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LETTER

Molecular ¹⁴C evidence for contrasting turnover and temperature sensitivity of soil organic matter components

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Abstract

Climate projection requires an accurate understanding for soil organic carbon (SOC) decomposition and its response to warming. An emergent view considers that environmental constraints rather than chemical structure alone control SOC turnover and its temperature sensitivity (i.e., Q_{10}), but direct long-term evidence is lacking. Here, using compound-specific radiocarbon analysis of soil profiles along a 3300-km grassland transect, we provide direct evidence for the rapid turnover of lignin-derived phenols compared with slower-cycling molecular components of SOC (i.e., long-chain lipids and black carbon). Furthermore, in contrast to the slow-cycling components whose turnover is strongly modulated by mineral association and exhibits low Q_{10} , lignin turnover is mainly regulated by temperature and has a high Q_{10} . Such contrasts resemble those between fast-cycling (i.e., light) and mineral-associated slow-cycling fractions from globally distributed soils. Collectively, our results suggest that warming may greatly accelerate the decomposition of lignin, especially in soils with relatively weak mineral associations.

KEYWORDS

compound-specific ¹⁴C, physical fractions, soil organic carbon, temperature sensitivity, turnover time

INTRODUCTION

Soils are the largest terrestrial reservoir of actively cycling carbon (Rattan, 2018). Changes in the turnover of soil organic carbon (SOC) in response to global warming

have the potential to influence atmospheric CO₂ concentrations and are hence extensively studied (Davidson & Janssens, 2006; Lugato et al., 2021). However, due to the inherent complexity of SOC, mechanisms governing SOC turnover and its response to warming remain

contentious (Bradford et al., 2016; Doetterl et al., 2015). Emergent consensus proposes that environmental constraints, such as physicochemical protection conferred by organo-mineral interactions, rather than chemical structure alone, determine SOC turnover and its sensitivity to warming (Chen, Fang, et al., 2021; Gentsch et al., 2018; Schmidt et al., 2011). Based on kinetic theory, organic carbon (OC) associated with soil minerals turns over more slowly, and its decomposition exhibits a higher temperature sensitivity (Q_{10} , the relative change in decomposition rate per 10°C temperature increase) than mineral-poor soil fractions such as aggregates or particulate organic matter with relatively weak mineral associations (Davidson & Janssens, 2006; Leifeld & Fuhrer, 2005). Alternatively, mineral protection may restrict substrate accessibility and microbial activity, thereby overriding thermodynamic controls on decomposition and attenuating Q_{10} (Gentsch et al., 2018; Qin et al., 2021). However, current studies mainly rely on operationally defined soil carbon pools (e.g. light and heavy soil density fractions) to examine their turnover (Cerli et al., 2012; Lugato et al., 2021), which encompass a continuum of compounds that hinder assessment on the turnover of structurally different molecular components of SOC. Some studies combining ¹³C-labeling techniques and molecular-level ¹³C analysis have been used to evaluate the turnover of specific compounds in artificial labeling experiments or natural isotope labelling systems (e.g. with known C3/C4 vegetation changes) over relatively short periods (months to decades; Dignac et al., 2005; Gleixner et al., 2002). However, they do not address the long-term (> centennial timescales) behaviour of SOC components in natural systems. It is crucial, therefore, to directly compare the long-term turnover of various SOC molecular components in natural soils to clarify the influence of chemical structure and mineral association on the turnover of SOC components and its Q_{10} .

Among the wide array of molecules residing in soils, lignin, lipids and black carbon together account for about half of SOC (Hall, Ye, et al., 2020) and exhibit distinct chemical structures, thermodynamic properties and propensities to associate with soil minerals or physical fractions (Lehmann et al., 2008). Lignin, the chemically recalcitrant macromolecule of vascular plants (Kirk & Farrell, 1987), is found to degrade slowly during litter decomposition (Bahri et al., 2008; Hall, Huang, et al., 2020). Therefore, lignin contents and lignin-to-nitrogen ratios have long been used as important variables in many soil-plant models to indicate SOC pools of differing lability (e.g. Century, CABLE and RothC). However, lignin is found to rarely persist in mineral soil profiles (Kögel-Knabner et al., 2008). Hence, the emergent view proposes that despite its chemical recalcitrance, the lignin macromolecule turns over relatively rapidly (Schmidt et al., 2011), partly because it is relatively concentrated in soil aggregates rather than mineral-associated fine soil fractions (Amelung et al., 1999, 2002).

In contrast, black carbon is also chemically recalcitrant, but enriched in mineral-associated fractions (Brodowski et al., 2005, 2006; Kögel-Knabner et al., 2008) and considered to be among the most persistent SOC components (Leifeld, 2008; Skjemstad et al., 2004). Plant-derived long-chain lipids also chemically associated with soil minerals (Kögel-Knabner et al., 2008; Lin & Simpson, 2016), while short-chain lipids that include microbial contributions may turn over relatively quickly in the soil (Wiesenberg, Schwarzbauer, et al., 2008). The above postulations, however, remain to be rigorously tested. Importantly, direct comparison of the cycling of these different molecular components may shed light on the relative importance of chemical recalcitrance and mineral protection on carbon turnover and its Q_{10} .

