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Potential responses of soil organic carbon to global environmental change

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ABSTRACT Recent improvements in our understanding of the dynamics of soil carbon have shown that 20–40% of the approximately 1,500 Pg of C stored as organic matter in the upper meter of soils has turnover times of centuries or less. This fast-cycling organic matter is largely comprised of undecomposed plant material and hydrolyzable components associated with mineral surfaces. Turnover times of fast-cycling carbon vary with climate and vegetation, and range from <20 years at low latitudes to >60 years at high latitudes. The amount and turnover time of C in passive soil carbon pools (organic matter strongly stabilized on mineral surfaces with turnover times of millennia and longer) depend on factors like soil maturity and mineralogy, which, in turn, reflect long-term climate conditions. Transient sources or sinks in terrestrial carbon pools result from the time lag between photosynthetic uptake of CO_2 by plants and the subsequent return of C to the atmosphere through plant, heterotrophic, and microbial respiration. Differential responses of primary production and respiration to climate change or ecosystem fertilization have the potential to cause significant interannual to decadal imbalances in terrestrial C storage and release. Rates of carbon storage and release in recently disturbed ecosystems can be much larger than rates in more mature ecosystems. Changes in disturbance frequency and regime resulting from future climate change may be more important than equilibrium responses in determining the carbon balance of terrestrial ecosystems.

Soil carbon inventories and turnover rates are influenced by climate, vegetation, parent material, topography, and time, the fundamental state factors outlined by Jenny (1, 2). Studies attempting to understand the influence of a specific factor (e.g., temperature or moisture) on soil properties have found it useful to identify a suite of soils for which the factor in question varies whereas the others are held constant (1–4). This approach has been used successfully to look at the role of temperature (3, 5) and time (6–10) on the turnover of soil C. Ecosystem models such as CENTURY (11, 12), CASA (13), or the Rothamsted model (14, 15) predict the sensitivity of soil C inventory and turnover to climate, vegetation, and parent material, but as yet few data exist to test these predictions. Parameterizations of decomposition used in these models are based on empirical fits to specific calibration sites and may not include enough basic understanding of the interaction between plant substrates and the soil environment to make successful predictions in different environments (16).

The reservoir of soil carbon has been proposed as both a significant source and sink of atmospheric CO_2. A soil source results when net decomposition exceeds C inputs to the soil, either as a result of human activities such as clearing forests for agriculture (17, 18) or because of increased decomposition rates due to global warming (12, 14, 19, 20). Net sinks of C in soils are postulated from the difference between net ecosystem C uptake and tree growth rates (21) or from presumed increases in net C inputs from CO_2 or N-fertilization of plants (19, 20, 22–24). In both cases, the magnitude and timing of the response depends on the amount of carbon in pools that respond quickly to changes in climate and vegetation, and to the time lag between fixation of C by plants and its subsequent release to the atmosphere during decomposition.

This paper will describe recent approaches used to study soil C dynamics, and preliminary applications of these tools to the problems of soil C response to global environmental changes. The results indicate the importance of the global soil C pool to the global C cycle on interannual to century time scales and suggest profitable areas for future research.

The Nature of Soil Organic Matter (SOM)

SOM is defined here as the nonliving component of organic matter in soil. The ultimate source of organic matter in soils is CO_2 fixed by plants, including leaf litter, roots, and root exudates. The activity of soil fauna (especially fungi and microbial communities) metabolizes some of these substrates and transforms others into more resistant organic compounds (collectively referred to as humus). The stabilization and fate of organic matter residues is affected by the quality of the original plant substrate (25), and the physical environment in the soil [clay content and mineralogy (26), pH, O_2 availability (27), formation and disruption of soil aggregates (28–30)]. Carbon is lost from soil mostly as CO_2 produced during decomposition of organic matter, though losses of carbon through leaching or erosion may be important when considering C balance in soils on long time scales (29, 31, 32). Organic matter in soils plays important roles in determining soil water-holding capacity and soil structure, and provides a long-term store of nutrients needed by plants. Thus changes in SOM will have important feedbacks on hydrology and plant productivity (33).

SOM is difficult to study because it is a complex mixture of substances having turnover rates that range from days to millennia. The average global turnover time for soil organic carbon (to 1-m depth) was estimated as 32 years by Raich and Schlesinger (34), who divided the total C stock in soils by the average CO_2 flux from soil (corrected for root respiration contribution). Turnover times varied from 14 years to 400 years for different ecosystems in their study. Radiocarbon measurements of bulk soil C, however, often show that the average age of C in soils is several hundred to several thousand years (35–38). Both results are explained if SOM contains components that turn over slower and faster than the several-decade average.

Abbreviation: SOM, soil organic matter.

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Much of the work in understanding and modeling soil C is the study of relative decomposition rates for various organic substrates and organic matter byproducts. While organic matter may actually be a continuum, best represented by a distribution of turnover times (39), continuous distributions are difficult to constrain with field measurements. There is general agreement that SOM contains at least three identifiable C pools: root exudates and rapidly decomposed components of fresh plant litter ("active" pool); stabilized organic matter that persists in soils over several thousands of years ("passive" pool); and a poorly defined "intermediate" or "slow" C pool that has turnover times in the range of years to centuries (Fig. 1). I will use these terms in this paper, and in addition will refer to fast-cycling C as the combined active and intermediate pools (all nonpassive C).

