-term temperature history influenced the mineralization of both SOM and of freshly added litter, and that these effects persisted for at least a week after temperature differences had ended. These observations were for soils from a single site, but potentially represent general phenomena. Further experimentation will be necessary to verify these findings in other soils and land-use contexts.

In line with our first hypothesis, we found that a short-term history of lower temperatures (Stage 1) resulted in higher SOM mineralization in the seven-day measurement period of Stage 2. We showed that SOM mineralization was lower in soils with a history of 25 °C compared to

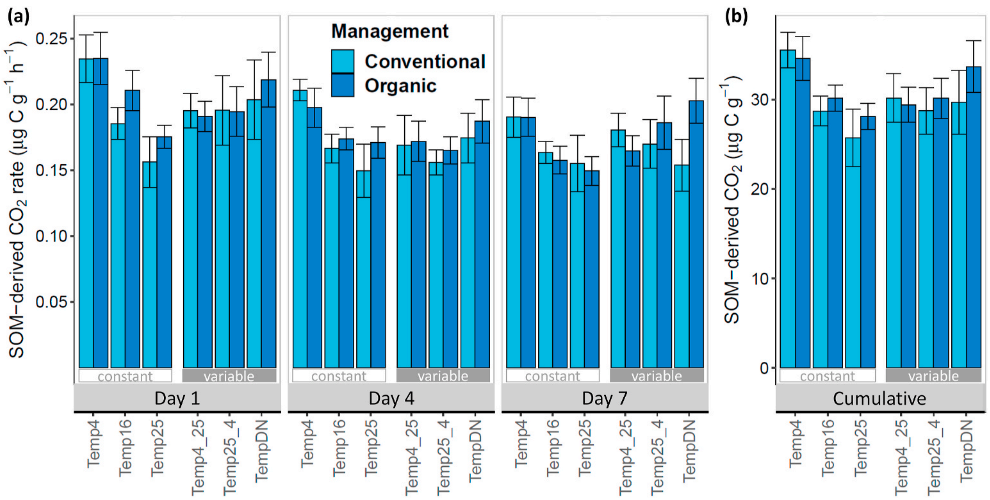

Fig. 2. SOM-derived CO_2 efflux in response to temperature history on the first, fourth and seventh day after returning soils to a common constant temperature of 16 °C (a) and the estimated cumulative production over this period (b). Temperature treatments over the preceding eight days were: Temp4, constant 4 °C; Temp16, constant 16 °C; Temp25, constant 25 °C; Temp4_25, four days at 4 °C followed by four days at 25 °C; Temp25_4, four days at 25 °C followed by four days at 4 °C; TempDN, day-night cycle between 21.1 and 10.4 °C. Error bars reflect standard errors of the mean (n = 4), with statistical comparisons described in the text.

4 °C and we found a decreasing trend in mineralization with increasing temperature across all three constant-temperature treatments. These results are in line with previous findings over different durations of temperature history (Koepf, 1953; Wei et al., 2014). In support of our second hypothesis, we found that temperature history also affected litter mineralization, although these effects were not as clear as for SOM mineralization. Temperature history therefore affected not only the mineralization of SOM that itself had experienced this history, but also influenced the mineralization of fresh organic matter that entered the soil only after temperature differences had ended. This suggests that temperature history effects in our experiment were not driven by differential depletion of labile organic compounds during the contrasting temperature treatments (Kirschbaum, 2006), because the newly added litter still contained all such compounds. Our findings do suggest that microbial acclimation plays a key role in driving litter mineralization (Bradford, 2013; Carrera et al., 2015): microbial decomposers were still under the influence of their temperature history, and therefore degraded the litter at different rates. Therefore, even on a short timescale of days, temperature history can drive microbial acclimation, with consequences for subsequent mineralization of organic compounds in soils. In contrast to the temperature history effects on mineralization, we did not find an effect on priming. This is consistent with SOM and litter mineralization being similarly affected by temperature history, without altering their interaction (Thiessen et al., 2013).