Here we use compound-specific radiocarbon analysis (Feng, Vonk, et al., 2013) in combination with bulk ¹⁴C measurements and soil ¹⁴C modelling to constrain the turnover time of various SOC molecular species in 13 soil profiles (down to depths of 1 m) across Qinghai-Tibetan to Mongolian grasslands that spans significant gradients in temperature, precipitation, vegetation and soil properties (Figure 1a and Appendix Tables S1–S3 in Supporting Information). This unprecedented molecular ¹⁴C data set, consisting of 225 ¹⁴C measurements on specific SOC compounds (including lignin-derived phenols, short-chain and long-chain lipids and black carbon; Figures S1 and S2), allows quantitative assessment on the turnover times of individual SOC components, which range from decades to tens of thousands of years in soils unaffected by grazing or other human activity (Torn et al., 2009). This detailed radiocarbon investigation of different constituents in soil profiles along the 3300-km transect offers a unique perspective on the environmental persistence of various SOC components in natural soils and provides a means to determine their turnover characteristics (including Q_{10}) as a function of environmental factors such as gradients in mean annual temperature (MAT). We hypothesize that on long-time scales, lignin-derived phenols turn over more rapidly and are more sensitive to warming relative to SOC components that tend to more closely associated with soil minerals (such as long-chain lipids and black carbon). The contrast may resemble that of soil fractions showing varying association with minerals. Hence, we further evaluate the turnover and Q_{10} of different SOC fractions by a synthesis of published ¹⁴C data on physical (density) fractions from globally distributed soils.

MATERIALS AND METHODS

Soil sampling

A 3300-km transect spanning alpine grasslands on the Qinghai-Tibetan Plateau and temperate grasslands across the Inner Mongolia of China is included in this

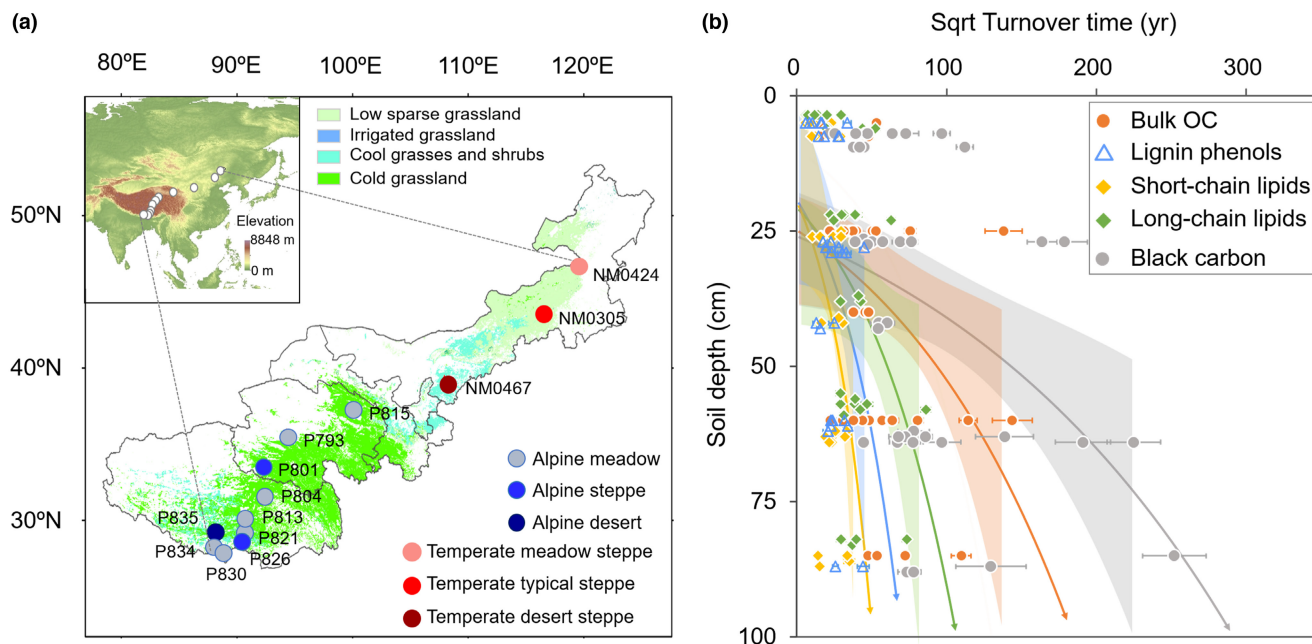


FIGURE 1 Distribution of sampling sites and turnover time of bulk organic carbon (OC) and various components in the soil profiles across the grasslands of northern China. (a) Spatial distribution of sampling sites. (b) Turnover time (square root) of bulk OC and various components versus soil depth (the longer turnover times are shown here for those OC components having two possible turnover times; the shorter turnover times are shown in [Figure S5](#)). Bulk OC is plotted at the midpoint of each sampling layer with components scattered around for improved visualization. Coloured lines represent fit curves using square root transformation (Sqrt) of the turnover time versus soil depth ($p < 0.05$). Coloured shades represent the 95% confidence intervals. Sqrt of the standard errors are given for turnover times. Invisible error bars are smaller than the data symbol.

study. Along this transect, MAT ranges from -4°C to 7.6°C and mean annual precipitation (MAP) ranges from 186 mm to 445 mm. An overview of the soil types, major vegetation types, environmental variables, mineral composition and major element contents for each sampling site can be found in [Tables S1–S3](#).

