

in $\text{La}_2\text{Mo}_2\text{O}_9$ form a lattice of slightly distorted parallelepipeds whose corners are occupied alternately by La and Mo cations, thus defining buckled alternated (LaMo) planes perpendicular to the three main crystallographic axes (Fig. 4a). Such an arrangement is reminiscent of that observed in the monazite structural type (LnPO_4), and can be described as a micro-twinning of the cationic arrangement of the monazite structure (Fig. 4b). In $\text{La}_2\text{Mo}_2\text{O}_9$, the relatively large shortest Mo–Mo distances (4.58 Å) make electron conduction improbable, as effectively measured.

The structural and electrical results reported above show that oxide-ion conductivity is strongly indicated in $\text{La}_2\text{Mo}_2\text{O}_9$. A more direct way to unequivocally demonstrate oxide ion transport is to perform concentration or permeation measurements on fully densified materials. These experiments are planned, and will be reported at a later stage.

A way to consider the high-temperature form of the $\text{La}_2\text{Mo}_2\text{O}_9$ structure is through its relationship with that of $\beta\text{-SnWO}_4$ (ref. 14). Both compounds crystallize in the same space group, $P2_13$, with identical cationic positions. Divalent tin is a $5s^2$ lone-pair element, and it is well known²⁰ that a lone pair occupies a volume equivalent to that of an oxide ion O^{2-} . $\text{La}_2\text{Mo}_2\text{O}_9$ can thus be viewed as $\beta\text{-SnWO}_4$ where tin has been replaced by lanthanum (with identical size but without a lone pair), and tungsten by iso-element molybdenum. As lanthanum is trivalent, an extra oxygen atom is necessary to fulfil its oxidation state, so that the formal substitution starting from $\text{Sn}_2\text{W}_2\text{O}_8\text{E}_2$ leads to $\text{La}_2\text{Mo}_2\text{O}_{8+\square}$ (here we use E to indicate a lone pair, and \square to indicate a vacancy). Two lone pairs are thus replaced by one oxygen atom and one vacancy, through which oxygen diffusion can progress, which suggests the origin of oxide-ion conduction in $\text{La}_2\text{Mo}_2\text{O}_9$. Oxygen localization with large thermal factors of $\sim 10\text{Å}^2$, and strongly modulated background with characteristic O–O distances as obtained from neutron diffraction data¹⁷, are consistent with both the conduction property and its interpretation. The substitution of lanthanum by bismuth, although it significantly increases the cell volume and stabilizes the high-temperature form, does not increase the oxide-ion conductivity because Bi^{3+} substitution reintroduces a lone pair in the system, which tends to block the conduction path.

These stereochemical considerations suggest a way to design new oxide-ion conductors: starting from a mixed oxide of a lone-pair element (like Tl^+ , Ge^{2+} , Sn^{2+} , Pb^{2+} , Sb^{3+} , Bi^{3+} , Se^{4+} , I^{5+} ...), and substituting the lone-pair element with oxidation state $(n)^+$ by a non-lone-pair element of the same size and oxidation state $(n+1)^+$. For each two substituted cations, this would create one extra oxygen and one vacancy, which is a favourable situation for oxygen diffusion. As far as possible, the counter-cation should withstand a variation of coordination (as does Mo^{6+}). \square

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Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature

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It has been suggested that increases in temperature can accelerate the decomposition of organic carbon contained in forest mineral soil (C_s), and, therefore, that global warming should increase the release of soil organic carbon to the atmosphere^{1–6}. These predictions assume, however, that decay constants can be accurately derived from short-term laboratory incubations of soil or that *in situ* incubations of fresh litter accurately represent the temperature sensitivity of C_s decomposition. But our limited understanding of the biophysical factors that control C_s decomposition rates, and observations of only minor increases in C_s decomposition rate with temperature in longer-term forest soil heating experiments^{7–12} and in latitudinal comparisons of C_s decomposition rates^{13–15} bring these predictions into question. Here we have compiled C_s decomposition data from 82 sites on five continents. We found that C_s decomposition rates were remarkably constant across a global-scale gradient in mean annual temperature. These data suggest that C_s decomposition rates for forest soils are not controlled by temperature limitations to microbial activity, and that increased temperature alone will not stimulate the decomposition of forest-derived carbon in mineral soil.

