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SOIL ORGANIC MATTER DYNAMICS ALONG GRADIENTS IN TEMPERATURE AND LAND USE ON THE ISLAND OF HAWAII[1]

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Abstract. We studied soil organic matter (SOM) dynamics in allophanic soils (Udands) along independent gradients of temperature (altitude) and land use (forest–pasture) on the island of Hawaii. Using an integrated ^{13}C signal derived from land conversion along with measurements of soil respiration and soil carbon, we separated rapid, intermediate, and very slow turnover SOM pools, and estimated turnover times for the large intermediate pool. These estimates were compared to independent estimates using either bomb-derived soil ^{14}C or the Century soil organic matter model. All calculations based on a three-pool SOM structure yield rates of turnover that are 3 times slower than those produced by a single pool model. Accordingly, analyses of potential feedbacks between changes in climate, atmospheric CO_2, and soil carbon should incorporate the heterogeneous nature of soil organic matter. We estimate that roughly three-quarters of the carbon in the top 20 cm of these soils has turnover times less than 30 yr. Turnover times for intermediate SOM double with a 10°C change in mean annual temperature, suggesting that recalcitrant pools of SOM may be as sensitive to changes in temperature as the smaller labile pools.

Key words: atmospheric CO_2; decomposition; soil carbon; soil respiration.

INTRODUCTION

More than 50 yr ago, Hans Jenny outlined the importance of the state factors climate, organisms, topography, time, and parent material in the regulation of soil organic matter (SOM) dynamics (Jenny 1941). Now that human activity is expected to alter the first two of these on a global scale, much attention has been given to how these changes could affect the role of SOM in the global carbon cycle (Schimel et al. 1990, Jenkinson et al. 1991, Fung 1993). The quantity of carbon stored in soils is double that in either the atmosphere or terrestrial vegetation (Ajtay et al. 1979, Post et al. 1982, Schlesinger 1991), and annual effluxes of CO_2 from soils (via decomposition) are ≈10 times those derived from the combustion of fossil fuels (Mooney et al. 1987). Although at steady-state net uptake of CO_2 by plants (net primary production, or NPP) balances the loss from soils globally, even a small disruption of this equilibrium could alter atmospheric concentrations. Losses of soil carbon during land conversion coupled with prolonged decreases in productivity due to soil degradation can cause large losses of carbon from deforested regions to the atmosphere (Emanuel et al. 1984, Houghton et al. 1987, Houghton 1989). The differing responses of NPP and decomposition to changes in temperature could also create an imbalance: in general, increasing temperatures cause rates of respiration and decomposition to increase exponentially (Reiners 1968, Medina and Zelwer 1972, Singh and Gupta 1977), whereas rates of photosynthesis and NPP have a linear to saturating response (Gates 1980, Fitter and Hay 1981). These patterns have raised concerns that climatic warming caused by elevated CO_2 could cause an additional net transfer of carbon from the terrestrial biosphere to the atmosphere, and a positive feedback to further warming (Woodwell 1990, IGAC 1990, IPCC 1990). However, our ability to predict such changes is impaired by an incomplete knowledge of how climate controls soil carbon turnover and storage.

One uncertainty results from the fact that our understanding of the effect of temperature on decomposition is derived mostly from short-term studies, the results of which are applied to all SOM as if it were a single undifferentiated pool. In fact, SOM is highly complex and heterogeneous (Kononova 1975, Schlesinger 1977, Van Veen and Paul 1981), with organic compounds that vary from labile microbial biomass and fresh plant material to extremely refractory components that can remain in the soil for millennia. A number of successful models of SOM dynamics (Jenkinson and Raynor 1977, Parton et al. 1987) therefore separate soil carbon into pools with different turnover times; a small fraction is labile (≈5%), with the remainder divided into a large (60–85% of the total) "intermediate" SOM pool with turnover times in the range of years to decades, and a smaller (10–40%) "passive" SOM pool with turnover times of thousands of years. The labile, or "active," pool can change quickly in response to

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climate or land use change, but is too small to affect total stocks on land (and therefore the atmosphere) significantly; the passive pool turns over too slowly to make any real difference for several centuries. In contrast, the large intermediate pool is likely to respond on the time scale of anthropogenic global change, and analyses of the consequences of such change need to determine rates and controls of its turnover.

The relatively slow decomposition of the intermediate and passive pools means that CO_2 efflux from soils (soil respiration) is dominated by decomposition of the small active pool and by root respiration. There have been many analyses of the relationship between soil respiration and environmental variables such as temperature, moisture or vegetation (Berg 1984, Schlentner and Van Cleve 1985, Gordon et al. 1987, Stewart and Wheatley 1990), and the functions derived from these comparisons have been used to predict SOM turnover (Raich and Schlesinger 1992, Townsend et al. 1992). However, since the bulk of SOM appears to account for only ≈10% of total CO_2 (Schimel et al. 1994), soil respiration dynamics may differ from the dynamics of most soil carbon, and simple models based upon measurements of respiration and total soil carbon may be misleading. Instead, we need measurements that reflect responses of the bulk of SOM, preferably ones that can distinguish labile and recalcitrant SOM fractions.

Several studies have estimated SOM turnover and pool structure using carbon isotopes: either stable ^{13}C (Cerri et al. 1985, Balesdent et al. 1987, Vitorello et al. 1989, Martin et al. 1990), or radioactive ^{14}C (O'Brien and Stout 1978, Anderson and Paul 1984, Jenkinson et al. 1992, Trumbore 1993). However, to improve understanding of the response of SOM to environmental change, such isotopic measurements are needed along independent gradients of the controlling state factors. We used both ^{13}C and ^{14}C to estimate SOM turnover and pool structure in forests and pastures along an altitudinal gradient on the island of Hawaii. The resulting data provide a functional relationship between temperature and turnover of the largest SOM pools, as well as information on the effects of forest to pasture conversion in a tropical environment.

Methods

Study sites

The sites are on the northeast flank of Mauna Kea volcano in the Laupahoehoe Forest Reserve and the adjacent Waipunalei tract. They consist of native *Metrosideros polymorpha* dominated rain forest (C_3) that ranges from 700 to 1700 m elevation, and of adjacent pastures, dominated by the African C_4 grass *Pennisetum clandestinum,* that were converted from this forest several decades ago. The pastures extend below the forest to sea level, and both forest and pasture sites can be found at all elevations on the same soil type. These soils are andisols, classified in the 1965 Hawaii Soil Survey as typic distrandepts, and all are derived from what is known in Hawaii as "Pahala Ash," a generic term for a series of large volcanic ash falls occurring between 12 000 and 20 000 yr ago (Peterson and Moore 1987). Although different ash falls can vary both physically and chemically, there is little variation in a single large event like the one that covered our sites (Peterson and Moore 1987).