In the summer of 2011, 2012 and 2015, a total of 41 soil samples from 13 soil profiles (down to 70 and 100 mm for the temperate and alpine grasslands, respectively; [Figure S1](#); three replicates for each sample) were collected along the transect using soil cores (diameter of 7 mm). Soils from the same depth of each profile were carefully mixed as one composite sample. Visible roots were manually picked out, washed, dried to constant weight at 65°C , and weighed. After homogenization and removal of stones, the soil was passed through a 2-mm sieve before drying. Soils from 0–10 or 5–10 cm were referred to as ‘topsoil’, 20–30 and 30–50 cm as ‘subsoils’, and 50–70 cm as ‘deep soils’.

Bulk and black carbon analysis

Soil texture was determined by laser diffraction using a Malvern Mastersizer 2000 particle analyser (Malvern Instruments Ltd.) after removal of organic matter and lime (Di Stefano et al., 2010). Dithionite-extractable iron and aluminium (Fe_d and Al_d) were extracted from soils

using the citrate-bicarbonate-dithionite method (Mehra & Jackson, 1960), and quantified on an inductively coupled plasma emission spectrometer (ICAP6300, Thermo Scientific, USA) to represent reactive Fe and Al (Wang et al., 2017). The abundance of major elements in bulk soils was determined by X-ray fluorescence spectrometry (Panalytical Axios mAX), while mineral composition was examined using X-ray diffractometer (Bruker D8 Advance instrument).

Black (or pyrogenic) carbon was isolated using the chemo-thermal oxidation method (Caria et al., 2011). Briefly, air-dried and weighed soil samples were thermally oxidized at 375°C for 24 h in a muffle furnace with air flow to remove non-pyrogenic OC. Vapour acidification (12-M hydrochloric acid; HCl) was then used to remove carbonate and the remaining OC was defined as black carbon (Caria et al., 2011). The possibility of thermal oxidation of non-pyrogenic OC into black carbon was ruled out by two additional chemo-thermal oxidation analyses (comparing soils prepared with different masses and lignin-soil mixtures; [Method S1](#)).

After removal of inorganic carbon by vapour acidification (Walther et al., 2010), the radiocarbon content of bulk OC and black carbon was measured on an integrated elemental analyser interfaced to the Miniturised radioCARbon DAting System (MICADAS) at ETH Zürich (Fahrni et al., 2013; Ruff et al., 2010).

Isolation and ¹⁴C analysis of individual compounds

Freeze-dried soil samples were subjected to sequential extractions to isolate individual compounds for compound-specific ¹⁴C analysis (Feng et al., 2015; Feng, Benitez-Nelson, et al., 2013). Briefly, soil residues after solvent extraction were hydrolysed with 1-M potassium hydroxide in methanol (100°C, 3 h) to release hydrolysable lipids. Dried soil residues were further subjected to alkaline cupric oxide (CuO) oxidation to release lignin phenols (Otto & Simpson, 2006). Isolation of specific hydrolysable lipids and lignin phenols was achieved by preparative capillary gas chromatograph and high-performance liquid chromatograph, respectively. The isolated individual compounds were purified and separately converted under vacuum into CO₂ with CuO at 850°C (5 h) before ¹⁴C measurement on a MICADAS (Wacker et al., 2013). To account for extraneous carbon introduced during sample processing, procedural blanks were assessed separately for black carbon, lipids and lignin phenols. Then, fraction modern (F¹⁴C) values were corrected for derivative carbon (for lipids) and respective procedural blanks with the errors propagated, and finally reported as Δ¹⁴C (Haghipour et al., 2019). Further details are given as Methods S2 and S3.

Calculation of turnover times

Since soil samples were collected in different years, Δ¹⁴C (Δ¹⁴C_{sample}) values and the sampling year were used to calculate the turnover time with a time-dependent steady-state model (Torn et al., 2009):

$$C_t \times R_{\text{sample}(t)} = I \times R_{\text{input}(t)} + C_{t-1} \times (1 - k - \lambda) \times R_{\text{sample}(t-1)} \quad (1)$$

$$R_{\text{sample}(t)} = (\Delta^{14}\text{C}_{\text{sample}} / 1000) + 1 \quad (2)$$

where C_t and C_{t-1} are OC contents of the soil sampled in year t and one year before that, respectively. I is the annual input of plant-derived OC during the sampling year. R_{sample} is the ratio of measured radiocarbon to a standard with a constant radiocarbon value. λ is the radioactive decay constant ($\lambda = 1.210 \times 10^{-4} \text{ year}^{-1}$) while k is the OC decomposition rate (inverse of turnover time). At the steady state, $C_t = C_{t-1} = I/k$.

$$R_{\text{input}(t)} = R_{\text{atm}(t)} = (\Delta^{14}\text{C}_{\text{atm}(t)} / 1000) + 1 \quad (3)$$

where Δ¹⁴C_{atm(t)} is atmospheric ¹⁴C content at year t and can be obtained from Levin and Kromer (2004), Levin et al. (2013) and website (<https://doi.org/10.11588/data/10100>), assuming no lag between the fixation of carbon from the atmosphere and plant inputs into the soil and constant

atmospheric ¹⁴C content prior to 1950. Equation (4) is then derived from Equation (1):

$$R_{\text{sample}(t)} = k \times R_{\text{atm}(t)} + (1 - k - \lambda) \times R_{\text{sample}(t-1)} \quad (4)$$

Based on Equation (4), a numerical model was constructed using MATLAB 2015 (MathWorks, Inc.) to find the optimal k to fit the given $R_{\text{sample}(t)}$. To estimate the error associated with the model-derived estimates of k , a Monte Carlo simulation was performed for each sample using the corrected F¹⁴C value and the propagated error. Uncertainties of k were the standard error of the solutions to the 200 Monte Carlo runs (Castaneda-Gomez et al., 2023).

