RESEARCH ARTICLE

Differences in SOM Decomposition and Temperature Sensitivity among Soil Aggregate Size Classes in a Temperate Grasslands

Qing Wang1,2, Dan Wang1, Xuefa Wen2, Guirui Yu2, Nianpeng He2*, Rongfu Wang1*

1 Resources and Environment College, Anhui Agricultural University, Hefei, China, 2 Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

* henp@igsnrr.ac.cn (NH); rfwang@ahau.edu.cn (RW)

Abstract

The principle of enzyme kinetics suggests that the temperature sensitivity ($Q_{10}$) of soil organic matter (SOM) decomposition is inversely related to organic carbon (C) quality, i.e., the C quality-temperature (CQT) hypothesis. We tested this hypothesis by performing laboratory incubation experiments with bulk soil, macroaggregates (MA, 250–2000 μm), microaggregates (MI, 53–250 μm), and mineral fractions (MF, <53 μm) collected from an Inner Mongolian temperate grassland. The results showed that temperature and aggregate size significantly affected SOM decomposition, with notable interactive effects ($P<0.0001$). For 2 weeks, the decomposition rates of bulk soil and soil aggregates increased with increasing incubation temperature in the following order: MA > MF > bulk soil > MI ($P<0.05$). The $Q_{10}$ values were highest for MA, followed (in decreasing order) by bulk soil, MF, and MI. Similarly, the activation energies ($E_a$) for MA, bulk soil, MF, and MI were 48.47, 33.26, 27.01, and 23.18 KJ mol$^{-1}$, respectively. The observed significant negative correlations between $Q_{10}$ and C quality index in bulk soil and soil aggregates ($P<0.05$) suggested that the CQT hypothesis is applicable to soil aggregates. Cumulative C emission differed significantly among aggregate size classes ($P<0.0001$), with the largest values occurring in MA (1101 μg g$^{-1}$), followed by MF (976 μg g$^{-1}$) and MI (879 μg g$^{-1}$). These findings suggest that feedback from SOM decomposition in response to changing temperature is closely associated with soil aggregation and highlights the complex responses of ecosystem C budgets to future warming scenarios.

Introduction

Soil aggregates play important roles in maintaining soil structure, fertility, and stability, and in influencing the decomposition dynamics of soil organic matter (SOM) [1–3]. Soil aggregates store large quantities of SOM [1,2], and therefore the distribution of SOM within aggregates is
Temperature is one of the most important factors influencing SOM decomposition, and is considered to be positively correlated with the decomposition rate of SOM. Under global warming scenarios, the response of SOM decomposition in different soil aggregates to temperature change is unquestionably important for predicting the global pattern and magnitude of soil carbon storage in the future.

The temperature sensitivity ($Q_{10}$) of SOM decomposition can be depicted by exponential models and Arrhenius models. Exponential models better reflect the effects of temperature on SOM decomposition, whereas Arrhenius models provide mechanistic explanations for SOM decomposition and $Q_{10}$. Recently, there has been a common assertion that the composition of SOM can affect the temperature sensitivity of SOM decomposition; however, experimental and model evidence have not been presented. Some studies have included a series of incubation experiments to investigate the effect of soil aggregation on SOM decomposition, but the results were inconsistent. Manna et al. demonstrated that macroaggregates (250–2000 μm) were dominant in the decomposition process of SOM; however, other studies have indicated that microaggregates (53–250 μm) or mineral fractions (<53 μm) are more important. Understanding the differences in SOM decomposition and its temperature sensitivity in different soil aggregates is therefore essential to accurately assess the effects of future warming on soil C storage.

The principle of enzyme kinetics suggests that the $Q_{10}$ value of SOM decomposition is controlled by the C quality of substrates utilized by microorganisms, and that a higher activation energy ($E_a$) is required to mineralize low-quality C substrates (C quality-temperature [CQT] hypothesis). The CQT hypothesis have been confirmed by the data of soil incubation experiments. However, the CQT hypothesis has not been experimentally tested for different soil aggregates with different C qualities resulting from different physical and chemical protective mechanisms.

In this study, incubation experiments were performed using soils of typical temperate grassland in Inner Mongolia, to assess the SOM decomposition and temperature sensitivity in different-sized aggregates (macroaggregates, microaggregates, and mineral fractions) and to test the CQT hypothesis. The main objectives of this study were to investigate (i) how decomposition of SOM varies among aggregate size and temperature; (ii) how $Q_{10}$ values differ among soil aggregates; and (iii) whether CQT hypothesis is appropriate for soil aggregates.

