



Temperature sensitivity of labile and stabilised organic carbon decomposition in different land uses

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Received: 7 July 2025 / Accepted: 14 April 2026 / Published online: 28 April 2026
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Abstract The temperature sensitivity of the decomposition of organic carbon pools is of key importance for modelling carbon turnover in soils. Therefore, examining the factors that determine and influence temperature sensitivity is extremely important. The decomposition of organic matter taken from three soil fractions in four land use areas (grass, spruce, oak and arable) was investigated in a 1-year incubation at 15, 25 and 35 °C. The particulate organic matter (POM) fraction corresponds to the labile C stock,

the sand + aggregate fraction (S + A) to aggregate-stabilized OM, and the silt + clay fraction (s + c) to mineral-associated OM. The rate of organic matter decomposition (k) in the labile fraction significantly exceeded that of the stabilised fractions (S + A and s + c) by 23–167%. However, no significant differences were found in the decomposition temperature sensitivity (Q_{10}) values, which ranged from 2.96 to 3.71. In the cultivated soil, very high Q_{10} values were detected in the aggregate fraction: 5.38. In contradiction to the kinetic theory, there were no significant differences in Q_{10} between the labile and stabilised pools. The chemical composition of the organic matter was found to regulate the temperature sensitivity of OM decay: the aryl C, methoxy C and carbonyl C content was positively correlated with Q_{10} , while the C/N ratio and O-alkyl C content proved to be negatively correlated with Q_{10} . The results highlight the vulnerability of the aggregate fraction of cultivated soils, a significant increase in the rate of organic matter decomposition and its temperature sensitivity.

Responsible Editor: Samantha R. Weintraub-Leff.

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Keywords Laboratory incubation · ^{13}C NMR ·
POM · Aggregates · MAOM

Introduction

The upper 1 m of soil contains about twice as much carbon as the atmosphere (Schimel 1995). Therefore, understanding the relationship between environmental

changes and the rate of organic matter decomposition in the soil is critical for projecting changes in the total carbon cycling of ecosystems (Houghton 2001). Furthermore, CO₂ efflux from soil organic matter (SOM) may cause further warming due to positive feedback (Jenkinson et al. 1991), which largely depends on the real temperature sensitivity of SOM decomposition. Therefore, this research field has been extensively studied, especially in recent years (e.g. Curiel Yuste et al. 2004; Domeignoz-Horta et al. 2023; Fierer et al. 2003; Li et al. 2021). However, despite much research on the temperature sensitivity of SOM decomposition, it is still a question how the temperature affects organic carbon decomposition (Davidson and Janssens 2006; Hakkenberg et al. 2008; Azizi-Rad et al. 2022).

This might seem strange, since empirical relationships between reaction rate and temperature have been known for nearly 150 years, based on the work of van't Hoff and Arrhenius (Arrhenius 1889). However, understanding and describing the temperature sensitivity of organic matter in the soil is much more complicated, because soil is a collection of many different organic molecules with different kinetic parameters. Confounding factors such as differences in the chemical structure of organic molecules and in the availability of organic carbon may cause conflicting results for the temperature sensitivity of SOM (Kirschbaum 2006). For example, based on the kinetic theory of Arrhenius, the greater activation energy of recalcitrant substrates should lead to greater temperature sensitivity (Davidson and Janssens 2006). Therefore, the theory predicts that stabilised, energy-rich OM will be more sensitive to warming than labile, low-energy OM. Although many laboratory incubation studies have provided empirical support for this idea (Biasi et al. 2005; Conant et al. 2008; Haddix et al. 2011; Bracho et al. 2016), others have found contrasting results (Fang et al. 2005; Gil-label et al. 2010).

Temperature sensitivity is governed not only by the quality and composition of soil organic matter (Liu et al. 2017), but also by vegetation type and land use (Gutiérrez-Girón et al. 2015; Bhattacharyya et al. 2020). The quality and quantity of organic molecules is largely determined by the type of vegetation, as the chemical composition of both the above-ground and below-ground parts of plants can differ considerably. For example, Gutiérrez-Girón et al. (2015) found that

the vegetation affected the temperature sensitivity of soil organic matter decomposition in Mediterranean high mountain soils. In contrast to this, the temperature sensitivity values (Q_{10}) of bulk soils were similar for both forest and pasture soils in the study of Bhattacharyya et al. (2020). Land use also influences the Q_{10} of macroaggregates in the soil, indicating that temperature sensitivity studies on the degradation of soil organic matter fractions are crucial for understanding the turnover of soil organic carbon (Bhattacharyya et al. 2020).

Soil organic carbon stocks with different kinetic properties can be characterised by soil fractionation methods (Mueller et al. 2014), in which the organic fractions represent differences in the resistance of organic C against microbial degradation. In these methods, the labile carbon is often matched to the unprotected POM fraction, while the organic pools containing physically and chemically stabilised carbon correspond to the protected C stocks. In the present study, the fractionation procedure yielded three different fractions based on the work of Zimmermann (Zimmermann et al. 2007): POM (particulate organic matter), S + A (sand + aggregates) and s + c (silt and clay). Each fraction can be characterised by a dominant stabilisation mechanism: non-stabilised, labile carbon (POM), carbon stabilised in aggregates (S + A), and carbon stabilised by organo-mineral interactions in the silt and clay fraction (s + c or mineral-associated organic matter, MAOM). Clay minerals and iron oxyhydroxides effectively protect the organic matter from decomposition through various mechanisms, such as ligand exchange, bridging of multivalent cations, hydrogen bonds, and van der Waals forces (Sollins et al. 1996; Lützow et al. 2006). The formation of stable macro- and microaggregates can physically protect soil organic matter through the following reasons: (i) reduces the access of micro-organisms and enzymes to OM, (ii) limits aerobic decomposition due to reduced oxygen diffusion, and (iii) isolates enzymes in the pores within the aggregates (Six et al. 2004; Lützow et al. 2006; Jastrow and Miller 2018).

Although using SOM fractions provides a closer estimate of the temperature sensitivity of fractions stabilised via different protection mechanisms (Swanston et al. 2002; Crow et al. 2009), few studies have examined the decomposition and temperature sensitivity of isolated soil fractions.

