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AGE OF SOIL ORGANIC MATTER AND SOIL RESPIRATION: RADIOCARBON CONSTRAINTS ON BELOWGROUND C DYNAMICS

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Abstract. Radiocarbon data from soil organic matter and soil respiration provide powerful constraints for determining carbon dynamics and thereby the magnitude and timing of soil carbon response to global change. In this paper, data from three sites representing well-drained soils in boreal, temperate, and tropical forests are used to illustrate the methods for using radiocarbon to determine the turnover times of soil organic matter and to partition soil respiration. For these sites, the average age of bulk carbon in detrital and Oh/A-horizon organic carbon ranges from 200 to 1200 yr. In each case, this mass-weighted average includes components such as relatively undecomposed leaf, root, and moss litter with much shorter turnover times, and humified or mineral-associated organic matter with much longer turnover times. The average age of carbon in organic matter is greater than the average age predicted for CO_2 produced by its decomposition (30, 8, and 3 yr for boreal, temperate, and tropical soil), or measured in total soil respiration (16, 3, and 1 yr). Most of the CO_2 produced during decomposition is derived from relatively short-lived soil organic matter (SOM) components that do not represent a large component of the standing stock of soil organic matter. Estimates of soil carbon turnover obtained by dividing C stocks by heterotrophic respiration fluxes, or from radiocarbon measurements of bulk SOM, are biased to longer time scales of C cycling. Failure to account for the heterogeneity of soil organic matter will result in underestimation of the short-term response and overestimation of the long-term response of soil C storage to future changes in inputs or decomposition.

Comparison of the ¹⁴C in soil respiration with soil organic matter in temperate and boreal forest sites indicates a significant contribution from decomposition of organic matter fixed >2 yr but <30 yr ago. Tropical soil respiration is dominated by C fixed <1 yr ago. Monitoring the ¹⁴C signature of CO₂ emitted from soils give clues as to the causes of seasonal and interannual variability in soil respiration in these systems.

Key words: belowground processes and global change; carbon cycle; global climate change; radiocarbon; sink; soil organic matter; soil respiration; source.

INTRODUCTION

Interest in the storage and cycling of organic matter in soils has increased recently because of its importance to the global carbon cycle. Organic matter in detritus and mineral soil organic matter, collectively referred to here as SOM, is the major reservoir of carbon in terrestrial ecosystems, storing some 1500 Pg (1 Pg = 10^{15} g) of carbon in the upper meter of mineral soils (Jobbágy and Jackson 2000). This is slightly more than twice the amount of carbon present in the atmosphere as CO₂. However, merely knowing the size of the reservoir of carbon stored in soils is insufficient for predicting its potential to influence atmospheric CO₂ concentrations. We must also know something about soil carbon dynamics.

Not all of the carbon in soils interacts with atmospheric CO_2 on the same time scale. Observational constraints require SOM to consist of several pools, with characteristic turnover times of \leq yr, years to decades, and over several hundred years (e.g., Parton et al. 1987). Most of the roughly 80–160 Pg C in surface detritus (Matthews 1997) and an estimated 200–300 Pg C in SOM is in forms that accumulate and decompose on time scales of a century or less (Schimel 1995, Potter and Klooster 1997). The remainder, constituting the majority of carbon stored in mineral soils, is stable on time scales of centuries to millennia.

Several issues have emerged recently to focus questions on the role of soils in the global carbon cycle over decade-to-century time scales. The first is the role that soils have played historically as sources or sinks of carbon associated with changes in land management (e.g., clearing of forest or abandonment of agricultural land to forest regrowth; Jackson et al. 2000). In general, forest clearing is associated with soil C loss and regrowth is associated with soil C gain in temperate ecosystems. Tropical soils have been observed to both gain and lose C on forest conversion, depending on the pro-

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ductivity of the subsequent pasture (e.g., Camargo et al. 1999). Changes in C storage occur not only in upper soil layers, but also affect distribution of organic matter with depth (Jackson et al. 2000).

Soil C stores are predicted to respond to climatic change because organic matter decomposition rates are linked to soil temperature and moisture regimes. In particular, enhanced decomposition associated with warming of 1°C has been predicted to release between 11 and 30 Pg C to the atmosphere from soils (Schimel et al. 1994). Given the general warming of nearly 0.5° C over the past century, deduced from observations and paleoclimate data, we should therefore expect soils to presently act as a global net source of CO₂ to the atmosphere. Of particular interest is the response of large stores of C in northern peatlands to potential future warming.

Another issue of interest is the observed interannual variability in the partitioning of fossil fuel derived CO_2 among atmospheric, terrestrial, and oceanic sinks. The annual transfer of CO_2 from soils to the atmosphere has been estimated at 60–80 Pg C/yr (Raich and Potter 1995), 12–16 times the annual rate of addition of fossil fuel CO_2 to the atmosphere. If a significant portion of that flux is derived from carbon that resides in SOM for several years to decades, then one cause of interannual variability may be due to differences in the timing of C addition to and release from soils (Fung et al. 1997).

A timely question is the present and future potential for storage of fossil fuel derived CO₂ in soil organic matter. With the Kyoto accords suggesting that enhancement of C sinks may be an acceptable way of offsetting fossil fuel emissions (Bolin 1998), there is increased interest in managing soils to take up carbon. The ability of a reservoir to act as a net CO₂ sink depends on both the fluxes of C into the reservoir and the residence time of carbon. Small reservoirs that adjust quickly to enhanced C inputs are not good longterm solutions for storing carbon, whereas large pools that turn over more slowly may remain net sinks of carbon long enough to partially offset fossil fuel addition to the atmosphere for a decade or two. Critical to the ability to predict how much and how long carbon can be stored in soils is an understanding of the residence time of carbon in SOM, and what processes determine it.