Materials and Methods

Study sites

Soil samples were collected from typical temperate grassland at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences (43°33′17.33″N, 116°40′32.44″E). This region is characterized by a semi-arid continental climate with mean annual precipitation of 345 mm and mean annual temperature of 1.1°C. The soil is classified as Calci Chernozem with loamy sand texture. The experimental plot was established at IMGERS in 1999 by fencing off a section of grassland that was previously open to free grazing by sheep and cattle. The predominant vegetation consists of grasses, including Leymus chinensis, Stipa grandis, and Cleistogenes squarrosa.

Sampling and pretreatment

Soil samples (0–20 cm depth layer) were randomly collected from 10 locations in the long-term experimental plot. In the laboratory, we manually removed roots and visible organic debris from the samples. After sieving (<2-mm mesh), approximately 100 g of soil from each sample was air-dried for analysis of basal properties, including C content, nitrogen (N) content.
and pH. The C and N contents of bulk soil and aggregates were measured using an elemental analyzer (Elementar vario max, Germany). Soil pH was determined using a pH meter (Mettler Toledo Delta 320, Switzerland) in a slurry of soil and distilled water (1:2.5).

The soil water holding capacity (WHC, %) of the soil and aggregates were measured by oven drying. The remaining soil was stored at 4°C. All samples were pre-sieved (2 mm diameter) prior to wet-sieving to remove stones and coarse organic matter and to define the initial dimensions of the aggregates for analysis. Water-stable aggregates were separated using two sieves similar in principle to a Yoder wet-sieving apparatus. The apparatus was modified to handle stacked sieves and to enable complete recovery of all particle fractions from individual samples [20]. Fresh soils were shaken for 2 min in two sieves (250 and 53 μm diameter) to generate three aggregate fractions: macroaggregates (MA, 250–2000 μm), microaggregates (MI, 53–250 μm), and mineral fractions (MF, <53 μm) [2].

Experimental design

Two incubation experiments were performed.

Experiment I was designed to investigate the difference in the temperature sensitivity of SOM decomposition among soil aggregates. In brief, 40-g samples of fresh bulk soil or aggregates, adjusted to 60% WHC, were placed into incubation bottles (5 cm diameter, 10 cm height) and mixed with 10 g of quartz sand. The soil samples were then pre-incubated at 20°C and constant humidity (80%) for 1 week. The samples were then incubated at different temperatures (5, 10, 15, 20, and 25°C) for 2 weeks (n = 3; for each temperature treatment), and SOM decomposition rates were measured six times, at 0, 1, 3, 5, 7, and 14 d.

Experiment II was designed to examine differences in decomposition over long-term incubation among aggregates. Soil samples (40 g of fresh soils or aggregates, adjusted to 60% WHC and mixed with 10 g of quartz sand) were pre-incubated at 20°C and 80% humidity for 1 week and then placed into incubation bottles (25°C). During the 169-d incubation, the SOM decomposition rate at 25°C was measured 14 times, on days 0, 1, 3, 5, 7, 14, 21, 28, 35, 42, 49, 56, 84, 112, 140, and 169.

SOM decomposition rates were measured using an automatic system, which was modified from the continuous gas flow system of Cheng and Virginia [21]. This system consisted of a Li-COR CO2 analyzer (Li-7000), an electric water bath to control incubation temperature, an airflow controller, soda-line equipment to control the initial CO2 concentration, an auto-sampler on a turn-plate, automatic transformation valves to control the sample bottle, and a data collector, which was the same as the equipment of He et al. [22].

Calculation method

The SOM decomposition rates was calculated from the slope of the CO2 concentration and conversion factors as follows:

\[ R = \frac{C \times V \times \alpha \times \beta}{m} \]  

where \( R \) is SOM decomposition rate (μg C g\(^{-1}\) h\(^{-1}\)); \( C \) is the slope of the change in CO2 concentration; \( V \) is the volume of the incubation bottle and gas tube; \( m \) is the soil weight (g); \( \alpha \) is the conversion coefficient for CO2 mass; and \( \beta \) is a conversion coefficient of time.
The $Q_{10}$ of SOM decomposition was calculated using the following exponential equations [23]:

$$R = A \times e^{bT} \quad (2)$$

$$Q_{10} = e^{10b} \quad (3)$$

where $R$ is SOM decomposition rate ($\mu$C g$^{-1}$ h$^{-1}$), $T$ is temperature ($°C$), and $A$ and $b$ are the exponential fit parameters that describe the intercept and slope of the line, respectively.