The mechanisms through which climate or land-use change may influence soil carbon cycling include a combination of biotic controls that affect the amount and resistance to decay of C added to soils by plants, and physical controls, including the area and chemistry of surfaces for stabilization of organic matter, and the availability of oxidants to decomposers. These mechanisms operate on vastly different time scales. Plant productivity and soil microbial communities respond to shifting climate conditions within hours (41), whereas changes in production and respiration on an annual basis are linked to interrannual variability in climate (42, 43). Persistent changes in climate can lead to species changes over time scales of decades to centuries (44), with concomitant shifts in plant production and litter quality (45). Soil minerals, forming over millennial time scales, control how much of the soil carbon is chemically/physically protected from decomposition (46–49). Finally, ecosystem disturbance caused by fire, flooding, tree blow-down, etc. will cause drastic changes in plant production and soil conditions for decomposition that far exceed those associated with interrannual variability. Thus the general design of experiments to understand soil C dynamics should depend on sampling existing environmental and disturbance gradients as well as manipulations to test soil forming factor effects on the amount and turnover times of C in active, intermediate, and passive C pools.

Tools to Study SOM

No single, satisfactory method yet exists to separate soil C into components with different turnover times. Instead, the dynamic makeup of soil C is deduced using many constraints, including: physical and chemical fractionation of organic matter, field and laboratory decomposition studies, measures of C fluxes into and out of the soil, measurements of ^{14}C in soils sampled at various times before and after the peak of atmospheric nuclear weapons testing, changes in the ^{13}C content of SOM after a vegetation change from plants with C3 to C4 photosynthetic pathway, and measurements of changes in the total amount of C in soils of different age or after disturbance. Each of these tools is suitable for determining different time scales of soil C dynamics, and much confusion may result from mixing of terms related to turnover times (active, intermediate, or passive) with those derived from measured soil parameters. For example, the increase in bomb ^{14}C, or changes in ^{13}C in SOM during the first several decades after conversion of a C3-dominated forest vegetation to C4-dominated pasture vegetation may be used to determine the amount and average turnover time of C that is fast-cycling (nonpassive). Fast-cycling C may be further comprised of active and intermediate pools with different turnover times, but isotopic techniques are not suitable for distinguishing this split.

Active Carbon Pools. Field decomposition studies involve both observation of loss of native plant litter and differences in decomposition of a common litter substrate at different sites. Isotope labeling studies usually follow specific compounds or compound classes (such as amino acids or carbohydrates), but also may follow the fate of below-ground C allocation, as in pulse-labeling studies. Although some incubations have been followed over periods of more than 10 years (26, 50), most are designed for shorter time periods. These studies are used to provide multiple rate constants for decomposition models like those of Jenkinson and Raynor (15).

Soil-respired CO_2 is produced either by metabolic root respiration or by decomposition of fast-cycling SOM pools (Fig. 1). In addition, CO_2 fluxes measured at the soil surface are most likely dominated by decomposition in near-surface layers (including surface detritus). With these caveats, CO_2 flux measurements provide an estimate of total decomposition C flux from the soil, if correction for root-respiration can be made (34). Radiocarbon measurements of respired CO_2 may help distinguish sources of respiration experimentally. Root respiration and CO_2 derived from decomposition of C with very rapid turnover should have $\Delta^{14}C$ close to atmospheric values for the year of sampling, whereas CO_2 derived from slow C pools will have higher or lower $\Delta^{14}C$ values, depending on the average turnover time.

Field measurements of decomposition and CO_2 flux often are complicated by seasonal differences in the quality and quantity of detrital material (for example, in temperate zones, deciduous leaves are shed in autumn, but may be responsible for a pulse of decomposition the next spring). Laboratory incubations, where soil is separated from roots, allow observation of the CO_2 evolved from decomposition alone (51). Long-term incubations (>1 year) allow estimation of the relative contributions of active and slow pools to soil CO_2 flux (5). However, the magnitude of laboratory fluxes of C may not be easily mapped to field conditions.

Experiments manipulating soil temperature to determine the net response of soils (19) or soils plus vegetation (52) to increased temperature are now in progress in several places. These treatments have been in place in most cases for <10 years, and preliminary results are reflective of adjustments in the fast-cycling pools.