Various tools have been developed to determine the dynamics of SOM, including direct observations of C fluxes and inventory, manipulations such as litter decomposition experiments and ¹⁴C labeling of substrates, and chronosequence studies. This paper will focus on the use of ¹⁴C produced by atmospheric weapons testing to study belowground C dynamics. The comparison of ¹⁴C in soil respiration with ¹⁴C in soil organic matter fractions demonstrates the heterogeneous nature of soil C, and may be used to determine the fraction of soil

respiration derived from decomposition of organic carbon with turnover times >1 yr. Examples taken from boreal, temperate, and tropical forest soils are used to demonstrate several issues: (1) determining turnover time of soil C fractions, including sources of uncertainty in the interpretation of radiocarbon data; (2) partitioning soil respiration into contributions from C recently fixed from the atmosphere and C that has resided for years to decades in soil organic matter; (3) investigating causes of seasonal and annual variability in soil respiration; and (4) using ¹⁴C measurements to verify whether managed systems are accumulating or losing carbon relative to unmanaged counterparts.

THE RADIOCARBON TRACER

Radiocarbon is useful for studying soil organic matter dynamics on two different time scales. Natural radiocarbon, which is produced at an approximately constant rate in the upper atmosphere during cosmic ray bombardment, reflects the dynamics of organic matter that has been stabilized by interaction with mineral surfaces and resides in soils long enough for significant radioactive decay to occur (14 C half-life = 5730 yr). Discussion here, however, will focus on radiocarbon produced during atmospheric testing of thermonuclear weapons during the early 1960s. Tracing this global isotopic "spike" for the C cycle into ocean and terrestrial C reservoirs provides information on exchanges that occur on time scales of years to decades (Broecker and Peng 1982). Radioactive decay on this time scale is negligible, and bomb ¹⁴C is essentially a conservative tracer.

Although the first radiocarbon measurements in SOM were made in the 1960s (e.g., Campbell et al. 1967), the recent advent of accelerator mass spectrometry (AMS), with its smaller sample size requirements and faster throughput capabilities, has led to a rapid expansion in the use of ¹⁴C to study organic matter dynamics in terrestrial ecosystems. The use of AMS also makes it feasible to monitor the ¹⁴C signature of CO₂ emitted from soils, and to sample soil atmosphere CO₂ for isotopic measurement.

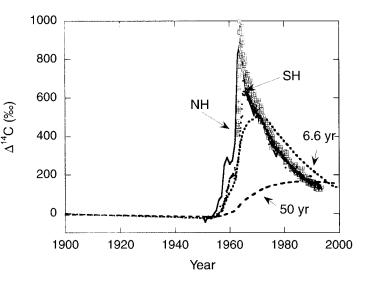
Radiocarbon data are reported as the permil (‰) deviation from a standard of fixed isotopic composition:

 $\Delta^{14} C = [F - 1] \times 1000 \tag{1}$

$$F = \frac{\begin{pmatrix} {}^{14}C\\ {}^{12}C \end{pmatrix} \text{sample}}{\begin{pmatrix} {}^{14}C\\ {}^{12}C \end{pmatrix} \text{standard}}.$$
 (2)

The standard is selected so that Δ^{14} C is zero (F = 1.000) for atmospheric CO₂ in 1950. Both sample and standard are corrected for mass-dependent fractionation of iso-

FIG. 1. Changes in the Δ^{14} C of atmospheric CO_2 in the northern and southern (solid circles) hemisphere since 1900, as recorded in air samples and wines (Stuiver and Quay 1981, Burcholadze et al. 1989, Manning and Melhuish 1995, Nydal and Lövseth 1995). A Δ^{14} C value of +1000‰ represents a doubling of the amount of ¹⁴C in atmospheric CO₂. The southern hemisphere (SH) record of bomb 14C lags that of the northern hemisphere (NH) due to the preponderance of atmospheric testing in the northern hemisphere and the time required to mix air across the equator. Also shown is the expected evolution of two steady state, homogeneous carbon reservoirs (in the northern hemisphere) with mean carbon residence times of 6.6 and 50 yr (dashed lines). The two lines cross in 1996.



topes, with all samples corrected to a common δ^{13} C value of -25%. Radiocarbon data reported in this way thus reflect the time since C was fixed and/or the ¹⁴C signature of CO₂ sources, and not isotopic discrimination during fixation or respiration of carbon. Positive Δ^{14} C values indicate the presence of bomb-produced radiocarbon (¹⁴C activities higher than the 1950 atmosphere). Negative Δ^{14} C values indicate that the bulk of the carbon has resided in soils long enough for significant radioactive decay to have occurred.

Fig. 1 illustrates changes in the amount of radiocarbon in atmospheric CO₂ during this century. Analysis of the ¹⁴C content of known-age tree rings shows that, for several thousand years prior to 1900, atmospheric ¹⁴CO₂ levels remained roughly constant. Radiocarbon decreased in the early part of the century because of dilution by CO₂ derived from the burning of ¹⁴C-free fossil fuels. The major feature seen in Fig. 1 is a neardoubling of atmospheric ¹⁴C levels between 1955 and 1964, due to ¹⁴C production by atmospheric nuclear weapons testing. With the cessation of most atmospheric tests in 1964, radiocarbon levels decreased as the excess ¹⁴C in the atmosphere began to be transferred into ocean and terrestrial C reservoirs. The radiocarbon signature of atmospheric CO₂ in the 1980s and 1990s continues to decline at a rate of about 8‰ per year (Levin et al. 1992) due to continued uptake by the oceans and dilution as CO2 derived from ¹⁴C-free fossil fuel is added to the atmosphere. The Δ^{14} C of CO₂ during the northern hemisphere growing season in 1996 was $+97 \pm 5\%$ (Gaudinski et al., *in press*). Because the annual rate of decline is greater than the precision of the ${}^{14}C$ measurement (±4-8‰, depending on the laboratory and method used), it is possible to identify the year in which C was fixed from the atmosphere to within 1–2 years over the past 30 years.

Few other methods exist to trace carbon dynamics on decadal time scales. Most rely on the presence of some form of disturbance; for example, observing the accumulation or loss of carbon associated with a change in land management, or the change in ¹³C following a vegetation change from C_3 to C_4 plants. The latter method has been used extensively in tropical ecosystems where C_3 forests are often replaced with C_4 grasses. However, it only gives information on C dynamics in the disturbed system. Ehleringer et al. (2000) discuss other assumptions and limitation of using stable isotopes to study SOM dynamics. A major advantage of using the bomb radiocarbon tracer is that it can be used in both disturbed and undisturbed ecosystems.