The response of k to MAT is described by the Arrhenius equation:

$$k = A \times \exp\left(\frac{-E_a}{R \times T}\right) \quad (5)$$

where A is the pre-exponential factor and E_a is the apparent activation energy required for an enzymatic reaction. R is the universal gas constant (8.314 J K⁻¹ mol⁻¹) and T is the absolute temperature in Kelvin. Then E_a can be calculated as the slope of the relationship between $-1/(R \times T)$ and the natural logarithm of k using linear least squares, while the error of E_a was the standard deviation (Std. Error) of the slope. Q_{10} was calculated based on E_a :

$$Q_{10} = \frac{k_{T+10}}{k_T} = \exp\left(\frac{E_a}{R} \times \frac{10}{T^2 + 10 \times T}\right) \quad (6)$$

For a given compound with specific E_a , Q_{10} changed with increasing temperature. Here changes of decomposition rates with temperature increasing from 5°C to 15°C were used to represent Q_{10} of bulk OC and various components. The error of Q_{10} was also estimated using a Monte Carlo simulation (200 runs) of E_a and its standard deviation. Given the temporal changes in atmospheric ¹⁴C over the last several decades, two turnover times may be calculated for certain Δ¹⁴C_{sample} (>20‰; Torn et al., 2009). In this case, both longer and shorter turnover times were separately chosen for further analysis.

For compounds firmly associated with soil minerals which may not be released by the conventional biomarker extraction (Cai et al., 2017; Hernes et al., 2013), the mineral-bound fraction of the targeted biomarkers were extracted after demineralization by HCl and hydrofluoric acid (Method S4). Mineral-bound compounds were quantified and their potential influence on the apparent turnover time of total compounds was assessed (Result S1), assuming that the turnover time of mineral-bound fractions was the same with that of black carbon in the same soil at the same depth. As soluble phenols may be partially lost to the aqueous phase during soil demineralization (Wang et al., 2017), three scenarios were used for lignin phenol assessment: Scenario 1 used the

measured proportions of mineral-bound lignin phenols in total lignin phenols with negative values arbitrarily assigned to zero; Scenario 2 assumed an average proportion (17%) of mineral-bound lignin phenols based on our measured, positive values; Scenario 3 assumed a higher proportion (44%) based on the highest proportion of mineral-bound lignin phenols in sorption studies with naked minerals (Hernes et al., 2013).

Compilation of published ^{14}C data

To compare the turnover and temperature sensitivity of our analysed molecular components with SOC pools isolated using other techniques, we further compiled published ^{14}C data for surface soils (0–30 cm) isolated into fast- (i.e. light) and slow-cycling (i.e. heavy) fractions by density fractionation from the international soil radiocarbon database ISRaD (Lawrence et al., 2019; <https://soilradiocarbon.org/>), supplemented by searching on 'Web of Science' containing words 'radiocarbon' and 'density fraction' published in 1993–2020. Studies that used sodium polytungstate solution to separate surface soils (0–30 cm) into light (<1.6 or 1.65 g cm⁻³), occluded light fraction and heavy fraction (>1.6 or 1.65 g cm⁻³) with reported $\Delta^{14}\text{C}$ or $F^{14}\text{C}$ values for fractions were selected. For this study, fraction <1.6 or 1.65 g cm⁻³ was treated as the 'light' fraction, while fraction >1.6 or 1.65 g cm⁻³ were treated as 'heavy' fraction (Cerli et al., 2012). In total, our data set included 185 observations for bulk OC, 127 for the light fraction and 376 for the heavy fraction which mainly originated from forests (49%–65%) and grasslands (~19%; Figure S3).

Ancillary data including sampling year, climate (MAT and MAP), net primary productivity (NPP) and soil texture (clay content) were also collected from the literature or obtained from the global climate database (Worldclim, Version 2.0) and high-resolution (250-m) gridded soil property database (<http://data.isric.org>), when not available from the literature.

The turnover times and temperature sensitivity of bulk OC and different physical fractions were calculated using the same method as for our molecular ^{14}C data. For some of the ^{14}C values with two possible turnover times, reported turnover times (if given in the original paper) were used. Otherwise, the shorter turnover time was chosen for the light fraction while the longer one was chosen for the heavy fraction, as the turnover time of bulk OC should be slower than the light fraction, but faster than the heavy fraction. Turnover times calculated using our method agreed well with those reported in the original literature (Figure S4).