Passive Soil Carbon and the Depth Distribution of ^{14}C. The existence of passive SOM is deduced from radiocarbon measurements and the fact that some C3-plant-derived organic matter persists in disturbed soils even after a century or more of cultivation with C4 plants. In general, the amount and ^{14}C content of SOM decrease with depth in soil profiles, indicating the increasing importance of passive organic matter with depth in the soil (37, 53).
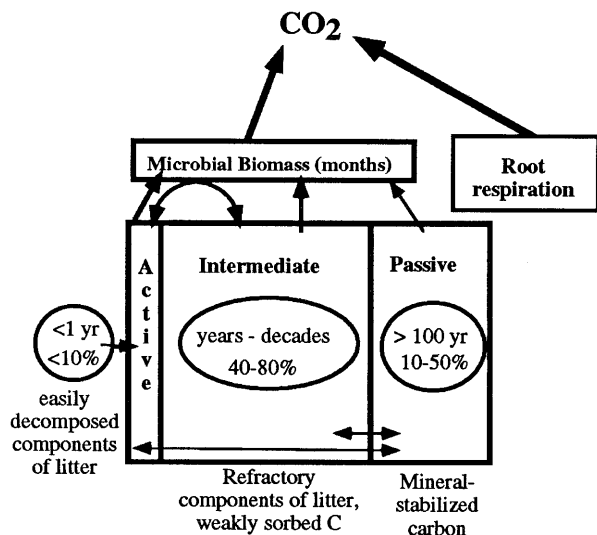

CO₂

Microbial Biomass (months)

Root respiration

Active

Intermediate

Passive

<1 yr
<10%

easily decomposed components of litter

years - decades
40-80%

> 100 yr
10-50%

Refractory components of litter, weakly sorbed C

Mineral-stabilized carbon

FIG. 1.   Conceptual model of SOM dynamics used in this paper (after ref. 40).

The ^{14}C age of passive organic matter may give clues to the mechanisms that cause C to persist in soil over millennial time scales. Three approaches to isolating the properties of passive C from the bulk soil have been used. The first, proposed by O'Brien and Stout (37, 54) and used by Harrison *et al.* (22) uses a ^{14}C measurement from deep in the soil as an estimate of the passive pool ^{14}C content. This approach attributes decreases in C and ^{14}C with increasing soil depth to a decrease in the abundance of fast-cycling C pools to near-zero at depth, while assuming that the abundance and properties of passive C remain constant over the same depth interval.

A second approach toward determining the ^{14}C content of passive SOM is based on operationally defined physical and chemical fractionation of the organic matter. Several investigators (36, 38, 53, 55–58) have shown that repeated extractions of SOM with acids and bases of increasing strength will leave a residue with a lower ^{14}C/^{12}C ratio than the starting material (a density separation is performed first to remove relatively intact vascular plant material, which can represent up to 80% of the C in soil A horizons).

A third way to estimate the turnover rates in the passive fraction is based on a chronosequence approach (9, 59, 60). A chronosequence is a series of soils of different age, but developed on the same parent material with the same vegetation and climate (for example, soils formed on a series of lava flows or river terraces of different age). During the first several hundred years of soil formation, C accumulation in chronosequences is rapid as vegetation is assumed to establish steady state with fast-cycling soil C components. Accumulation of passive C over millennial time scales in soils (perhaps as authigenic soil minerals are formed and provide new surfaces for organic matter stabilization) is presumably responsible for long-term C increases. Increases in the amount of passive C over time should cause a steepening of the ^{14}C-depth curve (6, 61). Goh *et al.* (8) reported decreasing ^{14}C contents in deeper soil horizons with increasing soil age in a chronosequence developed on aeolean sand.

Tools to Study the Intermediate Pool. The intermediate pool of soil C, with turnover times that vary from years to decades, is the largest fraction of organic matter in most soils. It is also the most difficult to study, as it is itself almost certainly made up of fractions with different turnover times. Ecosystem models such as CENTURY and the Rothamsted model subdivide fast-cycling soil C into readily decomposable and resistant plant debris, as well as an intermediate C pool. In temperate forests soils with low clay content, relatively undecomposed plant debris (the low-density fraction of SOM) can represent up to 80% of the C in A horizon SOM (3) and have turnover times of years to several decades. In tropical soils, low-density organic matter has turnover times of < 5 years and makes up roughly 10–30% of the total SOM in the upper 10 cm of soil. Mineral-associated (high-density) C that is hydrolyzable in acids and bases, makes up about 50% of the A horizon C, and has turnover times of 20–30 years (62). While it is tempting to map the hydrolyzable C onto the models' intermediate C pool, operationally defined extraction methods give little practical insight into the mechanisms that are stabilizing this organic matter fraction.

The Bomb ^{14}C Tracer. The incorporation of ^{14}C produced in the early 1960s by atmospheric thermonuclear weapons testing (bomb ^{14}C) into SOM during the past 30 years provides a direct measure of the amount of fast-cycling (active + slow) SOM (5, 22, 35, 37, 63–67). The most straightforward approach, which compares ^{14}C measurements of SOM sampled before 1960 with contemporary samples from the same location, is summarized in Fig. 2 (62, 64, 68). A large increase in ^{14}C content over the past 30 years indicates that significant portions of the SOM are exchanging carbon with atmospheric CO_2 on decadal and shorter time scales. Harrison *et al.* (22) modeled the ^{14}C increase with time for SOM measured over the past 30 years and reported in the literature (for mostly temperate soils) and obtained an average turnover time of about 25 years for fast-cycling C. Work in other locations has shown that turnover times may be either faster or slower than this average value.