Another method proposed to study more slowly cycling soil organic matter pools is long-term (>1-yr) incubations (e.g., Townsend et al. 1995). The rationale for using incubations is that all rapidly cycling organic matter will decompose within the first year, allowing estimation of the fraction of heterotrophic respiration derived from remaining C, which has turnover times >1 yr. However, soil incubations are limited in that they are not representative of in situ conditions. In addition, the C not respired after one year is likely to have a range of decomposition rates. Because those components with the fastest decomposition rates will dominate the production of CO_2 , care must be exercised when calculating a decomposition rate from incubation experiments.

Distribution of radiocarbon in SOM

The degree to which bomb ¹⁴C may be found in soil organic matter provides a direct measure of the degree to which soils have incorporated C fixed from the atmosphere over the past \sim 35 yr. This information may be used in conjunction with other measures of C inventory and flux to deduce the residence time of carbon in different components of SOM.

Fig. 2 shows the distribution of C and ¹⁴C with depth for moderately well to well-drained boreal, temperate

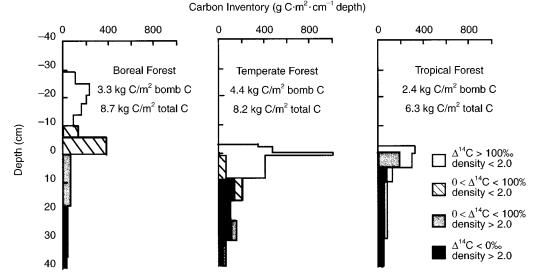


FIG. 2. Carbon density (in g C/m² per cm depth) and radiocarbon signatures (shading) with depth for boreal, temperate, and tropical forest soils. Zero on the depth axis is the mineral–organic boundary, negative depths are surface litter, and positive depths are within the mineral soil. Carbon is also identified as dense fraction (>2 g C/cm³) or low-density fraction (<2 g/cm³). See *Distribution of radiocarbon in SOM* for descriptions of sites and original references.

deciduous, and tropical forest soils, sampled 31-33 yr after the 1964 peak in bomb ¹⁴C. Surface detrital layers are shown in addition to the upper portions of the mineral soil. In mineral horizons, SOM has been separated by density. The dense fraction ($\leq 2 \text{ g C/cm}^3$) is carbon associated with soil mineral surfaces, whereas the lowdensity fraction ($\geq 2 \text{ g C/cm}^3$) is nonmineral-associated organic matter of varying degrees of degradation. The shading shows the radiocarbon content of the SOM in each depth interval. High values (>100‰) indicate that the soil organic matter has more ¹⁴C than the 1996 atmosphere, and is thus dominated by C fixed >1 yr but <35 yr ago. Low values (<0%) indicate that the organic matter, on average, has resided in the soil long enough for significant radioactive decay of ¹⁴C to have occurred (>300 yr). Intermediate values (0-100‰) represent either C that turns over on time scales of several decades to centuries, or a mixture of more rapidly (>100%) and more slowly (<0%) cycling material.

The boreal soil is in a mature black spruce–feather moss stand near Thompson, Manitoba, Canada, that burned ~120 yr ago (Harden et al. 1997, Trumbore and Harden 1997). Since then, ~30 cm of moss, root, and leaf detritus has accumulated above a residual layer of charred material underlain by humified organic matter in which plant fragments can no longer be identified. We infer from chronosequence studies that the site is continuing to accumulate C in surface moss in 1996 (Harden et al. 1997), although this gain is offset by carbon losses from net decomposition of deeper, ¹⁴Cdepleted carbon (Goulden et al. 1998). The temperatey forest soil is from the Harvard Forest in central Massachusetts, USA (Wofsy et al. 1993, Goulden et al. 1996). This mixed deciduous hardwood and conifer forest has regrown on abandoned farm land. All of the carbon in surface litter and the A horizon at this site has accumulated on the top of a plowed layer since abandonment, nearly a century ago (Gaudinski et al., *in press*). The tropical site is a deep-rooting, seasonally dry, but still evergreen broadleaf forest in eastern Amazonia, Brazil (Trumbore et al. 1995, Camargo et al. 1999).

Although Fig. 2 shows only the upper 40 cm, the C storage of both fast-cycling and more persistent C at depths >40 cm is significant for all three soils. This is particularly true of the tropical forest soil, which contains as much C with decadal turnover times below 1m as in the upper 1m of soil (Trumbore et al. 1995). Clay contents are highest in the mineral portion of the tropical and boreal soils and low in the temperate soil. The boreal and temperate soils are both developed on postglacial surfaces, whereas the tropical soil is probably >100 000 yr old.

At each site, the total amount of carbon in soil derived from the atmosphere since 1963 is on the order of 2.5–4 kg C/m², some 40–50% of the total organic matter in the soil to 40 cm depth. The ¹⁴C signatures of organic matter fractions clearly differ, with most of the bomb C in low-density organic matter (<2 g C/ cm³). The abundance of bomb carbon decreases with depth in the soil profile at all sites, although its presence at depth may be inferred from the ¹⁴C measured in soil CO₂ (see *Soil respiration*).

TABLE 1. Summary of turnover times derived from modeling radiocarbon in SOM fractions for the boreal, temperate, and tropical forest soils shown in Fig. 2.

Site and SOM fraction	C stock (g C/m ²)	TT† (yr)	Source of mean residence time (MRT)	
Boreal	5800	60		
Surface moss and detritus Humic layer	5800 9400	60 1000–1500	¹⁴ C and C accumulation since last fire; chronosequence ¹⁴ C and C accumulation since deglaciation	
Total to mineral (40 cm)	15 200	650–1250	C and C accumulation since degraciation	
Temperate				
O leaves + roots	400	3-8	¹⁴ C of leaf and root detritus	
O humics	1300	30-40	¹⁴ C and C accumulated since reforestation; CO ₂ fluxes	
A/Ap low density roots	100	3-8	¹⁴ C of root detritus	
A/Ap low density humics	2600	50-160	14 C of $< 2 \text{ g/cm}^3$ fraction	
A/Ap dense	600	160 - 400	14 C of > 2 g/cm ³ fraction	
B1 low density	1200	800-1000	14 C of $< 2 \text{ g/cm}^3$ fraction	
Total to 40 cm	6200	200-310		
Tropical				
O leaves	325	<1	litter flux and layer inventory	
A $(0-40 \text{ cm})$ low density	830	1-3	^{14}C of $< 2 \text{ g/cm}^3$ fraction	
A dense hydrolyzable	3110	10-30	¹⁴ C and C removed hydrolysis	
A dense nonhydrolyzable	1190	>6000	14 C of > 2 g/cm ³ residue	
Total to 40 cm	5460	1040	-	

Notes: Details and original data for each sites are given in Trumbore and Harden (1997) for boreal soils; Gaudinski et al. (*in press*) for temperate soils; and Trumbore et al. (1995) for tropical soils. Ages associated with total inventories are based on the mass-weighted ¹⁴C value for all elements.

