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Soil carbon pool structure and temperature sensitivity inferred using CO_2 and $^{13}CO_2$ incubation fluxes from five Hawaiian soils

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Abstract. We measured respiration and $\delta^{13}C$ values of respired and soil carbon in long-term incubations of soils from two forests and three pastures along an altitudinal gradient in Hawaii. CO_2 fluxes early in the incubations decreased rapidly, and then stabilized at approximately 20% of initial values for seven months. We suggest that the rapid drop and subsequent stabilization of respiration reflects a change in the dominant source of the CO_2 from labile (active) to much more recalcitrant pools of soil organic matter (SOM). Estimates of active SOM were made by integrating all of the carbon respired in excess of that attributable to respiration of the intermediate SOM pool; these values ranged from 0.7–4.3% of total soil C. $\delta^{13}C$ values for carbon respired from the pasture soils showed that older, forest-derived C contributed an increasing fraction of total soil respiration with time. Initial and late-stage respiration responded similarly to changes in temperature, suggesting that intermediate SOM is as sensitive to temperature as the active fraction.

Introduction

The steady increase in radiatively active gases in the atmosphere is likely to raise global temperatures over the coming century (IPCC 1990). One effect of such warming will be an increase in decomposition rates of soil organic matter (SOM) (Jenkinson et al. 1991; Schimel et al. 1994). Rates of SOM turnover are a major control over the supply of mineral nutrients to vegetation, and any change in those rates could alter both the productivity and community structure of ecosystems (Pastor & Post 1986). Globally, SOM contains twice as much carbon as the atmosphere (Schlesinger 1991), and the rate at which soils store or lose carbon in a warmer climate could either retard or accelerate anthropogenically-driven increases in atmospheric CO_2 (Schimel et al. 1990; Townsend et al. 1992).

Soil carbon turnover and storage are controlled in large part by climate (Jenny 1980), but the heterogeneous nature of SOM complicates analyses of the relationship between decomposition and climate. Soils contain thousands of different low to high molecular weight compounds that vary dramatically in their resistance to decomposition, with fractions of SOM that vary in turnover time from days up to thousands of years (Kononova 1975; Schlesinger 1977; Van Veen & Paul 1981). The most labile pools comprise only a small fraction of the total, but because they turn over so rapidly, day to day soil CO_2 efflux is dominated by their dynamics (Schimel et al. 1994), while more recalcitrant pools dominate the SOM inventory (Trumbore 1993). Correlations between climate and measurements of respiration in either field or short-term lab studies therefore may not apply to the bulk of SOM, but the response of these large pools to prolonged environmental changes will determine any major shifts in soil carbon storage.

Models of SOM often represent the continuum of labile through highly recalcitrant fractions by grouping SOM into a few discrete pools. In the CENTURY model (Parton et al. 1987), for example, it is partitioned into three major components: a small ($\sim$5%), highly labile 'active' pool consisting of microbial biomass and easily decomposable compounds, a large (60–85%) 'intermediate' pool with turnover times that range from less than 10 to more than 100 years, and a smaller (10–40%) 'passive' pool. The last is stabilized or physically protected material that can have a mean residence time of thousands of years. CENTURY attributes roughly 80% of heterotrophic soil respiration to decomposition of active SOM, with the remaining 20% arising from the intermediate pool, and turnover of all pools is controlled by the same exponential temperature function (Schimel et al. 1994).

We carried out a series of long-term (several months) incubations designed to test three assumptions common to several models of SOM: 1) that active and intermediate SOM are distinct fractions; 2) that the bulk of heterotrophic respiration arises from decomposition of active SOM; and 3) that the response of both pools to changes in temperature does not differ functionally. Figure 1 shows the theory behind the use of a long-term incubation; initially the flux should be dominated by the active pool, but with the soil removed from the plant-soil system, this pool should decompose rapidly and not be replaced. The total flux therefore should decrease with time, stabilizing when it is dominated by the decomposition of the larger, more recalcitrant intermediate pool. The response of this late-stage flux to temperature should yield a relationship that is applicable to a much larger fraction of SOM, and the ratio of the late-stage flux to the initial flux is an estimate of the fraction of total heterotrophic respiration that arises from intermediate SOM.