According to the Arrhenius equation, $SR$ is a function of a pre-exponential parameter ($A$), the activation energy ($E_a$), the gas constant $R$ and temperature ($T$)(Eq. 4). Eq. 5 was used to assess the relationship between $E_a$ and $Q_{10}$, derived from Eq. 4 [23].

$$R = A \times e^{E_a/RT} \quad (4)$$

$$E_a = R \times \frac{ln(Q_{10})}{ \frac{1}{T_1} - \frac{1}{T_2} } \quad (5)$$

where $R$ is the gas constant (8.314 J mol$^{-1}$) and $T_1$ and $T_2$ are temperatures (K) indicating the 10°C temperature range for the corresponding $Q_{10}$ (i.e., $T_1 + 10 = T_2$). In calculating $E_a$, it was assumed that $Q_{10}$ represented the range $T-5$ to $T+5$, where $T$ was the average incubation temperature.

**Statistical analysis**

One-way ANOVA and the least significant difference method (LSD) were used to explore the effects of aggregate size, incubation temperature, and their interactions on SOM decomposition. Regression analyses were used to evaluate the relationships between the C quality index and $Q_{10}$ and $E_a$. Differences were considered significant at $P<0.05$. All statistical analyses were conducted using SPSS 13.0 for windows (SPSS Inc., Chicago, IL, USA).

**Results**

**Soil properties**

The C and N content and C:N ratios differed significantly ($P<0.0001$) among bulk soil and aggregates (Table 1). The highest C content was observed in MA, and the lowest in bulk soil and MI; the similar trends were also observed for N content. The C:N ratio increased with increasing aggregate size.

|                | Total carbon content(%) | Total nitrogen content(%) | C:N ratio        |
|----------------|-------------------------|---------------------------|------------------|
| Bulk soil      | 1.855 (0.013)$^a$       | 0.175 (0.007)$^b$         | 10.611 (0.356)$^b$ |
| MA: 250–2000 μm| 2.089 (0.027)$^b$       | 0.182 (0.013)$^b$         | 11.546 (0.774)$^b$ |
| MI: 53–250 μm  | 1.383 (0.006)$^d$       | 0.148 (0.008)$^c$         | 9.343 (0.502)$^c$ |
| MF: <53 μm     | 2.268 (0.011)$^c$       | 0.247 (0.016)$^a$         | 9.200 (0.625)$^c$ |
| $F$            | 1986.467                | 49.256                    | 15.316           |
| $P$            | <0.0001                 | <0.0001                   | <0.0001          |

MA, macroaggregates; MI, microaggregates; MF, mineral fraction. Data are means (SD) ($n=3$); data with different superscript letters within a column are significantly different at $P<0.05$.  

doi:10.1371/journal.pone.0117033.t001
Decomposition rate and temperature sensitivity

Temperature and aggregate size had a significant influence on SOM decomposition rates, with notable interactive effects \( (P<0.0001) \). In addition, the \( Q_{10} \) values of SOM decomposition calculated using either the exponential model or the Arrhenius model differed significantly among aggregate sizes (Fig. 1, S1 Fig., Table 2), ordered as follows: MA > MF > bulk soil > MI. We also found that the differences in \( Q_{10} \) values decreased with increasing temperature \( (F = 299.98, P<0.0001) \) (Fig. 2, Table 3). Significant negative correlations were observed between \( Q_{10} \) and the C quality index \( (P = 0.001, \text{Fig. 3, S2 Fig.)} \). Similarly, negative correlations were observed between \( Q_{10} \) values and \( E_a \) \( (F = 374.43, P<0.0001, \text{Table 3}) \), which is consistent with the CQT hypothesis.