Data analysis

All statistical analyses were conducted using R version 3.5.3 (R Development Core Team, 2019) or SPSS 20

(SPSS). Multiple comparisons with paired *t*-test were used to examine differences in the turnover times between bulk OC and various components in the topsoil as well as along soil profiles. One-way ANOVA was used to compare differences in turnover times among bulk OC, light and heavy fractions. Relationships of turnover times with environmental variables were assessed by Pearson correlation using the R package Hmisc (Hollander & Wolfe, 1999). Further, hierarchical partitioning analysis was conducted using the 'hier.part' package in R to determine the independent contribution of each environmental variable (including MAT, MAP, Fe_d and Al_d/clay and root/NPP) to the total variability of the response variable (turnover time of bulk OC and various fractions) in a multiple regression model (Nally, 1996). The relative independent effects refer to their independent effects in the total variations. Differences or correlations are considered to be significant at a level of $p < 0.05$, or marginally significant at a level of $p < 0.10$.

RESULTS

Turnover time of bulk OC and its molecular constituents

Overall, the $\Delta^{14}\text{C}$ values of bulk OC and its molecular components (including black carbon, lignin phenols and lipids) were higher in surface soil horizons and decreased with soil depth (Figure S1). Based on soil ^{14}C modelling, SOC components with high $\Delta^{14}\text{C}$ values (>20‰) may yield two potential solutions for turnover times (Figure 1b and Figure S5). However, there was no significant difference in the turnover time of bulk OC versus its various components other than black carbon in the topsoil (0–10 cm, $p > 0.10$), even when the longer turnover time was chosen for those components with two solutions. With increasing soil depth, the turnover time exhibited the sharpest increase for black carbon, followed by bulk OC and long-chain lipids, while this increase was less substantial for lignin phenols and short-chain lipids (Figure 1b). Correspondingly, lignin phenols and short-chain lipids showed the fastest decomposition rates across all profiles, exhibiting short turnover times (204–1962 years) relative to bulk OC and long-chain lipids even at the greatest soil depth, while black carbon showed the longest turnover time at the same depth (~60,000 years; $p < 0.05$).

Demineralization released mineral-bound short-chain and long-chain lipids that on average amounted to $14.7 \pm 1.3\%$ (mean \pm standard error) and $7.0 \pm 1.1\%$ of total lipids in the soil, respectively. Different from lipids, only 46% of the examined soil samples exhibited elevated yields of lignin phenols after demineralization with mineral-bound lignin phenols accounting for $17.9 \pm 3.1\%$ of total lignin phenols in the soil ($n = 14$; Figures S6 and S7). After considering the mineral-bound fraction of each

molecular components, lignin phenols and short-chain lipids remained to be the fast-cycling molecules among all the analysed SOC components under Scenarios 1 and 2. With increasing proportions of mineral-bound lignin phenols, turnover time of total lignin phenols increased but did not surpass that of bulk OC under any of the scenarios (Result S1 and Figure S7c).

Drivers and temperature sensitivity for the turnover of specific SOC components

Correlation and hierarchical partitioning analyses suggested that the turnover time of lignin phenols was mainly associated with MAT in the topsoil, while soil minerals had minimal influence on the turnover of short-chain lipids in deeper soil layers (20–70 cm; Figure 2a and Figure S8). In contrast, Fe_d and Al_d had the largest independent effect on the turnover time of the slow-cycling components (long-chain lipids and black carbon) as well as bulk OC in all soil layers (less so for bulk OC in the topsoil), where higher Fe_d and Al_d contents correlated with slower turnover.

Furthermore, E_a and Q_{10} values calculated using the Arrhenius equation for modelling (Equations 5 and 6) were compared among various molecular components. The E_a (18 ± 2.7 – 104 ± 3.9 kJ mol⁻¹) of lignin phenols and short-chain lipids decreased with soil depths (except short-chain lipids in the topsoil), resulting in a range of Q_{10} from 1.64 ± 0.07 to 5.87 ± 0.37 , with the highest Q_{10} value (5.87 ± 0.37) observed for lignin phenols in the topsoil (Figure 2b). In contrast, the slow-cycling components

(black carbon and long-chain lipids) and bulk OC had low E_a and Q_{10} in all layers. Lignin phenols still exhibited the highest Q_{10} values compared with bulk OC and slow-cycling components, when the measured mineral-bound fraction of biomarkers was considered (Figure S9) or when the shorter turnover time was chosen for those OC components with two possible turnover times (mainly in the topsoil; Figure S10). Moreover, Q_{10} of total lignin phenols turnover decreased with increasing proportions of mineral-bound lignin phenols (Figure S9).

Global synthesis of turnover times and temperature sensitivities of SOC fractions

Published ¹⁴C data of bulk OC and different physical fractions from globally distributed surface soils revealed that light fraction had a relatively shorter turnover time (222 ± 24 years), followed by bulk OC (330 ± 22 years), while the heavy fraction exhibited a longer turnover time (430 ± 28 years; Figure 3a). Correlation and hierarchical partitioning analyses confirmed that MAT had a predominant, negative effect on the turnover time of the fast-cycling (light) fraction, whereas the turnover time of the slow-cycling (heavy) fraction was mainly and positively controlled by clay content (Figure 3b and Figure S11). Moreover, the light fraction had a much higher E_a (40 ± 1 kJ mol⁻¹) and Q_{10} (1.88 ± 0.03) than the heavy fraction (15 ± 0.3 kJ mol⁻¹ and 1.25 ± 0.01 , respectively; Figure 3c), again indicating that other environmental characteristics (i.e. mineral association) modulate the turnover of the