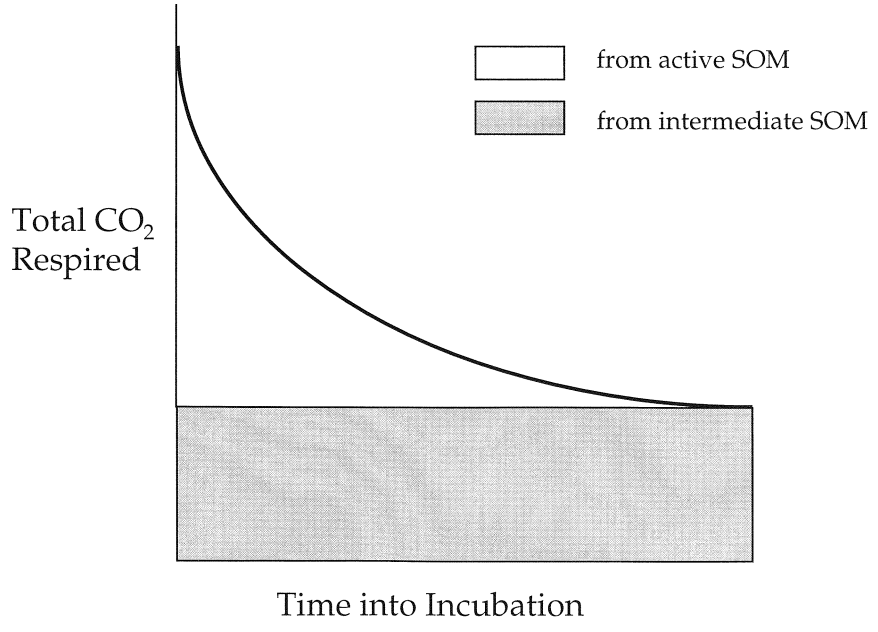

Figure 1. Theoretical contribution of active and intermediate SOM to respiration over the course of a long-term incubation.

We also used the carbon-13 signature of soil carbon and of CO_2 evolved from the soils to test the relative contribution of different SOM fractions to respiration. These isotope measurements are useful in sites where the photosynthetic pathway of the vegetation has changed. C_3 plants fractionate substantially against $^{13}CO_2$ during photosynthesis, while C_4 plants fractionate much less (Ehlringer & Osmond 1989), and this difference is reflected in the soils on which the plants grow. For example, after a change from C_3 forest to C_4 grassland, the soil gradually becomes enriched in ^{13}C, as the 'lighter' forest-derived carbon decomposes away and is replaced by 'heavier' grass-derived carbon. ^{13}C has been used to calculate the amount of soil carbon derived from C_4 versus C_3 vegetation (Cerri et al. 1985; Balesdent et al. 1987; Vitorello et al. 1989; Martin et al. 1990), and the same calculation can be made for respired CO_2.

In a situation where conversion from C_3 to C_4 vegetation occurred decades ago, the active pool should be wholly C_4-derived carbon. Therefore, CO_2 respired early in an incubation should be almost entirely C_4-derived, but as the flux becomes dominated by decomposition of intermediate SOM, the $^{13}CO_2$ values should display a greater fraction of the older, forest-derived carbon.

Methods

Study sites

We sampled sites on the northeast flank of Mauna Kea volcano in the Laupahoehoe Forest Reserve and in the adjacent Waipunalei tract. They consist of native *Metrosideros polymorpha* dominated rain forest (C_3) that ranges from 700 m to 1700 m elevation, and of pastures dominated by the African C_4 grass *Pennisetum clandestinum* that were converted from this forest several decades ago. The pastures extend below the lower limit of the forest to sea level, and both forest and pasture sites are found on andisols derived from the same 12,000–20,000 year old volcanic ash deposit (Peterson & Moore 1987).

Mean annual rainfall varies from 2000 mm to 3000 mm, with a positive water balance at all elevations (Juvik et al. 1978); therefore the gradient is essentially one of temperature, with a decrease in mean annual temperature of about 9 °C from the lowest pasture site at 100m (MAT ∼21 °C) to the highest at 1700m (MAT ∼12 °C). We selected five sites along this gradient: pastures at 100, 800, and 1700 m, and forests at 900 and 1500 m. The uppermost two pastures are 40–50 years old, and the lowest is approximately 100 years old (Townsend et al. 1995).

Thirty 20cm deep soil cores were collected in each of the five sites, put in a cooler, and taken back to the laboratory in Hawaii. The roots were then removed manually, and the remaining soil was refrigerated and shipped to Stanford, CA. Soils were either refrigerated (4 °C) or kept on ice in coolers at all times prior to the start of the incubations; the total time between sample collection and the start of the incubations was approximately ten days.

Soil Carbon and ^{13}C measurements

Total soil carbon was measured by passing samples through a 2mm sieve, after which the soils were 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.

To measure soil ^{13}C, homogenized samples of soil were combusted in a sealed quartz tube with CuO at 900 °C. The evolved CO_2 was trapped and purified by breaking the tubes under vacuum, and then analyzed for ^{13}C on a Finnigan Delta E mass spectrometer. 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 NBS19, and results are expressed vs. Pee Dee Belemnite. All soil samples were run at

the Stable Isotope Ratio Facility for Environmental Research at the University of Utah; analytical precision was $\pm 0.1‰$.

