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Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture

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Abstract

This experiment was designed to study three determinant factors in decomposition patterns of soil organic matter (SOM): temperature, water and carbon (C) inputs. The study combined field measurements with soil lab incubations and ends with a modelling framework based on the results obtained. Soil respiration was periodically measured at an oak savanna woodland and a ponderosa pine plantation. Intact soils cores were collected at both ecosystems, including soils with most labile C burnt off, soils with some labile C gone and soils with fresh inputs of labile C. Two treatments, dry-field condition and field capacity, were applied to an incubation that lasted 111 days. Short-term temperature changes were applied to the soils periodically to quantify temperature responses. This was done to prevent confounding results associated with different pools of C that would result by exposing treatments chronically to different temperature regimes. This paper discusses the role of the above-defined environmental factors on the variability of soil C dynamics. At the seasonal scale, temperature and water were, respectively, the main limiting factors controlling soil CO_2 efflux for the ponderosa pine and the oak savanna ecosystems. Spatial and seasonal variations in plant activity (root respiration and exudates production) exerted a strong influence over the seasonal and spatial variation of soil metabolic activity. Mean residence times of bulk SOM were significantly lower at the Nitrogen (N)-rich deciduous savanna than at the N-limited evergreen dominated pine ecosystem. At shorter time scales (daily), SOM decomposition was controlled primarily by temperature during wet periods and by the combined effect of water and temperature during dry periods. Secondary control was provided by the presence/absence of plant derived C inputs (exudation). Further analyses of SOM decomposition suggest that factors such as changes in the decomposer community, stress-induced changes in the metabolic activity of decomposers or SOM stabilization patterns remain unresolved, but should also be considered in future SOM decomposition studies. Observations and confounding factors associated with SOM decomposition patterns and its temperature sensitivity are summarized in the modeling framework.

Keywords: climate change, soil organic matter, decomposition, soil respiration

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Introduction

The soil is the largest terrestrial carbon (C) pool (Post *et al.*, 1982). Stored soil C results from an imbalance between organic matter produced by plants and its decomposition back into the atmosphere as CO_2. The large pool of C in the soil is vulnerable to climatic warming and its potential loss may amplify further

warming (Cox *et al.*, 2000). However, current predictions are based on empirical models because there is a general lack of knowledge about the mechanisms that influence decomposition of soil organic matter (SOM).

Among the factors affecting SOM decomposition, temperature, soil moisture and plant C inputs are perhaps the most relevant. Regarding the temperature sensitivity of decomposition, kinetic theory predicts that temperature sensitivity of SOM decomposition should increase as the degree of substrate complexity increases (Bosatta & Ågren, 1998). Because the bulk of SOM is formed of old, long-chained organic molecules, an increase of temperature will therefore affect the storage of these old organic fractions more. However, other studies have shown very contradictory results regarding temperature sensitivity of different organic matter fractions (Kirschbaum, 1995; Trumbore *et al.*, 1996; Katterer *et al.*, 1998; Liski *et al.*, 1999; Giardina & Ryan, 2000; Fierer *et al.*, 2003, 2005; Fang *et al.*, 2005).

Soil water content is another important variable for predicting organic matter decomposition and soil CO_2 efflux (Xu & Qi, 2001a; Reichstein *et al.*, 2002a, b; Xu *et al.*, 2004; Tang & Baldocchi, 2005). Drought limits the physiological performance of microbes and the diffusion of nutrients in the soil pore space (Harris, 1981; Papendick & Campbell, 1981; Robertson *et al.*, 1997). In general, soil metabolic activity decreases as soils dry out below a certain limit (Davidson *et al.*, 1998; Howard & Howard, 1999; Xu & Qi, 2001a, b; Reichstein *et al.*, 2002a, b; Curiel Yuste *et al.*, 2003). Most studies have focused on either temperature or water effects on SOM decomposition but only a few have explored the combined effect of both (Howard & Howard, 1999). Given the projected decreases in precipitation and increases in temperatures projected for Mediterranean systems (Gibelin & Deque, 2003; Kueppers *et al.*, 2005), it is particularly important to understand how the interaction of both factors may affect SOM decomposition.

At the scale of a plant canopy, soil respiration may become decoupled from temperature and, instead, be coupled to antecedent or current rates of photosynthesis. This is because photosynthate translocated to roots stimulates their autotrophic respiration and because root exudates feed microbes, which stimulates microbial respiration (Grayston *et al.*, 1997; Högberg *et al.*, 2001; Kuzyakov & Cheng, 2001, 2004; Bowling *et al.*, 2002; Gleixner *et al.*, 2005; Tang *et al.*, 2005a; Baldocchi *et al.*, 2006). The degree of coupling depends on the time scale at which soil respiration is correlated with photosynthesis. On seasonal/annual time scales, soil respiration correlates directly with gross primary productivity (*GPP*) (Raich & Tufekciogul, 2000; Janssens *et al.*, 2001). Conversely, soil respiration on hourly to weekly time scales is sensitive to antecedent rates of photosynthesis (Högberg *et al.*, 2001; Bowling *et al.*, 2002; McDowell *et al.*, 2004; Tang *et al.*, 2005a; Baldocchi *et al.*, 2006).

We designed an experiment to explore how these factors affect SOM decomposition at different time and spatial scales. The experimental design includes field respiration measurements and 'lab-based' studies of SOM. The ultimate aim of the manuscript is to create a conceptual framework to: (1) encourage new experimental directions in the quest for understanding the mechanisms involved in decomposition of SOM; and (2) inspire the development of new, mechanistic-based modeling exercises.