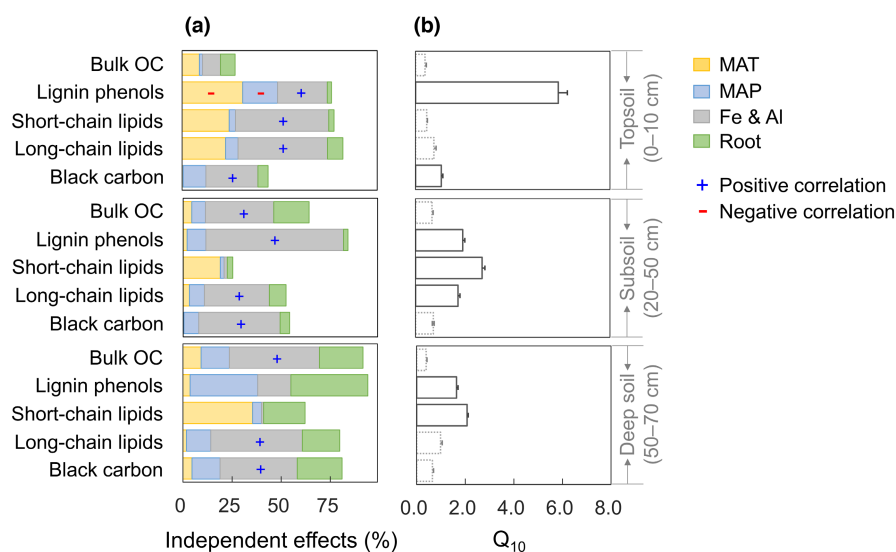


FIGURE 2 Influencing factors and temperature sensitivity (Q_{10} , changes of decomposition rates with temperature increasing from 5°C to 15°C) for the turnover of bulk organic carbon (OC) and various components in the grassland soil profiles of northern China. (a) Relative importance of different environmental variables influencing the turnover times. (b) Q_{10} values of bulk OC and various components in different soil layers. The longer turnover times are chosen here for those OC components having two possible turnover times. Dotted line indicates $Q_{10} < 1$. ‘-’ and ‘+’ in (a) represent significantly negative and positive correlations between turnover times and environmental variables based on Pearson correlation ($p < 0.05$). MAT, mean annual temperature; MAP, mean annual precipitation; Fe_d & Al_d , the summed contents of dithionite-extractable iron and aluminium in soil. Standard errors are given for Q_{10} .

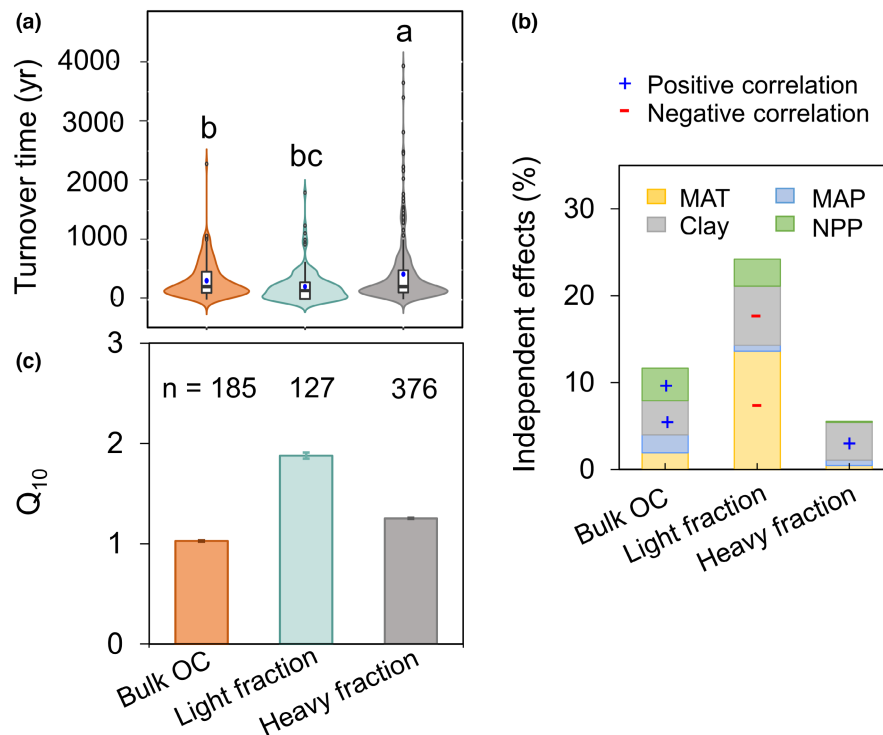


FIGURE 3 Influencing factors and temperature sensitivity (Q_{10} , changes in decomposition rates with temperature increasing from 5°C to 15°C) for the turnover of bulk organic carbon (OC), light and heavy fractions in globally distributed surface soils (0–30 cm). (a) Violin charts comparing the turnover times of bulk OC and OC associated with light and heavy fractions (based on meta-analysis). Solid line and circle in the box mark the median and mean of the data set. The upper and lower whisker caps denote the 0.25 and 0.75 percentiles, respectively. The upper and lower whisker caps denote the maximum and minimum values, respectively. Dots denote outliers. Shapes of the violin represent the distribution pattern of the turnover times. Different lowercase letters indicate different levels (one-way ANOVA, $p < 0.05$). (b) Relative importance of different environment variables for the turnover times. ‘-’ and ‘+’ represent significantly negative and positive correlations between turnover times and environmental variables based on Pearson correlation ($p < 0.05$). (c) Q_{10} values of bulk OC, light and heavy fractions. MAT, mean annual temperature; MAP, mean annual precipitation; NPP, net primary productivity. Standard errors are given for Q_{10} .