Incubation procedure

Eight 10 g samples of soil (dry weight) per site were incubated at 20, 30, and 40 degrees C, and the CO_2 evolved was measured on days 5, 15, 35, 85, 135, and 225 following the start of the incubation. For each soil sample, we drilled several holes in the bottom of a 50 ml polystyrene beaker, placed a glass fiber filter in the bottom of the beaker, and added 10 g of soil on top of the filter. Each beaker containing soil was then stacked into a second beaker used to catch leached water. Water was added to all soils to bring them to field capacity, and the beakers were placed in 1 qt mason jars (Figure 2). Evolved CO_2 was measured by trapping it in NaOH and then titrating with HCl and BaCl (Coleman et al. 1978); ten blanks (jars without soil) were used to estimate any CO_2 not due to respiration. Soil moisture was kept at field capacity, and soils were leached with distilled water three weeks into the incubation, and then two weeks after and before the final four sampling periods. The lids to the mason jars were removed at regular intervals in between sampling to prevent anoxic conditions within the jars.

$\delta^{13}CO_2$ measurements

We carried out a second, 120 day incubation at 30 degrees C to measure changes in δ^{13}C of respired carbon over time. Soils from all five sites were used, with eight 10 g samples of soil per site, and the incubation set-up was as described above. To capture the CO_2 for isotopic analyses, 30 cc glass Wheaton jars were annealed, fitted with red rubber Wheaton septa that had been boiled to prevent outgassing, and then evacuated and sealed with Apiezon N grease. The mason jar lids were fitted with Swagelok fittings connected to Teflon tubing equipped with clamps (Figure 2). The clamps were closed, lids sealed on the jars, and CO_2 was allowed to accumulate (no base traps were present at this time). A Luer-Lock syringe was then attached to the free end of the tubing, the clamp was opened, and a 30 cc sample was taken by drawing and plunging the syringe three 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 septum. All of the gas was plunged into the jar, the needle removed, and the septa again sealed with grease.

CO_2 in the samples was purified under vacuum prior to isotopic analyses. To separate dilute amounts of CO_2 from bulk air, the sample was pumped repeatedly across a series of cold traps through a closed-loop circuit. Two

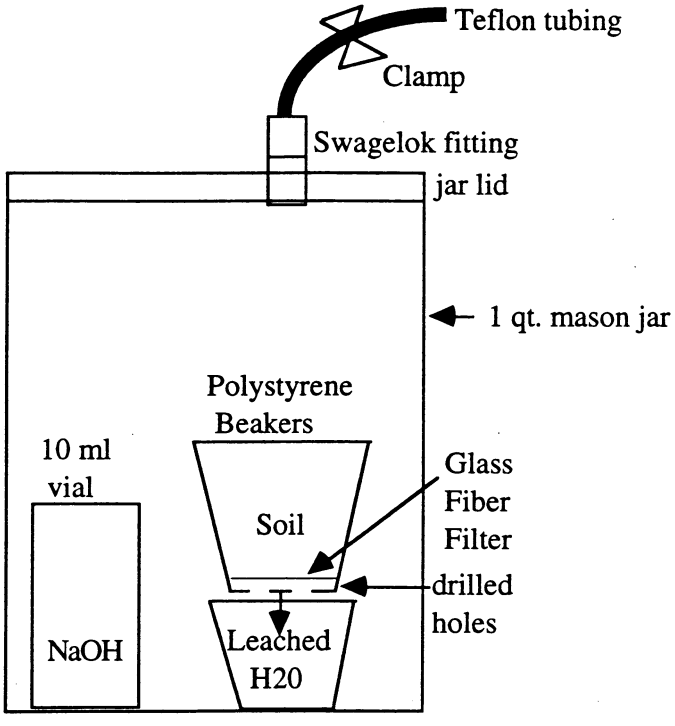

Figure 2. Diagram of the set-up for each sample of soil incubated. The Swagelok fittings, tubing, and clamps were used only in the incubation for $^{13}CO_2$.

needles connected the sample vial to the line. Each needle led to opposite sides of a mercury-driven Toeppler pump with a one-way valve; this pump was used to cycle the air sample for ten minutes over two traps used to remove water and impurities, and then for an additional ten minutes over the liquid-nitrogen CO_2 trap. Bulk air was then pumped out, and the CO_2 was transferred to a glass ampule and flame-sealed. This procedure produced 0.1‰ accuracy in analyses of the CO_2 isotope standard. All samples were analyzed on a Nuclide 6–60 mass spectrometer, and values are calibrated and reported as described above.

