# Seasonal and altitudinal variation in decomposition of soil organic matter inferred from radiocarbon measurements of soil CO<sub>2</sub> flux

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Abstract. The rate of carbon (C) cycling in soils is controlled by an array of processes and conditions. It has been widely accepted that an increase in temperature would accelerate microbial decomposition of soil organic matter (SOM) and provide a positive feedback to global warming, other factors being equal. However, soil moisture has received little attention in C cycle studies. In this project, we developed a technique for sampling soil-respired CO<sub>2</sub> for isotopic measurements and a model that relates the radiocarbon (14C) content of soil respired CO<sub>2</sub> to the rate of C cycling in soils. We measured soil CO<sub>2</sub> flux, carbon isotopic content (both <sup>13</sup>C and <sup>14</sup>C) of soil-respired CO2, soil temperature, and soil moisture on a monthly basis along an elevation transect in the Sierra Nevada in an attempt to determine the relationship between the rate of soil C cycling and soil environmental conditions. Both soil CO<sub>2</sub> flux and its <sup>14</sup>C content displayed significant variations (spatially and temporally), which reflect natural variations in the rate of SOM decomposition and in the relative amount of SOM-derived CO2 versus root-respired CO2 caused by seasonal changes in soil temperature, moisture, and plant activity. The relative contribution of SOM decomposition to total soil CO<sub>2</sub> production changed throughout the year from  $\sim 20 - 50\%$  at the peak of the growing season to close to 100% in the nongrowing season. The apparent decay rate of SOM determined from the <sup>14</sup>C content of soil-respired CO<sub>2</sub> varied from  $\sim 0.2 \text{ yr}^{-1}$  in the spring to  $\sim 0.01 \text{ yr}^{-1}$  in the fall at the lowest-elevation site and from 0.1 yr<sup>-1</sup> in the summer to  $\sim 0.01 \text{ yr}^{-1}$  in the late fall at the highest-elevation site. It appears that the apparent decay rate of SOM increased with increasing temperature when soil moisture was adequate but decreased with increasing temperature when soil moisture became limited. The apparent decay rate of SOM also varied with soil moisture. Higher soil moisture content accelerated decomposition of SOM until it reached an optimal level of ~ 14 - 25 wt % water content and then inhibited decomposition when more pores in soils became saturated with water and perhaps oxygen availability (for microbes) became limited. Although the rate of SOM decomposition varied throughout the year in response to fluctuations in soil temperature and moisture, the maximum apparent decay rate was higher at the low-elevation site (i.e., maximum apparent decay rate =  $0.22 \text{ yr}^{-1}$ ) than at the high-elevation sites (i.e., maximum apparent decay rate =  $0.10 \text{ yr}^{-1}$ ). Litter decomposition simulated by measuring changes in mass of litter in litter bags placed in the field also showed a similar decomposition pattern with decreasing decomposition rate with elevation. Multivariable regression analyses including various terms of soil temperature, moisture, and site variability suggest that soil moisture was a major factor, but not the only factor, controlling the rate of SOM decomposition and soil CO<sub>2</sub> flux in the Sierra Nevada soils. Both decay rate and total soil CO<sub>2</sub> flux are related significantly to soil moisture, temperature, and site effects.

### 1. Introduction

The importance of soil organic carbon in the global carbon budget has been recognized over the years [e.g., Schlesinger,

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Paper number 1999GB900074 0886-6236/00/1999GB900074\$12.00 1991; Denning et al., 1995; Eswaran et al., 1993; Post et al., 1997], but many knowledge gaps still exist as to how soils will respond to future environmental change. Evaluation of soil carbon sources and sinks is difficult because the dynamics of soil carbon storage and release are complex and still not well understood. Modeling the fluxes of soil CO<sub>2</sub> derived from soil organic matter (SOM) decomposition requires detailed knowledge of the factors regulating the soil C cycle. There is therefore a need to study the fundamental processes underlying

the CO<sub>2</sub> emissions from soils in a variety of environmental settings.

One method of assessing soil carbon dynamics is to model the observed changes in <sup>14</sup>C content of SOM pools during the last 30 years since atomic bomb testing ended assuming that soils are at steady state [Trumbore et al., 1989, 1990, 1996; Hsieh, 1989; 1992; Trumbore, 1993; Harrison et al., 1993; Wang et al., 1996, 1998, 1999]. The steady state approach assumes that the decay rate of SOM is constant with respect to time, local climate, and soil properties. As such, the decay rate derived from <sup>14</sup>C measurements of SOM represents an average rate over decades to millennia or longer timescales.

In this study, we developed a technique for sampling soilrespired CO<sub>2</sub> for isotopic measurements and a model that relates the <sup>14</sup>C content of soil-respired CO<sub>2</sub> to the rate of SOM decomposition and the fraction of soil CO2 flux derived from SOM decomposition. We also measured soil CO2 flux, stable and radioactive carbon isotopic ratios of soil-respired CO2, soil temperature, and soil moisture along an elevation transect of the western slope of the Sierra Nevada, California. The 14C content of soil-respired CO2 was the primary focus of this work and was interpreted in light of our model. Our objectives were (1) to examine the natural variations in soil CO<sub>2</sub> production and <sup>14</sup>C content of soil-respired CO2, (2) to determine the decay rate of SOM and the relative contribution of SOM decomposition versus root respiration to total soil CO2 flux, and (3) to establish statistically significant relationships between rates of organic carbon cycling in these soils and soil environmental parameters.

The approach presented here is different from the steady state approach in that we consider the decay rate of SOM as a dynamic character of a soil that varies with soil properties as well as soil environmental conditions. Our approach allows us to examine how seasonal variations in soil environmental conditions affect the dynamics of C cycling in soils and therefore provides an independent means of studying the soil C cycle on different timescales.

## 2. Methods

# 2.1. Field Measurements and Sampling of Soil CO<sub>2</sub> and Soil Respired CO<sub>2</sub>

We selected three natural soils and one disturbed (agricultural) soil along an elevation transect of the Sierra Nevada in central California for this study. Because the three natural soils (i.e., Fallbrook soil, Musick soil, and Chiquito soil) form a "climosequence" [Jenny et al., 1949] (a series of soils that are

similar to one another in major soil-forming properties such as parent material, soil age, and topography but experience different climate), they allow us to examine the effects of climate on the soil C cycle (Table 1). The soils have varying classifications due to their climatic and land-use history but are all developed on granodiorite. The disturbed soil (Fallbrook-OCD) was the same as the Fallbrook soil until it was converted to lemon orchard in 1972. Comparison of natural and disturbed soils allows us to evaluate the effect of land-use change on soil C cycling. The mean annual temperature decreases from ~18°C at the lowest elevation sites (i.e., the Fallbrook and Fallbrook-OCD sites) to ~3°C at the highest elevation site (i.e., the Chiquito site). The annual rainfall increases with elevation (from ~31 cm at the Fallbrook to ~ 127 cm at the Chiquito).

In this paper, soil-respired CO<sub>2</sub> represents the flux of CO<sub>2</sub> through a soil and into the overlying atmosphere [Cerling et al., 1991]. To examine how climate affects soil CO2 production and organic matter turnover, we measured the CO2 flux, C isotopic composition of soil-respired CO2, soil temperature, and soil moisture at these sites. CO2 flux from soil surface was measured with a portable LI-COR CO2 analyzer [Norman et al., 1992; Ben-Asher et al., 1994]. Soil temperature and moisture were measured by taking both temperature and resistance readings directly from permanently installed thermistor soil cells at depths of 10, 25, 50 and 100 cm. Field measurements of resistance were converted to moisture contents using moisture-resistance calibration curves for corresponding soils. The calibration relationship between soil moisture content and soil cell resistance for each soil was determined by taking a soil core close to the location where the soil cell was buried and then measuring the resistances at various moisture contents in the lab (SOILTEST manual, ELE International, Inc.). Soil-respired CO2 was collected from a large flux chamber with preevacuated glass bottles fitted with high vacuum glass stopcocks. The flux chamber consisted of a ring and a cap with a rubber gasket (Figure 1). The ring was inserted to a depth of ~ 12 cm to ensure no leakage to the atmosphere. The ring was installed permanently in the ground to minimize the disturbance of natural conditions. The cap was installed several hours before sampling and was removed after sample was withdrawn from the chamber to allow the chamber to reequilibrate with the ambient environment. Air samples (representing the air initially trapped inside the chamber) were collected from ~ 30 cm aboveground at each site for <sup>13</sup>C and <sup>14</sup>C measurements right before the installation of the chamber cap. After several hours, preevacuated sampling bottles were attached to the sample port, and stopcocks on sampling bottles were