slow-cycling carbon pool, resulting in its relative insensitivity to temperature variations. These findings agree with those based on our molecular ^{14}C data that slower turnover of black carbon and long-chain lipids along the soil profiles of the Qinghai–Tibetan–Mongolian grasslands was mainly conferred by mineral associations and that their temperature response may not be predicted well by Arrhenius kinetics (Figure 2; Figures S9 and S10). In contrast to slow-cycling carbon components, turnover of fast-cycling carbon constituents (i.e. lignin phenols, short-chain lipids and light fractions) was mainly controlled by MAT with higher Q_{10} .

DISCUSSION

In support of our working hypothesis, our molecular ^{14}C data set provides direct evidence for the faster cycling and higher Q_{10} of lignin phenols and short-chain lipids relative to slow-cycling SOC molecular components (i.e. long-chain lipids and black carbon) along the soil profiles of the Qinghai–Tibetan–Mongolian grasslands (Figures 1 and 2). Synthesis of ^{14}C data from globally

distributed soils confirms that slow-cycling (heavy, mineral-associated) fractions have lower Q_{10} than that of fast-cycling (i.e. light) fractions (Figure 3). Our regional observations and global synthesis thus collectively suggest that mineral association—rather than chemical recalcitrance—controls the turnover of SOC components and attenuates their response to global warming, potentially affecting the terrestrial carbon-climate feedback.

Across the grassland soil profiles, lignin phenols and short-chain lipids exhibit shorter turnover times relative to bulk OC, long-chain lipids and black carbon (Figure 1), regardless if the longer or shorter turnover times are chosen for those compounds with two potential turnover times based on ^{14}C modelling. For short-chain lipids, microbial utilization of modern carbon (such as from root exudates or via percolation of dissolved organic matter) may influence their ^{14}C contents, since short-chain lipids are partly derived from soil microbes (van der Voort et al., 2017; Wiesenberger, Schmidt, & Schwark, 2008). Vertical supply of modern dissolved organic matter may also partially contribute to the ^{14}C -enriched lignin phenols in deeper soil layers (Jia, Feng, et al., 2019). However, the proportion

of water-extractable lignin relative to total lignin in the bulk soil is minor (<0.5%; Jia et al., 2017; Jia, Cao, et al., 2019), suggesting limited influence of modern dissolved lignin on the observed lignin phenol ¹⁴C values and thus fast-cycling of lignin phenols. In contrast to the fast-cycling of lignin phenols and short-chain lipids, long-chain lipids and black carbon turn over slowly, consistent with previous findings (Leifeld, 2008; van der Voort et al., 2017), likely as a consequence of their intimate mineral association (Grant et al., 2022; Kögel-Knabner et al., 2008).

It should be noted that the above results did not account for the mineral-bound fractions (i.e. of lignin phenols and lipids) which may not be released by the conventional extraction methods (Cai et al., 2017; Hernes et al., 2013). However, even after accounting for the mineral-bound fraction of each molecular component based on our demineralization treatments, lignin phenols and short-chain lipids still turn over faster than long-chain lipids under common scenarios (1 and 2; Figure S7). The turnover times of lignin phenols do not surpass that of bulk OC even when the proportion of mineral-bound lignin phenols equals 44% (Scenario 3; Figure S7), the maximum fraction of 'hidden' lignin observed in sorption studies based on naked minerals (Hernes et al., 2013). Given that Scenario 3 represents an upper limit of mineral-bound lignin phenols which is rare in natural soils with myriads of competing molecules for mineral sorption sites, and the longest turnover time (same as black carbon; Leifeld, 2008; Skjemstad et al., 2004) is assumed for the mineral-bound fraction, we argue that lignin phenols and short-chain lipids turn over more rapidly than long-chain lipids and black carbon in the soil. Our results therefore provide direct evidence for the relatively rapid turnover of lignin phenols in mineral soils on long-term (> centennial) timescales, in contrast to the slow turnover of lignin during litter decomposition over a relatively short periods (months to decades; Bahri et al., 2008; Hall, Huang, et al., 2020).

The observed difference in the turnover of various SOC molecular components is most likely linked with their distinct propensities to associate with soil minerals (Kögel-Knabner et al., 2008). Lignin is relatively concentrated in mineral-poor soil fractions (such as particulate organic matter or large aggregates) with relatively weak mineral associations (Amelung et al., 2002; Kögel-Knabner et al., 2008) and may be more accessible to microbial degradation. In contrast, long-chain lipids and black carbon show strong affinity to mineral surfaces through covalent or electrostatical bonds that protect them against biological degradation (Brodowski et al., 2005; Brodowski et al., 2006; van der Voort et al., 2017). The strong impact of mineral association on OC turnover is confirmed by the increasing turnover time of total lignin phenols with increasing contributions of mineral-bound fractions (Figure S7c) and is also

manifested in the global synthesis of ¹⁴C-based turnover for light (fast-cycling) and heavy (mineral-associated) soil fractions (Figure 3a).