To examine the long-term influence of temperature on the decomposition of C_s in forest soils, we assembled results from studies that used one of two standard methods for estimating C_s loss from soil. Method 1 studies estimate C_s loss by measuring *in situ* changes in the ¹³C/¹²C ratio and total C_s content of soil after existing vegetation is replaced with vegetation that uses a different photosynthetic pathway (for example, C_3 forest to C_4 pasture)¹⁶. The

change in vegetation alters the $^{13}\text{C}/^{12}\text{C}$ ratio of new detritus, allowing an estimate of the loss of C_s formed before conversion. Method 2 studies estimate C_s loss by incubating soils in the laboratory for 1 yr at temperatures representative of field conditions, and quantifying the CO_2 evolved^{17,18}. The 82 sites examined here span 8 soil orders and the global range of mean annual temperature (MAT) for forests (see Supplementary Information).

Calculated C_s turnover times for method 1 studies were unrelated to MAT ($R^2 = 0.01$, $P = 0.50$; Fig. 1); turnover times under moist tropical conditions were similar to those in cool temperate soils. In these studies, soil clay content, which is thought to control C_s storage¹, did not explain the lack of a relationship between C_s decomposition rates and MAT. For soils with similar (15–27%) clay content, C_s turnover was still unrelated to MAT ($R^2 = 0.05$, $P = 0.28$). In method 2 studies, C_s turnover time was positively related to incubation temperature, with C_s decomposing more slowly at higher temperatures ($R^2 = 0.14$, $P = 0.02$; Fig. 2). The C_s lost from method 1 and method 2 soils is the most active, and therefore the most temperature-sensitive, carbon in mineral soil^{2,9,19}. However, the decomposition rates of forest-derived C_s reviewed here are insensitive to temperature, unlike the response predicted by models^{1–6}.

In our calculations of turnover time, we assumed a single-pool model for soil carbon. To test whether this assumption affected the results, we compared C_s mass loss per year across MAT, with method 1 sites segregated by time since conversion. For method 1 studies, C_s mass loss per year decreased with increasing MAT for sites sampled <11 yr after conversion ($R^2 = 0.66$; $P < 0.01$), and was unrelated to MAT for sites sampled 11–45 yr after conversion ($R^2 = 0.01$; $P = 0.72$) or >45 yr after conversion ($R^2 = 0.15$; $P = 0.35$). Despite a 20 °C gradient in MAT, C_s mass loss as a function of time since conversion was insensitive to temperature (Fig. 3). C_s mass loss was roughly constant with time until about 30 years or about 60% mass loss. After this time, C_s decomposition appears to slow dramatically or stop. For method 2 studies, C_s mass loss for the 1-yr incubations decreased with incubation temperature ($R^2 = 0.19$, $P < 0.01$). We conclude that our choice of a single-pool model did not cause the lack of a relationship between C_s decomposition rates and temperature.

Our results conflict with those of Trumbore *et al.*², who used ^{14}C -based estimates of light-fraction C_s age (separated from generally smaller quantities of heavy-fraction C_s during density fractionation of total C_s) to model the decomposition of light-fraction C_s across a gradient in MAT. These authors found that decomposition rates of

light-fraction C_s increased exponentially with increasing temperature. An explanation for the discrepancy with our findings may be that in the study of Trumbore *et al.*, other factors that alter C_s decomposition (moisture, disturbance, and litter quality^{20,21}) were highest at sites with the highest decomposition rates. The warmer sites were generally wetter, more disturbed, and supported vegetation that produced higher-quality litter.

Although many short-term studies of C_s or litter decomposition show that decomposition rates increase with temperature^{3,6,10}, transient responses to increasing global temperature are unlikely to represent the response of most detrital carbon in forests. First, detrital carbon in forests resides primarily in the mineral soil (up to 70% in boreal forests¹³ and 95% in the lowland tropics^{22,23}), and *in situ* C_s mass loss rates are much slower than losses of fresh litter or forest-floor material^{13,23}. Second, all method 2 studies show large, rapid declines in decomposition rates in the first weeks of incubation, during which <5% of total C_s is typically released^{9–12,18,21}. These declines indicate either the depletion of a very small, active pool of C_s , or—because soils are processed before incubation—a return to pre-disturbance conditions. Third, long-term incubations of forest soil^{9–12}, and *in situ* comparisons of C_s content in heated and unheated soil⁸ or C_s turnover along gradients in MAT^{13–15}, show responses to increased temperature that are small, ephemeral or non-existent (that is, Q_{10} values of 1.0–1.4, where Q_{10} = reaction rate at $T + 10$ °C/reaction rate at T , and T is temperature). Taken together, these data and the data presented in Figs 1 and 2 suggest that sustained, temperature-related increases in the decomposition rate of forest-derived C_s should not be expected.