Nevertheless, this approach eliminates the continuous transfer of OM from one organic carbon pool to another, a process that complicates the interpretation of data obtained from the incubation of bulk samples (Mueller et al. 2014). The main advantage of directly incubating SOM fractions is that the effects of different stabilization mechanisms on the mineralization rates of SOM fractions with varying degrees of stabilization can be examined separately. Furthermore, the effects of temperature on the protection of soil OM within soil aggregates has not been studied in great depth, so a particularly important objective of this study was to investigate the aggregate fraction in terms of temperature sensitivity, in order to test the hypothesis that land use is a key factor in the temperature sensitivity of soil organic matter decomposition due to differences in its chemical composition. The study thus involved similarly textured soils, with different vegetation coverage and land use: a grassland, a spruce forest, an oak forest and an arable area, leading to very different chemical composition in the organic matter input. The three fractions (POM, S + A and s + c) of the soil samples were incubated for 1 year at 15, 25 and 35 °C. The CO₂ evolution was measured during the incubation to calculate the decomposition rate constants (k) and the temperature sensitivity of SOM decomposition (Q₁₀ factor). Nuclear magnetic resonance (NMR) spectroscopy was used to characterise the OM in the fractions. The specific hypotheses were: (i) according to the kinetic theory the labile organic pool is less sensitive to temperature than the stabilised pools (aggregates and MAOM), (ii) the chemical composition of the organic matter in each fraction influences the decomposition and temperature sensitivity of OM.

Materials and methods

Site description and sampling

Composite soil samples (cca 1500 g) were collected from the top 20 cm of soils with different land use, from a native grassland, a spruce forest, an oak forest and a cultivated arable area. The sampling sites were very close to each other (within 20 km) so climatic differences could not have affected the transformation of organic carbon, though the vegetation-induced microclimate can influence distribution and quality of SOM by determining C and N turnover and availability (Burke 1989). The mean annual temperature (MAT) of this area is 9.2 °C, while the mean annual precipitation (MAP) is 725 mm year⁻¹.

The basic parameters of the air-dry soil samples sieved through a 2 mm sieve were determined: pH was measured in distilled water and KCl, the particle size distribution was determined by laser diffraction, while total organic carbon (TOC) content of the soils were determined using dry combusting method (Elementar Vario MACRO Cube, Elementar GmbH) (Table 1).

Soil fractionation

The SOM fractionation was carried out following the Zimmermann fractionation method modified by Poeplau and Don (2013). A detailed description of the method can be found in Filep et al. (2024). Briefly, the samples were wet-sieved over a 63 µm screen to separate the silt and clay fraction (s + c) from the sand and stabile aggregates (S + A) and particulate organic matter (POM). The sieving residue (S + A, POM) was separated based on density, using sodium iodide (NaI) with $\rho = 1.6 \text{ g cm}^{-3}$. After NaI treatment, the samples

Table 1 Basic properties of the sites

Site	Description	pH _{H2O}	pH _{KCl}	Sand	Silt	Clay	TOC	C/N
Faber meadow, Sopron, Hungary (N 47°39'56,508"; E 16°32'57,480")	Native Grass (<i>Festuca rubra</i>) cca 140 years old	5.48	4.21	21.7	70.9	7.4	3.1	10.9
Sopron Mountains, Hungary (N 47°39'20,082"; E 16°32'28,595")	Medium-aged spruce stands (30–40 years, <i>Picea abies</i>)	3.87	2.92	26.4	69.4	4.2	9.8	21.8
Sopron Mountains, Hungary (N 47°39'21,101"; E 16°32'26,645")	Medium-aged oak stands (30–40 years, <i>Quercus petraea</i>)	4.28	3.40	16.8	78.7	4.5	4.6	13.6
Harka, Hungary (N 47°37'08,208"; E 16°34'58,404")	Arable, cultivated, fertilised (for 30 years)	5.58	5.06	25.8	69.0	5.2	1.9	10.8

were washed out, but only twice, as washing more than twice can lead to significant SOM loss (Plaza et al. 2019). Crow et al. (2007) also concluded that the leaching of chemicals is not the primary cause of the difference between the respiration of the total fractions and that of the bulk sample.

Incubation experiment

30 g samples of the s + c and S + A fractions and 1.5 g of the POM fraction were incubated for 357 days at 15, 25 and 35 °C in three replicates. The air-dried fractions were preincubated at 60% of the water holding capacity (WHC) of them at 20 °C for two weeks (Franzluebbers 1999). The moisture content of the fractions was determined using the column method (Govindasamy et al. 2023). The soil fractions were adjusted to 60% WHC. The water evaporated during incubation was replenished at two-weekly intervals for incubation at 25 °C and weekly for incubation at 35 °C.

Measurement of CO₂ evaluation and elemental analysis

The respired CO₂ of the soil fractions was trapped in 15 ml of 2 M NaOH. The NaOH traps were replaced on days 7, 14, 21, 28, 35, 49, 63, 77, 105, 133, 161, 189, 217, 245, 273, 302, 330 and 357. The amount of CO₂ released from the samples was measured by titrating the NaOH solutions with 1 M HCl in the presence of BaCl₂ (Anderson 1982).

The TOC and total nitrogen (TN) content of soil fractions were measured using dry combustion method (Elementar Vario MACRO Cube, Elementar GmbH) at the initial stage of incubation (day 0).

Calculation of k and Q₁₀

The decomposition reactions were assumed to be first-order single pool kinetics for each fraction. A previous study showed that first-order, single-pool kinetics adequately describe the decomposition of soil organic matter (Zacháry et al. 2018). To calculate the decomposition rate constant (k) of SOC in individual fractions CO₂ evolution values measured in the course of incubation were fitted by means of non-linear curve fitting using Origin 2020b software.

The relationship between the decomposition rate (k) and temperature (T) was described by an exponential equation (Hamdi et al. 2013):

$$k = a \times e^{b \times T},$$

where a and b are fitted parameters, the unit of T is degrees Celsius.