 \dagger Turnover time of C in the plant + soil system. For a homogeneous, steady-state system, this is the same as the mean age of C in the fraction, or the mean time a C atom has resided in the SOM fraction since it was fixed from the atmosphere by photosynthesis.

Determining turnover times for soil organic matter from modeling radiocarbon

Changes in C storage in soils are the difference between annual carbon inputs (I, inputs of fresh plant detritus from leaves and roots) and losses to decomposition, leaching, and erosion. In a simple formulation, we assume that leaching and erosion losses are small (on an annual basis), and that decomposition may be represented as a first-order process:

$$dC/dt = I - kC \tag{3}$$

where C is the amount of carbon in the SOM fraction and k is the decomposition rate constant.

Trumbore and Torn (1999) and Gaudinski et al. (in press) discuss the time-dependent models used to calculate the mean turnover time of carbon (1/k) from radiocarbon data. As an example, the predicted evolution of Δ^{14} C in steady-state soil organic matter pools with mean residence times of 6.6 and 50 yr are compared with the atmospheric ¹⁴C record in Fig. 1. Both yield the same Δ^{14} C value (+160‰) in 1996, so the choice of the appropriate turnover time requires additional information. One approach is to measure the ¹⁴C in soil organic matter from archived soils sampled in the same location between 1940 and 1970 (e.g., O'Brien and Stout 1978, Harkness et al. 1986, Trumbore et al. 1989, 1996, Jenkinson et al. 1992, Harrison et al. 1993). If no archived soils are available, comparison of the flux implied from the C inventory in the fraction, divided by the mean residence time, with measured rates of soil C inputs (litterfall and root turnover) and losses (respiration), often may be used to distinguish between the two cases (Trumbore et al. 1995). Comparison of disturbed and undisturbed soils may also be used to constrain mean residence times (Hseih 1993, Townsend et al. 1995).

Some soils, such as the boreal forest moss layer (Fig. 2), are obviously accumulating carbon following disturbance. Because the amount of ¹⁴C in the atmosphere has changed considerably over the past 30 yr, the total amount of both carbon and ¹⁴C in the accumulated organic matter will uniquely determine *I* and *k*, assuming that the timing of disturbance is known (see Trumbore and Torn [1999], Gaudinski et al., [*in press*] for details). Radiocarbon measurements indicate that significant amounts of carbon fixed before 1960 (and since the last fire 120 yr ago) persist at the bottom of the moss layer (Fig. 2). Hence, decomposition rates must be slow. The mean residence time consistent with both C and ¹⁴C accumulation in moss detritus at this site is ~60 yr (Trumbore and Harden 1997).

Table 1 summarizes the turnover times derived from radiocarbon in physically and chemically fractionated organic matter for the boreal, temperate, and tropical forest soils shown in Fig. 2. Details of how turnover times and fractions were chosen are given in original references cited in Table 1. We have assumed in each case that the soil fraction isolated is homogeneous with respect to decomposition.

Turnover times inferred from ¹⁴C vary with soil depth and with soil organic matter fraction, as has been observed in other soils. Fractions with fastest turnover times (years to decades) are the least degraded organic matter: identifiable and relatively undecomposed leaves, root, and moss detritus. Mean residence times for this detrital carbon pool increase from tropical to boreal latitudes. Soil organic matter fractions with slowest turnover times (centuries to millennia) are either associated with mineral (clay) surfaces or kept from decomposing by conditions of waterlogging or soil freezing (boreal soil). Partially degraded (humified) organic matter in the temperate soil has intermediate residence times (decades to centuries), and makes up the bulk of the soil carbon to 40 cm depth. In the tropical forest soil, mineral-associated C that is hydrolyzed in acid and base has decadal turnover times, whereas the unhydrolyzed C has the longest turnover time measured in any of the soils.

Many studies in the literature report and interpret ¹⁴C measurements made only on bulk SOM. The mean soil carbon residence time to 40 cm, calculated as the inventory-weighted average in Table 1, ranges from 200 to 1300 yr. This age, which represents the ¹⁴C age that would be measured on bulk SOM integrated to 40 cm depth, is highly influenced by the amount of persistent (millennial cycling) carbon in the soil. Use of the mean ages derived from bulk SOM radiocarbon measurements would lead to severe underestimation of the dynamic nature of C in these soils, which contain \geq 40% of their SOM in forms that cycle on decadal and shorter time scales.

Appropriateness of assumptions and assessment of uncertainty

Two fundamental assumptions are made when using radiocarbon to determine turnover times for SOM fractions in soils. First, the use of a single decomposition rate (*k*) assumes that the probability that any given carbon atom in the SOM fraction will decay is the same. This is never true for bulk soil organic matter, and is probably only an approximation for SOM fractions isolated using density or chemical separations. Second, the assumption is made in calculating curves like those in Fig. 1 that the C added to the SOM fraction each year has the Δ^{14} C signature of that year's atmospheric CO₂. In other words, the assumption is made that the C added is fresh photosynthate and that no time lag exists between C fixation and addition to the soil as dead organic material.