Trumbore *et al.* (3) used the bomb ^{14}C technique to determine how the turnover time of fast-cycling organic matter varied along an elevation transect in the Sierra Nevada mountains of central California. Temperature decreases with elevation along the transect, though vegetation and annual precipitation also vary. C inventory in soil A horizons is predominantly in low-density fractions (<2.0 g/cm^3; 50–80% of the total SOM), with another 10–30% in the hydrolyzable fraction of organic matter in the >2.0 g/cm^3 fraction. Comparison of the ^{14}C content of these fractions isolated from 0–20 cm soil
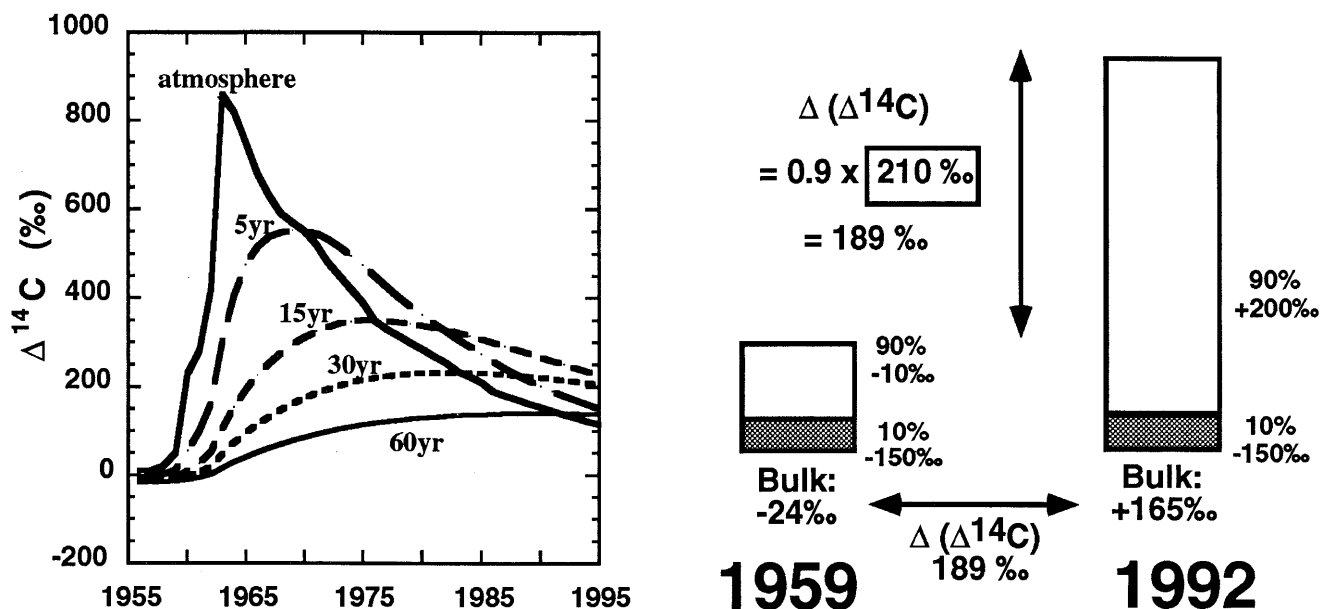

FIG. 2.   (*Left*) Change in Δ^{14}C in atmospheric CO_2 and in two homogeneous C pools with turnover times of 5, 10, 50, and 70 years. (*Right*) Effect of passive organic matter on $\Delta(\Delta^{14}$C) values in bulk SOM. Failure to account for 10% of the carbon in a passive fraction that does not change in ^{14}C content between 1959 and 1992 will result in an underestimate of the increase in fast-cycling Δ^{14}C and therefore of turnover time in that fraction. Thus it is important to assess whether passive components such as charcoal are present in presumed fast-cycling pools (such as low-density carbon).