Q₁₀ was calculated using the van't Hoff empirical equation (Hamdi et al. 2013):

$$Q_{10} = e^{10 \times b}$$

¹³C NMR analysis

Prior to NMR analysis, the SOM fractions (POM, S + A and sc) were treated with 10% HF at a ratio of 5 mL g⁻¹ to remove paramagnetic materials and concentrate the C in the samples (Kögel-Knabner 1997). The samples were successively reacted eight times for 2 h at 25°C. After each extraction the samples were centrifuged for 10 min at 3000 rpm. The supernatant was discarded and the solid part was again submitted to HF treatment. Finally, the samples were washed five times with ultrapure water, then freeze-dried and mixed thoroughly.

Magic angle spinning (MAS) solid-state NMR spectra were recorded for all the samples at 20 °C on a Varian NMR System spectrometer operating at ¹H frequency 400 MHz (100 MHz for ¹³C) with a Chemagnetics 4.0 mm narrow-bore double resonance T3 probe and a spinning rate of 10.0 kHz. The ¹H-¹³C cross-polarisation method was used with 15,000 scans, 2 ms of contact time and a repetition delay of 5 s to collect ¹³C NMR spectra. Glycine was used as external chemical shift reference. The spectra were processed with Agilent VnmrJ 4.2. software and deconvoluted with the Dmfit software package.

The carbon compound types were assigned to the following chemical shift regions: 0–50 ppm (alkyl C), 50–60 ppm (methoxy/N-alkyl C), 60–93 ppm (O-alkyl C), 93–110 ppm (di-O-alkyl C), 110–140 ppm (aryl C), 140–160 ppm (O-aryl C), and 160–190 ppm (carbonyl C). Alkyl/O-alkyl ratios were calculated by dividing the area of the alkyl region (0–50 ppm) by the area of the O-alkyl (60–110 ppm) region (Baldock et al. 1992). The ratio of hydrophobic C to hydrophilic C was further calculated by dividing the area of hydrophobic structures (0–50 and

110–160 ppm) by the area of hydrophilic structures (60–110 and 160–190 ppm) (Mao et al. 2022).

Statistical analysis

Differences in k and Q_{10} between the 4×3 combinations of land use and SOM fractions were tested by one-way ANOVA with Tukey's post-hoc test using SPSS (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.). Principal component analysis was performed to assess changes in the quality of the organic matter fractions using Origin 2020b software.

In order to analyse the distribution of different land use types and SOM fractions in the ordination space of the multivariate NMR spectra, redundancy analysis (RDA) was applied using Origin 2020b software. To achieve this, we plot the scores of variables characterizing SOM quality (alkyl C, methoxy C, O-alkyl C, di-O-alkyl C, aryl C, O-aryl C, carbonyl C, and alkyl/O-alkyl ratio) at the initial stage (before incubation) and final stages (after incubation at 15, 25 and 35 °C).

To study whether the four measures of decomposition (i.e., k_{15} , k_{25} , k_{35} and Q_{10}) are driven mainly by the land use type or the SOM fractions, variance

partitioning was conducted using the “vegan” package (Oksanen et al. 2025).

Results

CO₂ evolution and decomposition rate constants

The cumulative amount of CO₂ generated during the one-year incubation period differed significantly between the C fractions with different stabilization: the highest values were measured for the labile POM fractions (Fig. 1). There is no significant difference between the CO₂ efflux of the aggregate-stabilized C fraction (S + A) and MAOM C (s + c). However, it is clear that the increase in temperature had a strong effect on the CO₂ production of the fractions.

Temperature had a significant effect on the rate of organic matter decomposition (k); an increase of magnitude was measured for all fractions as the temperature increased from 15 to 35 °C (Table 2).

At all three temperatures, the soil of spruce forest showed the lowest degradation values for all SOM fractions. In contrast, the organic matter of the grassland soil showed great degradation at all three temperatures. However, the highest k values were found

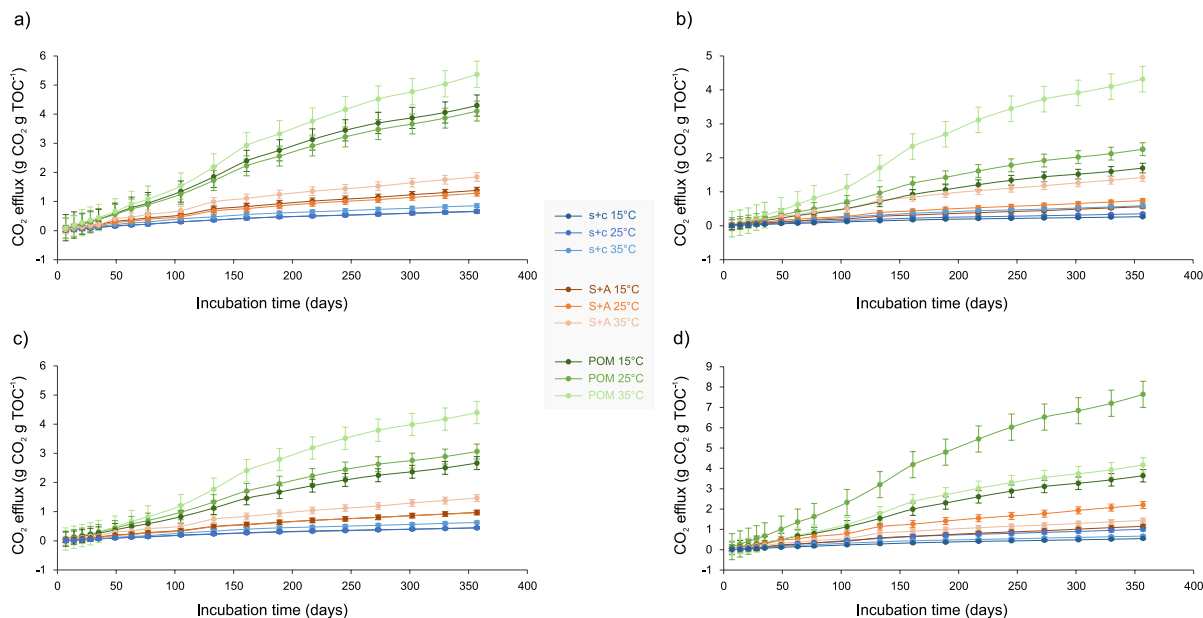


Fig. 1 Cumulative CO₂ efflux from soils with different land use: **a** grass, **b** spruce, **c** oak and **d** arable. CO₂ efflux is normalized to the total organic carbon (TOC) content of the samples. Line bars indicate standard deviation