Furthermore, our results show that the turnover of long-chain lipids and black carbon is mainly controlled by soil reactive minerals (Fe_d and Al_d), while MAT has a dominant control on the turnover of lignin phenols in the topsoil (Figure 2 and Figure S8). Similarly, MAT has a predominant, negative effect on the turnover time of light fraction in globally distributed soils, whereas the turnover time of heavy fraction is mainly and positively controlled by clay content (Figure 3b and Figure S11). These results jointly demonstrate the decisive role of soil minerals in the turnover of slow-cycling SOC fractions, while the turnover of fast-cycling carbon is mainly governed by thermodynamic constraints (i.e. temperature). It should also be pointed out that the turnover times of lignin phenols and short-chain lipids in the topsoil of Qinghai–Tibetan–Mongolian grasslands are longer than that of bulk OC and heavy fractions in the globally distributed surface soils, likely due to low temperature in the alpine grasslands (with average MAT of 0.86°C relative to 14.8°C globally) limiting microbial decomposition (Carvalhais et al., 2014).

Mineral association does not only mediate the decomposition rate of slow-cycling molecular compounds but also their response to warming. According to the kinetic theory, molecularly complex substances turn over slowly and exhibit high intrinsic Q_{10} (Davidson & Janssens, 2006). However, our results demonstrate that lignin phenols and short-chain lipids turn over faster and exhibit a higher Q_{10} than long-chain lipids and black carbon (Figure 2b). This discrepancy between kinetic theory and the observed apparent Q_{10} suggests that apparent Q_{10} is also mediated by mineral association. For long-chain lipids and black carbon which are strongly affected by mineral associations, access by extracellular enzymes may be hindered (Davidson & Janssens, 2006), complicating the response of enzymatic reactions to temperature variations and thus attenuating Q_{10} (Gentsch et al., 2018; Qin et al., 2021). Similarly, heavy fractions from globally distributed soils show lower Q_{10} than light fractions, and the Q_{10} of lignin phenol turnover decreases with increasing proportions of mineral-bound lignin phenols in our investigated grasslands (Figure 3c and Figure S9). For lignin with weak mineral associations, its high Q_{10} values imply that lignin decomposition may be accelerated under warming, consistent with recent observations based on field warming experiments (Feng et al., 2008; Jia, Cao, et al., 2019; Pisani et al., 2015; Tao et al., 2020). Given that lignin is a major component of organic matter in carbon-rich terrestrial environments (such as peatlands and forest organic layers; Chen, Hu, et al., 2021; Mason et al., 2012; Wang et al., 2017), future studies should pay more attention to lignin degradation under global warming.

CONCLUSIONS

Overall, our study provides the first direct evidence for rapid lignin turnover and its high Q_{10} compared with slower-cycling components of SOC such as black carbon and long-chain lipids in mineral soils, without or with considering mineral-bound fractions of biomarkers in the soil. The contrasting turnover times and Q_{10} values between molecular species resembles those of light and heavy SOC fractions, suggesting that mineral association—rather than chemical recalcitrance—controls the turnover of SOC components and suppresses temperature-regulated modulation of decomposition rates. These findings have two important implications for soil carbon cycling research. First, our results lend support to the view that the primary macromolecular structure of lignin does not necessarily confer resistance to decomposition in mineral soils (Schmidt et al., 2011). Although the biomarker method we employed targets relatively intact lignin molecules (not firmly associated with soil minerals) in the soil and may underrepresent transformed lignin derivatives (the latter requiring further investigation), the fast turnover of lignin phenols in mineral soils challenges the validity of carbon cycling models that parameterize SOC pools of differing lability based on lignin contents or lignin-to-nitrogen ratios. Instead, the content or fraction of mineral-associated carbon may be a more appropriate indicator of persistent SOC. Second, as a major plant carbon input into soils and a key component of organic matter in carbon-rich terrestrial environments, lignin is likely to decompose much faster with on-going global warming unless firmly associated with soil minerals. In contrast, the decomposition of slow-cycling SOC components may be more sensitive to disruptions of SOC-mineral associations (e.g. via shifting redox conditions or root exudation; Herndon et al., 2017) than direct warming. Factors that potentially affect organo-mineral associations hence warrant more attention regarding SOC-climate feedbacks on decadal to centennial timescales.

AUTHOR CONTRIBUTION

Xiaojuan Feng and Timothy I. Eglinton designed and supervised the study. Litong Chen, Jin-Sheng He and Xiaojuan Feng provided soil samples. Juan Jia, Zongguang Liu, Tian Ma, Yiyun Wang, Negar Haghypour and Hailong Zhang carried out chemical and ^{14}C analyses with help from Lukas Wacker, Timothy I. Eglinton and Meixun Zhao. Juan Jia, Ao Luo, Zhiheng Wang and Carlos A. Sierra performed statistical analysis with inputs from the others. Juan Jia and Xiaojuan Feng drafted the manuscript with contributions from all co-authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data supporting the results are archived in Figshare (<https://doi.org/10.6084/m9.figshare.22121720>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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