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collected in 1959 and 1992 (Fig. 3) shows turnover is fastest in low-density material and slowest in nonhydrolyzable organic matter. Translating the ^{14}C increases into turnover times according to procedures in Fig. 2 for the low-density + hydrolyzable organic matter gives turnover times of 8–12 years at low elevation (highest temperature) and 60 years at high elevation (low temperature). Fig. 3 also shows that the residue after repeated hydrolysis of mineral-associated organic matter
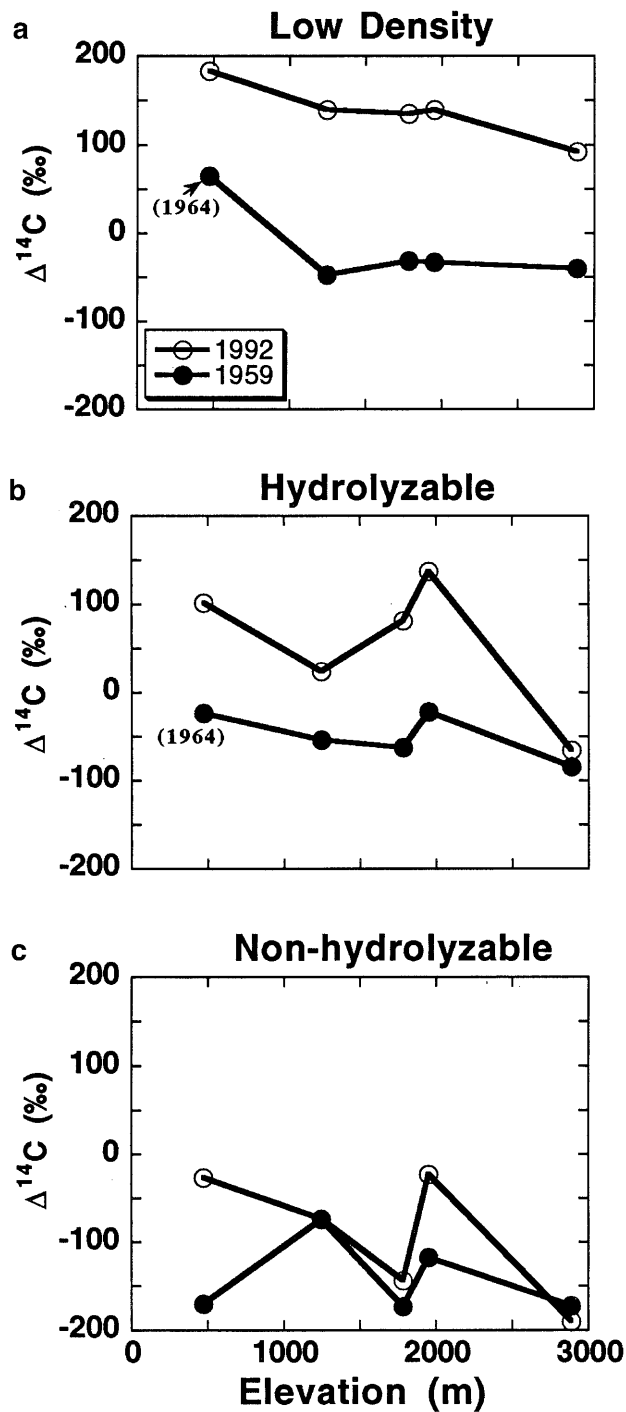

a   Low Density

b   Hydrolyzable

c   Non-hydrolyzable

FIG. 3.   Increases in Δ^{14}C between 1959 (1964 for lowest elevation site) and 1992 for (*a*) low density (<2.0 g/cm^3), (*b*) hydrolyzable (>2.0 g/cm^3), and (*c*) nonhydrolyzable (>2.0 g/cm^3) portions of SOM from an elevation transect in the Sierra Nevada (3). The fraction of organic matter with the fastest turnover time will have the highest pre-1963 ^{14}C values and show the largest increase in ^{14}C between 1959 and 1992 (*a*) while the fraction with slowest turnover has lowest initial ^{14}C values and shows little increase in ^{14}C over the past 30 years (*c*).

in acids and bases still may contain some fast-cycling carbon (as evidenced by an increase in ^{14}C in the past 40 years).

Without prebomb samples for comparison, ^{14}C measurements of contemporary soils may yield a very misleading picture of soil C dynamics. For example, the bulk ^{14}C contents of the 0–20 cm layer of tropical soils sampled in the early 1990s range from −70‰ (Hawaii; ref. 5) to +210‰ (Manaus; ref. 67). The average turnover times of fast-cycling components of these soils, derived from ^{14}C and other measures (see below), is similar (10–20 years). The amounts and ^{14}C contents of carbon in the passive carbon pool are responsible for bulk ^{14}C differences between these sites. The Hawaiian soils are developed on basaltic lava (Andisols) and stabilize large amounts of old carbon in noncrystalline minerals (6), whereas the soils in Manaus have very high percentages of sesquioxides that do not stabilize organic matter as well. Based on ^{14}C measured on bulk SOM alone, one could mistakenly assume very slow turnover rates for the Hawaiian soils. While this is true for average soil C, the average is not a useful number for predicting the response of Hawaiian soils to climate or land-use change.

Townsend *et al.* (5) report soil C turnover times for fast-cycling C along an elevation-based temperature transect of Andisols on the slope of Mauna Kea, near Lapahoehoe, Hawaii. No prebomb archived soil samples were available from these sites. Therefore, a suite of constraints, including ^{14}C measurements, were used to determine turnover times of active, slow, and passive organic matter. The ^{13}C changes in SOM accompanying C3 forest to C4 pasture conversion from three sites reflect the partitioning of fast-cycling ($\approx$75% of the total SOM) vs. passive ($\approx$25%) carbon pools in pastures that were roughly a century old. The application of this method is much the same as looking for the increase in bomb ^{14}C in soils; carbon turning over on decadal and shorter time scales will reflect recent isotopic changes in C sources, whereas passive carbon pools will not (26, 69–72). Townsend *et al.* (5) estimated the breakdown of fast-cycling C into active and intermediate C pools using long-term (1 year) incubations—the ratio of CO_2 evolution after 1 year to the initially observed CO_2 evolution was assumed to equal the ratio of CO_2 contributed from decomposition of intermediate C pools to that from active C pools. Estimates of passive pool ^{14}C content were made in two ways: using the method of O'Brien and Stout (37) or calculating from a knowledge of the soil age (15,000 years) and assuming constant accumulation of passive C since the time of soil formation (73). Intermediate pool turnover times then were constrained to reproduce 1990 ^{14}C values and CO_2 fluxes.