Mean annual rainfall varies from 2000 to 3000 mm, with a positive water balance at all elevations throughout the year (Juvik et al. 1978); therefore all soils are in a udic moisture regime and the gradient is essentially one of temperature, with a decrease in mean annual temperature of 9.4°C from the lowest pasture site at 100 m to the highest at 1700 m. We selected five main sites along this gradient: pastures at 100, 800, and 1700 m, and forests at 900 and 1500 m. The uppermost two pastures were 40–50 yr old, and the lowest was ≈100 yr old. We also selected two pastures at 800 m elevation that were ≈10–15 yr old and 15–27 yr old. The ages were determined by using air photos of the region taken in 1977, 1965, and 1954, and by talking with local landowners.

With the exception of stream cuts, the topography on a shield volcano such as Mauna Kea is quite consistent; all five sites were relatively level at a given altitude and all had a gradual slope towards the sea. Soil depth to older substrate was at least 1 m in all sites. To check our assumption that soil type was similar, we measured soil pH in $CaCl_2$ and in NaF of samples taken at 0, 20, 40, and 60 cm in each of the five sites. NaF pH is used as an index of allophane activity (Fieldes and Perrott 1965, Uehara and Gilman 1981). Soil pH values in both solutions were slightly lower at 0 cm in the forests (presumably due to surface litter), but overall values were extremely similar among the five sites (Fig. 1).

Soil carbon

With the exception of the samples for carbon-14, all soils were collected with a 5 × 20 cm corer. In each site, 15 cores were collected randomly along three 100-m transects. Sample sizes were between 100 and 200 g (dry mass), and all samples were passed through a 2-mm mesh sieve, after which any remaining root fragments were removed manually. The soils were then oven dried at 100°C, and kept at room temperature for analysis. Carbon contents were determined by combustion in a Carlo-Erba C/N analyzer; all samples were analyzed 2 or 3 times.

Soil respiration

CO_2 evolved from the soils in the field was determined using the soda lime technique (Raich et al. 1990). Approximately 60 g of soda lime in metal tins was dried at 100°C for 24 h immediately before sampling, then weighed and sealed. Fifteen plastic cham-

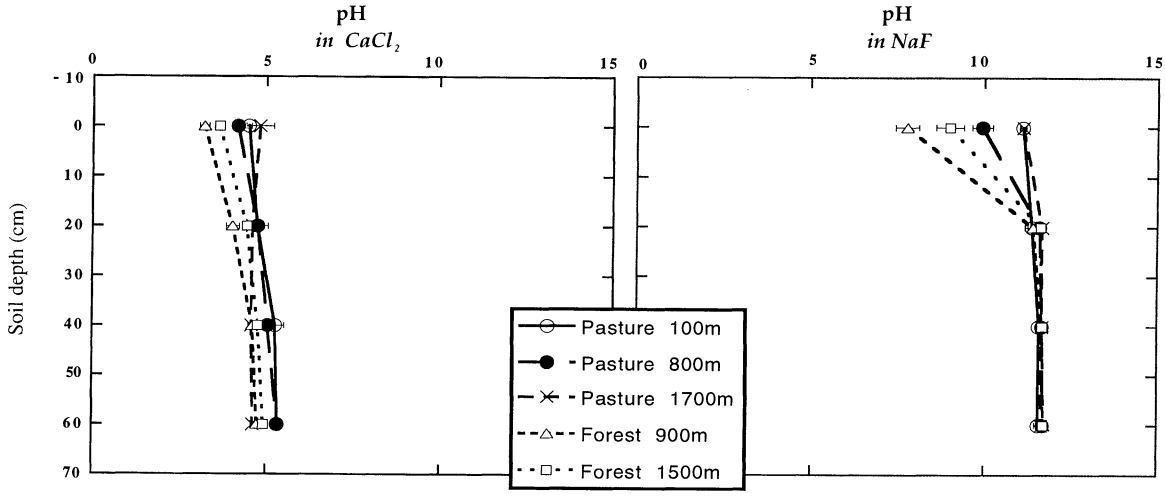

FIG. 1. Soil pH values in 20 cm depth increments from all five sites. Soil pH was measured in 0.01 mol/L $CaCl_2$ solution (Carter 1993) and in 1 mol/L NaF solution (Fieldes and Perrott 1965).

bers per site (33 cm diameter) were covered with aluminum foil, placed on the soil, and pushed in slightly to form a seal once all vegetation was clipped at the soil surface in the area encompassed by the chambers. The chambers were then removed, and allowed to equilibrate for 30 min. The soda lime tins were then opened and placed in the center of the cleared areas, the chambers were gently reinserted into the soil, and rocks were placed on top to keep the seal intact. Three tins per site were collected immediately and resealed to serve as blanks.

After 24 h, the chambers were removed and the remaining tins collected and sealed. A temperature probe was inserted ≈2–3 cm beneath the soil surface in all chamber locations, and soil temperatures were recorded. Soil cores were taken from within each chamber site and homogenized by hand. Subsamples were then taken from the homogenized cores, weighed, dried for 48 h at 100°C, and reweighed to determine soil moisture. The soda lime tins were dried at 100°C for 24 h and weighed; the difference between pre- and postsampling masses was assumed to be due to the CO_2 adsorbed during sampling. Sampling was done 6 times between November 1991 and September 1992. Values were converted to grams of carbon per square metre per day; annual values were computed by averaging all sampling days.

Carbon-13 of soils and vegetation

Homogenized samples of soil or vegetation were combusted in a sealed quartz tube with CuO at 900°C. The evolved CO_2 was released under vacuum and purified by trapping in liquid nitrogen; it was then analyzed for ^{13}C on a mass spectrometer (Finnigan Delta E) fitted with a triple-ion collector and dual inlet system that allows rapid switching between reference and sample. Results are expressed in $\delta^{13}C‰$ units:

$$\delta^{13}C‰ = (^{13}R \text{ sample}/^{13}R \text{ standard} - 1) \times 1000, \quad (1)$$

where $^{13}R = {}^{13}C/{}^{12}C$. The reference was calibrated using the standard NSB19, and results are expressed vs. Pee Dee Belemnite. All samples were run at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah; analytical precision was ±0.1‰.