Materials and methods

Sites description

Field measurements and soil sampling occurred at two ecosystems in northern California, a ponderosa pine plantation and an oak savanna. The pine plantation is located adjacent to the University of California Blodgett Forest Research Station at 38°53′42.9″N, 120°37′57.9″W at an altitude of 1315 m. The vegetation is dominated by ponderosa pine (*Pinus ponderosa* L.) with occasional other tree species. The major understory shrubs are *Arctostaphylos manzanita* (Manzanita) and *Ceonothus cordulatus* (Ceanothus). In spring 2003 tree density was ~510 trees per hectare; total one-sided leaf area index (L_{AI}) was 2.49, mean tree diameter at breast height was 12.0 cm, mean tree height was 4.7 m (mean shrubs height ~1.0 m) and basal area was 9.6 $m^2\,ha^{-1}$. The site is characterized by a Mediterranean climate, with warm dry summers and cold wet winters. Annual precipitation averages 1290 mm, with the majority of precipitation falling between September and May. Daily temperature averages range from 14 to 27 °C during summer and from 0 to 9 °C during winter. The soil is relatively uniform and comprised of 60% sand and 29% loam. The site is managed for commercial purposes. More information about management practices can be found in Misson *et al.* (2005).

The oak savanna field site (Tonzi Ranch) is located at 38.4311°N, 120.966°W. The altitude of the site is 177 m and the terrain is relatively flat. The woodland overstory consists of scattered blue oak trees (*Quercus douglasii*) with occasional grey pine trees (*Pinus sabiniana*). The understorey consists of exotic annual grasses and herbs; the species include *Brachypodium distachyon*, *Hypochaeris glabra*, *Bromus madritensis* and *Cynosurus echinatus*. The trees covered 40% of the landscape, with a mean height of 10.1 ± 4.7 m, mean trunk height of

1.5 ± 1.6 m, mean crown radius of 2.8 ± 1.6 m and leaf area index equals 0.65 (Baldocchi *et al*., 2004). The overstorey and understorey vegetation operate in and out of phase with each other over the course of a year. Soil is classified as loamy, mixed, superactive, thermic Lithic Haploxerepts (USDA). Depth of bedrock ranges from 25 to 70 cm but hardly exceeds the 50 cm, which makes this soil relatively shallow. The climate of the region is Mediterranean. The mean annual temperature is 16.3 °C, and 559 mm of precipitation fall per year, as determined from over 30 years of data from a nearby weather station at Ione, California.

The ecological and meteorological features of the two ecosystems under study have been characterized in other papers (Baldocchi *et al*., 2004; Misson *et al*., 2005).

Field measurements

During spring and summer 2005 soil respiration was measured twice a month at both ecosystems. We used a LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA). We used collars with a height of 4.4 cm and a diameter of 11 cm that were inserted into the soil for measuring soil respiration.

In the oak savanna site, 30 collars were used to cover the spatial variability of soil respiration in this ecosystem (Tang & Baldocchi, 2005). We defined understorey soil respiration as that recorded in the vicinity of the trees, ≤ 3 m away from the trunk while open soil respiration as that recorded far from the tree influence (Tang & Baldocchi, 2005) that we defined as at least 20 m away from trees. In the ponderosa pine ecosystems, two $20 \times 20\,m^2$ sampling plots were established, 40 m apart within the footprint area of the meteorological tower and a $3 \times 3\,m^2$ trenched plot. Typically, soil respiration was measured about three to four rounds in a day. Soil temperature at 5 cm in soil profile was collected with a soil thermistor next to each collar. Volumetric soil moisture content was measured continuously in the field at several depths in the soil with frequency domain reflectometry sensors (Theta Probe model ML2-X; Delta-T Devices, Cambridge, UK). Sensors were placed at various depths in the soil (5, 10, 20 and 50 cm) and were calibrated using the gravimetric method. In the oak savannah, profiles of soil moisture (0–15, 15–30, 30–45 and 45–60 cm) were made periodically and manually using an enhanced time domain reflectometer (Moisture Point, model 917; E.S.I. Environmental Sensors Inc., Victoria, Canada). In Blodgett, we also installed two moisture sensors at 10 cm, one in the control plot and one in the trenched plot (TDR, CS615 Campbell Scientific Inc., Logan, UT, USA) for continuously measuring soil moisture at 5 min intervals. Dataloggers (CR10X and 23X, Campbell Scientific Inc.) were programmed to store temperature and moisture data every 5 min. Owing to technical problems, only scarce data were available from this TDR during 2005.

For more methodological information about soil respiration measurements, see Tang & Baldocchi (2005) and Tang *et al*. (2005b). Soil water content was recorded continuously in the vicinity of the meteorological tower at each site.

Laboratory incubations design

Intact soil cores were collected during 29 and 30 July 2005. By this date rains at the site had stopped by 42 days, the grass was dead and the trees were still photosynthesizing. In the ponderosa pine site photosynthetic activity of vegetation was at its peak (personal communication). Undisturbed soil cores of $80\,cm^3$ ($4.4 \times 4.4 \times 5\,cm^3$) were collected using a stainless steel core soil sampler from the upper part of the soil profile (0–5 cm). Before core collection, the uppermost layer of litter (O_L) with visible undecomposed material (leaves, needles, etc.) was excluded. Soil cores were kept in their stainless steel container. By keeping intact cores with their original bulk density, we were able to assess changes in volumetric water content via gravimetric methods and apply water retention curves to assess changes in soil water potential. For this study, four different soils were chosen: in the oak savanna site soils were taken from open areas (oak savanna open) where only grass grows and contribution of trees is minimal (Baldocchi *et al*., 2004) and under the tree canopy (oak savanna understorey) where there is significant contribution from trees and grasses. In the ponderosa pine plantation, samples were taken from the two adjacent control plots (Misson *et al*., 2006), which we refer to as 'ponderosa pine control' and from the trenched plot ($3 \times 3\,m^2$) established in 2000, which we refer to as 'ponderosa pine trenched'. Because the trenched plot was established 5 years before the samples were taken for this study, we assume the mean age of the organic matter in the trenched plot to be older than in the control plot. The experimental design, therefore, includes treatments with most labile C burnt off (trenched plot), treatments with some labile C gone (dead grass of open areas in oak savanna) and treatments with fresh inputs of labile C (oak and pine understories areas).