Results

Respiration over time

CO_2 emissions from all five soils followed the same general pattern. Fluxes on the first day of sampling (day 5 of the incubation) were relatively high

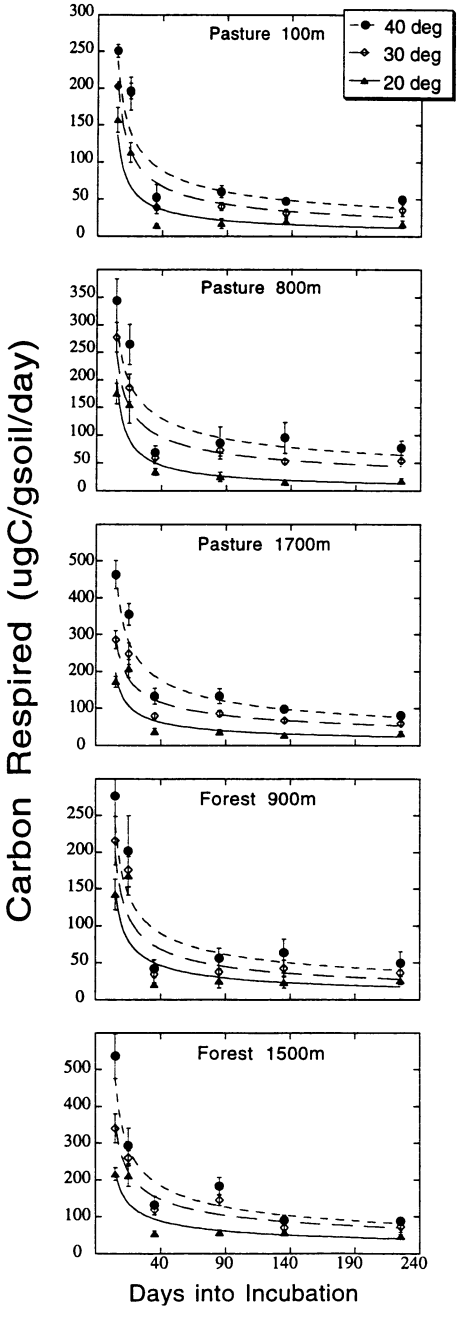

Figure 3. Respired carbon over time in ugC/g soil/day at three different temperatures for all five sites. Data are from 10 g (dry weight) samples of soil incubated with moisture kept at field capacity; error bars are standard errors.

Table 1. Initial (R_i) and intermediate (R_{int}) respiration, and estimates of % soil carbon respired, of 'active' soil carbon pool sizes, and of the fraction of initial respiration estimated to be from intermediate SOM. R_i values are the fluxes on day 5 of the incubation, when both active and intermediate pools are contributing to respiration; R_{int} values are the means of fluxes on days 135 and 225, when the active pool is assumed to have decomposed. Values for % soil C respired are from R_{total}/soil C x 100 (see Equation 3 in text for estimates of R_{total}). Active pool sizes are calculated from equations 2 and 3 in the text. The ratio R_{int}/R_i is an estimate of the fraction of total heterotrophic respiration that is derived from intermediate SOM.

Site	Soil carbon (%)	Temperature ($^{\circ}$C)	R_i (μgC/gsoil/d)	R_{int} (μgC/soil/d)	% Soil C Respired)	Active Soil C (% total soil C)	R_{int} / R_i
Pasture 100 m	9.6	20	128	19	5.8	1.4	.15
		30	203	34	11.1	3.4	.17
		40	251	49	15.0	3.8	.19
Pasture 800 m	15.1	20	176	27	4.7	0.7	.15
		30	278	54	10.6	2.7	.19
		40	344	87	14.6	1.9	.25
Pasture 1700 m	21.0	20	173	31	4.8	1.5	.18
		30	287	64	9.2	2.5	.22
		40	464	90	13.7	4.3	.19
Forest 900 m	14.4	20	143	25	5.2	1.4	.18
		30	216	40	7.7	1.6	.19
		40	277	57	10.4	1.7	.21
Forest 1500 m	26.0	20	217	53	5.7	1.2	.24
		30	341	73	9.5	3.3	.21
		40	537	90	11.6	4.0	.17
Means		**20**	–	–	**5.2**	**1.3**	**.18**
		30	–	–	**9.6**	**2.7**	**.20**
		40	–	–	**13.1**	**3.1**	**.20**
		all	–	–	**–**	**2.4**	**.19**

for any given soil at any given temperature, and fluxes from all soils at all temperatures dropped dramatically by day 35, remaining low and relatively constant through day 225 (Figure 3). We labeled the flux on day 5 'initial respiration' (R_i), and the average of fluxes on days 135 and 225 'intermediate respiration' (R_{int}); the latter ranged from 15–25% of initial respiration across all sites and temperatures. The mean at 20 degrees was 18%, compared to 20% for both 30 and 40 degrees; these values do not differ statistically.