Table 1. Climate and Related Characteristics of Sierra Nevada Study Sites

Site	Elevation,	Temperature,	Precipitation,	Soil	Vegetation	Land-Use
	m	°C	cm	Classification		Condition
Fallbrook	455	17.8	31	typic haploxevalf	annual grasses, blue oak	natural
Musick	1240	11.7	94	ultic haploxevalf	ponderosa pine, white fir, manzanita, incense cedar, sugar pine, bear clover	natural
Chiquito	2890	3.3	127	entic cryumbrept	western white pine, lodgepole pine, Sierra juniper	natural
Fallbrook -OCD	420	17.8	31	typic haploxevalf	lemon trees	disturbed

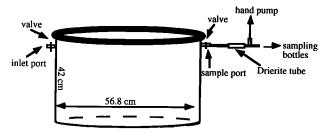


Figure 1. Flux chamber for measuring isotopic composition of soil-respired CO<sub>2</sub>. To collect gas sample from the chamber, preevacuated sampling bottles are connected to the sample port via capillary tubes and a commercial Drierite tube (for removing water from the gas sample).

opened carefully after the system between the valve and the bottles had been evacuated with a hand pump (Figure 1). Then the valve on the sample port of the flux chamber was opened, and at the same time the valve on the inlet port was cracked to let ambient air enter the chamber to minimize the total pressure change inside the chamber. Carbon dioxide samples were cryogenically purified in a multitrap flow-through vacuum line as soon as possible following field sampling.

Because the gas inside the flux chamber is a mixture of soil-respired CO<sub>2</sub> and atmospheric CO<sub>2</sub> initially trapped in the chamber, the isotopic composition of soil-respired CO<sub>2</sub> was calculated using the following mass balance relationships:

$$\Delta^{14}C_{respCO2} = [\Delta^{14}C_{sample} - (1-f)*\Delta^{14}C_{atmCO2}]/f,$$
 (1)

$$f = (\delta^{13}C_{\text{sample}} - \delta^{13}C_{\text{atmCO2}})/(\delta^{13}C_{\text{respCO2}} - \delta^{13}C_{\text{atmCO2}}), (2)$$

or

$$f = ([CO2]sample-[CO2]air)/[CO2]sample, (3)$$

where f is fraction of soil-respired CO<sub>2</sub> in the flux chamber,  $\Delta^{14}C_{respCO2}$  is the  $^{14}C$  content of soil-respired CO<sub>2</sub>,  $\Delta^{14}C_{atmCO2}$  and  $\delta^{13}C_{atmCO2}$  are the  $^{14}C$  and  $^{13}C$  content of atmospheric CO<sub>2</sub> initially trapped inside the chamber,  $\Delta^{13}C_{sample}$  and  $\delta^{13}C_{sample}$  are the  $^{13}C$  and  $^{13}C$  content of CO<sub>2</sub> inside the flux chamber at the time of sampling,  $\delta^{13}C_{respCO2}$  is the  $^{13}C$  content of soil respired CO<sub>2</sub> (which is same as the  $\delta^{13}C$  of SOM),  $[CO_2]_{air}$  is the CO<sub>2</sub> concentration in the air, and  $[CO_2]_{sample}$  is the CO<sub>2</sub> concentration inside the flux chamber at the time of sampling.

Our sampling technique was tested in two different ways. First, we compared air samples collected directly into preevacuated bottles with that passed through our sampling apparatus (consisting of Drierite and capillary tubes) into preevacuated bottles. We found that the addition of Drierite and capillary tubes did not fractionate carbon isotopes in CO<sub>2</sub>. Second, we selected a forested site on Berkeley Hill and collected air samples and soil-respired CO<sub>2</sub> samples using the flux-chamber technique described above for both CO<sub>2</sub> concentration and  $\delta^{13}$ C analyses. The  $\delta^{13}$ CrespCO<sub>2</sub> values determined from the experiments using (2) and (3) were essentially the same as expected (i.e.,  $\delta^{13}$ Com value of SOM: Cerling, 1984), suggesting that our sampling technique does not fractionate C isotopes of soil-respired CO<sub>2</sub> and provides a reliable method for studying the isotopic composition of soil-respired CO<sub>2</sub>.

In addition to CO2 flux measurements, we conducted field measurements of aboveground organic matter input at our study sites. At the annual grassland site, grasses (i.e., aboveground biomass) within a 1 m x 1 m area at four different locations were cut right above the surface of the soil in September (nongrowing season) and oven dried at 70°C for few days; the dry weight was measured for determination of the aboveground organic matter input. At the forested sites, four litter traps were placed on the ground surface at each site. The litter was collected periodically from the litter traps and oven-dried at 70°C for determination of litter inputs at the sites. We also collected litter from each site for litter decomposition study following the procedure of Steinberger and Whitford [1988]. The litter was oven dried at 70°C for 72 hours. Ten-grams samples of litter were placed in 20 cm x 20 cm Nylon mesh bags. For the Fallbrook site, 7-g litter bags were used because not enough litter was collected. Twelve 10-g litter bags were scattered on the ground surface at the Musick site, ten 10-g litter bags were placed at the Chiquito site, and ten 7-g litter bags were placed at the Fallbrook site on August 10, 1994. Litter bags were collected periodically for measuring the amount of litter lost through decomposition.

#### 2.2. Laboratory Methods

Air and soil gas samples were purified cryogenically via a multitrap flow-through vacuum line. The sample was first expanded sequentially into three liquid N2 traps and then was allowed to flow through the traps at a rate less than 20 cm<sup>3</sup> min<sup>-1</sup>. This procedure separates CO2 and H2O from other gases in the sample. Further separation of CO2 from H2O was accomplished using the conventional cryogenic method. This multitrap flowthrough CO<sub>2</sub> extraction method was tested with mixtures of N<sub>2</sub> and pure CO2 with a known carbon isotopic ratio and was found to be effective in stripping small amounts of CO2 from a large volume of gas sample without fractionating the carbon isotopes. In addition, we collected replicate air samples and sent one of them to S. Trumbore's lab at University of California at Irvine for independent analysis. The <sup>14</sup>C content measured in Trumbore's lab was the same within the analytical precision as that obtained in our lab on the replicate samples, confirming that our sample preparation procedure did not fractionate or contaminate the <sup>14</sup>C content of a sample. The stable C isotopic composition of the purified CO2 was measured on a stable isotope ratio mass spectrometer and reported as the standard  $\delta$  notation (i.e.,  $\delta^{13} C \!\!=\!\! \{[^{13}C/^{12}C]_{sample} \!\!-\!\! [^{13}C/^{12}C]_{PDB}\}/[^{13}C/^{12}C]_{PDB}1\;0\;0\;0\;)\;.$ radiocarbon (14C) analysis, the purified CO2 was reduced to graphite with H<sub>2</sub> over Fe, and its <sup>14</sup>C/<sup>13</sup>C ratio was measured on an accelerator mass spectrometer (AMS) at the Center for Accelerator Mass Spectrometry at the Lawrence Livermore National Laboratory. Carbon 14 data are reported as  $\Delta^{14}C$  =  $[A_{SN}/A_{ABS}-1]*1000\%$ , where  $A_{SN}$  is the specific activity of a sample (which is proportional to the <sup>14</sup>C/C ratio in the sample) normalized to  $\delta^{13}C$  =-25‰, and  $A_{ABS}$  is the absolute international standard activity which is equal to 0.95 times the specific activity of the international standard (NBS Oxalic Acid from the National Institute of Standards and Technology) normalized to  $\delta^{13}C = -19\%$  and the year 1950 [Stuiver and *Polach*, 1977]. Analytical precision (1  $\sigma$ ) for <sup>14</sup>C analysis is better than 9‰.

#### 2.3. Statistical Methods

Both univariate and multivariate polynomial and exponential regression models were used to establish the relationship between

the rate of C cycling in soils and soil environmental conditions. For example, let  $y_{ij}$  be the apparent turnover time (the inverse of the apparent decay rate of SOM) and  $T_{ij}$  be the average soil temperature measured in month i and at site j, where sites 1-4 are Fallbrook, Fallbrook-OCD, Musick, and Chiquito, respectively. We may consider the following univariate polynomial regression model:

$$y_{ij} = \mu + b_1 T_{ij} + b_2 T_{ij}^2 + e_{ij}$$

or a univariate exponential regression model:

Ln 
$$(y_{ii}) = \mu + b_1 T_{ii} + e_{ii}$$

where  $\mu$  is the intercept in the model,  $e_{ij}$  is a random noise term representing measurement errors, and  $b_1$  and  $b_2$  are coefficients. The  $e_{ij}$  values are assumed to be independent and normally distributed with mean zero and variance  $\sigma^2$ .

