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Vegetation control on soil organic matter dynamics

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Abstract

Soil organic matter (SOM) formation is one of the least understood steps of the global carbon cycle. An example is uncertainty around the role of plant communities in regulating SOM formation and turnover. Here we took advantage of the highly controlled conditions at the San Dimas lysimeter installation to quantify the influence of oak and pine vegetation on SOM dynamics. SOM turnover rates, estimated using total C and $^{14}$C content of litter and physically separable soil fractions, were faster under oak than under pine. In contrast to the rapid turnover for the oak litter (<2 years), the delay in litter incorporation into the mineral soil under pine was a controlling factor of SOM fluxes.

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1. Introduction

Conceptual models of pedogenesis, and ecosystem models such as CENTURY, distinguish between distinctive environmental controls over organic matter storage in soils, including climate, vegetation, and parent material (Schimel et al., 1994). Validation of these models is difficult, especially in the case of vegetation influence on SOM dynamics because vegetation and climate typically covary in a complex fashion. Here we take advantage of a long-term man-made experiment where scrub oak (\textit{Quercus dumosa} Nutt.) and Coulter pine (\textit{Pinus coulteri} B. Don) have been grown in adjacent lysimeters under the same climatic conditions. Initial soil conditions were identical, allowing us to compare organic matter formation and turnover where vegetation is the only environmental variable.

The detonation of thermonuclear weapons in the 1950’s and 1960’s enriched atmospheric CO\textsubscript{2} with “bomb” $^{14}$C, which subsequently was fixed in terrestrial plants and incorporated into SOM. This radiocarbon enrichment has been used as a tracer for assessing SOM turnover in situations where archived soils (i.e. samples taken prior to the 1960’s) are available for comparison with modern soils (O’Brien and Stout, 1978; Scharpenseel et al., 1989; Trumbore et al., 1996). In this study, litter and soil samples collected in 1987 were compared with soil samples archived in 1937 during construction of the lysimeters. Radiocarbon abundance was measured by accelerator mass spectrometry (AMS), using a sample size as small as 0.5 mg. The overall objective was to characterize processes controlling SOM turnover as a function of the oak and pine vegetation. Changes in SOM storage were combined with isotopic measurements to estimate inputs to the soils and SOM turnover rates.

2. Experimental

2.1. Site description

The lysimeter installation is located within the San Dimas Experimental Forest, a U.S. Forest Service...
Pacific Southwest Research Station facility about 56 km northeast of Los Angeles. The climate is Mediterranean, with a mean annual precipitation of 670 mm and a mean annual air temperature of 14.3°C (Dunn et al., 1988). The lysimeters consist of large (5.3 by 5.3 m horizontally and 2.1 m deep) earthen-valled pits that were filled in 1937 with fine sandy loam (58% sand, 31% silt, 11% clay) derived on site from the weathering of diorite (Colman and Hamilton, 1947). In 1946, the lysimeters were planted with monocultures of native woody species, including scrub oak and Coulter pine (Patric, 1961). Each planting covered a single lysimeter and buffer strips to eliminate edge effects. At the time of sampling in 1987, a 7-cm-thick A horizon composed nearly entirely of worm casts had developed in the oak lysimeter, while the soil under pine had a 1-cm-thick A horizon devoid of casts (Graham and Wood, 1991). Aboveground biomass as measured in 1993 was similar for the pine (304 Mg ha⁻¹) and the oak (301 Mg ha⁻¹) stands (Quideau et al., 1998).

2.2. Analyses

Four soil samples archived in 1937 during filling of the lysimeters, and triplicate samples from the 1987 litter and surface A horizons under oak and pine were selected for this study. Soil samples (< 2 mm) were fractionated using a combination of sedimentation and centrifugation techniques to separate four distinct carbon pools (Quideau et al., 1998): the floatables (50–2000 μm, isolated from the mineral fraction by floation in water), the sand + coarse and medium silt (5–2000 μm), fine silt (2–5 μm), and clay (< 2 μm) fractions. Litter samples and soil fractions were analyzed for total C by dry combustion using a Carlo Erba analyzer. The measured carbon concentrations correspond to organic carbon since the lysimeter soils contain no carbonates.