Cumulative C emission

Aggregate size significantly influenced cumulative C emission \( (F = 269.89, P<0.0001) \), with the highest values occurring in MA and the lowest in MI (Fig. 4). Differences in cumulative C

Table 2. Parameters for the empirical exponential equation of SOM decomposition.

| Aggregate Size          | \( A (\text{mg kg}^{-1} \text{d}^{-1}) \) | \( b \) | \( R^2 \) | \( Q_{10} \)          |
|------------------------|----------------------------------------|--------|--------|----------------------|
| Bulk soil              | 3.071 (0.101)                          | 0.048 (0.002) | 0.910 | 1.618 (0.028)\(^b\)  |
| MA, 250–2000 \( \mu \)m| 2.450 (0.070)                          | 0.070 (0.002) | 0.879 | 2.001 (0.031)\(^a\)  |
| MI, 53–250 \( \mu \)m    | 3.957 (0.042)                          | 0.033 (0.001) | 0.789 | 1.400 (0.008)\(^d\)  |
| MF, <53 \( \mu \)m         | 4.759 (0.094)                          | 0.039 (0.002) | 0.806 | 1.474 (0.026)\(^c\)  |
| \( F \)                |                                        |        |        | 354.698              |
| \( P \)                |                                        |        |        | <0.0001              |

MA, macroaggregates; MI, microaggregates; MF, mineral fraction. Data are means (SD) \( (n = 3) \); data with different superscript letters within a column are significantly different at \( P<0.05 \). \( A \) and \( b \) are the exponential fit parameters describing the intercept and slope, respectively. \( Q_{10} \) is the temperature sensitivity of SOM decomposition.

doi:10.1371/journal.pone.0117033.t002
emission increased with increasing incubation time, although the decomposition rate decreased for all soil aggregates.

Discussion

Decomposition of soil aggregates

Aggregate size had a significant influence on SOM decomposition. However, the decomposition rate of SOM still varied among soil aggregates. Some studies have found that SOM decomposition rates generally decrease with decreasing aggregate size [3,24], and that MA contains a greater proportion of decomposable C than whole soil [25]. However, others have reported that MI is a higher decomposition rate than MA [11,26]. The present results show that MA contains more organic C than MI (Table 1), which supports the concept of aggregate size classes [27,28]. Differences in organic C content among soil aggregates may result in the variability of cumulative C emission. One plausible explanation is that particulate organic matter in MA can

![Fig 2. Relationship between temperature sensitivity ($Q_{10}$) and incubation temperature. The $Q_{10}$ values were calculated using the Arrhenius equation.](image)

doi:10.1371/journal.pone.0117033.g002

Table 3. Temperature sensitivity ($Q_{10}$) and activation energy ($E_a$) for different aggregate size classes calculated using the Arrhenius equation.

| Temperature range (°C) | Temperature sensitivity ($Q_{10}$) | Activation energy ($E_a$) |
|------------------------|-----------------------------------|--------------------------|
|                        | 5–15°C | 10–20°C | 15–25°C | Mean (SD) | 5–15°C | 10–20°C | 15–25°C | Mean (SD) |
| Bulk soil              | 1.815 (0.128)$^b$ | 1.372 (0.068)$^{bc}$ | 1.569 (0.062)$^a$ | 1.586 (0.032)$^b$ | 33.258 (1.205)$^b$ |
| MA, 250–2000 μm        | 3.349 (0.309)$^a$ | 1.866 (0.144)$^a$ | 1.261 (0.062)$^b$ | 2.169 (0.053)$^a$ | 48.467 (0.979)$^a$ |
| MI, 53–250 μm          | 1.923 (0.017)$^b$ | 1.214 (0.053)$^c$ | 1.090 (0.046)$^c$ | 1.409 (0.007)$^c$ | 23.178 (0.399)$^d$ |
| MF, <53 μm             | 2.098 (0.012)$^b$ | 1.424 (0.041)$^b$ | 1.055 (0.033)$^c$ | 1.526 (0.023)$^b$ | 27.009 (1.184)$^d$ |

$^a$ MA, macroaggregates; MI, microaggregates; MF, mineral fraction. Data are means (SD) ($n=3$); data with different superscript letters within a column are significantly different at $P<0.05$.

doi:10.1371/journal.pone.0117033.t003
decompose into MI, which contains less organic C [17]. Moreover, the soil C:N ratio of the aggregates, as one of the indicators of the degradability of SOM, increases with increasing aggregate size [29], which results in the higher cumulative C emission in MA [30]. However, some studies have demonstrated that soils with lower C:N ratios generally have higher CO2 production up to a certain threshold [23,31].