Table 2 Decomposition rate constant (k) and temperature sensitivity of decomposition (Q_{10}) for soils with different land use

Land use	Fractions	k_{15}^* year ⁻¹	k_{25}^* year ⁻¹	k_{35}^* year ⁻¹	Q_{10}
Grass	s + c	0.07 ^{e**}	0.15 ^f	0.61 ^f	3.71 ^b
	S + A	0.07 ^c	0.14 ^{ef}	0.57 ^{ef}	3.66 ^b
	POM	0.09 ^f	0.21 ^g	0.83 ^g	3.60 ^b
Spruce	s + c	0.03 ^a	0.06 ^a	0.20 ^a	3.24 ^{ab}
	S + A	0.04 ^b	0.08 ^{ab}	0.28 ^{ab}	3.27 ^{ab}
	POM	0.06 ^{de}	0.16 ^f	0.56 ^{ef}	3.3 ^{ab}
Oak	s + c	0.05 ^c	0.11 ^{cd}	0.33 ^{bc}	2.96 ^a
	S + A	0.05 ^c	0.10 ^{bc}	0.40 ^{cd}	3.58 ^b
	POM	0.07 ^e	0.16 ^f	0.65 ^f	3.66 ^b
Arable	s + c	0.06 ^d	0.13 ^{de}	0.49 ^{de}	3.58 ^b
	S + A	0.12 ^g	0.25 ^h	1.50 ^h	5.38 ^c
	POM	0.07 ^e	0.16 ^f	0.64 ^f	3.67 ^b

* k_{15} , k_{25} and k_{35} denotes decomposition rate at 15, 25 and 35 °C

** Different letters mean significant differences within column based on Tukey's post hoc test

in the S + A fraction of arable soil with values of 0.12, 0.25 and 1.50 year⁻¹ at 15, 25 and 35 °C, respectively.

No significant difference in degradation rate was found between MAOM and aggregates, with the exception of the arable soil, where the S + A fraction had a very high rate constant at all temperatures. In general, the degradation rate of the labile POM fraction was significantly higher than that of the protected fractions (aggregates and MAOM).

Changes in chemical composition of SOM during incubation

The chemical composition of soil organic matter was characterised using ¹³C NMR spectroscopy under both pre-incubation and end-of-incubation conditions at three temperatures (Table 3). Significant differences in the organic matter composition of the fractions were found between the pre-incubation samples and the different land uses. For instance, the soil from the spruce forest contained a remarkably high amount of alkyl compounds, whereas all three fractions of the arable area were rich in aromatic compounds. The labile fraction of grassland contained very high amounts of O-alkyl organic matter, making up nearly half of the organic matter (~48%). The A/O-A ratio of the spruce soil was high, ranging from 1.2 to 1.4.

Principal component analysis of the NMR data visualises the effect of incubation at different temperatures and the effect of land use on these complex data and their changes (Fig. 2). A shift of the initial state point (start) in the ordination space visualises changes in the relative amounts of the chemical structures. This showed that the POM fraction of the arable soil, the s + c fraction of the oak forest and the s + c fraction of grassland had different chemical reactions to temperature; this was clear from the fact that the direction of the arrows indicating changes were very different. In contrast, for aggregates (the S + A fraction), no divergence was observed in response to temperature.

While changes in the chemical composition in the mineral fractions (aggregates and MAOM) during incubation generally resulted in a decrease in O-alkyl and di-O-alkyl compounds and an increase in aromatic structures, the picture was less clear for the POM fraction. The majority of POM fractions exhibited an enrichment of O-aryl compounds, while alkyl compounds accumulated in the POM fraction of the oak forest.

Temperature sensitivity of decomposition (Q_{10})

When considering the individual fractions, great variability in Q_{10} values were found in the s + c fraction, with the highest value for grass (3.7) and the lowest for oak (3.0) (Table 2). Variability was less pronounced in the other two fractions, although the high value recorded for aggregates in the arable soil (S + A: 5.4) stood out not only among the S + A fractions, but for all the organic matter fractions.

No significant differences were found between the labile (POM) and stabilised C pools (aggregates and MAOM) for either grassland or spruce soil. In contrast, the s + c fraction of oak forest had significantly lower temperature sensitivity than the S + A and POM fractions of the same soil.

Relationship between the chemical composition of SOM and Q_{10}

RDA explained 67% ($R^2_{adj}=0.668$) of the total variance of the data (Fig. 3a), in which the first two canonical axes (RDA 1 and RDA 2) contributed 75% and 2%, respectively. The NMR data, the carbon to nitrogen ratio and the ratio of Gram+ to

Table 3 The chemical composition of the SOM fractions of soils revealed by ^{13}C CP MAS NMR