To infer the minimum number of samples required, we used the standard deviation obtained from soil respiration measurements made during period of

maximal spatial variability and the equation:

$$n = \left[z_{\alpha/2} \times \alpha/E\right], \quad (1)$$

where n is the sample size, $z_{\alpha/2}$ is known as the critical value and α is the population standard deviation. To cover the spatial variability of soil respiration with a confidence interval of 95% and an error of not more than 25%, three collars were needed for the trenched plot and six for the other three soils. Three (trenched plot) and six (three other soils) soil samples per soil ($\times 4$) and per treatment ($\times 2$) were, therefore, collected.

Soils were sampled in a treatment from plots with a radius of 1 m separated by at least 30 m from each other. Sampling circles were defined randomly within the footprint of the micrometeorological tower. Within each of these locations, two sublocations were randomly defined and three samples were collected close to each other. From the three samples collected at each sublocation, one was used for analyses [soil water content, soil water potential, total C (TC) and nitrogen (N)], one was kept at field soil moisture (called dry) and the last one was placed over water-saturated sponges during 24 h, moistening the soil by capillarity until the soil matrix reached maximum water-holding capacity values (called wet). After 24 h, dry and wet samples were placed in the incubator at 20 °C. Soil water content at the samples was maintained by adding water periodically (approximately once a week) based on weight loss. In the trenched plot, the sampling strategy consisted of choosing randomly three sublocations within the 3×3 plot. As in the other three soil types, three samples were collected at each sublocation (one for analyses, one incubated dry and one incubated wet). Therefore, three samples were incubated for each treatment (dry and wet) and three samples were used for laboratory analyses (Table 1).

To assess the temperature sensitivity of soil decomposition at different stages of the incubation, seven temperature cycles were performed. These occurred at days 2, 7, 16, 24, 51, 81 and 111 after incubation started. During a cycle, temperatures were increased from 20 to 35 °C and then decreased again to the basal temperature (20 °C) with 5 °C steps every 4 h. In total, each temperature cycle took 32 h. Samples were maintained at 20 °C between temperature cycles. Three thermocouples were inserted at three different depths within the soil cores (0.5 cm from surface, 2.5 cm depth and 4.5 cm depth) to study possible gradients in temperature within the collars during these temperature cycles. Temperatures in the upper part of the sample equilibrated faster with the incubator temperature (data not shown), but the inner part of the sample needed at least 3 h to equilibrate with the incubator temperature. To avoid these temperature gradients, soil CO_2 evolution was measured 1 h after soil temperature was equilibrated within the sample.

Table 1 Biochemical and physical properties to 0–5 cm depth of the four soils, ponderosa pine trenched (bt), ponderosa pine control (bc), oak savanna open area (to) and oak savanna understorey (tu)

	bt	bc	to	tu
Roots ($kg\,m^{-2}$)	0	1.3(1.5)	1.5(1.0)	1.4(2.4)
Litter ($kg\,m^{-2}$)	3.0(29)	2.8(24)	0.6(3)	1.4(23)
% N	0.2	0.5	0.2	0.3
% C	6.4	13.9	1.7	3.9
Soil N_{total} ($kg\,m^{-2}$)	0.1	0.2	0.1	0.2
Soil C_{total} ($kg\,m^{-2}$)	2.9	5.1	1.4	2.6
C/N ratio	28.5	29.6	10.7	12.5
Moisture dry ($g\,g^{-1}$)	10	14.5	2.4	4.2
ψ dry (MPa)	−1.5	−0.25	−15	−10
Moisture wet ($g\,g^{-1}$)	24.3	28.9	18.9	22.1
Total C respired ($Kg\,C\,m^{-2}$)	0.2	0.2	0.22	0.43
% of C respired	7	4	16	16

Percentage of N and C represents the percentage of nitrogen and carbon, respectively. C and N represent the quantities of the same elements. 'Moisture dry' and 'ψ dry' represents, respectively, the soil water content and soil water potential of soil under field conditions. 'Moisture wet' was the soil water content after soils were rewetted (wet treatment).

Soil analyses

Several soil characteristics were measured using the soil samples spared from analyses, including bulk density, soil moisture, soil C and N concentrations. Analyses for N and C were carried out with a Europa scientific 2020 mass spectrometer interfaced to a Europa scientific SL elemental analyzer (PDZ Europa Scientific Instruments, Crewe, UK). The analysis was calibrated and adjusted for linearity with NIST standards calibrated against IAEA standards. The pH of both soils were acid (6.4 and 5.5 for oak savanna and pine stands, respectively) and, therefore, is unlikely that carbonates concentration were interfering with the analyses. Biomass of litter and fine roots present into the soil cores was estimated in the set of samples collected for analyses. Litter and fine roots were collected from the cores using tweezers. We defined litter as organic matter present in the soil samples still not completely degraded and that could be visually distinguished from the bulk of the organic matter and the soil (e.g. needles, burk, etc.). Fine roots were neither separated into live and dead nor were they divided into diameter classes. In the oak savanna open, all fine roots were from grasses and were dead at the time of sampling.