Our findings show that C emissions are derived mainly from MA during relatively short-term incubation (56 d) and from MF during longer-term (more than 56 d) incubation, which is consistent with the findings of Christensen [32]. Dou et al. demonstrated that the condensation and molecular complexity of humic acids decrease with increasing aggregate size, accompanied by an increase in activation grade [33]. Although recent studies have suggested that
recalcitrant molecules (e.g., lignin) contribute minimally to the long-term stability of SOM, except for somechar [34–36], the substrate molecular structure remains a critical factor during the early stages of SOM decomposition where the substrate is inaccessible to microbes. Moreover, the soil microbial biomass varies among aggregates of different particle sizes, with greater values generally observed in MA [37].

Temperature sensitivity related to aggregate size

Aggregate size had a significant effect on the temperature sensitivity of SOM decomposition. The most widely models for different SOM pools use fixed $Q_{10}$ values of 1.5–2 [38–42]. In the present study, the $Q_{10}$ values ranged from 1.4 to 2.2, which is similar to the results of previous incubation experiments [43–46]. On the basis of thermodynamic principle, the decomposition rates of SOM in different aggregates were more sensitive to lower temperature than to higher temperature [47]. Here, the maximum $Q_{10}$ value was observed for MA, from 5 to 15°C. In contrast, Tan et al. reported that the maximum $Q_{10}$ value occurred in MI [3]. These inconsistent results indicate that complex mechanisms control the temperature sensitivity of SOM decomposition, which depended on organic-mineral interactions [48–50], the quality and structure of the SOM [15,49], and other environmental factors, e.g., moisture [51].

Our findings show that MA and MF have higher $Q_{10}$, implying that they will be more sensitive to future climate warming and could generate a positive feedback for global warming. The variability in $Q_{10}$ and its dependence on aggregate size have important implications for regional and global ecosystem C modeling, specifically for predicting the response of terrestrial ecosystems to future global warming. Experiments have been conducted to explore the temperature sensitivity of the SOM decomposition of different aggregates and its underlying mechanisms, including substrate availability [6], physical and chemical protection [32], and microbial activity [52]. Craine et al. demonstrated that C quality was particularly important for the temperature sensitivity of SOM decomposition [41]. Inconsistent findings have been reported, including increases [53,54], no change [5,39], or decreases [55,56] in the $Q_{10}$ of SOM decomposition with increasing C quality. In the future, it will therefore be essential to investigate the important physical and chemical factors controlling SOM decomposition in different aggregates.

Similarly to other studies [41,57–59], we also observed that $Q_{10}$ and $E_a$ were both inversely related to this index. These findings are consistent with the CQT hypothesis [55], which proposes that the decomposition of low-quality SOM requires higher $E_a$ and is more sensitive to temperature than the degradation of high-quality SOM [9,59]. The present results provide new evidence that the CQT hypothesis is applicable to soil aggregates. The robust CQT relationship [41] deserves more detailed examination, because it may be used to improve models for predicting the SOM response to anticipated warming. As proposed by Wagai et al. [49], some issues for better understanding the CQT hypothesis need to be addressed in the future by (i) providing a better definition of “C quality” based on the actual molecular structure of organic compounds in soil; (ii) distinguishing the active or microbial accessible fraction from bulk SOM; and (iii) simultaneously assessing the temperature effect on easily soluble C pools and microbial biomass C in addition to microbial respiration.

Conclusion

The decomposition rates of SOM and the corresponding $Q_{10}$ values differed remarkably among aggregate sizes, and both increased with aggregate size. $Q_{10}$ and $E_a$ were inversely correlated with organic C quality in different soil aggregates, supporting the CQT hypothesis with respect to soil aggregate classes. Therefore, future research on the relationship between SOM
decomposition and C quality should consider not only C quality with different incubation times and different SOM, but also soil physical propertiesto explore internal mechanisms controlling the decomposition rates of SOM in aggregates, and their temperature sensitivity. Moreover, differences in SOM decomposition rates and temperature sensitivity are important and should be incorporated into models to improve prediction in the future.

Supporting Information
S1 Fig. Energy of activation ($E_a$) of SOM decomposition for different aggregate size fractions. Values are the mean ($n = 3$); bars indicate the SD. Different letters indicate a significant differences at $P < 0.05$.

(TIF)

S2 Fig. Relationship between energy of activation ($E_a$) and SOC quality. $E_a$ was calculated by the Arrhenius equation and SOC quality was calculated by the exponential equation. Values are the mean ($n = 3$); bars indicate the SD.

(TIF)

S1 File. Data of SOM decomposition rates for PONE-D-14-18377.