Trumbore *et al.* (62) use a different set of constraints with ^{14}C measurements to deduce the amount and turnover time of fast-cycling C in tropical forest soils in eastern Amazonia. Estimates of annual carbon input to the soil were derived from measurements of litterfall and fine root biomass. The ^{14}C content of CO_2 measured in the soil air space was greater than that of atmospheric CO_2 for the year in which it was measured (73, 74), indicating that a large portion of the carbon contributing to soil respiration was fixed from the atmosphere by plants over the past several years to decades. The ^{14}C content of CO_2 evolved from SOM decomposition can be used as an additional constraint to break fast-cycling organic matter into active and intermediate pools.

C Inventory Changes with Land Use. Changes in soil carbon accompanying human or natural disturbance also provide clues about C dynamics in soils. Decreases in soil C inventory associated with cultivation on average may be of the order of 10–40% of initial C inventories (18), but may be smaller and difficult to measure in some areas (62). Changes in ^{13}C abundance in SOM after a shift in vegetation with C3 to C4 photosynthetic pathway (or vice versa) can be used to identify fast-cycling organic matter. These methods rely on accurate

measures of C inventory change over time (26, 69–72), and a knowledge of the ^{13}C content of new and old vegetation C inputs to soil. Comparison of ^{14}C in paired undisturbed and disturbed ecosystems can be a sensitive measure of net C storage or loss over the past 30 years (62, 75). Soils that are accumulating C will have higher $\Delta^{14}C$ values compared with an undisturbed ecosystem (presumed at steady state), whereas soils that are losing C will have lower ^{14}C than the undisturbed site (73).

Prediction of the Response of Soil C to Global Change

Total C Inventory in Soils. Estimates of the amount of C stored in soils fall in the range of 1,200 to 1,500 Pg C (46, 76, 77). These estimates are based on relatively few soil C inventory data from many important regions, especially the tropics and northern wetlands. Global estimates are extrapolated using correlations of SOM content with vegetation/climate regime (46, 76) or by soil mapping unit (77). The apparent overall agreement between these estimates masks large uncertainties at the regional scale. For example, moist and wet tropical forest profiles reported in Schlesinger (76) have C inventories ranging from 6.5 to 20.5 kg C m^{-2} (average of 10.4 kg C m^{-2}). Post *et al.* (46) use values of 11.5 and 21 kg C m^{-2} as averages for tropical moist and wet forests, respectively. Davidson and Lefebvre (78) discuss potential uncertainties involved in estimating C stores from large-scale soil map units.

Present estimates of global soil C stocks are based on the upper meter of soils, without reference to what fraction of that organic matter is in active, intermediate, or passive pools. Sombroek (79) points out that many tropical soils extend deeper than 1 m, and adding deep C inventories can increase soil C stocks in the tropics markedly. The question of what depth should be the cutoff for counting soil C stores really depends on where and how much of the C is in fast-cycling pools, and how much of the passive soil C pool may be inherited in the case of sedimentary parent material. Ecological models that include cycling of SOM generally assume that only the 0- to 20- or 0- to 30-cm layer of soils contains significant amounts of fast-cycling organic matter. Estimates of fast-cycling SOM pools derived from these models (12, 13) range from about 250 to 530 Pg C globally.

The assumption that organic matter deep in soils is not important in C cycling is not always correct. The presence of live roots to depths greater than 15 m in 40-m deep soils of seasonal tropical forests in eastern Amazonia (74) drives a fast carbon cycle to depths of at least 8 m (62, 74). Although bulk C concentrations and ^{14}C contents of SOM at >1-m depths are low, estimates of turnover from fine-root inputs, CO_2 production, and the ^{14}C content of CO_2 produced at depth show that up to 15% of the carbon inventory in the deep soil has turnover times of decades or less. In these soils, the amount of fast-cycling soil carbon between 1- and 8-m depths (2–3 kg C m^{-2}, out of 17–18 kg C m^{-2}) is significant compared with the amount present in the upper meter of soil (3–4 kg C m^{-2} out of 10–11 kg C m^{-2}) (62).

Predicted Changes in Soil C Due to Increased Plant Production. The simplest approach to predicting the response of soil C changes in plant productivity is to assume that the size of C pools will adjust to a new steady state with increased in C inputs. Fast-cycling pools will adjust most rapidly to new steady state conditions. Harrison *et al.* (22), assuming a β (growth-enhancement) factor of 0.35 and turnover time of fast-cycling C of 25 years, calculated that increased C inputs to soils should have resulted in net storage of 0.5 Gt C/yr in fast-cycling C in the 1980s (with an additional 0.1 Gt C/yr added to surface litter). This approach assumes no change in decomposition rates due to changes in the quality of those plant substrates, an assumption that has yet to be tested.

The changes in C inventory predicted by Harrison *et al.* (22) are almost impossible to measure directly (62, 80). For example, even a predicted 0.5 Gt C/yr sink integrated over 30 years increases the total soil C pool only 1% (the fast-cycling pool by 3%). C inventory measurements, plagued by small-scale heterogeneity and comparatively large analytical uncertainties (for example, in bulk density measurements), cannot distinguish such small increases on local to regional scales. Thus, other methods must be discovered to determine whether C accumulation of this magnitude is actually occurring in soils.