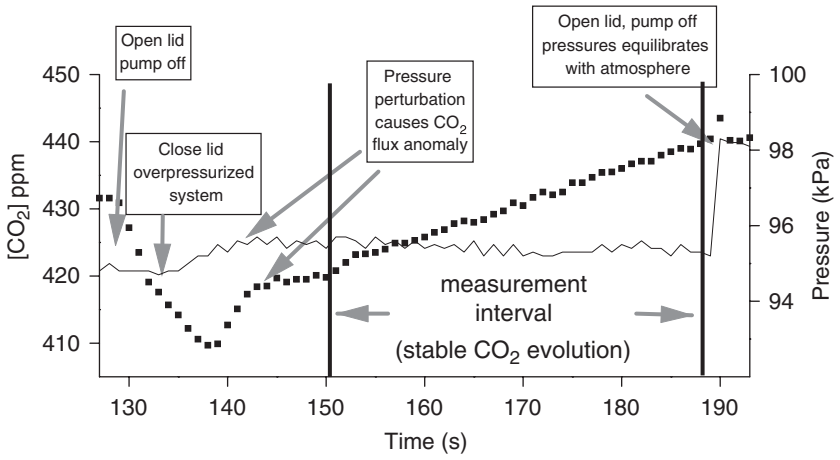

Fig. 1 Increase in CO_2 concentrations within the analysis chamber of the IRGA during a measurement period (around 40 s). Interval within the two vertical bars represents the measurement interval used to calculate the flux.

Soil moisture was estimated gravimetrically, by drying the samples during 48 h at 75 °C. By estimating the dry weight of the samples contained within the known volume of the collar (80 cm^3), we estimated the bulk density of the sample. Results are presented in Table 1.

Soil respiration system

To measure soil CO_2 efflux, we built a dynamic flow-through system that was operated under closed and nonsteady state conditions. Concentrations of CO_2 in the system were measured with a Li-Cor 6262 infrared gas analyzer (Li-Cor Inc.). Two-valved acrylic flow meters (10 LPM precision) maintained an air flow of around 1 LPM through the closed system including Teflon tubing (FEP 1/4″ OD 3/16″ ID) and the soil chamber. At this air flow pressure fluctuations within the system were minimal, which consequently minimized pressure-related variations in the CO_2 readings. A Campbell Scientific data logger (Model CR10X) recorded CO_2, water vapour, air temperature and pressure in the soil chamber every second. The parallel recording of temperature and pressure in the chamber allowed us to correct CO_2 concentrations for fluctuations in both parameters in real time using the ideal gas equation. To avoid pulses of CO_2 due to pressure fluctuations created by opening and closing the lid, we reduced the measurement interval to that interval with minimal pressure fluctuations (Fig. 1). The short time used to measure the increase in CO_2 within the jar head space (40–60 s) reduced diffusion artifacts that may affect the flux estimates (Pumpanen *et al.*, 2004). Moreover, the sampling frequency of the system (1 Hz) improves the statistical fit obtained over standard methodologies that produce a limited number of readings, such as closed static chambers that sample the air episodically with syringes (Livingston & Hutchinson, 1995).

Calculation of decomposition rates and SOM mean residence time

Soil respiration was calculated from the initial slope in CO_2 concentration increase as a function of time (normally 40 s time interval) within the closed loop (Livingston & Hutchinson, 1995)

$$F_c = (dCO_2/dt - a) \times 1/t/V_s, \quad (2)$$

where F_c is the total soil CO_2 evolved from the soil sample during the sampling interval (μmol), dCO_2/dt is the change in CO_2 concentration (ppm) within the system during the sampling interval, t is the sample interval (s), a is the intercept of the linear function and V_s is the volume of the system (L). Volume of the system was calculated by injecting within the system a known quantity of CO_2 and applying the following dilution function

$$V_s = R \times T/P \times \Delta CO_2/ppm_f, \quad (3)$$

where V_s is the unknown volume of the system (L), R the Universal Gas Constant (8.31×10^{-3} L kPa mol^{-1} K^{-1}), T and P are, respectively, the observed temperature (K) and air pressure (kPa) at measurement time, ΔCO_2 is a known injected quantity of CO_2 (60 mL of air with 600 ppm concentration of CO_2 = 0.94 μmol CO_2) and ppm_f the final CO_2 concentration within the closed system. Before CO_2 addition, the system was flushed with N to achieve zero CO_2 concentration. A second syringe was installed as buffering volume avoiding overpressure within the system when injecting the 60 mL air. Volume of the system was also corrected by

pore space of soil sample within the closed system based on the bulk density of the sample and the density of mineral particles (2.65 g cm^{-3}), assuming free pore space for dry samples and saturated pore space for wet samples.

Soil CO_2 efflux (F_c) was expressed on an area basis (F_a: μmol m^{-2} s^{-1}) by dividing the flux by the surface of the collar (12.6×10^{-6} m^2). Additionally F_c was also expressed on a mass basis (F_m: μmol gC^{-1} s^{-1}) by dividing it by the remaining grams of TC in soil. Fluxes normalized by the remaining C were used as a proxy of the efficiency of microbes decomposing SOM. Remaining C in soil was calculated by integrating the total soil CO_2 evolved (*TCR*) during sampling days using a simple linear function.

$$TCR = \sum (c \times t + b)\mathrm{d}t, \tag{4}$$

where *TCR* is the total amount of C (gC) respired during a given time interval, t is time in days within the given time interval and c and b are parameters. Total soil C remaining was then calculated by subtracting the cumulative amount of C respired from the initial amount of C.