Total soil carbon (dry weight %C) varied from 9.6% in the pasture at 100 m elevation to 26% in the 1500 m forest (Table 1), and respiration varied among the sites in proportion to these differences in soil C. Both initial and intermediate fluxes were lowest in the 100m pasture and highest in the 1500m forest at all three temperatures (Table 1).

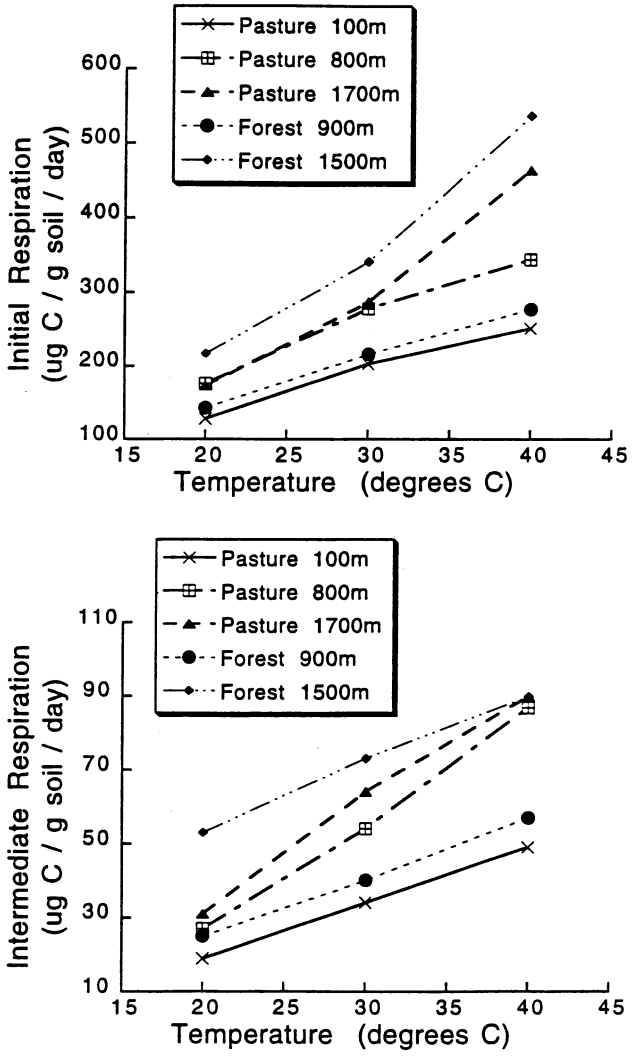

Figure 4. Initial (A) and intermediate (B) respiration versus temperature. Initial values are the fluxes on day 5 into the incubation; intermediate values are the mean of fluxes on days 135 and 225.

Respiration versus temperature

R_i increased by a factor of 1.6 between 20 and 30 degrees, and by 1.4 between 30 and 40 degrees; the values for R_{int} are 1.8 and 1.4 (Table 2). This difference in Q_{10}'s at 20–30 degrees is not statistically significant, while the decrease

Table 2. Q_{10}'s for R_i and R_{int}(initial and intermediate respiration). Values are ratios of the fluxes at higher temperatures to those at lower temperatures.

Site	Q_{10}'s for R_i		Q_{10}'s for R_{int}	
	20–30 °C	30–40 °C	20–30 °C	30–40 °C
Pasture 100 m	1.6	1.2	1.8	1.4
Pasture 800 m	1.6	1.2	2	1.6
Pasture 1700 m	1.7	1.6	2.1	1.4
Forest 900 m	1.5	1.3	1.6	1.4
Forest 1500 m	1.6	1.6	1.4	1.2
Means	**1.6**	**1.4**	**1.8**	**1.4**

in Q_{10}'s at the higher temperature interval is only marginally significant even for the intermediate fluxes ($t = 2.48$; $p = .048$).

Carbon-13

The $\delta^{13}C$ values for respiration in three of the sites were relatively constant throughout the incubation, remaining between -12.5‰ and -12.8‰ in the 100 m pasture, and between -25.2‰ and -25.9‰ in both forests. In the 800 m and 1700 m pastures, however, values decreased significantly between days 7 and 120 (Figure 5). At 800 m, they decreased from -14.6‰ to -16.0‰ (Single Factor ANOVA; $F = 2.99$, $p < .05$), and at 1700 m they dropped from -12.6‰ to -14.2‰ ($F = 6.32$, $p < .005$) (Figure 5).