Carbon-13 of soil respiration

Glass Wheaton jars (30-cm^3) were annealed at 300°C, sealed with red rubber Wheaton septa that had been boiled for 2 h, and then evacuated and sealed with Apiezon N grease. Plastic chambers fitted with Swagelok valves were connected to Teflon tubing equipped with clamps. The clamps were closed, chambers were placed over bare soil (see *Soil respiration* above), and CO_2 was allowed to accumulate within the chamber for 30 min. A Luer-Lock syringe was then attached to the free end of the tubing, the clamp was opened, and a 30-cm^3 sample was taken by drawing and plunging the syringe 3 times before locking the syringe valve.

A 22G surgical needle was then placed on the syringe and pushed through the thick portion of the Wheaton jar septa. All of the gas was plunged into the jar, the needle removed, and the septa again sealed with grease. We found that extracting samples through a needle directly from the chamber into the syringe can cause fractionation of >3‰; needles should be used only when the entire volume of gas is being transferred. The CO_2 in the samples was extracted and purified under vacuum, and then analyzed on a Nuclide 6-60 mass spectrometer in David Des Marais' laboratory at NASA/Ames Research Center. Values are calibrated and reported as described in the preceding section; analytical precision was ±0.1‰. All ^{13}C values for soil respiration are reported minus the fraction due to at-

TABLE 1. Soil carbon pools and fluxes, carbon isotopes, pasture ages, and the percent forest-derived soil carbon calculated from ^{13}C data using Eq. 3. Sites are three C_4 pastures and two C_3 forests on the northeast flank of Mauna Kea Volcano, island of Hawaii. Values in parentheses are standard errors, and $N = 15$ for all but soil respiration ($N = 75$) and soil ^{14}C

	Pasture (100 m)		Pasture (800 m)		Pasture (1700 m)	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Soil carbon (carbon, g·m^{-2}·20 cm depth^{-1})	9610[a]	123	13 620[b,c]	565	14 170[c,d]	543
Soil respiration (carbon, g·m^{-2}·yr^{-1})	3180[a]	91	2910[b]	80	2260[c]	71
Microbial biomass (carbon, mg/g soil)	1.78[a]	0.25	2.70[a,b]	0.57	3.55[b]	0.70
Microbial biomass (% soil C)	1.85		1.78		1.69	
$\delta^{13}C$ vegetation (‰)	−12.92[a]	0.15	−12.66[a]	0.20	−12.87[a]	0.18
$\delta^{13}C$ soil (‰)	−16.43[a]	0.18	−18.33[b]	0.25	−19.90[c]	0.30
$\delta^{13}C$ soil respiration (‰)	−14.65[a]	1.07	−15.21[a]	1.76	−13.28[a]	1.20
$\Delta^{14}C$ soil (‰)	−70	42	19	21	34	17
Pasture age (yr)	≈100		40–50		40–50	
% forest-derived soil C	25.4		41.5		52.3	

mospheric $^{13}CO_2$, determined by measuring the isotopic signature of eight atmospheric samples taken at each of the five sites, and by assuming the mean value from each site applied to 355 μL/L of the CO_2 in the chamber samples. The mean (± 1SE) for all five sites was −8.9 ± 1.4‰.

Carbon-14

Two 1 m deep soil pits were dug at each site; soil samples were collected at 20-cm increments to 1 m from the wall of the pit. These samples were taken by scraping free 2–3 cm from the surface of the walls to avoid contamination caused by digging, and then scraping an additional amount on to a clean trowel. Soils were processed and combusted in a quartz tube as described above; the resultant CO_2 was then analyzed for both ^{13}C (as above) and ^{14}C. ^{14}C was measured using Accelerator Mass Spectrometry (AMS; Trumbore 1993). The CO_2 was catalytically reduced to graphite AMS targets (Vogel et al. 1987), and measurements were made at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory. $\delta^{13}C$ corrections were made using results from the same samples. Values are expressed as $\Delta^{14}C$, the deviation in parts per thousand of the $^{14}C/^{12}C$ ratio in the sample from that of an absolute standard (oxalic acid decay corrected to 1950, Stuvier and Polach 1977). The values reported here are averages of the 0 and 20 cm samples, weighted by their respective carbon contents.

Microbial biomass

The microbial biomass for each site was estimated using the chloroform fumigation technique (Jenkinson and Powlson 1976). Ten 10-g samples of soil per site were fumigated in 100-mL beakers in a vacuum dessicator for 24 h; the beakers were then removed from the desiccator and placed into mason jars for 20 d. CO_2 evolved from the soils over days 1–10 and 11–20 was measured using base trap vials containing 5 mL of 1 mol/L NaOH (Coleman et al. 1978). The vials were removed following each sampling period, BaCl was added to precipitate out the CO_2 in solution, and each vial was titrated with 1 mol/L HCl. Five vials were placed in empty mason jars to serve as blanks. Microbial biomass C was computed using the equation of Chaussod and Nicolardot (1982):

$$\text{Mic C} = \frac{(\text{C evolved days 1–10}) - (\text{C evolved days 11–20})}{k}, \quad (2)$$

where k is the fraction of the carbon in the killed biomass that is mineralized to CO_2 under the conditions of incubation. We used a value of 0.45 (Jenkinson and Ladd 1981).

SOM fractionation

We attempted to separate bulk soil into fractions with different turnover times via two fractionation schemes. The first was a physical procedure described in full by Cambardella and Elliot (1994), in which the soils were dispersed in sodium hexametaphosphate for 16 h and then passed through a 53-μm mesh sieve. The second was a chemical procedure described by Trumbore (1991), in which the soils received alternating applications of HCl and NaOH (Trumbore 1991). The ^{13}C and ^{14}C values of each fraction were then determined.

Century model

Simulations of carbon dynamics of all five sites were done with the Century Soil Organic Matter model, which is described in detail in Parton et al. (1987, 1988). This model has been applied widely to both grassland and forest sites, has been validated extensively against sites in the Great Plains, and most recently, against a worldwide set of grassland sites (Parton et al. 1993). Existing parameter files for an

(N = 8). For each row, values with different superscripts (a,b,c, and d) are significantly different ($P < 0.05$).