More generally, if we let  $M_{ij}$  denote the soil average moisture measured in month i and at site j and treat the four study sites as a qualitative (or categorical) variable with four levels, then a multivariate polynomial regression model has the form

$$y_{ij} = \mu + \alpha_j + b_1 T_{ij} + b_2 T_{ij}^2 + b_3 M_{ij} + b_4 M_{ij}^2 + b_4 (TM)_{ij} + e_{ij}$$

and an exponential model has the form

$$\operatorname{Ln}(y_{ii}) = \mu + \alpha_i + b_1 T_{ii} + b_2 M_{ii} + b_3 (T_{ii} M_{ii}) + e_{ii}$$

where  $\{\alpha_j, j=1, ..., 4\}$  represent the effects of different soil sites and  $(T_{ij}M_{ij})$  is the product term of temperature and moisture that represents the interaction between the two environmental parameters (i.e., soil temperature and soil moisture).

It is well known that only three of the four parameters  $\{\alpha_j, j = 1, ..., 4\}$  are estimable, and various constraints can be imposed on the  $\alpha_j$  values to provide estimates of meaningful functions of the original parameters. In this study, the constraint  $\sum_{j=1}^{4} \alpha_j = 0$ 

was used. When  $\alpha_1$ ,  $\alpha_2$ , and  $\alpha_3$  are derived, the fourth parameter can be estimated based on the equation  $\alpha_4 = -(\alpha_1 + \alpha_2 + \alpha_3)$ .

Some terms in the multiple regression models may not be statistically significant. These terms should be identified and removed from the model. In this study, the stepwise regression procedure was applied to select models. This procedure allows selection of a final model that excludes all the non-significant terms. It is important to note that the four parameters  $\{\alpha_j: j=l, ..., 4\}$  together represent the impact of the site variable (reflecting differences in clay content, litter quality, soil texture, etc.) on the apparent turnover time of SOM.

# 2.4. A Model for Determining the Rate of Organic C Cycling in Soils Using $^{14}\mathrm{C}$

Since CO<sub>2</sub> is produced in soils by microbial decomposition of organic matter and by root respiration, the production of soil CO<sub>2</sub> can be expressed mathematically as follows:

$$\Phi_T = \Phi_R + \Phi_H \tag{4}$$

where  $\Phi_T$  is the total soil CO<sub>2</sub> production,  $\Phi_R$  is the CO<sub>2</sub> production by root respiration, and  $\Phi_H$  is the CO<sub>2</sub> production by organic matter decomposition.  $\Phi_H$  can also be defined as

$$\Phi_H = \Phi_T F = k C \tag{5}$$

where k is the apparent decay rate of organic matter which is a function of climatic variables and soil properties, and C is the soil carbon content, and F is the fraction of  $CO_2$  derived from SOM decomposition.

Although CO<sub>2</sub> produced by root respiration has about the same <sup>14</sup>C content as atmospheric CO<sub>2</sub> [Dorr and Munich, 1986], incubation studies suggest that the <sup>14</sup>C content of CO<sub>2</sub> derived from SOM decomposition is not the same as the <sup>14</sup>C content of bulk SOM (Y. Wang and T. Baisden, unpublished data, 1995). The <sup>14</sup>C content of CO<sub>2</sub> produced by SOM decomposition can be estimated by measuring the respired <sup>14</sup>CO<sub>2</sub> at a time when plant activity is at minimum. Once the <sup>14</sup>C content of CO<sub>2</sub> produced by SOM decomposition is known, the relative contribution of these two reservoirs to the soil <sup>14</sup>CO<sub>2</sub> production can be calculated with a two-component mixing model following the equation [Wang et al., 1994]

$$(^{14}C)_{Sr} = (1-F) (^{14}C)_{atm} + F (^{14}C)_{om},$$
 (6)

where  $(^{14}\text{C})_{SF}$  is the  $^{14}\text{C}$  content of soil respired CO<sub>2</sub>; and  $(^{14}\text{C})_{OM}$  and  $(^{14}\text{C})_{atm}$  are  $^{14}\text{C}$  content of CO<sub>2</sub> derived from organic matter decomposition and the atmosphere, respectively.

From (4), (5), and (6), we can calculate the value of F (i.e., the fraction of CO<sub>2</sub> produced by microbial decomposition of SOM) and also the apparent decay rate (k):

$$F = [(^{14}C)_{sr} - (^{14}C)_{atm}]/[(^{14}C)_{om} - (^{14}C)_{atm}]$$
 (7)

$$k = \Phi_T F/C. (8)$$

The relative contribution of root respiration to total soil CO<sub>2</sub> production is (1 - F). The apparent decay constant k defined here is different from the steady state decay constant used in previous studies [e.g., Paul et al., 1964; Trumbore et al., 1989, 1990; Trumbore, 1993; Trumbore et al., 1996]. Under the steady state assumption used previously, the decay constant is an integration of annual variations caused by temperature and precipitation. In this research, the time series of measurements allows us to examine the annual variations in k caused by variations in soil temperature and soil moisture. By measuring soil CO2 flux or total respired CO<sub>2</sub> ( $\Phi_T$ ), total carbon content of the soil (C), the <sup>14</sup>C content of total respired CO<sub>2</sub> [(<sup>14</sup>C)<sub>ST</sub>], and the <sup>14</sup>C content of  $CO_2$  produced by organic matter decomposition [( $^{14}C$ )<sub>om</sub>], we can calculate the F (i.e., the fraction of CO<sub>2</sub> derived from SOM decomposition), and the apparent decay rate (k) for a particular soil using (7) and (8). We then can determine how the seasonal variations in F, k and  $\Phi_T$  respond to local soil environmental parameters (i. e., temperature and moisture, etc.). The apparent decay rate of SOM defined in our study gives us a better indicator of the environmental influence on the dynamics of organic carbon cycling in soils than the annual average decay rates derived from SOM 14C studies and is a somewhat independent means of examining the rates of soil C cycling.

### 3. Results and Discussions

### 3.1. Natural Variations in Soil CO2 Flux

Along the Sierra Nevada transect there is a significant variation in soil CO<sub>2</sub> flux, both spatially and temporally (Table

	Table 2.	Field Measurements	of Soil CO2 Fluxes	Along the Sierra N	Nevada Transect
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Date	Fallbrook Soil	Fallbrook-OCD	Musick Soil	Chiquito Soil	Note
August 1994	1.88 ±0.12(4)		5.07±0.24(4)	2.51±0.15(5)	litter-free surface
September 1994	$1.66 \pm 0.18(18)$	11.32 <u>+</u> 0.64(8)	6.99 <u>+</u> 0.66(19)	3.76±0.43(23)	litter-free surface
	1.91 <u>+</u> 0.14(8)		5.57±1.73 (8)	7.97±0.93(6)	litter-covered surface
October 1994	14.63±7.58(12)	4.11±0.78(20)	24.60±5.89 (16)	10.36 <u>+</u> 0.72(8) <sup>a</sup>	litter-free surface
				3.95 <u>+</u> 0.14(8) <sup>b</sup>	
	21.25 ±4.88(19)	5.23±0.23(8)	18.99 <u>+</u> 2.66(19)	13.77 <u>+</u> 3.57(11) <sup>a</sup>	litter covered surface
				6.34 <u>+</u> 0.47(8) <sup>c</sup>	
				1.17 <u>+</u> 0.54(8)	snow-covered surface
November 1994	15.30 <u>+</u> 3.71(18)	6.41±1.40(23)	7.42 <u>+</u> 1.19(20)	snow covered	litter-free surface
	22.39±2.77(19)	19.12 <u>+</u> 2.84(23)	16.42±7.27(16)		litter covered surface
			1.12±0.16(8)		snow-covered surface
January 1995	10.81±3.17(23)	17.46±3.02(15)	snow covered	snow covered	litter-free surface
	15.23±2.81(20)	14.83±7.27(21)			litter-covered surface
February 1995	24.88±7.27(24)	9.61±1.40(20)	snow covered	snow covered	litter-free surface
	24.91±4.14(23)	17.86 <u>+</u> 4.21(22)			litter-covered surface
March 1995	25.92±7.20(18)		snow covered	snow covered	litter-free surface
					litter-covered surface
April 1995	26.91±2.48(55)	5.01±1.73(57)	27.43±2.34(31)	snow covered	litter-free surface
_	29.76±2.97(59)	22.89 <u>+</u> 11.61(18)	16.79 <u>+</u> 4.21(24)		litter-covered surface
May 1995	15.89±3.96(24)	10.02 <u>+</u> 5.18(24)		snow covered	litter-free surface
	20.30±2.77(24)	8.48±1.80(16)	22.40±1.33(8)		litter-covered surface
fune 1995	5.56±0.76(24)	8.27±3.20(31)	17.50±6.95(36)	snow covered	litter-free surface
	8.31±3.89(24)	7.08 <u>+</u> 6.01(24)	17.91±7.02(40)		litter-covered surface
July 1995	2.81±0.54(24)	13.78±9.58(27)	13.51±2.99(15)	7.46±3.38(28)	litter-free surface
	1.94±1.94(24)	9.94 <u>+</u> 4.46(15)	16.16 <u>+</u> 6.05(15)	8.24±0.97(27)	litter-covered
September 1995	1.00±0.20(31)	10.23±4.14(44)	6.98±2.41(28)	4.25±2.27(28)	litter-free surface
•	$1.02\pm1.01(32)$	7.54±5.33(20)	4.47±1.55(32)	2.48±0.54(36)	litter-covered surface
October 1995	1.31±0.42(36)	14.59±9.25(24)	$9.62 \pm 7.02(28)$	3.31±1.51(36)	litter-free surface
	0.78±0.79(24)	11.12±9.22(44)	6.22±2.59(32)	2.39±0.36(40)	litter-covered surface