A global-scale relationship between C_s decomposition rates and MAT is central to predictions that global warming will accelerate the release of carbon stored in mineral soil^{1–6}. However, decomposition is performed by enzymes, and enzyme activity is limited by

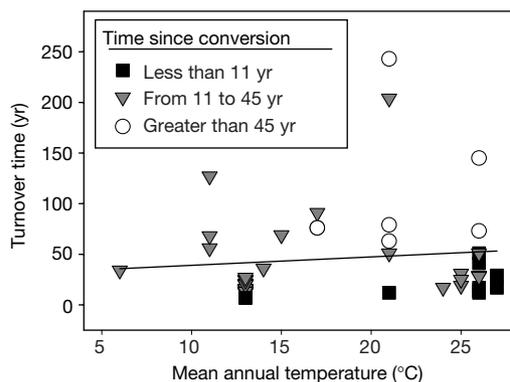


Figure 1 Relationship between turnover time for mineral soil carbon and mean annual temperature for method 1 studies. Turnover time is given by $1/k$ for a first-order decay reaction²¹, where $A_t = A_0 e^{-kt}$, A_t equals initial C_s content remaining when time since conversion equals t (in years), and A_0 equals C_s content when time since conversion equals zero. A_t and A_0 were estimated using $^{13}\text{C}/^{12}\text{C}$ ratios and C_s content for 44 sites (see Supplementary Information).

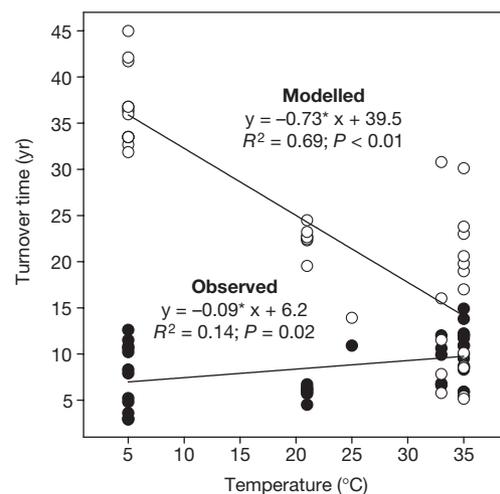


Figure 2 Relationship between observed or modelled C_s turnover time and incubation temperature for incubated forest soils. Observed points are first-order decay estimates of turnover times based on 1-yr cumulative C_s mass loss for single soils from 38 sites (see Supplementary Information). Modelled points were calculated from the equation controlling the sensitivity of soil C to temperature and texture in the widely used terrestrial ecosystem model CENTURY: $\tau_{\text{SOC}} = -16 + 41(\text{clay fraction}) + 46e^{-0.037T}$, where τ_{SOC} is the turnover time for total soil organic C, and T is temperature (ref. 1). In CENTURY, as with most models of terrestrial ecosystems^{3,4}, C_s turnover is defined to be exponentially related to temperature, with Q_{10} values ranging from ~1.2 at 35 °C to ~8 at 1 °C. The above equation, the “slow C pool” equation ($\tau_{\text{SOC}} = -67 + 9.1(\text{clay fraction}) + 159e^{-0.037T}$), and a more labile “detrital” soil C equation ($\tau_{\text{SOC}} = -0.1 + 0.6(\text{clay fraction}) + 7.3e^{-0.047T}$) were all poor predictors of observed C_s turnover (R^2 values <0.05), with CENTURY over-predicting the influence of temperature on C_s turnover in cold climate soils. Similarly, CENTURY over-predicted the influence of clay on C_s turnover, most obviously for the tropical soils.