Fig. 3 compares the Δ^{14} C of CO₂ within the soil pore space with the Δ^{14} C of SOM at the same depths for the tropical (Camargo et. al. 1999) and temperate (Gaudinski et al., *in press*) forest soils. The isotopic composition of carbon dioxide in the soil pore space reflects its sources: decomposition of organic matter and metabolic respiration by plants. (In both soils, CO₂ concentrations increase with depth and therefore the isotopes do not reflect downward diffusion of carbon dioxide produced near the surface.) The Δ^{14} C of CO₂ derived from decomposition should equal that of the homogeneous SOM fraction that is decomposing. The

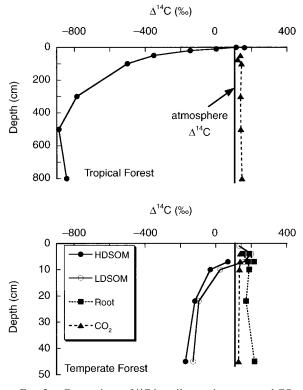


FIG. 3. Comparison of ¹⁴C in soil organic matter and CO₂ sampled in the soil pore space for tropical and temperate forest sites also depicted in Fig. 2. Abbreviations: LDSOM, low-density soil organic matter; HDSOM, high-density soil organic matter. The atmospheric Δ^{14} CO₂ value for 1996 was between +95‰ and +105‰, significantly less than ¹⁴CO₂ values measured in soil pore space at both sites.

 Δ^{14} C of CO₂ derived from plant metabolic respiration should equal that of the contemporary atmosphere, because the residence time of carbon respired by roots is expected to be <1 yr.

Fig. 3 shows that Δ ¹⁴C values in pore-space CO₂ are enriched in ¹⁴C compared to atmospheric CO₂ in the year of sampling (+95% to +105%), and organic matter fractions measured at the same depth. We must infer the presence of a SOM fraction at depth that has mean residence times of years to decades, which has $\Delta^{14}C$ values greater than atmospheric ¹⁴CO₂. The source of this deep, rapidly cycling C is either decomposition of fine roots (which have been identified as having high ¹⁴C at depth in Harvard Forest; Gaudinski et al., in press) or soluble organic matter transported down from surface layers. The amount of organic matter that we infer in this faster cycling pool is small enough that it does not significantly affect the low density SOM fraction ¹⁴C value, but it cycles rapidly enough that it dominates the decomposition flux. For example, deep soil organic matter that is 97% carbon with mean turnover time of ~850 yr (Δ^{14} C = -100‰), mixed with 3% carbon with mean turnover times of ~ 10 yr (Δ^{14} C = +200‰), would have an overall bulk Δ^{14} C value of

Variable	Boreal	Temperate	Tropical
$\label{eq:constraint} \hline Observed flux of CO_2 (g \ C\cdot \ m^{-2} \cdot yr^{-1}) \\ TT of C in SOM derived from C stock divided by 0.7 \times respiration (yr)^{\dagger} \\ TT determined from \ ^{14}C in SOM (yr)$	200	720	2200
	220	12	2.5
	650–1250	200–310	1040
Δ^{14} C of CO ₂ from decomposition (‰) ⁺ Mean age of decomposition flux (yr)	$+132 \\ 30$	$+165\\8$	+127 3
Measured Δ^{14} C of soil respiration (‰)	+110 to +120	+128	+103
Range of observed values (‰)	-97 to +160	+87 to +147	NA§
Mean age of soil respired C (yr)	16	3	1
Fraction of total respiration derived from SOM with MRT >1 yr	40-50%	40-50%	<20%

TABLE 2. Fluxes and isotopic signature of soil-respired CO₂ at the three forested sites.

[†] TT is turnover time of C in the plant and soil system.

 \ddagger Flux-weighted Δ^{14} C in CO₂ derived from decomposition of soil organic matter fractions listed in Table 1. Fluxes are calculated as k (= 1/TT) times C inventory from Table 1. The mean age of the decomposition flux is calculated using the flux-weighted TT, again from Table 1. The mean value is given here for simplicity of comparison; a range of values is calculated depending on assumptions about transfer of C between SOM fractions (see Gaudinki et al., *in press*).

§ NA, not measured seasonally.

-91%. The Δ^{14} C of CO₂ derived from decomposition of this organic matter would be +120%. Our results demonstrate that, although radiocarbon data in organic matter may give a reasonable estimate of the mean residence time for organic matter and the rate at which it will respond over decades, they are not useful for estimating C fluxes from the soil on an annual basis, particularly in mineral soil horizons.

Fung et al. (1997) point out that the age of C substrate added to the soil is not necessarily always ≤ 1 yr, as assumed when calculating the time course of ¹⁴C in hypothetical SOM fractions in Fig. 1. Woody debris, conifer needles, and roots that live >1 yr may make up a significant portion of the annual litter inputs to soil organic matter. If so, their ¹⁴C content will be higher than that assumed in the model (because the atmospheric ¹⁴C is decreasing at \sim 9 permil per year). In the case of woody debris, a significant component of litter inputs may pre-date atmospheric bomb testing and may have low Δ^{14} C values. In some cases, this difference may be used to determine the residence time of C in living organic matter pools. For example, the Δ^{14} C of conifer leaves in accumulating detritus in the boreal forest soil indicates that the average age of needles is ~ 10 yr older than that of deciduous leaves in the same layer (Trumbore and Harden 1997). However, interpreting radiocarbon data in terms of decomposition rates becomes problematic unless one knows how C inputs are allocated among long-lived species like conifer needles, woody debris, and coarser roots vs. litter components like deciduous leaves and very fine root hairs that may grow and die within one year. Hence, the turnover times derived from ¹⁴C reported here represent the average age of C in the entire plant plus soil system, and probably underestimate actual in situ decomposition rates.

RADIOCARBON IN SOIL RESPIRATION

Partitioning of soil respiration sources

The discussion of Fig. 3 illustrates how the Δ^{14} C of CO₂ respired from soils yields information about its

sources. Ehleringer et al. (2000) divide soil respiration into metabolic and heterotrophic components for study using stable isotopes. In terms of radiocarbon, soil respiration must be considered to be derived from three components: (1) decomposition of SOM fractions with turnover times of several years to decades, as deduced from ¹⁴C in organic matter substrates (Table 1); (2) decomposition of organic matter with very fast turnover times (<1 yr), which are a small component of SOM and therefore cannot be estimated from radiocarbon in the solid phase; and (3) metabolic respiration by plants. Components (2) and (3) are indistinguishable in their ¹⁴C content.

For the three forest soils discussed here, the predicted CO_2 flux from decomposition of SOM fractions with mean residence times >1 yr (calculated as $k \times C$ for each fraction), and the predicted $\Delta^{14}C$ of the resulting CO_2 , are given in Table 2. The mean age of this component of soil respiration (based on the fluxweighted mean age of what is decomposing) is also given in Table 2, and reflects the fact that faster cycling components contribute the most to the decomposition flux.