Radiocarbon measurements were made on the litter, unfractionated soil samples, and the floatable, fine silt and clay soil fractions. The ¹⁴C content of the sand + coarse and medium silt fractions was estimated from the measured ¹⁴C content of the other fractions and whole soil samples. Graphite targets for ¹⁴C analysis were prepared by combusting 0.5–1 mg carbon at 900°C with cupric oxide wire in evacuated, sealed quartz tubes (Trumbore, 1996). The evolved CO₂ was purified cryogenically in a vacuum line, catalytically reduced to graphite targets, and analyzed for ¹⁴C by AMS at Lawrence Livermore National Laboratory, California. Radiocarbon data were expressed as F, the fraction Modern carbon (where Modern is by definition 1950), and ¹⁴C, the % deviation from the ¹⁴C/¹²C ratio of oxalic acid standard, corrected for the radioactive decay of this standard since 1950. Average precision for the ¹⁴C values was ± 7%.

3. Results

3.1. Soil carbon storage and ¹⁴C measurements

The original fill material of the lysimeters contained no macroorganic matter (i.e. the floatables fraction), and most of the carbon was associated with the mineral clay fraction (Table 1). Since bomb ¹⁴C contamination was absent from these samples, the mean residence time (MRT) of carbon in each fraction was calculated as its radiocarbon age (Trumbore, 1996):

\[ \text{MRT} = -8267 \times \ln(F) \]  

(1)

where 8267 is the Libby mean life of ¹⁴C. Results indicated that the fractionation method was successful in separating SOM pools with diverse MRTs (Table 1).

Carbon concentration (g kg⁻¹) was roughly twice as high under oak as under pine (Table 2). Carbon accretion in the A horizon under the oak was an order of magnitude higher than under the pine when corrected for differences in horizon thickness. In contrast to the fill material, the major portion of soil carbon in the 1987 samples was recovered in the floatables fraction, indicative of recent litter inputs. This was particularly true for the soil under oak.

The 1987 soil samples and associated fractions reflected the incorporation of “bomb” ¹⁴C, as indicated by positive Δ¹⁴C values (Table 2). For each fraction, contribution of the carbon added to the soil between 1946 and 1987 (C₀) was separated from that originally present in the fill material (C₀), assuming that the decrease in C₀ with time followed a first-order reaction:

\[ C = C_0 + (C_0 \times e^{-k_{ot}t}) \]  

(2)

and

\[ \Delta^{14}C \times C = (\Delta^{14}C_n \times C_0) + (\Delta^{14}C_o \times C_0 \times e^{-k_{ot}t}) \]  

(3)

where C and Δ¹⁴C are the total measured carbon and ¹⁴C content in the 1987 samples, k₀ is the decomposition constant corresponding to C₀, and is equal to 1/MRT calculated using Eq. (1), Δ¹⁴C₀ is the ¹⁴C content in the fill material as presented in Table 1, and t is the time elapsed between construction of the installation and soil sampling (t = 41 years). Calculated C₀ and Δ¹⁴C₀ are shown in Table 2. For all soil fractions, the Δ¹⁴C₀ values were more positive under oak than under pine.

3.2. Modeling SOM dynamics

3.2.1. Model description

Changes in carbon content with time, dC₀/dt (g m⁻² year⁻¹), reflect the annual input of carbon to the soil, I (g m⁻² year⁻¹), and the output of carbon through
decomposition losses. In this modeling exercise, leaching losses were assumed negligible in front of decomposition fluxes, and loss by decomposition was assumed to be a first-order reaction:

\[ dC_n/dt = I - k_n C_n \]  

(4)

where \( k_n \) is the decomposition constant corresponding to \( C_n \). The amount of \(^{14}\text{C} \) (g m\(^{-2}\)) entering a given carbon compartment for a given year \( u \) was defined as: \( I_u \times ^{14}\text{C}_{u-\tau} \), where \( I_u \) is the input of carbon for year \( u \) \( \tau \) represents the lag time between photosynthetic fixation and the year of input into the carbon compartment, and \(^{14}\text{C}_{u-\tau} \) is equal to average \(^{14}\text{C} \) activity of atmospheric CO\(_2\) for year \( u-\tau \). The amount of \( I_u \times ^{14}\text{C}_{u-\tau} \) that is still present in this carbon compartment in 1987 thus is equal to: \( I_u \times ^{14}\text{C}_{u-\tau} \times e^{-\left(k_n + \lambda\right)(1987-u)} \), where \( \lambda \) is the rate constant for the radioactive decay of \(^{14}\text{C} \). The total amount of \(^{14}\text{C} \) present in the soil in 1987 can then be defined as the sum for all years over the 1946–1987 time interval (i.e. \( u \) varies between 1946 and 1987):

\[ \Delta ^{14}\text{C}_n = \Sigma I_u \times ^{14}\text{C}_{u-\tau} \times e^{-\left(k_n + \lambda\right)(1987-u)} \]  

(5)

Carbon inputs were assumed to increase linearly between 1946 and 1987, and Eq. (5) was solved to obtain \( \Delta ^{14}\text{C}_n \) as a function of \( k_n \) when \( \tau \) was fixed (Fig. 1). The \( k_n \) values corresponding to the measured \( \Delta ^{14}\text{C}_n \) for the litter layers and soil fractions were read from the obtained curves (Tables 2 and 3).