	Grass			Spruce			Oak			Arable		
	POM	S+A	s+c	POM	S+A	s+c	POM	S+A	s+c	POM	S+A	s+c
Alkyl C (b. i.) ¹	12.6	21.0	25.0	36.8	39.9	40.7	30.3	28.5	28.6	14.5	23.3	19.9
15 °C	10.1	24.3	21.2	31.6	42.4	35.1	31.0	30.4	27.5	15.2	22.9	18.1
25 °C	12.2	26.4	23.0	32.3	46.5	39.9	30.4	33.4	29.7	14.8	26.7	18.9
35 °C	13.8	26.2	26.4	35.9	40.9	43.7	36.1	32.8	28.5	20.1	26.3	20.5
Methoxy C (b. i.)	4.4	11.8	13.4	7.2	7.1	5.7	6.1	11.9	12.5	8.5	14.1	15.4
15 °C	5.2	11.4	8.4	8.6	3.4	10.7	6.5	12.2	12.5	5.8	16.9	15.5
25 °C	4.1	11.5	11.1	8.9	3.2	10.2	6.1	12.4	12.0	5.6	15.6	15.9
35 °C	5.9	11.3	13.3	8.4	3.8	6.0	6.4	13.4	12.1	6.1	16.2	16.6
O-alkyl C (b. i.)	47.6	30.3	30.1	24.4	23.3	24.7	27.5	28.5	29.1	31.4	20.8	21.7
15 °C	47.4	30.7	30.8	23.4	22.1	23.3	28.2	25.9	28.3	33.6	18.5	23.4
25 °C	41.1	25.2	28.4	22.2	20.9	22.8	28.6	23.0	29.3	32.8	13.6	21.3
35 °C	37.5	28.3	25.5	21.1	19.3	22.2	25.0	21.3	26.0	28.9	14.3	19.6
di-O-alkyl C (b. i.)	11.1	8.8	7.2	5.7	5.9	5.1	7.2	6.8	6.7	8.8	5.9	6.9
15 °C	11.3	7.0	8.8	5.3	4.1	3.6	6.0	7.1	7.9	9.6	6.8	6.6
25 °C	10.4	5.5	8.2	5.1	3.7	4.9	6.3	5.9	8.1	8.7	6.1	6.8
35 °C	9.0	6.5	6.8	4.4	3.6	3.8	4.8	6.1	7.7	5.6	5.4	5.2
Aryl C (b. i.)	13.6	12.2	9.1	13.3	10.6	10.5	14.0	11.5	11.0	19.3	21.5	20.7
15 °C	13.7	11.9	16.6	14.5	12.4	15.1	14.2	9.6	8.6	17.8	17.6	16.0
25 °C	17.0	13.6	14.4	15.3	11.7	10.8	15.1	10.1	7.3	19.8	21.0	18.0
35 °C	17.4	13.4	13.1	14.9	14.6	11.2	14.3	10.5	9.8	21.6	17.8	18.4
O-aryl C (b. i.)	5.2	5.7	3.9	8.6	5.3	4.9	7.7	3.5	2.8	10.1	4.9	4.5
15 °C	5.9	5.1	4.8	10.7	7.4	3.9	7.7	6.3	6.0	10.1	9.2	8.0
25 °C	7.6	7.4	4.8	10.3	6.0	3.9	6.7	6.2	5.0	10.8	10.1	7.2
35 °C	8.7	5.3	6.2	9.9	9.4	5.3	7.3	7.3	7.3	10.4	11.4	9.0
Carbonyl C (b. i.)	5.5	10.1	11.2	4.0	7.9	8.4	7.2	9.4	9.3	7.4	9.5	10.8
15 °C	6.4	9.6	9.3	5.9	8.1	8.2	6.3	8.4	9.0	8.0	8.0	12.4
25 °C	7.6	10.2	10.1	5.9	7.9	7.4	6.8	9.0	8.6	7.4	6.8	11.8
35 °C	7.6	9.1	8.6	5.5	8.3	7.7	6.2	8.5	8.6	7.4	8.5	10.6
A/O-A ²	0.2	0.5	0.7	1.2	1.4	1.4	0.9	0.8	0.8	0.4	0.9	0.7
15 °C	0.2	0.6	0.5	1.1	1.6	1.3	0.9	0.9	0.8	0.4	0.9	0.6
25 °C	0.2	0.9	0.6	1.2	1.9	1.4	0.9	1.1	0.8	0.4	1.3	0.7
35 °C	0.3	0.7	0.8	1.4	1.8	1.7	1.2	1.2	0.8	0.6	1.3	0.8

¹ before incubation²Alkyl/O-alkyl ratio

Gram-bacteria (GP/GN) were used in the initial stage. Data for C, N and the GP/GN ratio in the SOM fractions were taken from study of Filep et al. (2024).

Among the factors that determine the degradation of organic matter, the amount of di-O-alkyl and O-aryl compounds showed a clear positive correlation with the k values calculated at the three temperatures, while the HB/HL, alkyl and A/O-alkyl ratio exhibited a negative correlation. The chemical

composition of the organic matter, in terms of the relative proportions of aryl, methoxy and carbonyl-like compounds and the GP/GN ratio, was positively correlated with Q_{10} , the parameter expressing the temperature sensitivity of organic matter degradation. In addition, a strong negative correlation was found between the C/N ratio of the organic matter, the relative amount of O-alkyl compounds and the Q_{10} values.

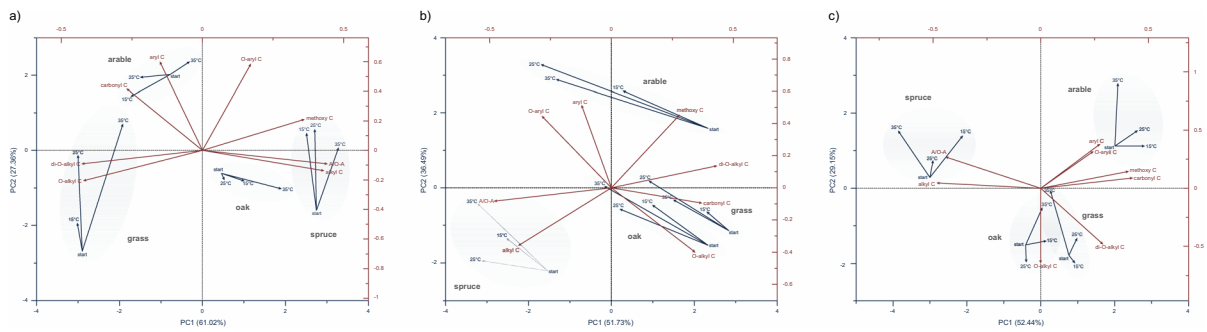


Fig. 2 PCA biplots with loadings for the POM (a), S+A (b) and s+c (c) fractions of different land uses showing changes in chemical composition during incubation. “Start” points represent the initial stage of the chemical composition of the fractions, the arrows represent the changes in chemical composition during the incubation

represent the initial stage of the chemical composition of the fractions, the arrows represent the changes in chemical composition during the incubation