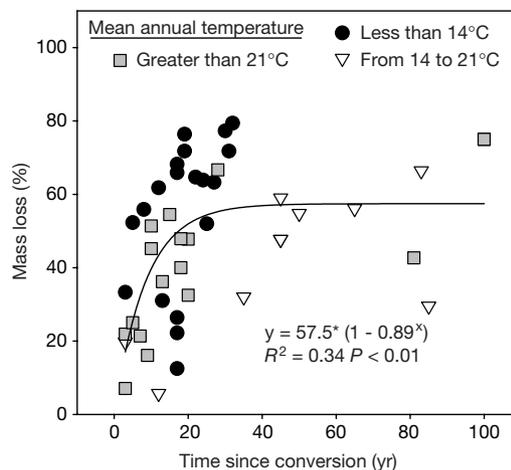


Figure 3 Relationship between C_s mass loss and time (in years) since conversion of vegetation type. These results are for the same sites as presented in Fig. 1.

temperature only when the supply rate of substrate exceeds the reaction rate for that substrate. Therefore, the most tenable explanation for the apparent temperature insensitivity of C_s decomposition is that heterotrophic microbes in mineral soil (those organisms responsible for decomposing C_s) survive on a supply of substrate that is sub-optimal for growth^{7,21,24}. Soil clay content, available moisture, and C_s quality are three factors that may influence substrate availability^{1,21}.

The binding of C_s to clay particles and physical protection within soil aggregates are thought to lower C_s availability^{1,21}. At a given location, where variations in climate and biota are more uniform, turnover times are longer for C_s associated with clay than with sand^{20,25}. If clay controls substrate availability, we would expect C_s turnover times to increase as clay content increases. However, data from method 1 and method 2 studies provide only weak support for clay limitations to substrate availability. For both method 1 and method 2 studies, C_s turnover time was nearly constant across sites, and variation among soils within a region was similar to global variation. For method 1 studies, where clay varied from 7% to 84%, there was no relationship between C_s turnover time and soil clay content ($R^2 = 0.05$, $P = 0.14$; see Supplementary Information). In method 2 studies, C_s mass loss was weakly related to clay content in soils with 7–30% clay ($R^2 = 0.15$, $P = 0.05$; Supplementary Information). For clay >30%, C_s mass loss decreased with increased clay ($R^2 = 0.41$, $P = 0.06$; Supplementary Information). While these results conflict with established modelling assumptions¹, other studies have also found weak relationships between clay content and C_s decomposition rates^{17,26}.

Available moisture exerts a large influence on soil microbial activity²¹, and low soil moisture probably reduces microbial populations. However, available moisture did not affect substrate availability in method 2 studies because soils were maintained at or near field moisture capacity for the length of the incubation. Although we have no information on differences in soil moisture among method 1 sites, method 1 data were taken primarily from sites that had previously supported closed-canopy forests, which indicates moisture regimes that are at least adequate for decomposition.

Low C_s quality may limit substrate availability for microbes, and perhaps also limit microbial populations²¹. Forest-derived C_s consists of lignin-dominated remains and precipitated by-products of plant and microbial residue decomposition. These compounds are poor carbon sources for microbes, because energy yields are low for the energy expended to digest them²¹. Evidence that low quality of C_s limits C_s decomposition rates in mineral soil includes low C_s decomposition rates compared with rates for fresh litter²³ and rapid

increases in CO_2 release from non-rhizosphere soils that are amended with labile substrate²⁴. ^{13}C nuclear magnetic resonance analyses of forest-derived C_s show that the relative abundance of C_s functional groups (for example, alkyls, O-alkyls, aromatics and carbonyls) varies minimally across global-scale gradients in MAT (ref. 27). If C_s quality limits decomposition rates, then low global-scale variation in C_s decomposition rates may reflect low variation in the chemical composition of C_s .

Whether C_s decomposition is controlled by temperature or by substrate availability will change predictions for the effect of global warming on the large quantity of C_s stored in tropical soils^{1,2,28} and in soils that are frozen for most of the year^{28,29}. If temperature limits C_s decomposition, as assumed in most current ecosystem models, then tropical soils would provide the main source of additional carbon released in a warmer climate because C_s decomposition rates in high-latitude soils would be constrained by perennially low soil temperatures^{1,2}. In contrast, if substrate availability limits C_s decomposition rates, increased global temperatures alone would have little influence on C_s decomposition rates in the tropics. Warming at high latitudes, however, would expose larger amounts of C_s to microbial activity by lowering the depth of frozen soil, lowering the water table, and extending the duration of thawed conditions²⁹. Once these soils are thawed or the water table lowered, C_s decomposition rates would be constrained by substrate quality and moisture rather than by low temperatures.