If the radiocarbon content of total soil respiration is measured, the partitioning of soil respiration among components with turnover times of greater and less than one year may be estimated from the mass balance of ¹⁴C (details are given in Gaudinski et al., *in press*):

$$\sum \text{SOM}_{i}F_{i} + RF_{atm} = TF_{T}$$
(4)

where SOM_i represents the flux of CO₂ estimated from each identified SOM fraction (i) with ¹⁴C signature F_i ; R is the flux of CO₂ from root respiration and decomposition of carbon that was fixed within the past year with ¹⁴C signature F_{atm} ; and T is the total respiration flux, with measured ¹⁴C signature F_{T} . Because

$$\sum \text{SOM}_{i} + R = T \tag{5}$$

the ratio of R to T may be derived from knowing the isotopic signatures (F_i, F_{atm}, F_T) alone. In practice, in-

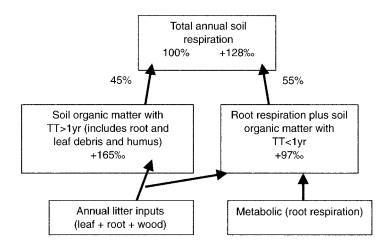


FIG. 4. An example of partitioning soil respiration into sources from organic matter with turnover times >1 yr and turnover times <1 yr, including metabolic respiration. Data in this figure are summarized from observations made in 1996 at the Harvard Forest site (Gaudinski et al., *in press*); estimates for other soils are shown in Table 2.

dependent measurement of the overall CO_2 flux (*T*), avoids uncertainty associated with estimating decomposition rates (and therefore fluxes, SOM_i) from the plant + soil mean age of C in roots or conifer needles. Additional uncertainties arise because of the transfer of C from one SOM fraction to another.

Table 2 shows the flux-weighted mean and range of ¹⁴C measured in total CO₂ (*T*) emitted from the three forest soils. Gaudinski et al., (*in press*) describe the

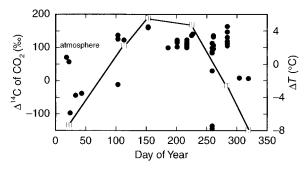


FIG. 5. Δ^{14} C of CO₂ (solid circles) sampled from soil pore space (12, 24, or 40 cm depth) and emitted from the soil surface near the black spruce-moss site depicted in Fig. 2. Data were collected, analyzed, and corrected for the presence of atmospheric air as discussed in Winston et al. (1997) and Gaudinski et al., (in press). Data were collected between November 1993 and August 1997; the range in atmospheric ¹⁴CO₂ values during these four years is shown (box). Samples include Sphagnum and feather moss cover. Open square symbols (connected by lines) represent the difference in temperature (ΔT in °C) observed at one site (in 1996) between the 12 cm and 40 cm depths below the moss surface. In summer, this difference is positive (the surface soil is warmer than deeper soil), coinciding with high Δ^{14} C values in respired CO2. In winter, although overall temperatures decrease to below freezing, the temperature difference is negative, indicating that the deep soil is warmer than the surface (and still warm enough for decomposition to occur, except in the very coldest months). CO_2 respired at this time is depleted in ¹⁴C, indicating different sources for CO₂ emitted from the soil during winter and summer months. Some of these data were published in Winston et al. (1997); others are previously unpublished.

method used for measurement of ¹⁴C in soil respiration. Comparison of these values with those predicted from decomposition of SOM fractions with >1 yr turnover times allows partitioning of the total annual CO₂ flux (Table 2). Fig. 4 illustrates this overall approach. The contribution of slower cycling SOM to soil respiration is <20% in the tropical forest, and some 40-50% of respiration in temperate and boreal forest sites. The average age of respired carbon is calculated assuming that the decomposition flux is diluted with CO₂ with a mean age of 1 yr (root respiration plus decomposition of carbon with turnover time of ≤ 1 yr). Carbon respired from tropical, temperate, and boreal forest soils has mean ages of 1, 3, and 16 yr, respectively. Temperate and boreal soils are net sources of ¹⁴C to the atmosphere, as the decadal-cycling pools contribute significantly to soil respiration.

Seasonal and interannual variability in soil respiration sources

Table 2 gives the range of observed values for Δ^{14} C in soil respiration, as well as the annual mean used to compute respiration partitioning. Significant seasonal variability in the Δ^{14} C of respired CO₂ is observed in temperate and boreal soils (see also Dörr and Munnich 1986). Seasonal differences may reflect changes in the contribution of root respiration and the availability of C substrates with turnover time <1 yr.

Fig. 5 shows the seasonal variation of ¹⁴C measured in CO₂ (solid points) in soil pore space and emitted from the soil surface near the boreal forest site shown in Fig. 1. Data from a number of years and sites near the soil pit sampled for SOM are combined; the range of atmospheric ¹⁴CO₂ values during that time period is shown for comparison. The line shows the difference obtained by subtracting the temperature measured at 40 cm from that at 12 cm (for one year only). Highest Δ^{14} C values in respiration are observed during the height of the growing season, when the temperature at 12 cm exceeds that at 40 cm (and when CO₂ fluxes are largest). These can exceed the range of atmospheric Δ^{14} C values over the same period, indicating the contribution from decomposition of carbon in the upper detrital layers that was fixed during the past three decades (Fig. 2). Low Δ^{14} C values are observed when the deeper soil is warmer than at 12 cm depth. Comparison with Fig. 2 shows that Δ^{14} C values of organic matter at 40 cm below the surface of the moss are negative; the predominance of decomposition from deeper soil layers is reflected in the negative Δ^{14} C values of soil respiration in fall and winter months. At high latitudes, the interaction of the seasonal temperature profile with the depth profile of organic carbon leads to a large range in the Δ^{14} C of respired CO₂.

Mean C residence times derived from interpreting the amount of bomb ¹⁴C in soil organic matter represent conditions averaged over several decades. In any given year, the actual amount of carbon decomposed may vary with climate conditions or plant productivity. Such short-term variability in decomposition rates may be assessed using measurements of ¹⁴C in soil respiration.