Forest (900 m)		Forest (1500 m)	
$\bar{X}$	SE	$\bar{X}$	SE
11 390[b]	762	15 360[d]	343
2630[d]	77	2400[c]	67
2.49[a,b]	0.42	2.64[a,b]	0.53
1.73		1.01	
−26.98[b]	0.14	−26.32[b]	0.18
−26.70[d]	0.17	−25.90[d]	0.13
−26.16[b]	0.46	−25.99[b]	0.52
−24	35	51	44
NA		NA	
100		100	

evergreen rain forest and a tropical grassland were modified to represent the climate, and litter and vegetation chemistry of the sites. Where possible, parameter values were taken from data collected in or near the sites; otherwise best estimates from the literature were used.

Century's default structure causes fine-textured soils to retain a substantial fraction of rainfall. The allophanic soils in these sites are fine textured but macroporous so that the high rainfall in the sites does not cause the soils to flood. Consequently, we decreased the model's fraction of rainfall that is stored by 30% so that both texture and drainage were reasonable. Monthly mean temperatures and rainfall for each site were taken from Giambelluca et al. (1986) and the Atlas of Hawaii (1983), and the model was run to equilibrium for each site. Final equilibrium values for respiration, soil carbon, and SOM turnover are reported here.

Results

Soil carbon and respiration

Total soil carbon varies from 15 360 g/m^2 in the highest forest to 9610 g/m^2 in the lowest pasture (Table 1). In general, soil carbon increases with increasing altitude, but there are no significant differences between forest and pasture sites at a given elevation. There was considerable variation in soil respiration at each site from month to month (Table 2), but mean annual values (calculated from an average of the six sampling dates) also show a decreasing trend with altitude, with the greatest respiration occurring in the lowest pasture (Table 1). Mean annual respiration was not significantly different between the high elevation forest and pasture, but was higher in the 800 m pasture than in the 900 m forest. Soil moisture contents were relatively high at all sites and sampling dates, reflecting the high, relatively constant rainfall of the area (Table 2). The decrease in soil moistures seen in March of 1992 resulted from the driest spring of the century in the region; nevertheless, soil moisture never dropped below 40%. Soil temperatures also varied little throughout the year, but as expected, decreased with increasing elevation (Table 2).

Carbon-13

The ^{13}C values of the vegetation in each site reflect the two different photosynthetic pathways: the pastures range from −12.92 to −12.66‰, while the forest values are −26.98 and −26.32‰ (Table 1). In contrast to altitudinal gradients on younger substrate (Vitousek et al. 1990), we observed no distinct difference in ^{13}C

TABLE 2. Seasonal variation in soil respiration, surface soil temperature (≈2–3 cm depth), and gravimetric soil moisture content. Values are means of 24-h samples taken one day in each month (N = 15).

	Nov 1991		Jan 1992		Mar 1992		Jun 1992		Jul 1992		Sep 1992	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Soil respiration (g·m^{-2}·d^{-1})												
Pasture (100 m)	8.33	0.40	8.97	0.37	7.76	0.38	11.02	0.62	8.32	0.35	7.88	0.42
Pasture (800 m)	9.44	0.46	7.23	0.29	8.34	0.34	9.65	0.41	6.78	0.39	6.32	0.37
Pasture (1700 m)	7.67	0.32	6.08	0.34	5.67	0.29	5.46	0.32	6.97	0.37	5.32	0.35
Forest (900 m)	6.05	0.31	7.99	0.25	6.77	0.33	8.54	0.40	7.15	0.26	6.78	0.33
Forest (1500 m)	6.04	0.47	7.69	0.25	6.34	0.24	7.77	0.35	5.67	0.34	5.99	0.48
Soil temperature (°C)												
Pasture (100 m)	26.0	0.48	26.3	0.76	25.1	0.68	27.3	0.77	26.3	0.76	25.3	0.87
Pasture (800 m)	21.6	0.73	20.3	0.54	20.0	0.47	21.3	0.49	20.9	0.44	20.2	0.39
Pasture (1700 m)	15.5	0.38	14.8	0.35	14.6	0.25	15.1	0.21	15.3	0.30	15.0	0.22
Forest (900 m)	19.2	0.32	18.9	0.23	18.7	0.21	19.7	0.38	19.4	0.21	19.0	0.33
Forest (1500 m)	16.4	0.33	16.6	0.22	16.2	0.34	16.3	0.24	16.1	0.27	16.0	0.27
Soil moisture (% moisture)												
Pasture (100 m)	43.1	0.89	44.3	0.84	40.2	0.61	46.0	0.58	42.8	0.55	41.2	0.66
Pasture (800 m)	48.3	0.95	48.6	1.13	44.9	1.53	52.7	0.84	49.9	1.07	48.2	0.89
Pasture (1700 m)	50.2	1.24	52.3	0.95	46.2	0.84	55.5	1.10	51.8	0.89	50.9	1.15
Forest (900 m)	58.8	0.98	59.2	1.10	52.0	0.89	59.0	1.36	58.0	1.59	57.9	1.36
Forest (1500 m)	65.1	1.07	63.7	0.78	56.8	0.81	65.9	0.95	64.1	1.36	62.3	1.44

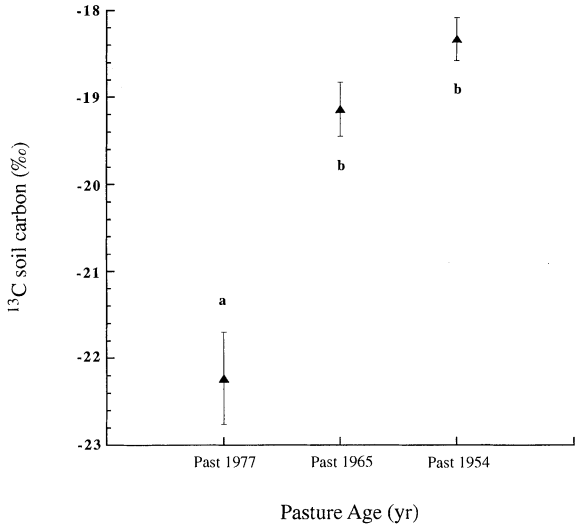

FIG. 2. $\delta^{13}C$ in parts per thousand of three pasture soils at 800 m elevation as a function of pasture age. All pastures are on the same soil type (andept), and all are dominated by the same C_4 grass species (*Pennisetum clandestinum*). The pasture ages are approximate; all could be as much as 10 yr older than shown.

with altitude in the forests. Soil ^{13}C values in the forest sites are close to those of the vegetation, at −26.77 and −25.90‰, whereas those in the pastures lie in between forest and pasture vegetation values, ranging from −19.90‰ in the highest pasture to −16.44‰ in the lowest (Table 1). Soil ^{13}C values in the youngest pasture at 800 m (10–15 yr old) are significantly lighter than in the two older pastures (Fig. 2).