Discussion

The results are consistent with the existence of at least a small, labile carbon pool and a much larger, more recalcitrant pool. It is possible that physical disturbance of the soil during sampling and preparation of the incubations caused initial rates of respiration to be artificially high; such an effect could produce patterns such as those seen here. However, we believe that several lines of evidence suggest that the patterns observed are not simply a product of disturbance, but instead reflect a relatively rapid change from initial respiration that is dominated by active SOM to later fluxes that are principally derived from 'intermediate' SOM. First, the mean ratio of intermediate to initial respiration was 19% (Table 1); this value is close to CENTURY's calculation that 23 ± 6% of respiration comes from intermediate SOM (Schimel et al. 1994), suggesting that late stage fluxes in the incubation are mostly from recalcitrant pools. Second, estimates of turnover times for SOM based on the

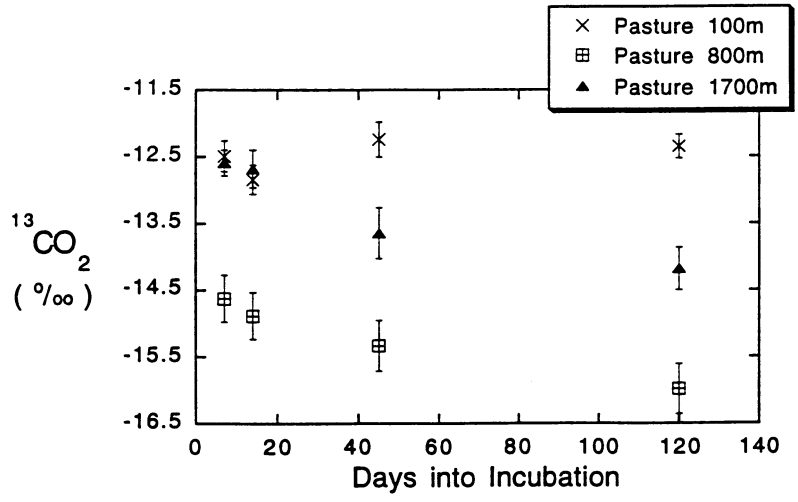

Figure 5. $^{13}CO_2$ for respiration versus time into the incubation for the three pasture soils. Values are in parts per thousand relative to the PDB standard.

Table 3. Comparison of three different approaches to estimating turnover times for intermediate SOM in these Hawaiian soils. Turnover times are reported as half-lives, or the time it takes for 50% of the carbon to decay, where $t_{1/2} = \ln 2/k$, and k is a decomposition constant estimated from the ratio of annual respiration to total soil carbon (see Jenny 1980). The values labeled 'Field Data' are derived from isotopic and respiration data taken in these sites, and are described in full in Townsend et al. (1995), as are the CENTURY simulation values. The incubation values are means of all five sites for each temperature, calculated from: $k = R_{int}$/total soil C.

Estimates of Turnover Times (years) for Intermediate SOM			
Temperature (°C)	Field Data	Century	Incubations
20	15.5	16.8	11.1
30	7.4	8.8	6.1
40	3.5	4.6	4.4

late stage respiration values are relatively consistent with other estimates for intermediate SOM turnover in these sites (Table 3). Third, if the decrease in flux over time was due to the disappearance of active SOM, we would have expected respiration from the soils incubated at higher temperatures to drop first, and a comparison of mean fluxes on day 5 versus day 15 shows significant decreases at higher temperatures, but no change at 20 degrees (Figure 6).

Finally, if the drop and stabilization of respiration over time represents a near complete loss of active SOM, then the total amount of CO_2 evolved over