Number in the bracket represents the number of measurements. Fluxes are given in mmol m<sup>-2</sup> hr<sup>-1</sup>.

2). Total soil CO<sub>2</sub> flux varied from ~1 mmol m<sup>-2</sup> hr<sup>-1</sup> (or 12 mg C m<sup>-2</sup> hr<sup>-1</sup>) on snow-covered surfaces at the Musick and Chiquito sites to ~ 30 mmol m<sup>-2</sup> hr<sup>-1</sup> (or 360 mg C m<sup>-2</sup> hr<sup>-1</sup>) in the spring at the Fallbrook site. The simple correlation between soil CO2 flux and average soil temperature was significant but explains only ~22% of the variance (Table 3). The simple correlation between soil CO2 flux and average soil moisture was also significant. Soil moisture alone explains ~55% of the variance in soil CO2 flux. However, multiple regression models including site effects (owing to differences in clay content, litter quality, etc.), soil moisture, and soil temperature have significant improvement (R<sup>2</sup> =0.723) over the simple regression models as shown in Table 3. Because it is known from incubation studies [e.g, O'Connell, 1990] that CO<sub>2</sub> production is exponentially related to temperature, we also applied exponential regression models to our field-based data to establish the relationship between soil CO<sub>2</sub> flux and soil environmental parameters. As shown in Table 4, the simple exponential correlation between soil CO2 flux and average soil temperature for all soils was significant; but temperature alone explained only 19% of the variance in soil CO2 flux. However, inclusion of site effects in the simple exponential model significantly improved the correlation between CO2 flux and soil temperature and explained 52% of the variation in soil

CO<sub>2</sub> flux. The simple exponential correlation between CO<sub>2</sub> flux and soil moisture for all soils was also significant with moisture alone explaining about 40% of the variance.

Our statistical analyses (whether polynomial or exponential regressions) suggest that total soil CO2 flux was significantly related to not only soil temperature but also soil moisture and the study site. By applying the stepwise regression procedure to our data, we selected a final model, which includes only significant terms, for describing the relationship between soil CO2 flux and soil environmental conditions. In our final polynomial regression model (Table 3), the three terms- temperature squares  $(T^2)$ , the interaction term between temperature and moisture (TM), and the site variable  $(\alpha_i)$ - together explain about 72% of the variation in soil CO2 flux along the transect. Similarly, in our final exponential model (Table 4), soil temperature (T) and the interaction term (TM) together explain 51% of the variance in CO<sub>2</sub> flux from Sierra Nevada soils examined in this study. Assuming that soil CO<sub>2</sub> fluxes during winter months were the same as those measured on the snow-covered surfaces in the late fall, we calculated the average soil CO2 flux at each site. The calculated average soil CO2 flux for the project period (from August 1994 to August 1995) decreased with increasing elevation (Figure 2).

a In the sun.

b On frozen ground.

<sup>&</sup>lt;sup>c</sup> In the shade.

Table 3. E	Estimated (	Coefficients ir	ı the	Multivariable	Pol	lvnomial 1	Regression	Model
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Coefficients In	Soil CO <sub>2</sub> Flux			
Regression Model	Simple Model 1	Simple Model 2	Full Model	Chosen Model
	( <i>T</i> only)	(M Only)		
Intercept $\mu$	4.09	4.619	12.7008	10.0474
(p value)			(0.5607)	(0.0044)*
$lpha_{\scriptscriptstyle 1}$			6.7978	6.5287
(p value)			(0.0243)*	(0.0023)*
$lpha_2$			-2.7812	-2.1788
(p value)			(0.4117)	(0.3528)
$lpha_3$			2.0989	1.5305
(p value)			(0.4972)	(0.4278)
$b_1$	-0.781		-0.2864	
(p value)	(0.0148)*		(0.9003)	
$b_2$			-0.0282	-0.0313
(p value)			(0.5808)	(0.0000)*
$b_3$		0.7662	-0.1780	
(p value)		(0.0003)*	(0.8748)	
$b_4$			-10.0022	
(p value)			(0.9148)	
$b_5$			0.0749	0.0550
(p value)			(0.2188)	(0.0029)*
$R^2$	0.223	0.545	0.723	0.719
Sample size	26	26	26	26

Regression model has a form of  $y = \mu + \alpha_1 + b_1T + b_2T^2 + b_3M + b_4M^2 + b_5(TM) + e$ .

Here T, average soil temperature (in the upper 50 cm of a soil profile); M, average soil moisture (in the upper 50 cm of a soil profile); e, the random error term in the model.

### 3.2. Carbon Isotopic Variations in Soil-Respired CO2

Radiocarbon isotopic composition of soil-respired CO2 varies significantly along the Sierra Nevada Transect (Figure 3). The  $\delta^{13}$ C values of the air samples collected close to the ground along the transect range from -8% to -11%, and the  $\Delta^{14}$ C values range from 57% to 114%. The low-C isotopic values are primarily due to the addition of CO2 from burning of fossil fuels (which are free of <sup>14</sup>C) in the nearby Fresno metropolitan area, which is directly upwind from the Fallbrook site. Soil-respired CO<sub>2</sub> at our study sites were all significantly enriched in <sup>14</sup>C relative to atmospheric CO<sub>2</sub> (Figure 3). Prior to the early 1950s, the  $\Delta^{14}$ C values of the atmosphere were relatively constant and were around 0%. In the 1950s and the early 1960s, the <sup>14</sup>C content of the atmosphere increased by several orders of magnitude by atmospheric testing of thermonuclear weapons [Dorr and Munnich, 1986]. This pulse of <sup>14</sup>C or "bomb" <sup>14</sup>C has been steadily declining toward prebomb levels since the test-ban agreement in 1963 [O'Brien and Stout, 1978; Trumbore et al., 1989, 1990; Trumbore, 1993; Harrison and Broecker, 1993; Harrison et al., 1993; Wang et al., 1997]. Therefore positive  $\Delta^{14}$ C values indicate significant amounts of "bomb"  $^{14}$ C, whereas negative  $\Delta^{14}$ C values would indicate that the CO<sub>2</sub> is derived from a C pool that has a mean turnover time long enough to reflect radioactive decay of cosmogenic  $^{14}$ C. The very positive  $\Delta^{14}$ C values of soil-respired CO2 in the Sierra Nevada soils indicate that decomposition of organic matter that was photosynthesized over the past 30 - 40 years contributed significantly to soil CO2 production. In other words, it appears that much of the soil C is turning over on a decadal timescale. The <sup>14</sup>C measurements of

SOM in these soils [Trumbore et al., 1996; Wang et al., 1999] show decreasing  $\Delta^{14}$ C values of SOM with depth. Comparison of the  $\Delta^{14}$ C values of soil-respired CO<sub>2</sub> with the <sup>14</sup>C content of SOM suggests that SOM-derived CO<sub>2</sub> was primarily from the upper 10 or 15 cm of the soil, below which SOM has negative  $\Delta^{14}$ C values.