(XLSX)

Author Contributions
Conceived and designed the experiments: QW NH RW. Performed the experiments: QW DW. Analyzed the data: QW XW. Contributed reagents/materials/analysis tools: XW GY. Wrote the paper: QW NH.

References
1. Wang X, Yost RS, Linquist BA (2001) Soil aggregate size affects phosphorus desorption from highly weathered soils and plant growth. American Journal of Soil Science Society 65: 139–146.
2. De Gryze S, Six J, Brits C, Merckx R (2005) A quantification of short-term macroaggregate dynamics: influences of wheat residue input and texture. Soil Biology & Biochemistry 37: 55–66. doi:10.1016/j.canlet.2015.01.036 PMID: 25641340
3. Tan WB, Zhou LP, Liu KX (2013) Soil aggregate fraction-based $^{14}$C analysis and its application in the study of soil organic carbon turnover under forests of different ages. Chinese Science Bulletin 58: 1936–1947.
4. Yamashita T, Flessa H, John B, Helfrich M, Ludwig B (2006) Organic matter in density fractions of water-stable aggregates in silty soils: Effect of land use. Soil Biology & Biochemistry 38: 3222–3234. doi:10.1016/j.canlet.2015.01.036 PMID: 25641340
5. Fang CM, Moncrieff JB, Smith JU (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433: 57–59. PMID: 15635408
6. Gershenzon A, Bader NE, Cheng WX (2009) Effects of substrate availability on the temperature sensitivity of soil organic matter decomposition. Global Change Biology 15: 176–183.
7. Thiessen S, Gleixner G, Wutzler T, Reichstein M (2013) Both priming and temperature sensitivity of soil organic matter decomposition depend on microbial biomass—An incubation study. Soil Biology & Biochemistry 57: 739–748. doi:10.1016/j.canlet.2015.01.036 PMID: 25641340
8. Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165–173. PMID: 16525463
9. Sierra CA (2012) Temperature sensitivity of organic matter decomposition in the Arrhenius equation: some theoretical considerations. Biogeochemistry 108: 1–15.
10. Manna MC, Bhattacharyya P, Adhya TK, Singh M, Wanari PH, et al. (2013) Carbon fractions and productivity under changed climate scenario in soybean–wheat system. Field Crops Research 145: 10–20.
26. Seech AG, Beauchamp EG (1988) Denitrification in soil aggregates of different sizes. America Journal of Soil Science 50: 627–633.

27. Tisdall JM, Oades JM (1982) Organic matter and water-stable aggregates in soils. Journal of Soil Science 33: 141–163.

28. Elliott ET (1986) Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. America Journal of Soil Science Society 50: 627–633.

29. Qin SP, Hu CS, He Y, Dong WX, Cui JF, et al. (2010) Soil organic carbon, nutrients and relevant enzyme activities in particle-size fractions under conservational versus traditional agricultural management. Applied Soil Ecology 45: 152–159.

30. Zhang WD, Wang XF, Wang SL (2013) Addition of external organic carbon and native organic carbon decomposition: a meta-analysis. Plos One 8: e54779, doi:54710.51371/journal.pone.0054779 PMID: 23405095

31. Riffaldi RSA, LeviMinzi R (1996) Carbon mineralization kinetics as influenced by soil properties. Biology and Fertility of Soils 22: 293–298.

32. Christensen BT (2001) Physical fractionation of soil and structural and functional complexity in organic matter turnover. European Journal of Soil Science 52: 345–353.
33. Dou SZ, Xu XC (1992) Study on organic matter characteristic in different particle-size microaggregates under brown soil. Chinese Journal of Soil Science 22: 52–54.

34. Dungait JAJ, Hopkins DW, Gregory AS, Whitmore AP (2012) Soil organic matter turnover is governed by accessibility not recalcitrance. Global Change Biology 18: 1781–1796.

35. Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, et al. (2011) Persistence of soil organic matter as an ecosystem property. Nature 478: 49–56. doi: 10.1038/nature10386 PMID: 21979045

36. Kleber M, Nico PS, Plante A, Filley T, Kramer M, et al. (2011) Old and stable soil organic matter is not necessarily chemically recalcitrant: implications for modeling concepts and temperature sensitivity. Global Change Biology 17: 1097–1107.

37. Chiu CY, Imberger K, Tian GL (2006) Particle size fractionation of fungal and bacterial biomass in subalpine grassland and forest soils. Geoderma 130: 265–271.