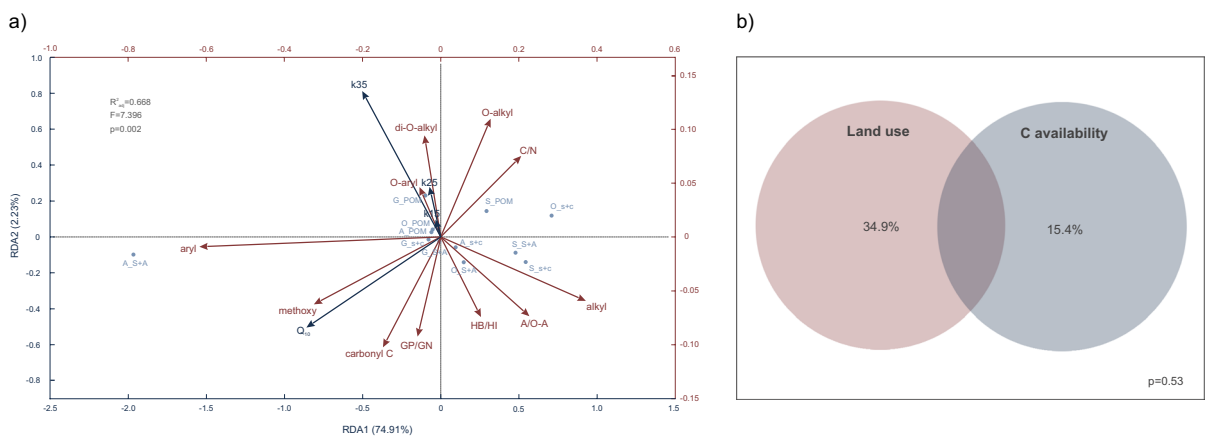


Fig. 3 RDA triplot for the relationship between the chemical composition of organic matter and the temperature sensitivity of decomposition of organic matter (Q_{10}) (a), and variance partitioning analysis for Q_{10} (b)

The variation partitioning results showed that land use could explain 34.9% of the variance, while the carbon availability (SOM fractions) only accounted for a smaller part (15.4%) of the variance for Q_{10} values (Fig. 3b).

Discussion

Decomposition of SOM is affected by both the type of soil organic matter stabilisation mechanism and land use

The fractionation procedure makes it possible to compare the degradation kinetics of organic matter from C pools with different stabilisation mechanisms. In

this study, significant differences were found in the decomposition rates of stabilised organic C pools (S+A and s+c fractions) and unprotected labile C stock (POM fraction): the degradation rate of the labile fraction significantly exceeded that of the physically and chemically protected C stocks (aggregates and MAOM) at all three temperatures (Fig. 1, Table 2). Well-documented results indicate that the mineralisation rate decreases with a decrease in soil particle size, which can be attributed to the increased protection against microbial mineralisation due to the stabilisation of carbon in microaggregates or by binding to clay and silt particles (Van Veen and Kuikman 1990; Hassink 1995; Ozlu and Arriaga 2021). The lower decomposition rate of protected C pools could be due to the fact that microbial respiration is

strongly regulated by C availability, which may limit the access of microorganisms to SOM (Garcia-Pausas and Paterson 2011; Gutiérrez-Girón et al. 2015). Earlier studies also demonstrated that the decomposition rate of the POM fractions was higher than that of mineral-associated organic matter. For example, Garten and Wulschleger (2000) used the ^{13}C natural abundance technique in switchgrass fields to show that the decomposition rate of POM was much higher ($0.10\text{--}0.26\text{ year}^{-1}$) than that of MAOM ($0.025\text{--}0.038\text{ year}^{-1}$).

The decomposition of organic stocks in soils with different vegetation types is also determined by external environmental factors such as soil pH and C/N ratio. In a previous study, it was shown that the degradation of the POM fraction is controlled by soil pH and C/N ratio: in spruce soils there was a significant accumulation of POM, as the soil pH ($\text{pH}_{\text{H}_2\text{O}}=3.87$) and low relative N content (C/N ratio: 21.8) inhibited the degradation processes of microbes (Filep et al. 2024). In the present study, this inhibition of degradation was clearly evident in the case of forest soils (spruce and oak), which had the lowest degradation rates in all three fractions. In contrast, higher rates were recorded for arable soils, but especially for grassland, as the conditions without the constraints of low pH and high C:N ratio in these soils.

In addition, significant differences in the chemical composition of plant litter may also contribute to differences in soil organic matter decomposition rates. The high degradability of organic matter in grassland can also be explained by the chemical structure of the plant residues, since grass contains much more easily degradable carbohydrates compared to forest litter, which has high O-alkyl content (Table 3). In this context, redundancy analysis showed that both high lignin content (O-aryl) and high di-O-alkyl and O-alkyl abundance were positively correlated with the rate constant of decomposition at all temperatures (Fig. 3a), indicating that both the quantity and quality of the substrate are critical for the microbial degradation of organic compounds. The alkyl/O-alkyl ratio (A/O-A) has also been proposed as an indicator for the overall decomposition process of organic matter in soils (Baldock et al. 1997; Leifeld et al. 2002), so it is not surprising that it is negatively correlated with the rate of organic matter decomposition. The hydrophobic/hydrophilic ratio (HB/HI) of plant residues can indicate the extent to which they contain

apolar organic matter, which is not readily available to microbes, thus preventing the degradation of the substance (Piccolo et al. 2004), which is why the HB/HI ratio is negatively correlated with the rate of SOM degradation.

Divergent response of SOM decomposition to the temperature and SOM fractions

The quality of organic matter changed in different ways during incubation at various temperatures, as shown by the divergence of the arrows on the PCA plots (Fig. 2). This indicated that the incubation temperature could have diverse effects on the chemical composition of individual soil organic matter fractions. For example, very divergent temperature arrows were observed for the POM fraction of arable soil. Similarly, the s+c fraction of the oak, spruce and arable soils showed significant differences in the decomposition of organic matter in response to temperature. This could be attributed to shifts in the microbial community composition at different temperatures, due to significant differences in chemical composition (Table 3) and the fact that some organic compounds are difficult for microbes to break down at lower temperatures (Zogg et al. 1997; Haddix et al. 2011).