Our data (Figure 3) also show that  $\Delta^{14}$ C of soil-respired CO<sub>2</sub> varies throughout the year in response to changes in soil environmental conditions (e.g., soil temperature and soil moisture). At the low-elevation sites (Fallbrook and Fallbrook-OCD) where we have an almost complete 1-year cycle of measurements, Δ14C values were lower during the growing season when soil CO2 fluxes were high and were higher when soil CO2 fluxes were low. This enrichment in <sup>14</sup>C content of soil-respired CO<sub>2</sub> in nongrowing season is due to a decreasing influence of root respiration and a relatively increased contribution of microbial decomposition of organic matter to total soil CO2 production. We were unable to make monthly measurements throughout a year at the high-elevation sites because these sites were covered with deep snow during the winter and spring. The first measurements soon after snow melted at both the Musick and the Chiquito sites show high- CO<sub>2</sub> fluxes with Δ<sup>14</sup>C values significantly higher than that of the atmospheric CO2. This is probably because that high soil moisture content after snow melted accelerated decomposition of SOM. In the summer when plants were active at these sites, the  $\Delta^{14}$ C values of soil-respired CO2 became closer to the atmospheric values due to an increased relative contribution of root respiration.

To determine the apparent decay rate of organic matter using the model described in section 2.4, we need to know the <sup>14</sup>C

<sup>\*</sup> Statistically significant (p < 0.05) based on the t test.

Table 4. Estimated Coefficient	s in the Ex	ponential l	Regression Mo	odel of Soil CO <sub>2</sub>	Flux

Coefficients	Soil CO <sub>2</sub> Flux					
In Regression	Simple Model 1	Simple Model 2	Simple Model 3	Simple Model 4	Full Model	Chosen Model
Model	(T only)	(T + site)	(M only)	(M + site)		
Intercept $\mu$	3.1260	3.7481	1.2196	1.2908	4.0077	2.465
(p value)	(0.0000)*	(0.0000)*	(0.0002)*	(0.0005)*	(0.0000)*	(0.0000)*
$\alpha_1$		0.4753		-0.0157	0.5906	
(p value)		(0.0809)		(0.9478)	(0.0198)*	
$\alpha_2$		0.5686		-0.0277	-0.0753	
(p value)		(0.0398)*		(0.9166)	(0.7991)	
$\alpha_3$		0.3817		0.2769	0.4256	
(p value)		(0.1392)		(0.3480)	(0.0720)*	
$b_1$	-0.0587	-0.1117			-0.1954	-0.0882
(p value)	(0.0250)*	(0.0006)*			(0.0005)*	(0.0003)*
b <sub>2</sub>			0.0775	0.0696	-0.1049	
(p value)			(0.0008)*	(0.0067)*	(0.0608)	
$b_3$					0.0134	0.0063
(p value)					(0.0097)*	(0.0007)*
$R^2$	0.1923	0.5217	0.3826	0.4094	0.6966	0.5131
Sample size	26	26	26	26	26	26

Regression model has a form of Ln  $(y) = \mu + \alpha_i + b_1T + b_2M + b_3(TM) + e$ .

Here, y, soil  $CO_2$  flux; T, average soil temperature (in the upper 50 cm of a soil profile); M, average soil moisture (in the upper 50 cm of a soil profile); e, the random error term in the model.

content of CO<sub>2</sub> derived from SOM decomposition. We estimated the  $\Delta^{14}C$  values of SOM-derived CO<sub>2</sub> based on measurements of the  $^{14}C$  content of soil-respired CO<sub>2</sub> during the nongrowing season when plant activity is at minimum. These values are 199.6% for Fallbrook soil, 172.4% for Musick soil, and 168.0% for Chiquito soil. Using these  $\Delta^{14}C$  values and the measured  $\Delta^{14}C$  values of atmospheric CO<sub>2</sub> and total soil C content at each site, we estimated the relative contribution of SOM decomposition to total soil CO<sub>2</sub> production (Figure 3) and the apparent decay rate of SOM (Figure 4) in each soil using (7) and (8). We are

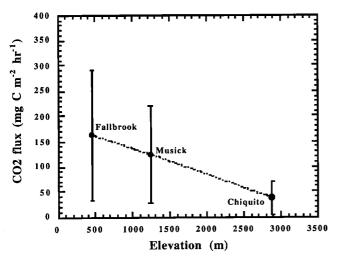
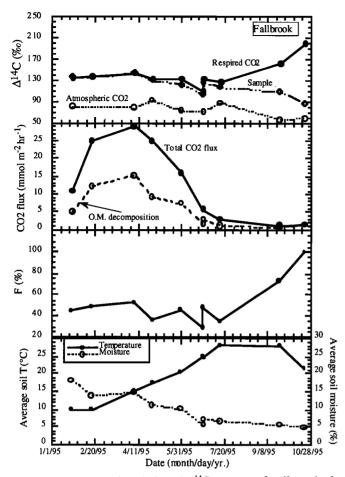


Figure 2. Average soil CO<sub>2</sub> flux for the period of August 1994 to August 1995 along the Sierra Nevada transect, assuming that the fluxes in the winter months were the same as measured on snow-covered surfaces in the late fall (Table 2). Vertical bars indicate the standard deviation based on all measurements at each site.

confident in our estimate of SOM-derived 14 CO2 at the Fallbrook site because grasses had dried out completely and there were few trees around which were dropping leaves. However, it is likely that we did not catch the pure SOM-derived CO2 at the Musick and Chiquito sites because of an incomplete sampling cycle and also the presence of perennial trees and shrubs. Therefore our calculated F and k values may overestimate the amount of CO<sub>2</sub> produced by organic matter decomposition as well as the rate of decomposition at both sites. At the disturbed site (Fallbrook-OCD), adequate moisture and warm temperatures kept the lemon trees active throughout the project period and prevented us from catching the pure SOM-derived CO<sub>2</sub>. We estimated the F and kin this soil by assuming that SOM-derived CO2 in this soil had the same <sup>14</sup>C content as that in its natural counterpart (i.e., the Fallbrook soil). However, this assumption may not be valid because years of agricultural activity could have changed the <sup>14</sup>C value of SOM being decomposed. Therefore the F and k values calculated for this soil very likely underestimate the rate of SOM decomposition at this site, but the seasonal trend in decomposition should still be valid. Another confounding factor is that the <sup>14</sup>C content of SOM-derived CO<sub>2</sub> may change with changes in soil temperature and moisture regimes and should be evaluated in future studies.

Trumbore et al. [1996] determined the steady state turnover times of carbon in these same soils from measurements of  $^{14}$ C in SOM, and their predicted  $\Delta^{14}$ C value of SOM-derived CO<sub>2</sub> based on steady state turnover time is similar to our estimated value for the Fallbrook soil but differs significantly for other soils. Their model-predicted  $\Delta^{14}$ C value of SOM-derived CO<sub>2</sub> is 46% higher at the Musick site and 22% lower at the Chiquito site than the highest  $\Delta^{14}$ C value of respired CO<sub>2</sub> measured at these two sites, respectively. Using their predicted  $\Delta^{14}$ C values for SOM-derived CO<sub>2</sub> and (7) and (8), the relative contribution of SOM-derived CO<sub>2</sub> would range from 21 to 66% in the Musick soil, lower than

<sup>\*</sup> Statistically significant (p < 0.05) based on the t test.



**Figure 3a.** Seasonal variations in  $^{14}$ C content of soil-respired CO<sub>2</sub>, soil CO<sub>2</sub> flux (both total soil CO<sub>2</sub> flux and flux from decomposition of organic matter), the values of F (i.e., the relative contribution of CO<sub>2</sub> from organic matter decomposition to total soil CO<sub>2</sub> production), average soil temperature and average soil moisture (in the upper 50 cm of the soil) at the Fallbrook site (a natural grassland). Sample refers to gas sample collected from the flux chamber.

our estimates of 33 – 100%, and vary from 33 to 142% in the Chiquito soil, higher than our estimates of 20 – 100%. Our measurements of soil CO<sub>2</sub> fluxes are 1428±1130 g C m<sup>-2</sup> yr<sup>-1</sup> at the Fallbrook site, 1356±799 g C m<sup>-2</sup> yr<sup>-1</sup> at the Musick, and 573±60 g C m<sup>-2</sup> yr<sup>-1</sup> at the Chiquito (Table 2). The predicted maximum CO<sub>2</sub> fluxes from SOM decomposition based on their steady state turnover times are 460 g C m<sup>-2</sup> yr<sup>-1</sup> for the Fallbrook soil, 600 g C m<sup>-2</sup> yr<sup>-1</sup> for the Musick soil and 260 g C m<sup>-2</sup> yr<sup>-1</sup> for the Chiquito soil, which would suggest that SOM-derived CO<sub>2</sub> was on average less than 33, 43 and 46% of the total soil CO<sub>2</sub> flux at the Fallbrook, Musick and Chiquito sites, respectively.