### Table 1
Carbon and \(^{14}\text{C} \) concentration in the original fill material (0–7 cm depth). Numbers in parentheses are an estimate of the sampling error, and represent one standard error from the mean (\( n = 4 \)).

| Soil sample\(^{a}\) | C (g kg\(^{-1}\)) | C (% total C) | C (g m\(^{-2}\)) | \( \Delta ^{14}\text{C} \) (%) | F Fract. Mod. | MRT\(^{b}\) |
|---------------------|----------------|--------------|----------------|----------------|----------------|----------------|
| SA                  | 1.2 (0.1) | 35.7 (1.5) | 90 | -514 | 0.489 | 5910 |
| FS                  | 7.3 (0.1) | 22.5 (0.3) | 57 | -187 | 0.818 | 1660 |
| CL                  | 8.7 (0.4) | 41.8 (1.9) | 106 | -15 | 0.991 | 75 |
| WS                  | 2.3 (0.1) | 100 | 253 | -232 | 0.773 | 2130 |

\(^{a}\) SA = sand + coarse and medium silt (5–2000 \( \mu \)m); FS = fine silt (2–5 \( \mu \)m); CL = clay (<2 \( \mu \)m); WS = whole soil (<2 mm).

\(^{b}\) Calculated using Eq. (1) as described in text.

### Table 2
Carbon storage, \(^{14}\text{C} \) concentration, estimated decomposition constant (\( k_n \)), and 1987 carbon input (\( I_{1987} \)) for the A horizons under oak (0–7 cm depth) and pine (0–1 cm depth) vegetation. Numbers in parentheses are an estimate of the sampling error, and represent one standard error from the mean (\( n = 3 \)).

| Sample\(^{a}\) | C (g kg\(^{-1}\)) | C (% total C) | C (g m\(^{-2}\)) | \( \Delta ^{14}\text{C} \) (%) | \( C_n^{b} \) (g m\(^{-2}\)) | \( \Delta ^{14}\text{C}_n^{b} \) (%) | \( \tau \) (year) | \( k_n^{c} \) (year\(^{-1}\)) | \( I_{1987} \) (g m\(^{-2}\)) |
|----------------|----------------|--------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| Oak lysimeter  |                |              |                |                |                |                |                |                |                |
| FL             | 406 (23) | 46.0 (4.5) | 963 | 319 | 963 | 319 | 1 | 0.07 | 102 |
| SA             | 8 (1) | 23.5 (3.1) | 492 | 154 | 402 | 302 | 1 | 0.09 | 51 |
| FS             | 62 (3) | 15.8 (1.2) | 331 | 274 | 275 | 367 | 5 | 0.08 | 32 |
| CL             | 43 (1) | 14.7 (1.1) | 308 | 225 | 247 | 285 | 1 | 0.13 | 41 |
| WS             | 33 (1) | 100 | 2093 | 259 | 1887 | 318 | – | 0.08 | 226 |
| Pine lysimeter |                |              |                |                |                |                |                |                |                |
| FL             | 341 (18) | 32.2 (6.4) | 55.5 | 220 | 55.5 | 220 | 1–25 | 0.08 | 6.6 |
| SA             | 8 (1) | 28.4 (2.6) | 49.0 | -90 | 36.0 | 61 | 1–28 | 0.005 | 1.9 |
| FS             | 41 (6) | 18.1 (2.0) | 31.0 | 108 | 23.2 | 209 | 1–25 | 0.07 | 2.5 |
| CL             | 38 (2) | 21.3 (3.1) | 36.5 | 115 | 27.9 | 156 | 1–25 | 0.02 | 1.7 |
| WS             | 16 (3) | 100 | 172.0 | 90 | 142.6 | 166 | – | 0.04 | 12.7 |

\(^{a}\) FL = floatables (50–2000 \( \mu \)m); SA = sand + coarse and medium silt (5–2000 \( \mu \)m); FS = fine silt (2–5 \( \mu \)m); CL = clay (<2 \( \mu \)m); WS = whole soil (<2 mm).