According to the manufacturer (Li-Cor), the IRGA can detect changes of 0.2 ppm at 10 Hz (sensitivity). Translated to fluxes units and the sampling frequency of the system (1 Hrtz) means that at standard conditions (40 s range, at ambient CO_2 concentrations, 25 °C and 101 kPa air pressure) the detection limit of our system was of 0.06 μmol m^{-2} s^{-1}, typically one order of magnitude smaller than the fluxes detected in dry soils.

The contribution of any live root respiration to total efflux was assumed to be marginal. First, it is likely that living fine roots in the soil cores died soon after excision because fine roots exhaust their carbohydrate storage quickly due to their high rates of respiration (Pregitzer *et al.*, 1998). Second, fine roots of grasses were dead by the time of sampling, which makes only the scarcer tree fine roots the active ones. And thirdly, to minimize confounding effects of respiration by any residual live fine root on soil CO_2 efflux, we initiated our first set of respiration measurements 48 h after field sampling.

Sensitivity to temperature and soil moisture of soil CO_2 efflux

To assess the relative increase in soil decomposition with temperature, we used the Q_{10} function. Q_{10} computes the relative increase in decomposition rate per 10 °C difference. To avoid errors associated with multiple parameter fitting (Hyvönen *et al.*, 2005; Reichstein *et al.*, 2005), we reduced the parameter fitting to Q_{10}, using the known values of F_{a20} as basal respiration rates.

$$F_a = F_{a20} \times Q_{10}^{T-20/10} \tag{5}$$

In Eqn (5), F_a is the measured soil CO_2 efflux [F_c on Eqn (2)] normalized for the amount of remaining soil C, F_{a20} is the measured F_a at 20 °C, Q_{10} is the relative change in F_a with 10 °C increases and T is the temperature of soil at measurement time. We fitted this exponential function at each temperature cycle, for each of the four studied soils for each water treatment (wet and dry). The function was also fitted to the seasonal evolution of soil respiration and soil temperature obtained from field measurements in the ponderosa pine site during 2005 (no correlation was found with temperature for oak savanna respiration).

Seasonal evolution of soil respiration, as a function of soil moisture, was fitted to a sigmoidal Boltzman-type function:

$$SR = b + (a - b)/(1 + \exp((SWC - c)/d)), \tag{6}$$

where SR is soil respiration (μmol m^{-2} s^{-1}) recorded in the field, a, b, c and d are parameters and SWC is the soil water content (%vol) at 15 cm into the soil. This equation was applied to field soil respiration recorded in the oak savanna soils during 2005.

Calculation of soil C pools

There are several equations that have inferred the labile and recalcitrant C pools based on the changes in the slope of the C mineralization along the incubation period (Townsend *et al.*, 1997; Katterer *et al.*, 1998; Sleutel *et al.*, 2005). These equations assume that the C mineralized initially has a fast turnover and is labile (fast pool), while the remaining fraction has a slow turnover and is recalcitrant (slow pool) (Townsend *et al.*, 1997). In this study, we used and compared results from three different two-pool C models

$$C_{cum}(t) = C_f \times [1 - (e^{-k_f \times t})] + (C_{total} - C_f) \times [1 - (e^{-k_s \times t})], \tag{7}$$

$$C_{cum}(t) = C_f \times [1 - (e^{-k_f \times t})] + k_s \times t, \tag{8}$$

$$C_{rate}(t) = k_f \times (C_f \times e^{-k_f \times t}) + k_s \times ((C_{total} - C_f) \times (e^{-k_s \times t}). \tag{9}$$

$C_{cum}(t)$ is the cumulative mineralized C at a certain time of the incubation, expressed as F_a (g C day^{-1} m^{-2}), k_f and k_s are the rate constants of the fast and slow C

Table 2 Calculated values and statistics (t tail and P-value) of the coefficients (C_f, k_f and k_s) obtained when flux data expressed as F_a was fitted to Eqns (7)–(9)

Treatments	Model	$C_{f\ (g\,m-2)}$	$K_{f\ (d-1)}$	$K_{s\ (d-1)}$	Adj R^2	P-value
bt	1	0	0	6.00E-04*	0.99	<0.0001
	2	1.4(0.2)*	0.04(6e-3) *	3.00e-03*	0.99	<0.0001
	3	2.1(6.5)	0.3(1.4)	8.00E-04*	0.85	<0.0001
bc	1	17.8(0.9)*	0.06(0.01)*	4.0E-04*	0.99	<0.0001
	2	22.6 (3)*	0.05 (0.01)*	4.00E-03*	0.99	<0.0001
	3	9.2 (4.2)*	0.15 (0.09)*	4.00E-04	0.91	<0.0001
to	1	32.2(3.4)*	0.08(0.01)*	1.4E-03*	0.99	<0.0001
	2	42.2 (5.7)	0.06(0.01)*	3.00E-03*	0.99	<0.0001
	3	20(3)*	0.16(0.03)*	0.1*	0.97	<0.0001
tu	1	61.4(6.8)*	0.08(0.01)*	1.3E-03*	0.99	<0.0001
	2	78 (10)*	0.06(0.01)*	0.05*	0.99	<0.0001
	3	51.2(8)*	0.1(0.02)*	1.20E-03*	0.98	<0.0001

Adjusted correlation coefficient (Adj R^2) and P-value (P) of the regression are also reported.
*Represent coefficients significantly different from 0 for a 95% confident interval. The treatments are ponderosa pine trenched (bt), ponderosa pine control (bc), oak savanna open area (to) and oak savanna understorey (tu).

pool (day^{-1}), C_f is the C content of the fast pool and C_{total} the calculated soil C (Table 2) ($KgC\,m^{-2}$). Equation (7) has been used in Breland (1994), Franzluebbers *et al*. (1994) and Bernal *et al*. (1998), Eqn (8) has been used in Alvarez & Alvarez (2000) and Eqn (9) is attributed to Robertson *et al*. (1997). The fit was improved by constraining the size of the slow pool (assumed C_s as $C_{total}-C_f$) (McLauchlan & Hobbie, 2004).