Along the Sierra Nevada transect, the climate changes progressively from warm/hot and dry to cold and moist with increasing elevation. The apparent decay rates determined from <sup>14</sup>C measurements of soil-respired CO<sub>2</sub> in the Sierra Nevada soils displayed a strong seasonal cycle at each site (Figure 4) and are clearly related to soil environmental conditions but not in a simple linear fashion (Figure 5). It seems from our limited data that the apparent turnover time (which is equal to 1/k) decreases

with increasing soil temperature until an optimal temperature (for decomposition) is reached and then increases with increasing soil temperature. This decomposition pattern may suggest that soil moisture becomes a limiting factor for decomposition under the hot and dry conditions in the summer and hence reflects a confounding of temperature and moisture effects, rather than an effect of temperature alone. Although soil temperature alone explains ~ 70% of the variation in organic matter decomposition in the Fallbrook soil, it explains only 22% of the variance in apparent turnover time in all soils (Figure 5a, c). This is probably because different soils have different optimal temperatures for microbial decomposition of organic matter due to variations in the composition of organic substrates, clay content, and soil texture, etc. Soil moisture alone can explain ~55% of the variance in organic matter decomposition in all soils examined in this study (Figure 5b, d). Our data also show that apparent turnover time decreases with increasing soil moisture content until an optimal soil moisture (for decomposition) is reached and then increases (or decay rate decreases) with increasing soil moisture content. This is likely because that oxygen becomes less available for microbes when more and more pores are becoming saturated with water. In other words, above certain optimal soil moisture level, oxygen availability becomes a limiting factor for microbial decomposition.

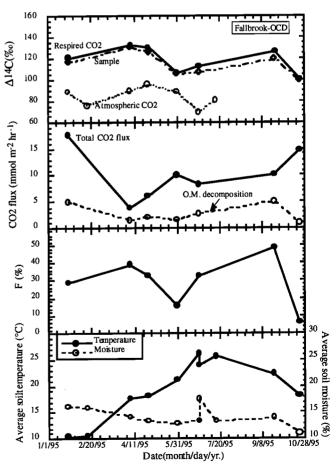


Figure 3b. Same as Figure 3a, except for Fallbrook-OCD site (a lemon grove).

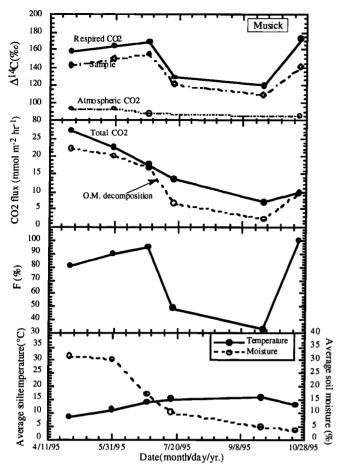


Figure 3c. Same as Figure 3a, except for Musick site (a temperate forest).

Laboratory incubation studies [Alexander, 1977; Orchard and Cook, 1983; Kucera and Kirkham, 1971; O'Connell, 1990; Howard and Howard, 1993] suggest that the maximum decomposition of organic matter seems to take place at 30°-40°C and that the rate of organic matter decomposition appears to increase as soil water contents increase from the permanent wilting point to ~ 60-80% saturation and decrease at higher or lower water contents. Some field studies also show that moisture levels have an effect on soil CO2 production [e.g., Wildung et al., 1975; Schlentner and Van Cleve, 1985; Amundson and Smith, 1988; Oberbauer et al., 1992; Hanson et al., 1993; Davidson et al., 1998, 1999; Saleska et al., 1999; Wang et al., 1999]. Our observations are in general agreement with the previous results except that the optimal temperatures for decomposition in the soils examined here seem to be in the range of 15°-22°C, which is lower than the accepted range of 30°-40°C [Alexander, 1977; O'Connell, 1990]. One possible explanation for this discrepancy is that we did not have enough measurements from the higherelevation soils. Another possibility is that the soil moisture levels were extremely low at the low-elevation site (where most of the measurements were made) and became a limiting factor for decomposition in the summer when soil temperatures were higher than 22°C.

We have also applied exponential regression to our data and the results are shown in Table 5. The simple exponential correlation between the apparent turnover time and soil temperature was not significant ( $R^2 = 0.1098$ ), but adding the site variable in the model significantly improved the model ( $R^2 = 0.4315$ ). The correlation between turnover time and soil moisture content was significant and did not appear to be influenced by the site variable (Table 5). Our final exponential model that includes soil temperature, moisture, and site variable explains ~ 65% of the variation in turnover time.

In our calculations, we used the measured atmospheric  $\Delta^{14}$ C value on a particular sampling date to derive the F, k, and  $\tau$  for that date. Because root respiration is likely from C fixed at different times, an integrated  $\Delta^{14}$ C value for atmospheric CO<sub>2</sub> during the growing season or the year, which can be determined by analyzing the <sup>14</sup>C content of annual grass or deciduous leaves, may improve the correlation between C turnover time and soil environmental conditions. Unfortunately, we did not analyze any leaves or grasses for <sup>14</sup>C content in this project.

It is widely accepted that CO<sub>2</sub> production from microbial decomposition of organic matter in soils is mostly dependent on soil temperature and increases with increasing temperature [e.g., Wiant, 1967a,b; Witkamp, 1969; Parada et al., 1983; Amundson and Smith, 1988; Raich and Potter, 1995]. However, soil moisture has received little attention in soil C cycle studies. Although our regression analyses do not reveal the underlying mechanisms controlling organic matter decomposition and soil

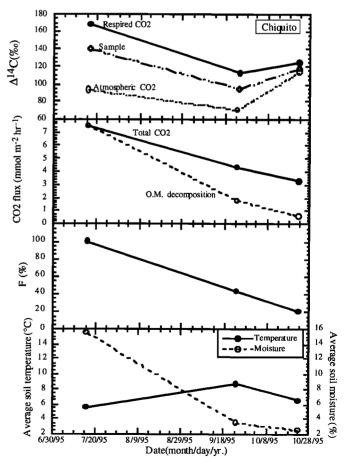


Figure 3d. Same as Figure 3a, except for Chiquito site (a temperate forest).

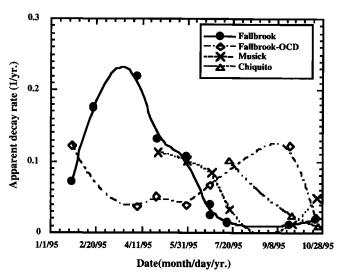
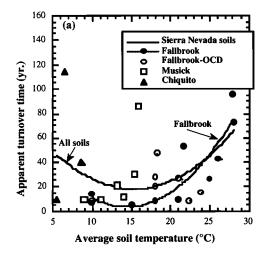
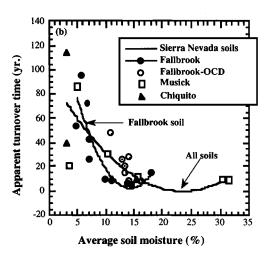


Figure 4. Seasonal variations of the apparent decay rate of SOM along the Sierra Nevada transect.

CO<sub>2</sub> flux, these analyses demonstrate significant correlations of apparent turnover time or decay rate of soil C and soil CO<sub>2</sub> flux with soil moisture and site variable, in addition to soil temperature. This suggests the need for further study of the response of soil C cycle to changes in soil environmental conditions.

Along the Sierra Nevada transect, the apparent decay rate of SOM changed from ~0.2 yr¹ (i.e., apparent turnover time  $\tau=5$  years) in the spring to ~0.0105 yr¹ (i.e.,  $\tau=95$  years) in the fall at the Fallbrook site, from 0.111 yr¹ (i.e.,  $\tau=95$  years) in the spring to 0.0116 yr¹ (i.e.,  $\tau=86$  year) in the fall at the Musick site, and from 0.1 yr¹ (i.e.,  $\tau=10$  years) in the summer to ~0.01 yr¹ (i.e.,  $\tau=100$  years) in the late fall at the Chiquito site. Our data demonstrate that (1) decomposition of SOM varies seasonally in response to changes in soil temperature and moisture conditions (Figures 4 and 5) and (2) higher temperatures accelerate decomposition when adequate soil moisture is available but inhibit decomposition when soil moisture is limited (such as in hot and dry summer). For natural soils (i.e., Fallbrook, Musick, and Chiquito soils), the peak decay rate of





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(C)	Apparent turnover time $(\tau) = \mu + b_1 * [Temperaturn Temperaturn $	aturei + Dami i emperaturei

	Fallbrook	Fallbrook-OCD	Musick	Chiquito	All soils
μ	87.55				85.68
b <sub>1</sub>	-11.691 (n.s.)	Too few	Too few	Too few	-8.841 (n.s.)
$b_2$	0.402	data points	data points	data points	0.290
$R^2$	0.787				0.217
Sample size	10	7	6	3	26

(d) Apparent turnover time  $(\tau) = \mu + b_1 * [Moisture] + b_2 * [Moisture]^2$ 

(-) -		1 2 2			
	Fallbrook	Fallbrook-OCD	Musick	Chiquito	All soils
μ	175.34				95.411
b <sub>i</sub>	-24.266	Too few	Too few	Too few	-8.130
$b_2$	0.849 (n.s.)	data points	data points	data points	0.173
$R^2$	0.724				0.548
Sample size	10	7	6	3	26

n.s. = not significant at p < 0.05.