After CO_2 fertilization, the most often-cited mechanism leading to a terrestrial carbon sink is enhanced nitrogen availability to plants due to enhanced nitrate deposition (19, 20, 22, 23, 81). Nitrogen availability also will be increased if there is net decomposition of SOM, because SOM is a major source of nitrogen for plants. Although nitrogen mineralization is accompanied by CO_2 efflux, the transfer of nitrogen from soil to plants would result in net carbon sequestration because the C:N ratio of plants is roughly 10 times the ratio in SOM. Decomposition rates are predicted to increase as a result of warmer temperatures (see below).

Response of Fast-Cycling Soil C to Climate Change. The amount of organic matter in soils is positively correlated with moisture and negatively correlated with precipitation (2, 46). Carbon turnover rates for combined fast-cycling C pools discussed above from the Sierra Nevada, Hawaii, and Paragominas, Brazil are plotted against mean annual temperature in Fig. 4. Although these soils differ in vegetation cover, precipitation (greater than 90 cm/yr with one exception), and soil parent material, a strong relation between turnover time of the fast-cycling C pools and mean annual (air) temperature is observed. This suggests that temperature is a major control of the turnover rate of fast-cycling soil C, in accord with recent modeling and data-based studies (5, 12, 20, 34, 50, 82–84). The overall gradient with latitude from the tropics to boreal forests is in accord with trend derived from local elevation gradients.

Fig. 4 also plots temperature-turnover time relations predicted by the CENTURY model (12) and a literature review of surface litter decomposition rates (51). Turnover times derived from CENTURY are longer than values derived from field measurements, and show a less steep relation to temperature. The relation derived by Kirschbaum (51) plotted on Fig. 4 is a literature summary of the rates of decomposition derived from laboratory incubations of surface litter. These data suggest turnover of surface detrital pools is faster and has greater temperature dependence than fast-cycling organic matter in soils. Mean annual air temperature is plotted in Fig. 4, but obviously soils (especially surface detritus) experience seasonal and diurnal temperature extremes that may exceed those of the air above.

Both vegetation inputs and decomposition rates are expected to increase with increases in temperature (all other factors remaining equal). Soils become an amplifying feedback if the temperature dependence of decomposition is steeper than that of plant productivity (e.g. ref. 5). At present, this is still an open question. Kirschbaum (51) summarized data from incubation experiments for various types of plant litter and found that Q_{10} values for decomposition ranged from about 2.5 at 20°C to about 4.5 at 10°C. Data from field-based studies using climosequences (summarized in Fig. 4) suggest a Q_{10} for fast-cycling SOM of around 3, but are too few (particularly in tropical regions) to distinguish between cases with constant and changing Q_{10} values over a wide range of temperatures.

Schimel *et al.* (12) summarize modeling and data-based predictions of C release from SOM for a 1°C increase in global mean annual temperature. The calculated net release ranges from 11.1 to 33.8 Pg C once a new steady state is reached. The lowest value is predicted by CENTURY, which accounts for feedbacks between plant productivity and release of nutrients that accompanies net SOM decomposition. In N-limited plant
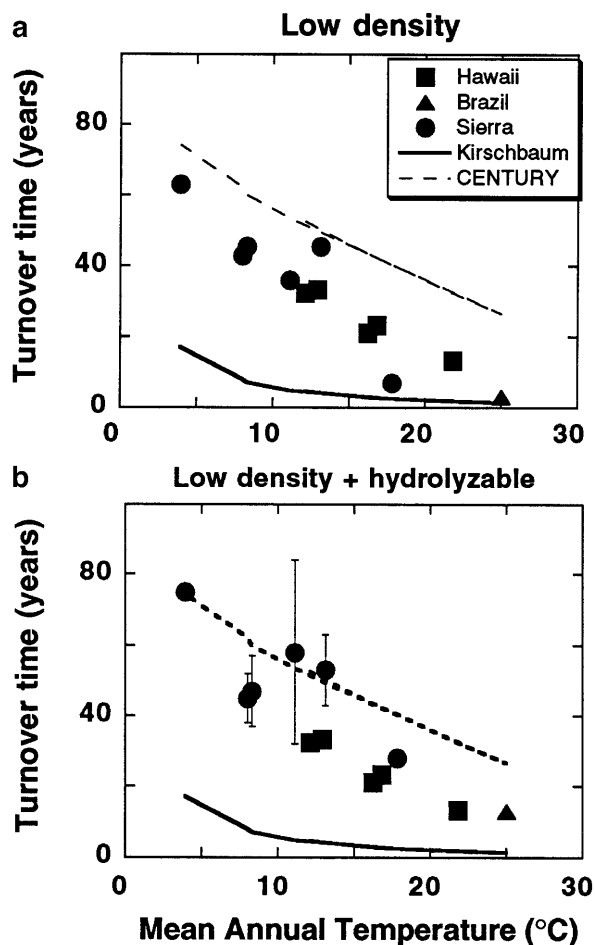
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FIG. 4. Turnover times for fast-cycling fractions for a number of sites plotted against mean annual temperature: (*a*) low-density C in the Sierra Nevada transect (3); combined active plus slow C from the Hawaii temperature transect (5); low-density C from a mature seasonal tropical forest in eastern Amazonia (60); (*b*) using low-density plus hydrolyzable carbon for Sierra and Brazil sites. All data represent approximately the upper 20 cm of soil. Also shown are predicted turnover time-temperature relationships estimated from the CENTURY model and from the literature review of Kirschbaum (51). The CENTURY curve is based on model results reported in Schimel *et al.* (12) assuming the temperature dependence reported in that paper, and combining pools assuming 5% of the C to 0–20 cm is contained microbial biomass pool, 20% in the detrital pool, and 50% in the slow pool.