Statistics

Analysis of variance and nonlinear regressions were performed using the curve fitter routines in ORIGIN 5.0.

Results and discussion

Soil respiration- and soil decomposition-derived CO_2 efflux

In general, field- and lab-based estimates of soil CO_2 efflux were in good agreement (Figs 2 and 3). However, disagreements between field- (Fig. 2) and lab-based (Fig. 3) soil CO_2 efflux occurred and are informative, too. For example, in the pine-trenched plot, soil CO_2 emissions were higher than lab-based soil CO_2 estimates (Figs 2a and 3a). In contrast, lab-based estimates of soil CO_2 efflux in open oak savanna dry soils (Fig. 3c) were higher than those obtained in the field (Fig. 2d). Lower lab-based rates of SOM in the trenched pine soils were expected since soil cores only covered the first 5 cm of soil, whereas Blodgett soil stores more C below this depth (Goldstein *et al*., 2000). Regarding the disagreement of fluxes in the dry savanna soils, soil respiration measurements during the driest periods were taken at higher soil temperatures (around 30–40 °C, see Fig. 2e) than those of the incubation (20 °C). The agreement between field- and lab-based soils CO_2 efflux was, therefore, better when they were normalized to similar temperature and soil moisture levels (Fig. 4c and d).

Two-pool models, fit to cumulative mineralized C data, are commonly used to quantify SOM fractionation (McLauchlan & Hobbie, 2004; Sleutel *et al*., 2005). Here, we compared three different models to assess the accuracy of these techniques. On the nontrenched plots, the three models fitted the data collected in this study well and had coefficients significantly different from 0 on the 95% confidence interval (Table 2). In addition coefficient values were within those published using similar models in other studies (Alvarez & Alvarez, 2000; Dalias *et al*., 2001; Sleutel *et al*., 2005).

Generally, longer (>6 months) lab incubation periods are used to produce reliable coefficients for two-pool models (Townsend *et al*., 1997). To assess if the duration of our 111-day incubation study introduced any bias or error on the determination of the two-pool model coefficients, we performed the following calculation. We assumed that decomposition rates at day 180 were 33% lower than those of 111 and recomputed the model coefficients. This artificial extension of the incubation period was found to modify the computation of rate coefficients by <10%.

Comparison of soil C dynamics of two contrasting ecosystems

Soil respiration peaked during early spring in the oak savanna soils and during summer in ponderosa pine

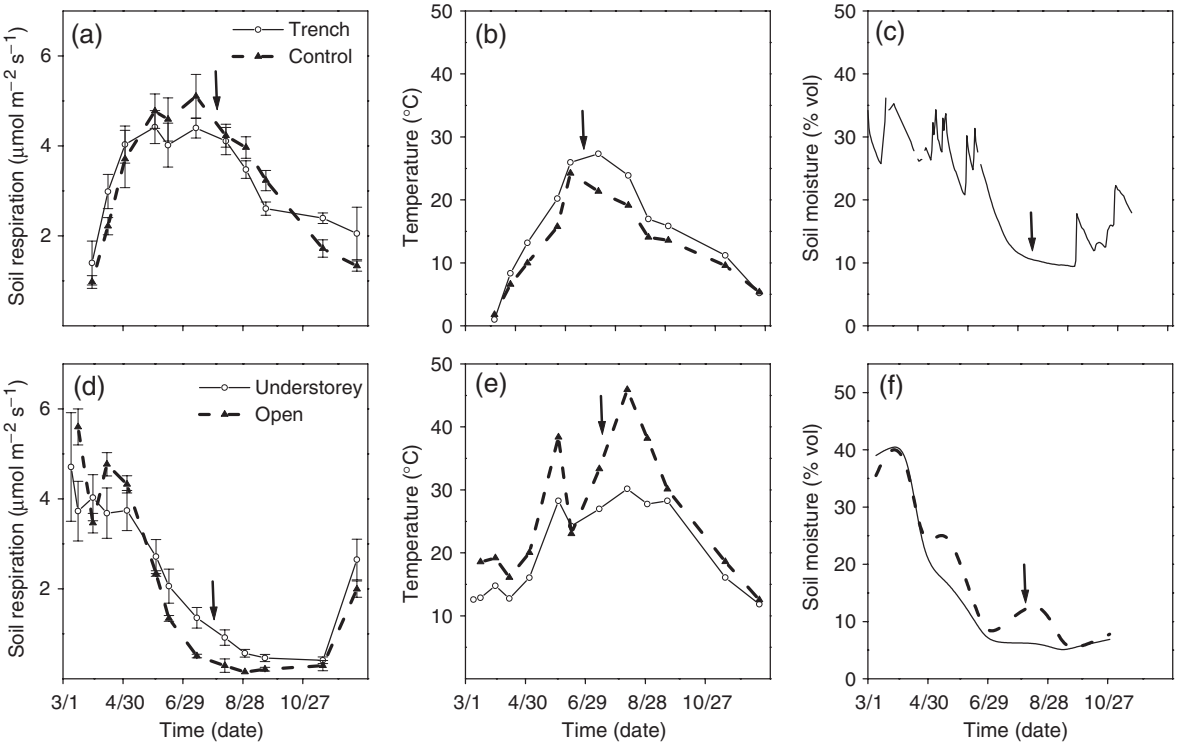

Fig. 2 A 2005 seasonal evolution of soil respiration (μmol m^{-2} s^{-1}; left panels), soil temperature (°C; middle panels) and soil volumetric water content (% vol; right panels), for the four studied soils. Data from the ponderosa pine soils (trenched and control) are represented in the above panels, while oak savanna soils (understorey and open) are represented in the panels below. Arrows in left panels indicate the sample collection date. Vertical bars in soil respiration panels represent the standard error of the mean.