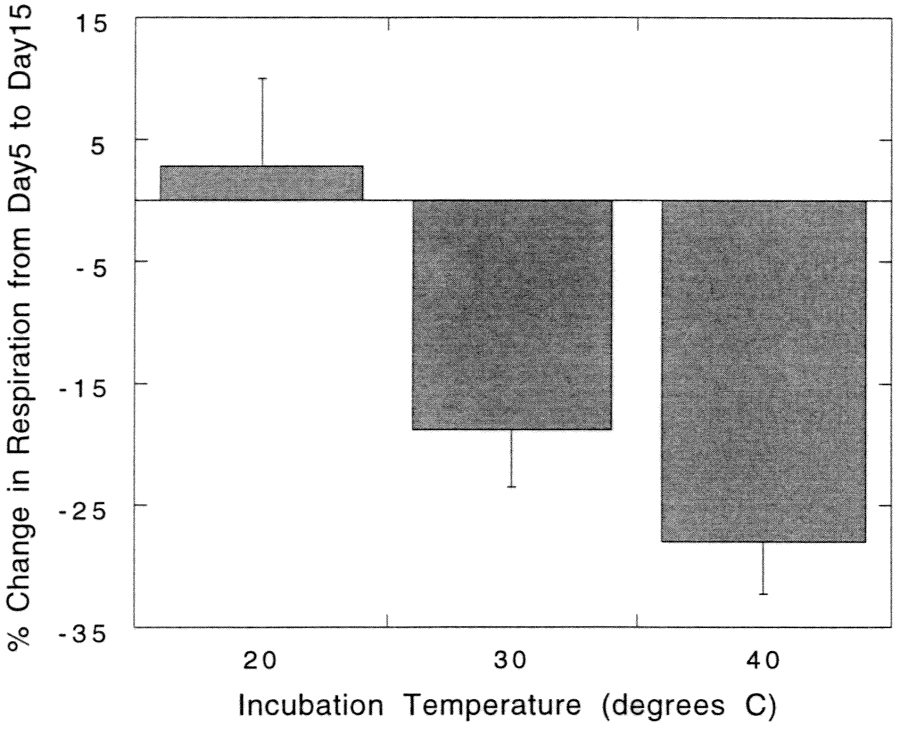

Figure 6. The average percent change in respiration between days 5 and 15 for 20, 30 and 40 degrees. Negative values indicate a decrease in respiration from day 5 to day 15, and error bars are standard errors.

the course of the incubation – above that attributed to intermediate SOM – should be roughly equal to the size of the active pool. This can be calculated from:

$$\%\text{Active C} = \frac{\text{R}_{\text{total}} - \text{R}_{\text{int}} \times 220}{\text{Soil Carbon}} \times 100 \tag{2}$$

where R_{total} is the total carbon evolved over the couse of the incubations, and R_{int} is the mean of fluxes on days 135 and 225. We assumed that respiration from intermediate SOM did not vary with time, therefore R_{int} is multiplied by 220 days to get the total amount of intermediate respiration. Since fluxes were not measured every day, we estimated R_{total} by fitting the best curve to the data for each site and temperature, and then integrated under these curves. The best fit curves in all cases could be described with the general equation $\text{y} = \text{ax}^{-b}$, therefore all estimates for R_{total} were made as follows:

$$\text{R}_{\text{total}} = \int_{x=5}^{x=225} (\text{ax}^{-b}\text{d}x) \tag{3}$$

Specific values for a and b are shown below.[1] The resulting estimates of active C range from 0.7–4.3% of total soil carbon, with a mean of 2.4% (Table 1). These values are similar to most reported values for microbial biomass C (Anderson & Domsch 1980; Srivastava & Singh 1988), including those from these same soils (Townsend et al. 1995).

The estimates of the size of the active pool are not independent of temperature, as they increase significantly from a mean of 1.3% at 20 degrees to 3.1% at 40 degrees (Table 1). However, the percent drop in respiration from day 5 to day 225 does not differ among the three temperatures, suggesting that the active pool has decomposed equally at all three temperatures by the end of the incubation.

Sensitivity of respiration to temperature

One objective of this study was to determine if more recalcitrant SOM fractions differ from the small labile pool in their sensitivity to changes in temperature. The results suggest not – both initial and intermediate respiration changed less at higher temperatures, and the Q_{10}'s do not differ statistically between fluxes from the two pools for either temperature range (Table 2). All Q_{10}'s are within the reported range in the literature (Singh & Gupta 1977; Raich & Schlesinger 1992), and are similar to those measured in a short-term incubation of soils from this same region, in which respiration was shown to increase exponentially between 15 and 55 degrees C (Holland et al. 1995). It is not possible to distinguish clearly between an exponential versus a linear relationship for either R_i or R_{int}, but it does appear that their respective sensitivities to temperature are not different. We note, however, that estimates of intermediate SOM turnover based on both field data from these sites and on CENTURY simulations (Townsend et al. 1995) show greater sensitivity to changes in temperature than the incubation data suggest (Table 3).

Carbon isotopes

Values of δ^{13}C for SOM and respiration in the pastures may be used to calculate how much soil and how much respired carbon is derived from earlier forest vegetation. The pastures have a mixture of grass- and forest-derived SOM, taking on values from -16.5‰ at the lowest pasture to -19.9‰ at the highest, versus about -13‰ for the grasses and -26‰ for the forest

[1] Best fit curves to data on respiration over time were all of the form $y = ax^{-b}$. Specific values for a and b are as follows, with the values for each site listed as a, b for 20°; 30°; and 40°: Pasture 100 m: 385, .642; 507, .547; 511, .476 Pasture 800 m: 629, .708; 518, .454; 587, .407 Pasture 1700 m: 477, .548; 601, .444; 1020, .476 Forest 900 m: 361, .552; 456, .513; 504, .466 Forest 1500 m: 454, .441; 696, .421; 1005, .460.