communities, the release of N through increased decomposition in a warmer world could further stimulate plant growth, and even cause net sequestering of C as nutrients are transferred from soils (low C:N ratios) to plant reservoirs with higher C:N ratios (19).

One consequence of all studies of C turnover as function of temperature is that soils already should be a net source of C to the atmosphere due to increased decomposition rates because of documented temperature increases over the past century. This present net C loss presumably would offset hypothetical increases in soil C stores from increased plant production due to CO_2 fertilization.

The rate at which steady state is approached when fast-cycling C pools respond to a temperature change demonstrates the importance of recognizing differences in turnover rates of soil C between ecosystems. Trumbore *et al.* (3) estimate the response after changes in net primary production in tropical, temperate, and boreal forest soils. According to these calculations, interrannual variations in net primary production may cause significant interrannual variability in soil-atmosphere

CO_2 fluxes, with largest and fastest response in tropical regions.

Moisture changes. Soil organic carbon inventories increase regionally from arid to wet environments (2, 46), whereas incubation and field decomposition studies show increases in decomposition rates with added moisture in aerobic soils. Decomposition rates for organic matter decrease dramatically under waterlogged conditions. Low C inventories in arid soils may be due to decreased C inputs, faster C turnover, or differences in the quality of plant material. As yet, the relative contributions of these factors are unknown.

Disturbance. Soils accumulate organic carbon over at least the first 10,000 years of development (1, 9). Schlesinger (7) showed that the rates of C accumulation in young (thousands of years old) soils are an order of magnitude lower those needed for soils to be a significant C sink for anthropogenic CO_2. The changes in C inventory over millennial time scales in soils most likely are caused by the development of secondary soils minerals with stabilization on new mineral surfaces (6).

More rapid rates of C accumulation and loss may occur over shorter time scales as the large component of fast-cycling soil C responds to disturbance such as a change in vegetation. As discussed above, soils may lose a significant portion of their carbon after cultivation; these changes represent a loss of fast-cycling C rather than passive C pools (30, 33, 62). Work in boreal forest ecosystems (85) shows high rates of net C sequestration in regrowing surface moss layers in the decades after stand-killing fire events. In these systems, decomposition in mosses is so slow as to be less important than periodic fire at controlling the status of these soils as net C sinks. Thus, particularly in regions where decomposition rates are slow, changes in fire frequency linked to climate or to land use (fire suppression) may be the ultimate control of regional status as a C source or sink. The same may be true in other fire-dominated ecosystems, such as chaparral (68), where organic matter accumulates rapidly between fire events.

Wetland areas store organic matter that is climatically stabilized; it is decomposing slowly only because of a lack of oxidants. Warming and draining of wetlands results in a loss of this stored organic matter (86, 87). In northern wetland soils (which contain an estimated one-fifth of total global soil C reservoir), this could lead to large positive feedbacks in warming.

Conclusions

Climate, vegetation, parent material, and time all affect the processes controlling accumulation and decomposition of organic matter in soils as has been known for decades. The quantification of these insights, however, is still in the beginning stages. Of the roughly 1,500 Gt of C stored in organic matter in soils, an estimated 250–530 Gt resides in C pools with turnover times of decades or less. Models extrapolating the response of the fast-cycling soil C pool on the global scale show its importance in affecting atmospheric CO_2. A great deal of work remains to be done to improve our assessments of the role of soils in the global C cycle. Some areas of particular importance are:

(*i*) Tying soil C pools with different turnover times to specific organic compound classes or structures found in soils, to understand how soil environment and plant litter quality interact to stabilize organic matter.

(*ii*) Better understanding of C accumulation and turnover in wetlands and how these will be affected by climatic and land use change. Present ecosystems models usually exclude wetland C pools from global studies.

(*iii*) Investigation of the role of landscape-scale disturbances, such as fire, in switching soils from net sinks to net sources of C.

(*iv*) Manipulations (field incubations) to look at specific responses of coupled soil and vegetation pools to changes in CO_2, N deposition, or climate change. Most manipulations presently are taking place in temperate ecosystems; short-term manipulations may yield larger signals in the tropics, where turnover times for fast-cycling soil C are shorter.

(*v*) For larger scale responses over longer timescales, more work needs to be done along naturally occurring environmental gradients, especially those that may have been previously studied and may have archived soils for isotopic analysis.

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