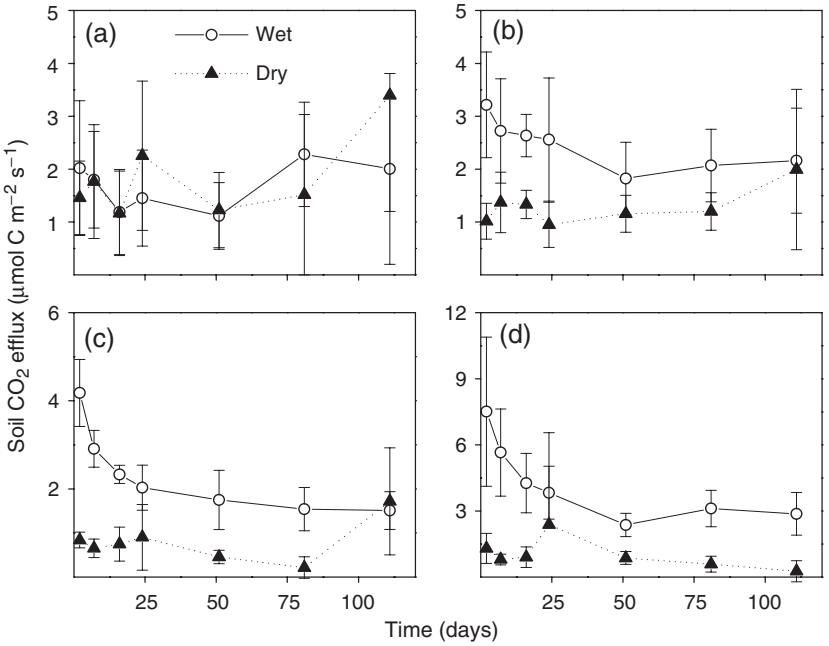

Fig. 3 Temporal evolution of decomposition-derived soil CO_2 fluxes in the wet (open circles) and dry (closed circles) treatments in the four studied soils: ponderosa pine trenched (a), ponderosa pine control (b), oak savanna open (c) and oak savanna understorey (d). Error bars represent the standard error of the mean. [Correction added after online publication 21 August 2007: '... wet (closed circles) and dry (open circles)...' has been changed to '... wet (open circles) and dry (closed circles)...'.]

soils (Fig. 2a and d). Sampling collection date (arrows in Fig. 2) in the pine plantation were the hottest and driest of the year. Soil moisture levels in the pine site nonetheless sufficed to maintain high soil metabolic rates, in contrast to the strong metabolic limitations observed at the savanna site (Fig. 2a and d). In the oak savanna soil, temperatures were near its peak, soil moisture at its nadir and soil respiration close to the lowest values of that year by sampling collection date (below panels in Fig. 2).

Environmental control over the variation of metabolic activity in the field appeared very different at both sites (Fig. 4). While seasonal variation of soil CO_2 efflux in the ponderosa pine ecosystem was mainly limited by temperature (Fig. 4a and b), soil moisture was the factor limiting the seasonal variation in metabolic activity in the oak savanna site (Fig. 4c and d). The low winter temperatures in the ponderosa pine ecosystem limited substantially the activity of organisms (plants and microbes) and only the seasonal increase in temperature allowed organisms to increase their soil metabolic activity (Misson *et al*., 2006). Temperature remained relatively high in the savanna site during winter and early spring, which stimulates the activity of plants and microbes (panels below Fig. 2). The increase in temperature coincided with the decrease in soil water availability during spring, triggering the senescence of the annual grasses in the open areas (Baldocchi *et al*., 2004). Because grasslands occupy approximately 60% of the savanna ecosystem, this decline resulted in an overall decrease in soil metabolic activity of the savanna during spring and summer. Despite the proximity of both Mediterranean ecosystems, intraregional differences in climate and phenology of vegetation, therefore, define the seasonal evolution of soil respiration.

Role of plant activity on soil C dynamics

The relative absence of fast pool C (C_f) in the trenched soils, in contrast to nontrenched soils (Table 2), suggests