Table 4. δ^{13}C values for vegetation and soil organic matter, and estimates of δ^{13}C values for intermediate SOM (described in Townsend et al. (1995)).

	Pasture (100 m)	Pasture (800 m)	Pasture (1700 m)	Forest (900 m)	Forest (1500 m)
δ^{13}C of SOM	−16.4‰	−18.3‰	−19.9‰	−26.7‰	−25.9‰
δ^{13}C of vegetation	−12.9‰	−12.6‰	−12.8‰	−27.0‰	−26.3‰
Forest-derived SOM	25%	41.5%	52.3%	100%	100%
δ^{13}C of Intermediate SOM	−12.9‰	−15.9‰	−17.9‰		
Forest-derived Intermediate SOM	0%	23.1%	38.2%	100%	100%

vegetation (Table 4). These values can be used to calculate the percent forest-derived carbon in the soils with the equation:

$$\%\text{Forest C} = \left\{ \frac{^{13}\text{C Pasture Soil} - ^{13}\text{ C Pasture Veg.}}{^{13}\text{C Forest Soil} - ^{13}\text{ C Pasture Veg.}} \right\} \times\ 100 \qquad (4)$$

which calculates that roughly 25% of the soil carbon in the lowest pasture is forest-derived, versus more than half in the highest (Table 4).

Earlier, we estimated that 25% of the soil carbon in all three pastures was in the passive pool (Townsend et al. 1995). δ^{13}C values for soil carbon show that 25% is forest-derived at 100m elevation, 41.5% at 800 m, and 52.3% at 1700 m (Table 4). This means that no intermediate SOM is forest-derived at 100 m, about 23% is at 800 m and about 38% is at 1700 m (Table 4). These fractions (F_i) can be used to estimate the ^{13}C signature of intermediate SOM from:

$$^{13}\text{C}_{\text{int}} = (\text{F}_{\text{C3 int SOM}})(^{13}\text{C forest}) + (\text{F}_{\text{C4 int SOM}})(^{13}\text{Cgrass}) \qquad (5)$$

yielding values that range from −12.9‰ at 100 m to −17.9‰ at 1700 m (Table 4).

If the drop in respiration with time reflects a change from active pool- to intermediate pool-dominated decomposition, then the ^{13}C signature of the CO_2 from the pasture soils should change from that of active SOM towards that of intermediate SOM. At 100 m, both pools are completely grass-derived, and the ^{13}C values for respiration remained between −12.5‰ and −12.8‰ throughout the incubation. In the 800 m and 1700 m pastures, however, the intermediate pool contains some forest-derived carbon, and the respiration values exhibited a significant decrease between days 7 and 120 in both cases (Figure 5).

These results raise a couple of questions. First, the ^{13}C values for respiration from the 800m pasture soils are consistently lower than those at 1700 m, even though there is much more C_3-carbon in the higher elevation soils. One possibility is that this is the smallest of the three pastures, and is closest to the intact forest, so that it may receive some inputs of more labile forest carbon. Alternatively, although all three pastures are dominated by the C_4-grass *Pennisetum*, the 800 m pasture has more subordinate herbaceous species, some of which are C_3.

Second, the $\delta^{13}C$ values of respiration decreased continuously with time in the two highest pastures (Figure 5), while respiration itself dropped rapidly and then stabilized (Figure 3). Additionally, the value on day 120 of $-14.2‰$ from the 1700 m pasture is still much higher than the estimated value for intermediate soil C of $-17.9‰$. These results may be due to the existence of a range of turnover times for carbon *within* the intermediate pool; although 38% of this pool may be C_3 at 1700 m, this 38% is still a minimum of 40 years old. The remaining 62% is a maximum of 40 years old, and it is this younger, C_4-carbon which will comprise the more labile components of the intermediate pool. Just as active SOM dominated respiration at the beginning of the incubation, so will the more labile fractions of intermediate C dominate respiration during the initial decomposition of this pool, but the decrease in respiration over time should be far slower.

The widely employed division of SOM into active, intermediate, and passive fractions is an operational separation of a continuum. Nevertheless, the rapid drop and subsequent stabilization of respiration in this study suggests that there is a small, highly labile SOM pool that is relatively discrete, and ^{14}C data have shown that there must be a distinct very old SOM fraction even in soils where 80% of the carbon is turning over ten years or less (Trumbore et al. 1990; Townsend et al. 1995). Thus while a continuous distribution of turnover times from days to millennia exists within SOM, it can be modeled reasonably with a few (at least three) distinct pools.

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