The ^{13}C values of CO_2 respired from the soil are relatively constant among pasture or forest sites. Pasture values lie between −15.2 and −13.3‰, while the forest values are −26.2 and −26.0‰ (Table 1); there are no significant differences among sites of the same vegetation type.

The soil ^{13}C data from the pastures can be used to estimate the amount of SOM that has turned over since conversion from forest:

$$\%\text{Forest C} = \frac{^{13}\text{C pasture soil} - {}^{13}\text{C pasture veg}}{^{13}\text{C forest veg} - {}^{13}\text{C pasture veg}} \times 100. \quad (3)$$

Using this equation, we find that only ≈25% of the soil C in the 100 m pasture is forest derived, but that at 1700 m, more than half of the carbon in the soil is still derived from the forest (Table 1).

Carbon-14

The soil ^{14}C values vary widely among sites, and the error associated with the value for each site is large. Values in the pasture sites range from −70 to +34‰, and the two forest sites are −24 and +51‰ (Table 1). The large errors associated with these values are due to spatial variability; we could not overcome it with more sampling due to the expense of AMS measurements.

Microbial biomass

Microbial carbon biomass varies from 1.78 mg/g soil in the lowest pasture to 3.55 mg/g soil in the highest (Table 1). Values for the two forest sites fall between these two, and only the lowest and highest pasture values were significantly different. These values represent a relatively small fraction of total soil carbon (1.01–1.85%; Table 1).

SOM fractionation

The absence of aggregate structure makes allophanic soils notoriously difficult to fractionate (Sollins et al. 1983). Although the ^{14}C bulk soil data shows that very old carbon must exist in these soils, we were unable to separate fractions by age; there were no significant differences in ^{14}C or in ^{13}C among the fractions derived from either the physical or the chemical procedure.

Century modeling

In general, Century simulated observed carbon pools and fluxes in these sites reasonably well. The model overestimated soil carbon by 4.8–28.2%, and underestimated soil respiration by 5.5–36.8% (Table 3). Because Century's values for respiration do not include roots, the comparison between respiration values required an estimate of root respiration for the data; we used a literature-based estimate that 50% of total CO_2 evolved from the soil is due to roots (Raich and Schlesinger 1992).

MODELS OF SOM TURNOVER

The values for ^{13}C in the pastures show how much soil carbon has turned over in the decades since con-

TABLE 3. Simulated soil carbon and respiration numbers from the Century model, and the percent difference in simulated vs. observed values.

	Pasture (100 m)	Pasture (800 m)	Pasture (1700 m)	Forest (900 m)	Forest (1500 m)
Soil carbon ($g \cdot m^{-2} \cdot 20\ cm^{-1}$)	10 060	10 180	11 470	14 610	16 030
% difference	4.8	25.3	19.1	28.2	4.4
Soil respiration* ($g \cdot m^{-2} \cdot yr^{-1}$)	1420	4920	4800	1240	1040
% difference	10.5	36.8	29.2	5.5	13.3

* Assuming 50% of measured soil respiration is due to roots.

TABLE 4. Turnover of intermediate SOM expressed as half-lives ($t_{1/2}$) from one-pool model, three-pool model, ^{14}C-model, and Century model.

	Pasture (100 m)	Pasture (800 m)	Pasture (1700 m)	Forest (900 m)	Forest (1500 m)
$t_{1/2}$ one-pool (yr)	4.2	6.5	8.7	6.0	8.9
$t_{1/2}$ three-pool (yr)	14.8	23.3	31.4	21.7	32.1
$t_{1/2}$ ^{14}C-model (yr)	10.5	21.8	31.3	20.4	32.4
$t_{1/2}$ Century (yr)	13.6	22.0	30.3	24.5	31.6

version, but since the pastures vary in age as well as in climate (Table 1), the effects of temperature on turnover times cannot be determined directly from ^{13}C. However, the isotope signal provides excellent validation for modeled estimates of SOM turnover. We used the data on soil carbon stocks and fluxes in simple models based on either a one- or three-pool SOM structure, and then compared these estimates of turnover to the ^{13}C data.

First, we assumed a single undifferentiated SOM pool that turns over according to the generalized decay equation:

$$C_t = C_0 \cdot e^{-kt}, \quad (4)$$

where C_0 is the initial pool of organic matter, C_t is the amount left at time t, and k is a fractional loss constant (Jenny 1980). This approach has been used in several global analyses of the terrestrial carbon cycle (Raich and Schlesinger 1992, Townsend et al. 1992). Values for k are estimated by dividing total heterotrophic respiration by total soil carbon:

$$k = \frac{\text{total soil respiration} - \text{root respiration}}{\text{total soil carbon}}. \quad (5)$$

Literature-based estimates of root respiration vary from ≈30 to 60% of total soil respiration, with a mean near 50% (Schlesinger 1977). Since it was not possible to directly measure this component of soil CO_2 efflux in these sites, we used 50% in the above equation. These values for k can then be used to estimate turnover times for the soil carbon. A convenient index is the half-life ($t_{1/2}$) of SOM, or the time it takes for 50% of the carbon to decay, which is calculated from:

$$t_{1/2} = \frac{\ln 2}{k}. \quad (6)$$

This one-pool model calculates turnover times for SOM in our sites that vary from ≈4 yr at the warmest end of the gradient to ≈9 yr at the coolest (Table 4).

To the extent the structure of SOM is important, however, these calculated turnover times could be a misleading average. To account for the structure of SOM, a model could incorporate the decomposition constants for each pool (arrived at by dividing the size of the pool by the flux from that pool) into an equation describing multiple exponential decay:

$$C_t = a \cdot C_{act} \cdot e^{-k_{act}t} + b \cdot C_{int} \cdot e^{-k_{int}t} + c \cdot C_{pass} \cdot e^{-k_{pass}t}, \quad (7)$$

where a, b, and c are the fractions of active, intermediate, and passive SOM. However, it is difficult (if not impossible) to directly measure these stocks and fluxes. Attempts to fractionate soils into pools with different turnover times have had only limited success (Trumbore 1993, Cambardella and Elliott 1994), and there is no generally accepted procedure. Successful attempts have found older carbon to be associated with small clay particles (cf. Martin et al. 1990), consistent with the notion that passive SOM is carbon stabilized as organo-mineral complexes on and within clay aggregates. Allophanic soils, however, do not form a stable aggregate structure, and may instead stabilize carbon within amorphous silica gels (Uehara and Gillman 1981). The two fractionation methods we tried were unsuccessful in separating SOM into fractions with different isotopic signatures.