Feng and Simpson (2008) monitored CO_2 respiration in a one-year laboratory incubation and noted that different OM compounds showed varying temperature sensitivity. However, the previously mentioned study used isolated organic compounds rather than those found in complex systems, such as organic fractions. Thus, this result is not necessarily relevant to the present study; however, Creamer et al. (2015) also reported alterations in the decomposition trajectories of the substrates when the decomposition of higher-quality (fresh) and lower-quality (aged) eucalyptus leaf litter was investigated at two different temperatures. In the present experiment, a significant divergence in the decomposition pathways was detected for the lignin-dominated (high relative amount of aryl C) arable POM fraction (Table 3). Although lignin substances are often believed to be stable, this study suggested that lignin is susceptible to advanced degradation caused by soil warming. Consistent with this, some studies showed greater losses of lignin at higher temperatures (Suseela et al. 2013; Datta et al. 2017), supporting the kinetic theory

that kinetically stable compounds have greater temperature sensitivity. In addition, Feng et al. (2008) employed NMR to study soil OM composition before and after 14 months of in situ warming (+5 °C) in a temperate mixed forest and found that lignin was sensitive to accelerated decomposition at elevated temperatures. Other studies have found that POM is closely related to inputs of plant litter (Gunina and Kuzyakov 2014), so in the present study, where samples from areas with different vegetation were incubated, the POM could be expected to exhibit different chemical composition and chemical changes in response to temperature.

While the chemical composition of MAOM-stabilised carbon pools (s+c fraction) from different soils was affected very differently by temperature-induced effects during incubation at different temperatures, the decomposition of organic matter molecules in the aggregates (S+A fraction) responded in a very similar way to increasing temperature (Fig. 2, Table 3). This is consistent with the study of Cates et al. (2022), which led to the conclusion that temperature effects were most visible in the silt and clay fractions, where carbohydrate- and tannin-like compounds were associated with C content. It is likely that the temperature-induced increase in the mineralisation rate of C was more pronounced outside the aggregates, while the temperature within the aggregates was more protected, thus confirming the present finding that soil aggregates, as a habitat, buffered OM against certain environmental fluctuations, and suggesting that the warmer conditions associated with climate change may alter the MAOM C content significantly.

Tillage causes a dramatic increase in the temperature sensitivity of aggregates

Although no significant differences were generally found in the Q_{10} values of the SOM fractions of different land uses, the aggregate fraction of the cultivated soil exhibited significantly higher temperature sensitivity (Table 2). It is well documented that tillage and fertilisation cause significant changes in the characteristics of particle size composition in aggregates of soil organic matter. Previous studies demonstrated that frequent tillage, combined with chemical fertilisers, reduced the formation and stability of macroaggregates, and exposed the formerly occluded C to microbial attack (Poeplau et al. 2020; Tamura and

Suseela 2021). Furthermore, the faster turnover of organic carbon under tillage leads slower rate of formation of microaggregates causing less stabilisation of organic matter (Six et al. 2000). Despite these clear research findings, somewhat contradictory results were obtained when measuring the temperature sensitivity of cultivated and non-cultivated areas. For instance, Plante et al. (2010) found that cultivation did not result in significant trends in Q_{10} values compared with other land uses, while Conant et al. (2008) found higher Q_{10} values for cultivated soils, which have less labile soil OM, than for undisturbed grassland soils.

The extremely high Q_{10} value obtained for cultivated land in the present study, compared to the other land uses, highlighted the fact that the temperature sensitivity of cultivated soils could not be fitted to current organic C degradation models, since land use changes that reduce soil C may accelerate decomposition-derived CO₂ emission during warming to a greater extent than is predicted by currently used SOM models (Wagai et al. 2013).

There are no statistical differences in Q_{10} between labile and stabilised C

Although the aim of the current study was to investigate the temperature sensitivity of the isolated fractions in order to reduce the possible attenuating effect of physical protection (e.g., Gillabel et al. 2010; Plante et al. 2010), the results contradicted the predictions of the kinetic theory, according to which, the temperature sensitivity of stabilised, high-energy C pools should be higher than that of labile, unprotected pools because of the higher activation energy required to decay them. However, no statistically verifiable difference was found in the temperature sensitivity of the labile pool (POM) and the stabilised pools (S+A and s+c) except for the aggregate fraction of cultivated arable soil, discussed above, and the MAOM fraction of the oak forest (Table 2). In spite of the theoretical clarity, several contradictory results have been obtained in this field (see in Conant et al. 2011).

The temperature sensitivity of organic matter is confounded by litter and SOM quality and quantity, i.e. substrate availability (Kirschbaum 2006; Gershenson et al. 2009), thus leading to results that contradict the theory. In the study of Haddix et al. (2011), for instance, six sites and land-use types were examined

and two of the soils did not follow the trend described by kinetic theory. This suggested that determining the temperature sensitivity of SOM decomposition on a single soil might lead to false conclusions about the temperature sensitivity of SOM. Furthermore, the total heterotrophic Q_{10} values determined in short-term laboratory incubations may under- or overestimate the temperature sensitivity of SOM decomposition, depending on the soil type, the initial labile carbon content and the temperature range used for measurements (Karhu et al. 2010). Ågren and Bosatta (2002) also drew attention to the fact that the degradation of SOM in the steady state was much less responsive to temperature than the decay rates estimated after short-term incubation. The importance of the length of incubation was underlined by Qin et al. (2024), who found that, although MAOM had lower Q_{10} values than the labile POM fraction when the entire incubation period was considered, the results of the “equal-C” method they employed revealed that the difference was only significant when the C content was in the 1%–4.5% range, highlighting how the length of incubation is crucial in assessing the temperature sensitivity of a fraction.

Chemical composition of SOM regulates Q_{10}

To evaluate the effect of SOM composition on the Q_{10} values, RDA was performed using the NMR data, carbon to nitrogen ratio and GP/GN ratio of samples from the initial stage (before incubation). The chemical composition of the fractions proved to have a significant effect on the Q_{10} values (Fig. 3a). At the molecular level, the kinetic theory, which states that the temperature sensitivity of molecules with high activation energy, is higher than that of labile, low-energy molecules, was confirmed in the present study, since the increase in the amount of aromatic C, methoxy C, carbonyl C and GP/GN ratio in the organic matter increased the temperature sensitivity of organic matter degradation.

The high abundance of aromatic compounds in OM is often considered to make it more stable, since these energy-rich compounds restrict microbial availability and decomposition (Weishaar et al. 2003). According to the kinetic theory, the oxidation of these compounds is complicated by the need for higher activation energies for their oxidation, which would imply an increased Q_{10} reaction with higher

aromatic content, as confirmed by the present results. Zimmermann et al. (2012) also found a positive correlation between the aryl C content of organic matter and Q_{10} . In addition to aromatic compounds, methoxy groups are common in lignin (Nelson and Baldock 2005), which is generally considered to be a recalcitrant material, therefore causing higher temperature sensitivity.