\(^{b}\) Calculated using Eqs. (2) and (3) as described in text; note that for the floatables, \( C = C_n \) and \( \Delta ^{14}\text{C} = \Delta ^{14}\text{C}_n \).

\(^{c}\) Calculated using Eqs. (4) and (5) as described in text, and the \( \tau \) value indicated in table.
3.2.2. Model fitting for the oak lysimeter

Intense earthworm activity under the oak contributes to the rapid mixing of fresh plant residues into the mineral soil (Graham and Wood, 1991). Therefore, a time lag \( \tau \) of 1 year was selected to solve Eq. (5). This provided a good experimental fit for the different soil fractions, with the notable exception of the fine silt fraction (Fig. 1a). The maximum \( \Delta^{14}C_n \) obtained with \( \tau = 1 \) was 351%, less than the measured value of 367% for this fraction. The estimated \( \Delta^{14}C_n \) increased as \( \tau \) increased, and it was possible to fit the fine silt value when \( \tau \) was equal to 5 years (Fig. 1a). These results suggest that fresh plant residues transit through coarser size fractions before they enter the fine silt fraction. Estimated decomposition constants correspond to a turnover of 8–14 years depending on the size fraction (Table 2).

Carbon input to the A horizon of the oak lysimeter was calculated by simultaneously solving Eqs. (4) and (5) to fit the measured \( C_n \) and \( \Delta^{14}C_n \) values for each soil fraction. This yielded a total input of 226 g C m\(^{-2}\) for 1987 (Table 2). By comparison, surficial litterfall for 1997–1998 was 225 g C m\(^{-2}\) (Quideau, unpublished data), suggesting that the entire litterfall would have to be added to the mineral soil in order the supply the necessary carbon flux. It is more likely, however, that part of the input is supplied by root turnover, which may constitute a substantial carbon flux into the mineral soil for chaparral ecosystems. Graham and Wood (1991) reported the presence of common fine and very fine roots in the A horizon under oak. Assuming it had reached steady state in 1987, the decomposition constant of the oak litter was estimated by dividing its biomass by the annual litterfall. The obtained value of 0.46 year\(^{-1}\) was slightly less than the corresponding \( k_n \) (0.61 year\(^{-1}\)) estimated from the measured \( \Delta^{14}C_n \) (Table 3), although both values imply a very rapid turnover for the oak litter.

3.3. Model fitting for the pine lysimeter

The litter layer under pine was composed of three distinct horizons: an Oi1 of fresh pine needles, an Oi2 with partially decomposed pine needles, and an Oe of mostly decomposed needles (Graham and Wood, 1991). The estimated decomposition constant \( k_n \) decreased with increasing depth in the litter layer, indicating an increasing resistance to decomposition as the pine needles decayed and became buried under fresher needles (Table 3). The modeled turnover rate for the Oe horizon was 33 years. These results emphasize the slower decomposition rate of the pine litter as compared to the oak.

Assuming a constant time lag \( \tau \) throughout the course of the experiment did not provide a good experimental fit for the measured \( \Delta^{14}C_n \) values in the soil under pine (Fig. 1a). In particular, for the sand + coarse and medium silt fraction, the measured \( \Delta^{14}C_n \) was equal to 61%, a much lower value than was predicted with the model. Two scenarios may explain a \( ^{14}C \) signature in soil carbon as low as 61%. First, the increase in soil carbon for

![Graph](image-url)

**Fig. 1.** Modeled \( \Delta^{14}C_n \) content (%) as a function of \( k_n \), calculated using Eq. (5) in the text: (a) the time lag \( \tau \) is assumed to stay constant; and (b) \( \tau \) is assumed to increase gradually from 1946 to 1987.

![Table 3](image-url)

**Table 3**

| Horizon | Depth (cm) | \( C \) (g kg\(^{-1}\)) | C (g m\(^{-2}\)) | \( \Delta^{14}C \) (%) | \( k_n \) (year\(^{-1}\)) |
|---------|------------|------------------------|-----------------|----------------------|---------------------|
| Oak lysimeter | 6–0 | 448 (16) | 493 | 212 | 0.61 |
| Oi | 6–0 | 448 (16) | 493 | 212 | 0.61 |
| Oi2 | 6–4 | 491 (3) | 65.1 | 238 | 0.27 |
| Oe | 4–0 | 448 (12) | 347.4 | 343 | 0.03 |

\( a \) Numbers in parentheses are an estimate of the sampling error, and represent one standard error from the mean (\( n = 3 \)).