Consequently, it was necessary to make indirect estimates of the size and turnover time of each pool. Since the intermediate pool is both the largest of the three, and the one that can respond on the time scale of global environmental change, we concentrated on estimating its turnover. To do so, we separated the total soil carbon and respiration values into active, intermediate, and passive components. First, we used the soil ^{13}C value of the lowest pasture to estimate the amount of passive SOM. This pasture was converted from forest ≈100 yr ago, and essentially all C_3-derived forest carbon (other than the passive fraction) should have been replaced with C_4-derived grass carbon. If no passive fraction existed, the soil ^{13}C value here would reflect the grass signature of −12.66‰, but the observed value is −16.5‰ (Table 1); therefore ≈25% of the soil carbon is from the forest. We suggest that this is the passive fraction. Moreover, since all sites are on the same soil type, we assumed this fraction remained relatively constant across the sites, and subtracted it from the total soil C values. We further assumed that decomposition of passive C makes no contribution to soil respiration.

Second, we used long-term incubations of soils collected in all five sites to estimate the fraction of heterotrophic respiration derived from decomposition of intermediate SOM (Townsend 1993). Respired carbon was measured for 8 mo in these incubations. We assumed that the active SOM pool would decompose rapidly in soils removed from the plant–soil system, but that decomposition of the large intermediate pool would be much slower. Fluxes of CO_2 therefore should drop rapidly early in the incubation as active SOM is lost, and then stabilize as respiration becomes dominated by decomposition of intermediate SOM. Incubations of soils from our sites all followed this pattern, with fluxes stabilizing between 15 and 25% of initial levels after the 1st mo (Table 5). This range is in close agreement with simulations for a broad spectrum of sites generated by the Century model (Schimel et al.

TABLE 5. Incubation results used in three-pool model to separate active and intermediate respiration, and to estimate the size of the active pool. The data are CO_2 fluxes from soils sampled in these five sites ($N = 15$) and incubated at 30°C and field capacity soil moisture.

	Pasture (100 m)	Pasture (800 m)	Pasture (1700 m)	Forest (900 m)	Forest (1500 m)
Initial CO_2*	203	278	287	216	341
(carbon, $\mu g \cdot g\ soil^{-1} \cdot ^{-1}$)	(11.3)	(45.8)	(19.7)	(21.1)	(40.6)
Intermediate CO_2*	34	54	64	40	73
(carbon, $\mu g \cdot g\ soil^{-1} \cdot ^{-1}$)	(4.0)	(9.7)	(12.2)	(3.4)	(36.3)
% initial flux from intermediate C†	17	19	22	19	21
% soil carbon in active pool‡	4.3	3.4	2.8	2.8	2.7

* Initial values are the fluxes measured on day 5 of the incubation; intermediate values are the average of days 135 and 225. Values in parentheses are standard errors.
† Values calculated from (Intermediate CO_2)/(Initial CO_2) × 100.
‡ Values calculated from Eq. 8.

1994). We used a mean value of 20% for the fraction of heterotrophic respiration that arises from decomposition of intermediate SOM.

We also used the incubations to estimate the size of the active pool. Assuming that the active pool is not replenished, the sum of all respiration above that attributed to intermediate C is an estimate of the size of the active pool:

$$\%\text{active C} = \frac{\sum_{\text{day 1}}^{\text{day 225}} (R_{\text{total}} - R_{\text{int}})}{\text{soil carbon}} \times 100, \qquad (8)$$

where R_{total} is the total C respired each day of the incubation, and R_{int} is C respired from the intermediate pool. This approach yields estimates of active C that range from 2.7 to 4.3% of total soil carbon (Table 5).

With these estimates, we could then calculate the decomposition rate constant for the intermediate pool from:

$$k_{\text{intermediate}} = \frac{R_{\text{total}} - R_{\text{root}} - R_{\text{act}}}{C_{\text{total}} - C_{\text{pass}} - C_{\text{act}}} \qquad (9)$$

or

$$k_{\text{int}} = R_{\text{intermediate}}/C_{\text{intermediate}}, \qquad (10)$$

where C_x is the amount of carbon in each pool, and R_x is the amount of respiration, from each pool. The k values were then used to calculate half-lives of intermediate SOM using Eq. 7 (Table 3).

The ^{13}C data can be used to test the accuracy of both the one- and three-pool models. For the one-pool model, we set C equal to the percent forest-derived soil carbon and t to pasture age (Eq. 6), and found that the model predicts that <5% of the carbon in any of the pasture soils should be forest derived (Fig. 3). We know from the isotope data that this is much too low, and therefore this model estimates turnover times that are too rapid for the bulk of SOM.

A similar comparison can be made with the three-pool model. To predict the relative proportions of forest- and grass-derived carbon in each pasture, we used the decomposition constant estimated for intermediate SOM in the following equation:

$$\text{forest C} = C_{\text{int}} \cdot e^{-k_{\text{int}} t} + C_{\text{pass}} - C_{\text{act}}. \qquad (11)$$

This model assumes that all passive carbon is forest derived, and that all active carbon is grass derived. In contrast to the one-pool model, it is in close agreement with the field data (Fig. 4). With the exception of the lowest pasture, where ^{13}C was used to estimate the

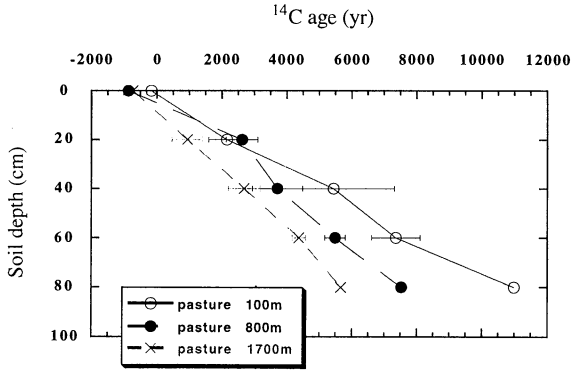

FIG. 3. ^{14}C ages of soil samples taken at 20-cm increments to 80 cm depth in the three main pasture sites. Ages at the surface are negative due to the influence of nuclear bomb-derived ^{14}C.