38. Fang C, Moncrieff JB (2001) The dependence of soil CO₂ efflux on temperature. Soil Biology & Biochemistry 33: 155–165. doi: 10.1016/j.soilbio.2001.03.036 PMID: 25641340

39. Conen F, Seth B, Alewell C (2006) Warming mineralises young and old soil carbon equally. Biogeosciences 3: 515–519.

40. Davidson EA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165–173. PMID: 16525463

41. Craine JM, McLaughlan KK (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. Nature Geoscience 3: 854–857.

42. Hamdi S, Sall S, Bernoux M, Chevallier T (2013) Synthesis analysis of the temperature sensitivity of soil respiration from laboratory studies in relation to incubation methods and soil conditions. Soil Biology & Biochemistry 58: 115–126. doi: 10.1016/j.soilbio.2015.01.036 PMID: 25641340

43. Lloyd J (1994) On the temperature dependence of soil respiration. Functional Ecology 8: 315–323.

44. Kätterer T, Andrén O, Lomander A (1998) Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models. Biology and Fertility of Soils 27: 258–262.

45. Boddy E, Roberts P, Hill PW, Farrar J, Jones DL (2008) Turnover of low molecular weight dissolved organic C (DOC) and microbial C exhibit different temperature sensitivities in Arctic tundra soils. Soil Biology & Biochemistry 40: 1557–1566. doi: 10.1016/j.soilbio.2008.04.017 PMID: 18527196

46. Farrar J, Hill PW, Jones DL (2012) Discrete functional pools of soil organic matter in a UK grassland soil are differentially affected by temperature and priming. Soil Biology & Biochemistry 49: 52–60. doi: 10.1016/j.soilbio.2012.03.017 PMID: 25641340

47. Timothy GW, Michael DM (2013) Native temperature regime influences soil response to simulated warming. Soil Biology & Biochemistry 60: 202–209. doi: 10.1016/j.soilbio.2015.01.036 PMID: 25641340

48. Creamer CA, Filley TR, Boutton TW (2013) Long-term incubations of size and density separated soil fractions to inform soil organic carbon decay dynamics. Soil Biology & Biochemistry 57: 496–503. doi: 10.1016/j.soilbio.2015.01.036 PMID: 25641340

49. Wagai R, Kishimoto-Mo AW, Yonemura S, Shirato Y, Hiradate S, et al. (2013) Linking temperature sensitivity of soil organic matter decomposition to its molecular structure, accessibility, and microbial physiology. Global Change Biology 19: 1114–1125. doi: 10.1111/gcb.12112 PMID: 23504889

50. Zimmermann M, Leifeld J, Bird MI, Meir P (2012) Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity? Biogeochemistry 107: 423–436.

51. Suseela V, Conant RT, Wallenstein MD, Dukes JS (2012) Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Global Change Biology 18: 336–348.

52. Sharon AB, Ford BI (2013) How interactions between microbial resource demands, soil organic matter stoichiometry, and substrate reactivity determine the direction and magnitude of soil respiratory responses to warming. Global Change Biology 19: 90–102. doi: 10.1111/gcb.12029 PMID: 23504723

53. Jari L, Hannu I, Annikki M, Carl JW (1999) CO₂ Emissions from soil in response to climatic warming are overestimated—the decomposition of old soil organic matter is tolerant of temperature. Ambio 28: 171–174.

54. Christian P, Giardina MGR (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404: 858–861. PMID: 10786789

55. Bosatta E, Agren GI (1999) Soil organic matter quality interpreted thermodynamically. Soil Biology & Biochemistry 31: 1889–1891. doi: 10.1016/j.soilbio.2015.01.036 PMID: 25641340

56. Roland B, Thomas B, Raymond C, Declan L (2003) Recalcitrant soil organic materials mineralization more efficiently at higher temperature. Journal of Plant Nutrition and Soil Science 166: 300–307.
57. Xu X, Zhou JZ (2012) Carbon quality and the temperature sensitivity of soil organic carbon decomposition in a tallgrass prairie. Soil Biology & Biochemistry 50: 142–148. doi: 10.1016/j.soilbiol.2015.01.036 PMID: 25641340

58. Fierer N, McLauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. Ecology 86: 320–326.

59. Wetterstedt JAM, Agren GI (2010) Temperature sensitivity and substrate quality in soil organic matter decomposition: results of an incubation study with three substrates. Global Change Biology 16: 1806–1819.