Fig. 6 shows two years' data for ¹⁴CO₂ measured in soil respiration along a moisture gradient (from the well-drained end member, shown in Fig. 2, to a very poorly drained swamp) in the temperate Harvard forest site. Both seasonal and interrannual variations in the ¹⁴C signature of soil respiration are seen, although spatial variability is small with the exception of the swamp site. The most striking feature is a decrease in the ¹⁴C of CO₂ respired from the swamp in the summer of 1997. This coincided with a period of drought and higher CO₂ emission rates (Fig. 6, bottom). We infer that the drying of the swamp allowed for aerobic decomposition of organic matter that normally is waterlogged and decomposing only slowly. Hence, overall slow decomposition rates inferred over decades in the swamp may be the long-term average of a few years with fast decomposition rates and many years with slower decomposition in waterlogged soils. With a record of ¹⁴C in soil respiration, it is possible to assess what fraction of the year-to-year variability in soil respiration is due to enhanced decomposition vs. metabolic respiration.

DISCUSSION

Comparing radiocarbon with box model approaches for determining turnover time

Turnover times for soil organic matter are often based on the inventory of carbon divided by the measured efflux of CO_2 , corrected for the estimated contribution of root respiration (the "box model" method; see for example, Raich and Schlesinger 1992). The assumptions inherent in this method are (1) that the soils are all at steady state, and (2) that the bulk organic matter is homogeneous with respect to decomposition. The residence times of carbon to 40 cm depth calculated in this way (2.5, 12, and 220 yr for tropical,

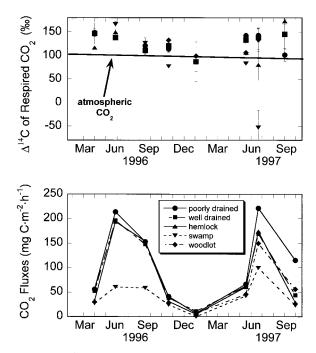


FIG. 6. Δ^{14} C of CO₂ emitted from soils (top) and CO₂ fluxes (bottom) at the Harvard Forest site in 1996 and 1997. Details of measurement methods are given in Gaudinski et al. (in press). Soil respiration data are from Davidson et al. (1998). Error bars in the top panel represent ± 1 SD of the mean for three chambers deployed at each site, and are larger than the analytical error for Δ^{14} C. The Δ^{14} C of atmospheric CO_2 during the same period is shown by the horizontal line. Data are given for a range of stands with different drainage, vegetation cover, and land use histories. The isotopic signature of soil respiration shows both seasonal and interrannual variations, although site-to-site variability is not large, with the exception of the swamp site. The most striking change occurred in late summer of 1997, when the swamp site dried out and older carbon was exposed to oxygen and decomposed. Data for the well-drained site (the temperate forest soil in this paper) are reported in Gaudinski et al. (in press); others are new.

temperate, and boreal forest soils, respectively) are between the ages derived for bulk soil C and decomposition flux from ¹⁴C (Table 2). It is clear from the ¹⁴C data for SOM fractions in Table 1 that the assumption of homogeneity for bulk organic matter does not hold, and that SOM is made up of C that turns over more rapidly and more slowly than the average calculated from inventory and flux measurements alone.

Fig. 7 shows the estimated response of total SOM in the three forest soils to an increase in annual C inputs of 15%, the amount productivity was enhanced in the FACE experiment reported in Allen et al. (2000). Because both productivity and C residence times differ between the sites, the overall magnitude of response differs in terms of grams of C sequestered per square meter. Two scenarios are compared in each case. The solid lines are the response calculated for each soil using turnover times based on radiocarbon measured

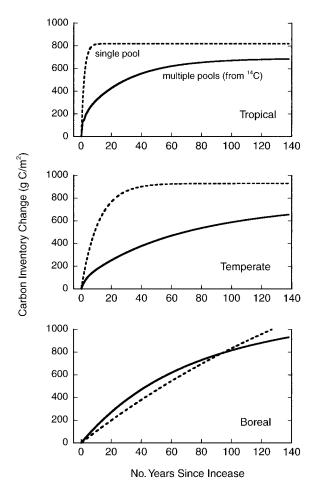


FIG. 7. Increase in the C stored by tropical, temperate, and boreal forest soils in response to a step increase in soil C inputs of 15%. The increase in inputs occurs in year 1; C increases are those above C inventory prior to the increase. The solid line is the predicted response with multiple SOM pools based on the fractions identified in Table 1. The dashed line is the response expected with the box-model approach, in which C turnover time is determined by dividing the total C inventory to 40 cm depth by 70% of the total soil respiration flux (Table 2).

in SOM fractions listed in Table 1. The dashed lines use the single turnover time derived from the box model approach (Table 2). Use of the box model approach will overpredict the decadal-to-century response in each case because of it does not account for large stores of very recalcitrant carbon. The box model approach also underestimates short-term response, although that effect is only significant in the boreal soil. Soil respiration will respond more quickly than soil organic matter, because it is dominated by SOM fractions that turn over on time scales of years or less. This is in general agreement with the results reported in Allen et al. (2000) that soil respiration responds quickly to enhanced C inputs, whereas other soil responses may take longer to be large enough to measure.

Variations in turnover with state factors

The total amount of C stored in soils is controlled by edaphic factors: the type of parent material, the degree of soil development, the type and productivity of vegetation, the presence of soil organisms, and climatic conditions. On long time scales, and at the landscape scale, the amount of C stored varies with factors such as soil drainage and soil texture and mineralogy (e.g., Torn et al. 1997; Table 1).

The three soils compared in Fig. 2 and Table 1 are all moderately well- to well-drained forest soils. Significant variations in mean residence times for carbon may exist in the vicinity of each sampling location depending on local vegetation or soil microclimate factors, in particular soil drainage. For example, turnover times derived from ¹⁴C for relatively undecomposed moss and surface detritus in soils sampled within an area of a few hundred square kilometers surrounding the boreal forest site ranged from 6-15 yr in welldrained soils with lichen and jack pine cover, to 20-50 yr in fen and bog environments, and 35-250 yr for a series of poorly drained uplands with Sphagnum and underlain by permafrost (Trumbore and Harden 1997). These differences are probably caused by changes in the decomposability of substrate material (e.g., Sphagnum mosses vs. feather mosses, lichens, leaves, roots, and woody debris). The degree of soil inundation (and therefore potential oxidant limitation) also varies across the sites, although fens, arguably the wettest sites, do not have the slowest turnover. Another difference may be in soil temperature; the number of soil degree-days increases with mean residence time across sites. Whatever the reason, differences in turnover across local drainage and vegetation gradients can be as great as those across large latitudinal gradients. Thus, the relationship between mean annual air temperature and fast-cycling organic matter turnover time developed by Trumbore et al. (1996) for well-drained soils is probably a poor predictor for soil carbon turnover rates across landscapes.