\( b \) Calculated using Eq. (5) as described in text with \( \tau = 1 \) year.
the pine lysimeter occurred at an early stage following planting, i.e.; before the 1960's and the increase in \(^{14}\text{C}\) content of atmospheric CO\(_2\) due to thermonuclear explosions. A second, and more probable, explanation would be an increase in the time lag \(\tau\) over the course of the experiment. Earthworms were absent under pine vegetation, and there was no mixing between the litter and the mineral soil (Graham and Wood, 1991). As the litter horizon gradually built up following planting, the delay between litterfall and the time of incorporation of these freshly fallen pine needles into the mineral soil would gradually increase. Allowing \(\tau\) to linearly increase from 1 year in 1946 to \(\geq 25\) years in 1987 provided the required fit for the measured \(\Delta^{14}\text{C}_n\) concentrations in the floatables, fine silt and clay fractions, while it was possible to fit the \(\Delta^{14}\text{C}_n\) value of 61% when \(\tau\) increased from 1 to \(\geq 28\) years (Fig. 1b).

Estimated turnover rate for total carbon contained in the pine A horizon was 25 years, twice as slow as that under oak vegetation (Table 2). Differences between species were particularly apparent for the sand and medium silt as well as the clay fractions. Carbon retention in soils may be promoted by the interaction between organic and inorganic components, such as the formation of organo-mineral complexes with clay particles, and of resistant coatings on larger, sand-sized particles. Since the two lysimeters were constructed with homogenized material, observed differences in carbon turnover should be related to the chemical make-up of the litter material entering the soil pool, and/or to the nature and activity of the decomposing community.

Total input to the A horizon under pine was 12.7 g C m\(^{-2}\) in 1987 (Table 2), while measured litterfall was 135 g m\(^{-2}\) in 1997–1998 (Quideau, unpublished data). The difference between these two values implies that a substantial part of the pine litter (i.e. >90%) is either decomposed to CO\(_2\) before it is incorporated into the mineral soil, or is leached as DOC below the A horizon depth. An additional carbon input to the mineral soil may be provided by root turnover, as Graham and Wood (1991) described the presence of common fine roots and many very fine roots in the A horizon under pine. Allowing \(\tau\) to increase throughout the course of the experiment assumes that roots accumulate and show an increasing time lag before incorporation into the mineral soil similar to that of the surficial litter.

4. Conclusion

The simple model described in this paper allowed us to estimate SOM turnover rates based on carbon and \(^{14}\text{C}\) concentration in litter and physically separated soil fractions. The model included three parameters: (1) the time lag \(\tau\) between photosynthetic fixation and litter incorporation into the mineral soil, (2) the carbon output through decomposition loss, and (3) the carbon input rate. A comparison of results indicated distinct SOM dynamics for the oak and pine lysimeters. In particular, these results demonstrated the dependence of the time lag parameter \(\tau\) on vegetation type. For the oak lysimeter, the measured \(^{14}\text{C}\) concentration was effectively modeled using a constant \(\tau\) of \(\leq 5\) years, which implied rapid incorporation of the fresh litter into the mineral soil. For the pine lysimeter, on the other hand, a successful fit of measured \(^{14}\text{C}\) values required \(\tau\) to increase throughout the growth period to reach \(\geq 25\) years in 1987. This suggested that the delay in incorporation of the plant residues into the mineral soil was a significant regulator of SOM fluxes under pine vegetation.

Comparing measured litterfall with the modeled carbon input rate provided an estimate of the efficiency of surficial litter incorporation into the A horizon. A much smaller portion of the surficial litter was added to the A horizon under pine than under oak. This model, however, does not allow partitioning between the different processes of carbon incorporation into the mineral soil. Diffusion, which includes mixing through the biological action of soil fauna was likely an important process at the oak lysimeter where earthworm activity was prominent. On the other hand, convection, which reflects the transport of DOC, may be the dominant mechanism at the pine lysimeter. In turn, this raises the question of how the age of DOC relates to the accumulated litter layer, and experiments are needed that would measure these different carbon fluxes and help clarify their respective role in SOM processes. Regardless, the model results demonstrate distinctly different SOM dynamics under different tree species which implies that similar differences exist among shrubs, herbs and grasses. Thus we conclude that the global mosaic of vegetation exerts significant influence on the accumulation and turnover of soil organic matter directly by determining the palatability of plant material and indirectly by conditioning the pathways of biomass incorporation into soil.

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