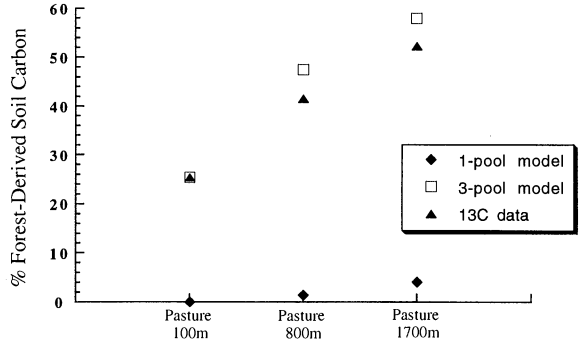

FIG. 4. The percent forest-derived carbon in the pasture soils estimated by the one-pool model, three-pool model, and ^{13}C data.

TABLE 6. The percent of total SOM in the passive pool as estimated by an assumption based on the ^{13}C value of soil at 100 m elevation, by the ^{14}C model, and by the Century model.

	Pasture (100 m)	Pasture (800 m)	Pasture (1700 m)	Forest (900 m)	Forest (1500 m)
^{13}C estimate	25	25	25	25	25
^{14}C model	38	25	22	24	21
Century	34	31	28	29	30

fraction of passive C, the soil isotope values provide independent validation of the model results.

Support for the three-pool approach is also seen in Fig. 2, which plots soil ^{13}C for pastures along an age gradient at 800 m. The values show a change from ≈70 to 40% forest-derived carbon between the youngest and oldest pastures, and a decrease in the rate of change with time. This pattern is consistent with an intermediate pool that has a half-life in the range of 15–20 yr, and with the existence of a passive pool. In contrast, the one-pool model predicts <50% forest carbon in the youngest pasture, and a continued rapid decrease to near zero in the oldest.

The low turnover times calculated by the one-pool model are due to the disproportionate amount of CO_2 produced by decomposition of the small active SOM pool. The dominance of active SOM and roots over respiration is shown by the ^{13}C data for soil respiration in the pastures (Table 1). If decomposition of the bulk of SOM dominated respiration, the ^{13}C values for respiration would equal those of the bulk soil; instead, they show a much greater proportion of grass-derived carbon in the CO_2 than in the bulk soil.

Carbon-14

The ^{14}C data (Table 1) provide another check of the three-pool model's estimates via the modeling approach described in Trumbore (1993). Briefly, turnover of SOM is based on the three-pool model shown in Eq. 7, and each pool incorporates the changes in atmospheric $^{14}CO_2$ using the decomposition rate constants. The active and intermediate pools are affected by the changes in atmospheric ^{14}C produced by bomb testing in the late 1950s and early 1960s because they turn over on time scales of decades or less; in contrast, the passive pool's ^{14}C value is dominated by its age, as its extreme recalcitrance renders it essentially inert to changes over the past 40 yr. The model assumes steady-state conditions, and calculates annual respiration and annual bulk soil ^{14}C values via a weighted average of the values for each pool. The bulk soil ^{14}C estimates are highly sensitive to the age and size of the passive fraction. Again, we assumed that 20% of heterotrophic respiration arises from intermediate SOM, and in this case, that active SOM has a 1-yr turnover time. The model is empirical, in that it solves for combinations of pool sizes, k_{int} and k_{pass} that match both the annual

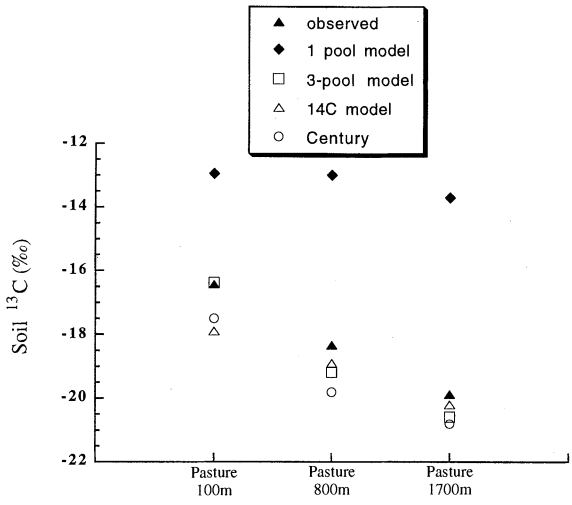

FIG. 5. Modeled vs. observed soil ^{13}C values for the three pasture sites.

soil respiration data and the soil ^{14}C data at the time of sampling (1992). These two constraints require a narrow range of solutions, and calculated turnover times for intermediate SOM are close to those generated with the ^{13}C-based model (Table 4).

The ^{14}C model's estimates of passive SOM, however, differ from the 25% value used above (Table 6). This discrepancy is largest in the lowest pasture; the value calculated from ^{14}C is 38%, whereas the ^{13}C data that shows that no more than ≈25% of SOM can be passive in this site. This difference could be due to the sensitivity of ^{14}C to small changes in very old SOM. ^{14}C ages at just 40 cm depth in this site are >5000 yr old (Fig. 4), and sampling errors caused by erosion of surface soils or by accidental incorporation of very small amounts of deeper soil could have profound effects on the ^{14}C values, causing the results to err in the direction of too much passive SOM. These processes would have little effect on the ^{13}C data.

Erosion following conversion could also cause the consistently greater ^{14}C ages at all depths at lower elevations (Fig. 3). If more surface soil has been removed in the lower pastures, then each sampling point in the depth profile is in effect representative of a deeper layer in lower pastures as compared to higher ones. Greater soil loss seems especially likely in the lowest pasture since it has been under human influence for twice as long as the higher two.