The turnover of C_s in forest soils appears to be remarkably constant on a global scale, and insensitive to differences in MAT. However, the relationship between C_s turnover and MAT presented here serves only as a proxy for the changes that will occur *in situ* in response to global warming. The influence of temperature on C_s decomposition rates needs to be directly examined across a range of sites to better constrain predictions of the effects of warming on carbon release from soil. □

Methods

Method 1 studies primarily examined the loss of forest-derived C_s . All sites were disturbed during conversion, but land management varied during and following conversion. Details on methodology for a typical method 1 study are given in ref. 16. For method 2 studies, all soils were sampled from closed-canopy forests, similarly processed, and maintained at constant moisture levels near field capacity for the length of the incubation period. We used studies in which soils were incubated for at least 1 yr, because long-term incubations provide information on the mineralization potential of both the small labile C_s pool and the larger intermediate C_s pool⁹. Microbial activity and C_s decomposition rates also may be less sensitive to sampling disturbance in long-term incubations than in short-term incubations. Method 2 studies have some important limitations. Soil macro-structure is altered during sampling and processing. Soils are incubated at a constant temperature and high moisture, whereas field environments fluctuate and are generally drier. Finally, incubations eliminate carbon inputs, which can shift microbial populations¹⁸. Although

incubation-derived indices of C_s decomposition rates will probably differ from those developed in the field, relative differences among sites are presumably real^{17,18,21,26}.

We used single-pool exponential decay models to estimate C_s turnover time in method 1 and method 2 studies. Single-pool models are widely used to describe C_s turnover, but they may over-estimate rates because the approach assumes that all C_s will behave as did the C_s released during the study³⁰. It is unlikely, however, that our single-pool approach masked a relationship between the turnover of a large, temperature-sensitive C_s pool and temperature. In method 1 studies, we would suspect masking if C_s mass loss per year increased with temperature early in the decomposition sequence. However, for sites with <11 yr since conversion, C_s mass loss per year was higher for cool sites (9.5% yr⁻¹) than for warm (4.5% yr⁻¹) climate soils ($P < 0.01$). In method 2 studies, we would suspect masking if the total quantity of C_s released per gram of soil increased with temperature because the release of this C_s is independent of total C_s pool size. However, C_s released per kilogram of soil in one year declined with increasing incubation temperature ($R^2 = 0.11$, $P = 0.04$). Further, for masking to have occurred, the proportion of total C_s that is temperature sensitive or fast-cycling must decline steeply with increasing temperature. Using the best techniques available, Trumbore *et al.*² found no relationship between the proportion of fast-cycling C_s (from 50% to 80% of total C_s) and MAT. Nonetheless, we tested the potential for masking by assuming that all C_s released in method 2 studies was fast cycling and that 50%, 65% and 80% of total C_s in tropical, temperate and subalpine soils, respectively, was fast cycling. We then recalculated turnover times for fast-cycling C_s alone. Overall, patterns of C_s decomposition were unchanged.

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Respiration as the main determinant of carbon balance in European forests

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Carbon exchange between the terrestrial biosphere and the atmosphere is one of the key processes that need to be assessed in the context of the Kyoto Protocol¹. Several studies suggest that the terrestrial biosphere is gaining carbon^{2–8}, but these estimates are obtained primarily by indirect methods, and the factors that control terrestrial carbon exchange, its magnitude and primary locations, are under debate. Here we present data of net ecosystem carbon exchange, collected between 1996 and 1998 from 15 European forests, which confirm that many European forest ecosystems act as carbon sinks. The annual carbon balances range from an uptake of 6.6 tonnes of carbon per hectare per year to a release of nearly 1 t C ha⁻¹ yr⁻¹, with a large variability between forests. The data show a significant increase of carbon uptake with decreasing latitude, whereas the gross primary production seems to be largely independent of latitude. Our observations indicate that, in general, ecosystem respiration determines net ecosystem carbon exchange. Also, for an accurate assessment of the carbon balance in a particular forest ecosystem, remote sensing of the normalized difference vegetation index or estimates based on forest inventories may not be sufficient.

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