RDA also revealed a positive relationship between the GP/GN ratio of the SOM fractions and the Q_{10} factor (Fig. 3a). Gram-positive bacteria are known to prefer older, more complex organic carbon, whereas Gram-negative bacteria preferentially use fresh OM as SOC sources (Kramer and Gleixner 2006). The positive relationship between Q_{10} and the GP/GN ratio thus supports the kinetic theory. This is consistent with the results of a study made by Wang et al. (2018), who found that GN bacteria was the major controlling factor for Q_{10} .

The positive relationship between the carbonyl content of SOM and the temperature sensitivity indicates enhanced decomposition (Preston et al. 2006), which contradicts our expectations, as the temperature sensitivity of degraded decomposed organic matter is theoretically lower than that of less degraded organic matter. However, carbonyl groups may be linked to organic compounds that cannot be identified using the CP-MAS NMR methodology (Nelson and Baldock 2005).

A strong negative correlation was found between the Q_{10} values and the O-alkyl content of SOM (Fig. 3a). Wagai et al. (2013) noted that the low temperature sensitivity of organic matter could be due to the abundance of labile, O-alkyl type compounds, which is consistent with the present findings.

The C/N ratio also proved to have a negative influence on the temperature sensitivity of OM. There is controversy in the literature as to whether the C/N ratio controls the temperature sensitivity of organic matter decomposition, since some experiments indicate a positive correlation between Q_{10} and the C/N ratio (Meyer et al. 2018; Wang et al. 2018), and others a negative relationship (Wei et al. 2022; Liu et al. 2024). These differences are likely related to methodological differences, since the experiments performed by Meyer et al. and Wang et al. were very short incubations (12 h and 21 days, respectively), in which the temperature sensitivity is dominated by the degradation of labile organic

matter, whereas protected pools also played a role in the temperature sensitivity of SOM in the one-year incubation in the present experiment.

In evaluating our results, we must emphasize that the correlations between Q_{10} and the chemical components of organic substances identified during the statistical analysis do not represent the so-called intrinsic temperature sensitivity of the given molecule, which refers to the specific molecular structure without the modifying influence of environmental conditions, but rather to its apparent temperature sensitivity.

Land use rather than C availability determines Q_{10}

It is widely accepted that the enzymatic degradability and availability of substrates, rather than chemical recalcitrant, regulate SOM degradation (Schmidt et al. 2011; Dungait et al. 2012; Lehmann and Kleber 2015). If the availability of organic matter is indeed the rate-limiting step in the degradation of physico-chemically protected SOM (Kemmitt et al. 2008), then the temperature sensitivity of degradation also involves the mechanisms that ensure the stabilisation of SOM (Moinet et al. 2018). Nevertheless, the present findings indicated that the quality of the organic matter, i.e. its chemical composition, also played a very important role in shaping the temperature sensitivity of organic matter degradation, as shown by the variance partitioning results (Fig. 3b), where land use explained a larger proportion of the total variance than the "C availability" factor representing the availability and stabilisation mechanisms of organic C. It should be emphasised, however, that the different land use areas also differed as regards environmental factors such as pH and the C/N ratio (Table 1). Thus, the substantial differences in the organic matter composition (SOM quality) of the fractions were partly responsible for the results obtained. Furthermore, it should be noted here that these two factors, quality and availability, are difficult to separate in an experiment of this nature, since the intrinsic properties of organic molecules also largely determine their availability, for instance, the hydrophobic compounds of the organic matter could be protected from further degradation (Spaccini et al. 2002).

Conclusions

Although the theoretical background seems to have been established, it is still important to understand how SOM quality and availability affect the temperature sensitivity of organic matter decomposition. The present research showed that although there were statistical differences between the rate of organic matter degradation in the labile and stabilised C pools, there were no differences in the temperature sensitivity of degradation between the labile and stabilised fractions. Chemical composition was found to be the determining factor of Q_{10} at the molecular level, following the kinetic theory, the temperature sensitivity of molecules with high activation energy, is higher than that of labile, low-energy molecules. The research also suggests the fact that soil tillage drastically increased the temperature sensitivity of degradation for organic C stabilised in aggregates, while the Q_{10} values of the other two fractions (labile and MAOM) did not differ significantly from that of the SOM fractions of grassland and forest areas. However, it should be noted that, the physical fractionation of soil organic matter alters the physical constraints on decomposition, so these results cannot be generalized to the entire soil due to physical differences between fractions, such as porosity and tortuosity, which fundamentally influence CO_2 transport in SOM fractions.

Further research is needed to investigate factors, e.g. the length of incubation, that cause inconsistencies in the results of temperature sensitivity assessment. It would also be important to clarify, explore and understand more deeply the relationship between OM quality and availability.

Author's contribution Tibor Filep: Conceptualization, Supervision, Writing – original draft, Writing – review and editing. Dóra Zacháry: Data curation, Writing – review and editing. Marianna Ringer: Methodology. Attila Domján: Methodology, Data curation. Bence Balterer: Methodology, Data curation. Ákos Bede-Fazekas: Formal analysis. Gergely Jakab: Investigation, Data curation. Orsolya Tőke: Visualization. Zoltán Szalai: Conceptualization.

Funding Open access funding provided by HUN-REN Research Centre for Astronomy and Earth Sciences. The research was financed by the National Research, Development and Innovation Fund, Hungary [Project N° FK 142936]. Project no. [FK 142936] has been implemented with the support provided by the Ministry of Culture and Innovation of Hungary from the National Research, Development and Innovation

Fund, financed under the [NRDI—Young researchers' excellence programme] funding scheme. Á.B.-F. was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences.

Data availability The dataset is available at: Filep, Tibor; Zachary, Dora (2025), "Decomposition_rate_constant_Q10_SOM_fractions", Mendeley Data, V1, <https://doi.org/10.17632/dgysfygc3.1>.

Declarations

Competing interest The authors declare no competing interests.

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