Neither SOM nor litter mineralization were much affected by the variable temperature treatments. Instead, the mineralization patterns of these treatments resembled the constant 16 °C treatment, to which they were closest in time-averaged mean temperature. Previous studies have reported divergent effects of short-term (e.g. diurnal) temperature cycles relative to constant temperatures (Akbari and Ghoshal, 2015; Bai et al., 2017; Chang et al., 2011; Zhu and Cheng, 2011), but interpreting these results is often complicated by the choice of reference temperature (e.g., mean versus maximum of the cycle) and the timing of CO_2 measurement. The comparison of our treatments was simplified because all soils were incubated at the same, constant temperature during Stage 2. Our results suggest that, on a timescale of days, mean temperature has a stronger influence on future soil responses than the short-term temporal temperature pattern. Verifying such principles of short-term behaviour may help to understand soil responses to climate change, which is impacting not only long-term climate averages but also daily weather patterns (Sippel et al., 2020).

In contrast to our third hypothesis that temperature history effects would subside within a week after temperature differences were removed, we found that SOM mineralization showed no significant interaction between temperature treatment in Stage 1 and measurement time in Stage 2. Thus, although microbial acclimation could occur in just 8 days, these effects were not readily reversible and persisted for at least a week after temperature differences had been removed. While seasonal and climatic differences are already recognized as key drivers of mineralization (Wardle, 2002), this finding suggests that it may also be important to take recent weather or temperature fluctuations into account. For example, field comparisons between different locations or timepoints should avoid strongly contrasting weather histories, since these differences could introduce variability, and potentially even bias, to measurements of mineralization. Temperature in laboratory experiments is typically more precisely controlled than in the field, and initial pre-incubation is common to avoid artefacts from soil handling. However, pre-incubation periods are often less than a week, which may impact the accuracy of subsequent soil respiration measurements. Also, storing samples at 4 °C between field sampling and experimentation may have a lasting effect on soil respiration after a return to field temperatures. Our results suggest that longer pre-incubations than generally used may be necessary to counteract the influence of short-term temperature history, especially in experiments involving soils that have recently experienced different conditions.

Neither mineralization nor its response to temperature history differed between organic and conventionally managed soils. The moderately significant management × time interaction for litter mineralization likely arose from slightly different effect sizes for time, rather than a strong direct influence of management. This was unexpected, considering that these agricultural systems are known to have substantially different microbial communities (Lori et al., 2017), including at the experimental site from which the soils for this study were collected (Lupatini et al., 2019; Martínez-García et al., 2018). The similar responses between organic and conventional soils could be due to the similar SOM contents of the two management systems, even after a 13-year difference in management (Martínez-García et al., 2018). Alternatively, despite differences in taxonomic composition, the functional redundancy of soil microbial communities might enable different communities to maximize the utilization of these carbon resources within the limits imposed by abiotic conditions (Allison and Martiny, 2008; Louca et al., 2018).

5. Conclusions

Mineralization of both SOM and newly added litter are sensitive to the temperature regime experienced by the soil in the preceding eight days. Lower mean temperatures during preliminary treatment were associated with higher mineralization during the subsequent common-temperature incubation. The history sensitivity of litter mineralization, with litter added after temperature differences had ended, provides evidence of short-term microbial acclimation to temperature.