Century model

Finally, we compared estimates of SOM turnover from both the three-pool model and the ^{14}C model to those generated by Century, and found all three approaches to be remarkably similar (Table 3). Century predicted lower soil carbon and respiration values in the pastures than we observed, but its estimates of turn-

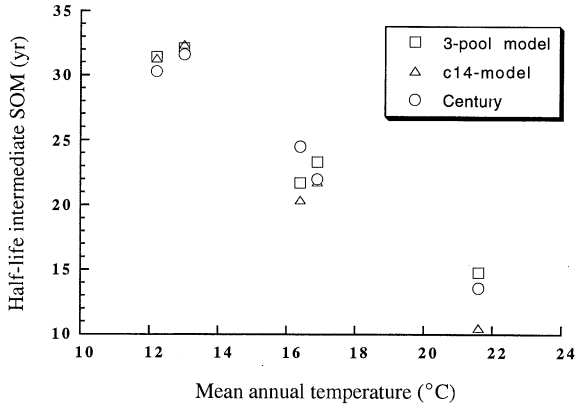

FIG. 6. Modeled values for intermediate SOM turnover vs. mean annual temperature. Values are expressed as half-lives (Eq. 6).

over in the pastures are very close to those of the data-based models because the model was allowed to run to equilibrium before the turnover times were calculated, and its ratio of respiration to soil carbon at equilibrium is close to that of the data, even though the values differ. Century also predicts somewhat different amounts of passive SOM than do the other two models. Like the ^{14}C model, it estimates that the passive fraction increases slightly with decreasing elevation in the pastures, though there is almost no difference between the two forest sites (Table 6).

Model validation

The soil ^{13}C data in the pastures provides a test of all three models' estimates of pool sizes and turnover times. Each model assumes that the active pool has the same ^{13}C value as the grass, that the passive pool's signature is equal to that of the forest vegetation, and that the intermediate pool's ^{13}C value depends on its turnover time and the pasture age. Fig. 5 compares the observed soil ^{13}C data to the predicted values generated by the one-pool model, the three-pool model, the ^{14}C model, and the Century model. This is an independent test of all four models with the exception of the three-pool model at 100 m elevation, since the ^{13}C data from this site was used to estimate the amount of passive SOM. Again, the one-pool model does a poor job, predicting ^{13}C values that are far too high in all three sites, while all three models that account for pool structure come much closer to the data. Agreement among these three models and between the models and the data is quite good for the uppermost two sites, with a total range of $<1‰$ in both cases. At 100 m elevation, both the Century and the ^{14}C model predict ^{13}C values that are slightly too low. Estimates of turnover by all three models are quite similar at all sites (Table 4); differences in their predicted values for ^{13}C result from differences in their estimates of passive SOM (Table 6).

Sensitivity analyses of simple three-pool models

The three-pool model (Eq. 7) presents a simple approach to calculating SOM turnover that still accounts for its structure, and that is consistent with the field results. A problem with this approach, however, is that it is highly sensitive to the estimated fractions of root, active pool, and intermediate pool respiration. Table 7 shows the results of a sensitivity analysis in which values for root respiration, intermediate respiration, and passive soil carbon were varied within ranges reported in the literature. A twofold change in either root or intermediate pool respiration resulted in twofold differences in calculated turnover times. In contrast, the passive pool is not a highly sensitive component in the calculation of intermediate pool turnover; doubling its size increases the half-life of intermediate SOM by only ≈20% (Table 7).

DISCUSSION

It has been suggested that increasing atmospheric CO_2 and a warmer climate could cause feedbacks in soil carbon cycling spanning a range from positive, where carbon losses from soils to the atmosphere accentuate warming, to negative, where increased carbon storage offsets the changes in the atmosphere (Prentice and Fung 1990, Woodwell 1990). Whether such feedbacks will occur, and if so which direction will prevail globally, will depend greatly on the response of intermediate SOM. The sites studied in this research pro-

TABLE 7. Sensitivity of three-pool model (Eq. 9) to estimates of root respiration (R_{root}), intermediate pool respiration (R_{int}), and total passive carbon (C_{pass}). The ranges for R_{root} and C_{pass} are best estimates from the literature; the range for R_{int} is from the long-term incubations (Table 5). Sensitivities for each parameter are turnover times using the high and low end of each reported range, computed by holding the other two parameters constant at the value used in this study.

Model parameters	Values used in this study (%)	Reported range (%)	Turnover times for intermediate SOM (yr)	Calculated from model	Sensitivity to R_{root}	Sensitivity to R_{int}	Sensitivity to C_{pass}
R_{root}	50	30–60	Pasture (100 m)	14.8	12.3–24.6	9.9–19.7	11.7–17.9
R_{int}	20	15–30	Pasture (800 m)	23.3	19.4–38.7	15.5–31.0	18.4–28.1
C_{pass}	25	10–40	Pasture (1700 m)	31.4	26.1–52.3	20.9–41.8	24.9–37.9
			Forest (900 m)	21.7	18.1–36.1	14.4–28.4	17.2–26.2
			Forest (500 m)	32.1	26.7–53.4	21.4–42.8	25.4–38.7

vided a unique opportunity to examine the effects of temperature on decomposition of intermediate SOM.

Decomposition rates are thought to increase exponentially with temperature, with numerous studies reporting Q_{10} values of ≈2 (Singh and Gupta 1977, Raich and Schlesinger 1992). These studies, however, are all of SOM fractions that turn over in ≤2 yr; the response of the larger recalcitrant fractions to temperature is not well known. Fig. 6 shows our estimates of the half-life of intermediate SOM from all three models plotted against mean annual temperature. The values range from ≈14 yr at the warmest end to 30 yr at the coolest, roughly a twofold increase in turnover over a 10°C range. This rate of change suggests a Q_{10} of ≈2, but given the error associated with these estimates, it is impossible to determine if the relationship is indeed exponential, or whether it is linear. Nevertheless, for at least the range provided by these study sites, the twofold change in turnover times suggests that decomposition of more recalcitrant fractions may be as sensitive to temperature as is that of the smaller labile pools.

Conclusions

1) We used four different approaches to estimating turnover of intermediate SOM, the largest of the three major SOM pools. The soil ^{13}C data showed that the three models that accounted for pool structure did a much better job of predicting SOM turnover following conversion from forest to pasture than did the simple one-pool model. All three multipool models were in close agreement, and all predict rates of SOM turnover that are three times slower than those from the one-pool model.

2) Intermediate soil carbon still can respond rapidly to environmental changes. We estimate that ≈75% of the SOM in the top 20 cm of these soils has turnover times of ≤30 yr, even at the coldest end of the temperature gradient. At the warmest end, a site with a climate that is representative of much of the lowland tropics, the turnover time of the large intermediate fraction is <15 yr.

3) The approximate doubling of intermediate SOM turnover times with a 10°C decrease in temperature suggests that decomposition of the larger, recalcitrant soil carbon pools may be as sensitive to temperature as the more labile active fraction.

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