Determining whether soils are net sources or sinks for carbon

The management of soils for carbon sequestration implies the need to develop methods that can verify that systems are accumulating or losing carbon. Detecting an increase of 10 Pg C (a decade's net sequestration) in a global store of 200–300 Pg C requires that we be able to measure carbon stocks to better than 1%. However, direct measurements of carbon storage at the 10% level is difficult due to the heterogeneity of soils and the difficulty of bulk density measurements needed to determine inventories. Therefore, verification of C storage must come from either long-term plots or pairing of plots experiencing different management.

Trumbore et al. (1995) and Camargo et al. (1999) demonstrate that bomb radiocarbon is a more sensitive

indicator of the recent accumulation or loss of carbon than carbon inventory measurements, when comparing soils that have experienced different land management in eastern Amazonia. Soils that have accumulated carbon during the past 30 yr will have more bomb ¹⁴C than those that have remained at steady state, whereas those that are losing C will have less ¹⁴C. For soils in which changes in C inventory are large enough to be detectable, the combination of ¹⁴C and total C mass balance can be used to study dynamics of various C pools (e.g., Hseih 1993, Wang et al. 1999).

Wetland and frozen soils provide a special case in which decomposition is limited not because of the inherently recalcitrant nature of the substrate, or by the association of organic matter with a mineral surface, but because of lack of O₂ supply (waterlogging) or temperature limitation of biological activity. Sudden changes in climate conditions, such as drying of wetlands, may result in the rapid release of "old" carbon when conditions for more rapid decomposition occur, as in the case of the Harvard forest swamp shown in Fig. 6, or in a boreal forest stand that experiences a temporary warming (Goulden et al. 1998). Monitoring of radiocarbon in soil respiration should be useful for confirming net oxidation of older organic carbon and the contribution of SOM decomposition to year-to-year differences in C storage at a site.

Implications for global ecosystem models

Radiocarbon measurements in SOM and soil respiration provide ideal tests for ecosystem models that predict the dynamics of soil carbon. Several models now predict radiocarbon signatures for organic matter pools and decomposing organic matter (e.g., CASA, Thompson and Randerson 1999). However, few comparisons have been made between models and measurements at specific sites. Part of the difficulty lies in mapping SOM pools assigned by models to the fractions that may be isolated and measured in soil organic matter. For example, the decomposition rate constant (k(t)) for a given organic matter fraction in soil models is calculated as:

$$k(t) = k' \times f(\text{temperature}) \times f(\text{moisture}) \times f(\text{texture})$$
(6)

where k' is the rate constant under "ideal" conditions for decomposition; f(temperature), f(moisture), and f(temperature) are functions with values <1.0 that modify that rate constant to non-ideal temperature, moisture, and texture conditions present in the particular time step in the model; and t indicates time. The turnover time derived from radiocarbon (1/k) is essentially k(t) averaged over several decades:

$$k = \int_{\text{decades}} k(t) \, dt. \tag{7}$$

As previously discussed, radiocarbon-derived turnover

times may underestimate decomposition rates unless residence times of C in living plant material can be determined independently. Increased collaboration between those measuring ¹⁴C in soils and those modeling C dynamics in soils will be required to take advantage of the constraints offered by radiocarbon data.

Determining ¹³C isotope disequilibrium

Our investigations in boreal, temperate, and tropical forests demonstrate that soil respiration contains significant contributions from the decomposition of carbon that resides in the plant-soil system for several years to decades (Tables 1 and 2). Hence, soil respiration is presently a source of ¹⁴C to the atmosphere globally. The fact that significant time lags may exist between C uptake by photosynthesis and return to the atmosphere by respiration implies that net C storage or loss can occur if vegetation production and soil decomposition rates respond differently to environmental variables (Schimel et al. 1997). It also has implications for the ¹³C isotope disequilibrium, the degree to which ¹³C fixed by ecosystems differs from that respired by ecosystems due to the decline in ¹³C in atmospheric CO₂ over time (Fung et al. 1997, Ehleringer et al. 2000) Predicted differences in ¹³C uptake and loss are small compared to variability due to changes in plant photosynthesis with climate conditions. Using radiocarbon measurements to determine the average age of respired C, we may easily infer the ¹³C isotope disequilibrium.

CONCLUSIONS

Soil organic matter is heterogeneous with respect to decomposition, as evidenced by the different ¹⁴C signatures measured in physically and chemically fractionated SOM components, and in comparisons of ¹⁴C in SOM with respired ¹⁴CO₂. Methods that presume homogeneity to estimate turnover times, such as dividing inventory by heterotrophic respiration flux, obscure the fact that SOM is composed of both more rapidly and more slowly cycling components. These methods underestimate short-term response and overestimate long-term response of carbon in soils to perturbations. Similarly, bulk soil radiocarbon measurements, which are biased toward longer turnover times because those pools make up most of the SOM, provide misleading estimates of the short-term SOM response to disturbance.

Comparisons of ¹⁴C in soil respiration with ¹⁴C measurements of SOM are useful for determining the relative contribution of substrates that decompose more slowly to overall soil respiration. The ¹⁴C signature of CO₂ is a useful indicator of seasonal to interrannual changes in the sources of respired carbon, and also may be used to confirm net C loss from a soil in response to disturbance. Seasonal variability in the Δ^{14} C of soil respiration is greatest at high latitudes, where changing soil temperatures interact with the depth profile of soil organic matter. Large interannual variability may be expected for systems with long time lags between photosynthesis and respiration. Slow decomposition rates may represent the long-term integration of sporadic periods when decomposition is faster (e.g., when a wetland dries out), interspersed with periods of much slower decomposition (e.g., when a wetland is inundated).

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