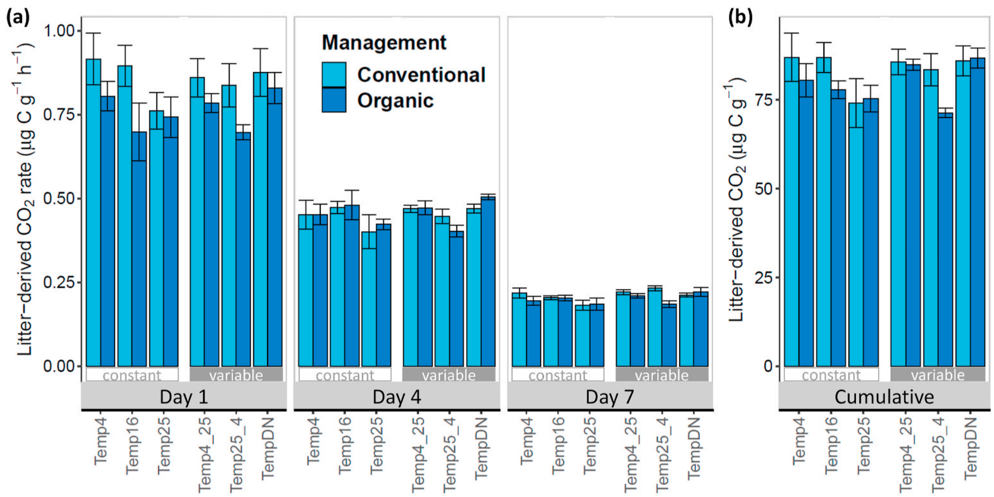

Fig. 3. Litter-derived CO_2 production in response to temperature history on the first, fourth and seventh day after returning pre-incubated soil to a common constant temperature of 16 °C and adding ^{13}C-labelled litter (a) and the estimated cumulative production over this period (b). Temperature treatments over the preceding eight days were: Temp4, constant 4 °C; Temp16, constant 16 °C; Temp25, constant 25 °C; Temp4_25, four days at 4 °C followed by four days at 25 °C; Temp25_4, four days at 25 °C followed by four days at 4 °C; TempDN, day-night cycle between 21.1 and 10.4 °C. Error bars reflect standard errors of the mean (n = 4), with statistical comparisons described in the text.

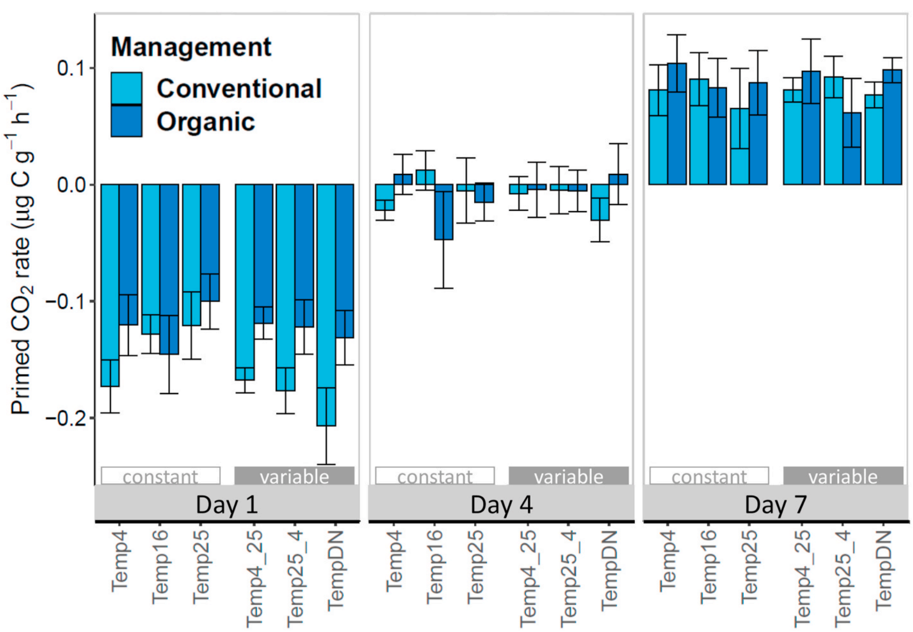

Fig. 4. Primed CO_2 efflux in response to temperature history on the first, fourth and seventh day after returning pre-incubated soil to a common constant temperature of 16 °C. Temperature treatments over the preceding eight days were: Temp4, constant 4 °C; Temp16, constant 16 °C; Temp25, constant 25 °C; Temp4_25, four days at 4 °C followed by four days at 25 °C; Temp25_4, four days at 25 °C followed by four days at 4 °C; TempDN, day-night cycle between 21.1 and 10.4 °C. Error bars reflect standard errors of the mean (n = 4), with statistical comparisons described in the text.

Furthermore, effects of temperature history can persist for at least a week, indicating that SOM and litter mineralization rates may be dependent on recent weather conditions. Thirteen years of different agricultural management (conventional or organic) did not affect SOM or litter mineralization. We conclude that organic matter mineralization, a key process in the carbon cycle, is sensitive to short-term temperature history. We suggest that future investigations of litter decomposition and soil CO_2 efflux take short-term dynamic temperature effects into consideration, as well as determine how these phenomena will respond to the weather extremes predicted under global change.

Declaration of competing interest

The authors declare that they have no known competing interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Many thanks to Gerard Korthals, both for the use of the Soil Health Treatment experiment and for his contributions to the Vital Soils project. Thank you also to Johnny Visser and Harry Verstegen for arranging access to the Vredepeel experimental farm, and to Hans Zweers for his assistance with CO_2 measurements at the NIOO. We gratefully acknowledge the NWO for funding of the Vitals Soils project under the 'Programma NWO Groen 2015' (ALWGR. 2015.5).

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