Figure 5. Variations of apparent turnover time (=1/k) with (a) average soil temperature and (b) average soil moisture along the Sierra Nevada transect. The data are fitted with 2nd-order polynomial models for (c) average soil temperature and (d) average soil moisture.

Table 5 Estimated	Coafficients in	the Exponential	Pegression !	Model of Car	hon Turnover Time

Coefficients In Regression Model	Turnover time Simple Model 1	Turnover Time Simple Model 2	Turnover Time Simple Model 3	Turnover Time Simple Model 4	Turnover Time Full Model	Turnover Time Chosen Model
Intercept $\mu$	2.2744	1.3819	4.0329	4.1855	1.8567	2.4683
(p value)	(0.0001)*	(0.0101)*	(0.0000)*	(0.0000)*	(0.0222)*	(0.0001)*
$\alpha_1$	(511111)	-0.7628	, ,	-0.2774	-0.7946	-0.6986
(p value)		(0.0160)*		(0.2446)	(0.0050)*	(0.0078)
$\alpha_2$		-0.6982		-0.0355	0.0369	-0.0962
(p value)		(0.0259)*		(0.8910)	(0.9079)	(0.7456)
$\alpha_3$		0.0743		0.2649	0.1311	0.2176
(p value)		(0.7923)		(0.3594)	(0.5926)	(0.3539)
b <sub>1</sub>	0.0457	0.1176			0.1699	0.1213
(p value)	(0.0982)	(0.0011)*			(0.0033)*	(0.0001)*
b <sub>2</sub>	, ,	,	-0.0832	-0.0918	0.0629	
(p value)			(0.0004)*	(0.0006)*	(0.2820)	
$b_3$					-0.0121	-0.0069
(p value)					(0.0268)*	(0.0024)*
$R^2$	0.1098	0.4315	0.416	0.4653	0.6672	0.6457
Sample size	26	26	26	26	26	26

Regression model has a form of Ln  $(y) = \mu + \alpha_i + b_1T + b_2M + b_3(TM) + e$ .

Here, y, turnover time; T, average soil temperature; M, average soil moisture; e, the random error term in the model.

SOM (Figure 4) is much higher at the low-elevation site (i.e., Fallbrook, warm/hot climate) than at the high-elevation sites (cooler climate). Our litter bag study also shows that litter decomposition was much faster at the low-elevation site than at the high-elevation sites (Figure 6a). At the Fallbrook site, over 50 wt % (weight percentage) of the litter in litter bags was lost in 8 months, and then the loss due to decomposition seemed to have reached a plateau during the dry season. Litter decomposition at the Musick site was slightly faster than at the Chiquito site. After 11 months, the litter loss due to decomposition was ~16 wt % at the Musick site and ~8 wt % at the Chiquito site. Aboveground organic-matter input also changes with elevation. Our measurements for the period from July 1994 to September 1995 show that the aboveground input was highest at the Fallbrook site, decreased slightly at the Musick, and was lowest at the Chiquito (Figure 6b). The balance between C input and decomposition determines the amount of C stored in soils. Because of the relatively high input and slow decomposition rates at the Musick site, Musick soil has higher C content than either Fallbrook or Chiquito soils (Figure 6c).

It is also clear from our data that conversion of grassland to agricultural land affects the soil C cycling rates (Figure 3). Both soil CO<sub>2</sub> flux and <sup>14</sup>C content of soil respired CO<sub>2</sub> at the disturbed site (i.e., Fallbrook-OCD) differ significantly from those measured at the corresponding natural site (i.e., Fallbrook). The apparent decay rate of organic matter in the agricultural soil was higher in the summer but lower in the spring compared to its natural counterpart (Figure 4). This is because very low soil moisture content in the hot and dry summer limited decomposition at the natural site. However, adequate moisture was available year-round in the agricultural soil due to irrigation and therefore decomposition was accelerated by higher temperatures.

# 4. Conclusions

Although temperature has been recognized as the major control on C turnover in soils [e.g., Jenkinson, et al., 1991; Trumbore, et al., 1996; Houghton, et al., 1998], soil moisture has received less attention in soil C cycle studies. Our study of soils along an elevation transect in the Sierra Nevada shows that both soil CO2 flux and SOM decomposition vary significantly throughout the year in response to changes in soil environmental conditions (e.g., soil temperature and soil moisture, etc.). Despite the large seasonal variations in soil CO<sub>2</sub> flux (from ~ 1 mmol m<sup>-2</sup>  $hr^{-1}$  or 12 mg C  $m^{-2}$   $hr^{-1}$  to ~ 15 - 30 mmol  $m^{-2}$   $hr^{-1}$  or 180 - 360 mg C m<sup>-2</sup> hr<sup>-1</sup>) at each site, the average soil CO<sub>2</sub> flux decreased with increasing elevation along the Sierra Nevada transect. The relative contribution of SOM decomposition to total soil CO2 flux changed with season from as low as 20% to nearly 100% in these soils. The apparent turnover time of soil organic C determined from <sup>14</sup>C content of soil-respired CO<sub>2</sub> varied from ~ 5 years (i.e.,  $k = 0.2 \text{ yr}^{-1}$ ) in the spring to ~ 95 years (i.e., k = 0.011yr<sup>-1</sup>) in the fall at the lowest elevation site and from ~ 10 years (i.e.,  $k = 0.1 \text{ yr}^{-1}$ ) in the summer to little over 100 years (i.e., k =0.01 yr<sup>-1</sup>) in the late fall at the highest-elevation site. Although decomposition of organic matter varied throughout the year in each soil, the maximum apparent decay rate of SOM as well as the rate of litter decomposition decreased with increasing elevation. Our data show that higher temperatures enhance decomposition of SOM only when soil moisture is adequate and reduce decomposition under moisture-limited conditions. Similarly, higher soil moisture content enhances decomposition of SOM until an optimal soil moisture level (~ 14 - 26 wt % water content) is reached and then inhibits decomposition when more pores in soils become saturated with water and oxygen availability (for microbes) becomes limited. Our multivariable

<sup>\*</sup> Statistically significant (p < 0.05) based on the t test.

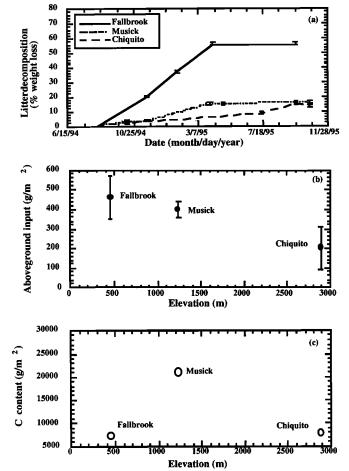


Figure 6. (a) Variations of litter decomposition, (b) aboveground organic-matter input and total soil C inventory to the bottom of the B horizon (i.e., to a depth of 75 cm for Fallbrook soil, 85 cm for Musick soil and 70 cm for Chiquito soil) along the Sierra Nevada transect. Vertical bars indicate the standard deviation based on replicate measurements. Because of the small number of litter bags and traps employed, the litter input and decomposition data may not be very accurate, but the general trends are valid.

regression analyses suggest that soil moisture is a major factor controlling the rate of organic matter decomposition in the soils along the Sierra Nevada transect. Both soil organic C turnover time and soil CO<sub>2</sub> flux seem to correlate significantly with soil moisture, soil temperature, and the study site. A multivariable polynomial regression model including the site variable, average soil temperature, and moisture can explain over 70% of the variation in soil CO<sub>2</sub> flux along the Sierra Nevada transect. An exponential model including the same variables explains about 65% of the variance in the apparent turnover time of soil organic C along this transect.

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## References

- Alexander, M., Introduction to Soil Microbiology, 2nd ed., 467pp. John Wiley, New York, 1977.
- Amundson, R. G., and V. S. Smith, Annual cycles of physical and biological properties in an uncultivated and irrigated soil in the San Joaquin Valley of California, Agric., Ecosyst., Environ., 20, 195-208, 1988.
- Ben-Asher, J., G. E. Cardon, D. Peters, D. E. Rolston, J. W. Biggar, C. J. Phene, and J. E. Ephrath, Determining root activity distribution by measuring surface carbon dioxide fluxes, Soil Sci. Soc. Am. J., 58, 926-930, 1994.
- Cerling, T. E., The stable isotopic composition of modern soil carbonate and its relationship to climate, Earth and Planetary Science Letters, 71, 229-240, 1984.
- Cerling, T. E., D. K. Solomon, J. Quade, and J. R. Bowman, On the isotopic composition of carbon in soil carbon dioxide, *Geochim. Cosmochim. Acta*, 55, 3403-3405, 1991.
- Davidson, E. A., E. Belk, and R. Boone, Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, Global Change Biol., 4, 217-227, 1998.
- Davidson, E. A., L. Verchot, J. H. Cattanio, I. L. Ackerman, and J. E. M. Carvalho, Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia, *Biogeochemistry* (in press), 1999.
- Denning, A. S., I. Y. Fung, and D. Randall, Latitudinal gradient of atmospheric CO<sub>2</sub> due to seasonal exchange with land biota, *Nature*, 376, 240-243, 1995.
- Dorr, H., and K. O. Munnich, Annual variations of the <sup>14</sup>C content of soil CO<sub>2</sub>, *Radiocarbon*, 28, 338-345, 1986.
- Eswaran, H., E. V. Berg, and P. Reich, Organic carbon in soils of the world, Soil Science Society of America Journal, 57, 192-194, 1993.
- Harrison, K., and W. S. Broecker, A strategy for estimating the impact of CO<sub>2</sub> fertilization on soil carbon storage, Global Biogeochem. Cycles, 7, 69-80, 1993.
- Harrison, K., W. S. Broecker, and G. Bonani, The effect of changing land use on soil radiocarbon, *Science*, 262, 725-726, 1993.
- Hanson, P. J., S. D. Wullschleger, S. A. Bohlman, and D. E. Todd, Seasonal and topographic patterns of forest floor CO2 efflux from an upland oak forest, *Tree Physiol.* 13, 1-15, 1993.
- Houghton, R. A., E. A. Davidson, and G. M. Woodwell, Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance, Global Biogeochem. Cycles, 12, 25-34, 1998.
- Howard, D. M., and P. J. A. Howard, Relationships between CO2 evolution, moisture content and temperature for a range of soil types, Soil Biol. and Biochem. 25, 1537-1546, 1993.
- Hsieh, Y. P., Dynamics of soil organic matter formation in croplands -Conceptual analysis, Sci. Total Environ., 81/82, 381-390, 1989.
- Hsieh, Y. P., Pool size and mean age of stable organic carbon in cropland, Soil Sci. Soc. Am. J., 56, 460-464, 1992.
- Jenny, H., S. P. Gessel, and F. T. Bingham, Comparative study of decomposition rates of organic matter in temperate and tropical regions, Soil Sci., 67, 419-432, 1949.
- Jenkinson, D. S., D. E. Adams, and A. Wild, Model estimates of CO<sub>2</sub> emissions from soil in response to global warming, *Nature*, 351, 304-306, 1991.
- Kucera, C. L., and D. L. Kirkham, Soil respiration studies in tallgrass prairie in Missouri, *Ecology*, 52, 912-915, 1971.
- Norman, J.M., R. Garcia, and S.B. Verma, Soil surface CO<sub>2</sub> fluxes and the carbon budget of a grassland, J. Geophys. Res., 97, 18845-18853, 1992.
- Oberbauer, S. F., C. T. Gillespie, W. Cheng, R. Gebauer, A. Sala Serra, and J. D. Tenhunen, Environmental effects on CO2 efflux from riparian tundra in the northern foothills of brooks Range, Alaska, USA, Oecologia, 92, 568-577, 1992.
- O'Brien, B. J., and J. D. Stout, Movement and turnover of soil organic matter as indicated by carbon isotope measurements, *Soil Biol. Biochem.*, 10, 309-317, 1978.
- O'Connell, A. M., Microbial decomposition (respiration) of litter in eucalypt forests of south-western Australia: An empirical model based on laboratory incubations, *Soil Biol. Biochem.*, 22, 153-160, 1990.
- Orchard, V. A., and F. Cook, Relationship between soil respiration and soil moisture, Soil Biol. Biochem., 15, 447-453, 1983.

- Parada, C. B., A. Long, and S. N. Davis, Stable-isotopic composition of soil carbon dioxide in the Tucson Basin, Arizona, U. S. A., Isot. Geosci., 1, 219-236, 1983.
- Paul, E., C. Campbell, D. Rennie, and K. McCallum, Investigations of the dynamics of soil humus utilizing carbon dating techniques, In: *Transactions 8th International Soil Science Society*, Buchaarest, Romania, pp. 201-208, 1964.
- Post, W., W. King, and S. Wullschleger, Historical variations in terrestrial biospheric carbon storage, Global Biogeochem. Cycles, 11, 99-109, 1997.
- Raich, J. W., and C. S. Potter, Global patterns of carbon dioxide emissions from soils, Global Biogeochem. Cycles, 9, 23-36, 1995.
- Saleska, S., J. Harte, and M. Thorn, The effect of experimental ecosystem warming on CO2 fluxes in a mountane meadow, Global Change Biol., 5: 125-141, 1999.
- Schlentner, R. E., and K. Van Cleve, Relationships between CO2 evolution from soils, substrate temperature, and substrate moisture in four mature forest types in interior Alsks, Can. J. For. Res., 15, 97-106, 1985.
- Schlesinger, W. H., Biogeochemistry: An Analysis of Global Change, 443 pp, Academic, San Diego, Calif., 1991.
- Steiberger, Y., and W. G. Whitford, Decomposition process in Vegev ecosystems. *Oecologia*, 75, 61-66, 1988.
- ecosystems, Oecologia, 75, 61-66, 1988. Stuiver, M. and H. Polach, Reporting of <sup>14</sup>C data. Radiocarbon, 19, 355-363, 1977.
- Trumbore, S. E., Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements, Global Biogeochem. Cycles, 7, 275-290, 1993.
- Trumbore, S. E., J. S. Vogel, and J. R. Southon, AMS 14C measurements of fractionated soil organic matter: an approach to deciphering the soil carbon cycle, *Radiocarbon*, 31, 644-654, 1989.
- Trumbore, S. E., G. Bonani, and W. Wolfli, The rates of carbon cycling in several soils from AMS <sup>14</sup>C measurements of fractionated soil organic matter, in *Soils and the Greenhouse Effect*, edited by A. F. Bouwman, pp. 405-414, John Wiley, New York, 1990.
- Trumbore, S. E., O. A. Chadwick, and R. Amundson, Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change, *Science*, 272, 393-396, 1996.

- Wang, Y., R. Amundson, and S. Trumbore, A model for soil <sup>14</sup>CO<sub>2</sub> and its implications for using <sup>14</sup>C to date pedogenic carbonate, *Geochim. Cosmochim. Acta*, 58, 393-399, 1994.
- Wang, Y., R. Amundson, and S. Trumbore, The impact of climate and land use change on C turnover in soils, Paper presented at the Fourth International Symposium on The Geochemistry of The Earth's Surface, Int. Assoc. of Geochem. and Cosmochemistry and Minerol. Soc., Ilkley, Yorkshire, England, 1996.
- Wang, Y., A. H. Jahren, and R. Amundson, Potential for <sup>14</sup>C dating of biogenic carbonate in hackberry (*Celtis*) endocarps, *Quat. Res.* 47, 337-343, 1997.
- Wang, Y., et al., Carbon cycling in the terrestrial environments, in *Isotope Tracers in Catchment Hydrology*, edited by C. Kendall and J. McDonnell, Elsevier Sci., New York, 1998.
- Wang, Y., R. Amundson, and S. Trumbore, The impact of land-use change on C turnover in soils, Global Biogeochem. Cycles, 13, 47-57, 1999
- Wiant, H. V., Influence of temperature on the rate of soil respiration, *J. For.*, 65, 489-490, 1967a.
- Wiant, H. V., Influence of moisture content on "soil respiration," J. For., 65, 902-903, 1967b.
- Wildung, R. E., T. R. Garland, and R. L. Buschbom, The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils, *Soil Biol. Biochem.*, 7, 373-378, 1975.
- Witkamp, M., Cycles of temperature and carbon dioxide evolution from litter and soil, *Ecology*, 50, 922-924, 1969.
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