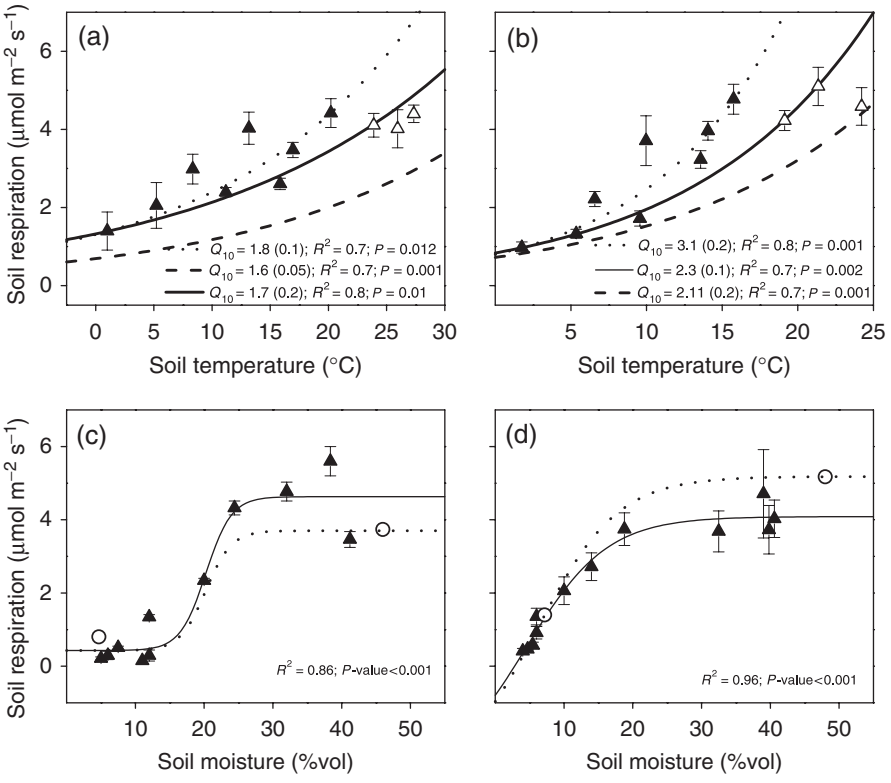

Fig. 4 Field estimates of soil respiration as a function of soil temperature (5 cm depth soil) under no water limitations in (a) ponderosa pine trench and (b) ponderosa pine control. Solid lines represent the Q_{10} fit of the field data under no water limitations (solid triangles), dotted lines the same but including data obtained under water limitations (open triangles) and dashed lines the initial Q_{10} fit obtained in soil incubations for the same soils. Field estimates of soil respiration as a function of soil moisture at 15 cm depth in (c) open areas and (d) understorey areas of the oak savanna ecosystem. Solid lines represent the fit of field data (solid triangles) to the Boltzman sigmoid function [Eqn (6)]. Dotted lines represent the fit to the SOM decomposition data obtained in the lab (open circles). Error bars represent the standard error of the mean. Values of temperature sensitivity (Q_{10}), correlation coefficient (R^2) and *P*-values are also given. SOM, soil organic matter.

 Global Change Biology, doi: 10.1111/j.1365-2486.2007.01415.x

a connection between plant activity and the existence of a labile pool quickly decomposable. Within the oak savanna site, C_f under the active trees doubled that under the dead grasses of the open areas (Table 2). Despite the higher soil temperatures and moisture, both soil respiration (Fig. 2d) and microbial decomposition rates (Fig. 3c and d) were higher under active trees than under dead annual grasses. Moreover, this fast C pool exerted a strong influence on the total decomposition-derived CO_2 efflux (Fig. 5), which indicates its important contribution to short-term temporal variation of soil respiration. Active plants are continuously exudating organic material to soil in the form of easily decomposable substrates such as of simple sugars, amino acids and organic acids (Lynch & Whipps, 1990; Norton & Firestone, 1991; Grayston *et al.*, 1997; Gleixner *et al.*, 2005). Studies in spring wheat and maize plants indicate that photosynthetic-induced priming effect via root exudation may account for a substantial increase in SOM decomposition rates and its short-term temporal variation (Kuzyakov & Cheng, 2001, 2004). Tang *et al.* (2005a) showed how photosynthesis strongly controlled soil respiration in the studied oak savanna system, with a lag of 7–12 h during the summer. This photosynthetic effect on SOM decomposition, therefore, may account for part of the unaccounted variation typically associated with current soil respiration models, parameterized with only temperature and moisture.

The role of plant activity on soil CO_2 efflux was also observed at longer temporal scale (Fig. 4). In contrast to the similarity in Q_{10} values between lab and seasonal data in trenched pine soils (Fig. 4a), values of seasonal Q_{10} of the control plot were substantially higher than the Q_{10} of approximately 2 obtained from lab estimates (Fig. 4b). These differences between control and root-free soils may reflect the confounding effect of seasonality of fine root growth, activity and exudates deposition, which in turn depends on photosynthetic supply from plants (Curiel Yuste *et al.*, 2004; Davidson *et al.*, 2006; Sampson *et al.*, 2007). In oak savannah soils, the effect of seasonality of C inputs in soil respiration can also be noticed (Fig. 4c and d). Lab decomposition rates (calculated using the initial lab-obtained Q_{10} and normalized for field temperatures and soil moistures) were lower than field respiration rates for open area soils (Fig. 4c). This is probably because the period at which soil respiration values were recorded (spring; closed symbols) grasses were active, but when soil cores were collected (summer, open symbols) grasses were already dead. In contrast SOM decomposition rates were higher than field soil respiration for understorey area soils (Fig. 4d), probably because soil respiration was recorded when the trees were dormant while soil cores were collected when the trees were active.

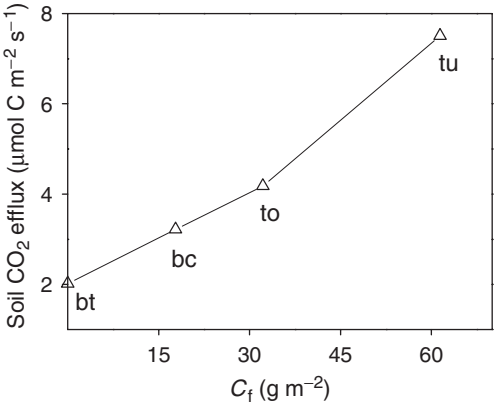

Fig. 5 Measured decomposition-derived CO_2 effluxes at time 0 and 20 °C vs. initial C_f quantity calculated with Eqn (7).

Microbial decomposition efficiency

Fluxes normalized by the amount of remaining C also suggested that microbial SOM decomposition of oak soils was more efficient than that of pine soils (Fig. 6). There was three times more N per unit of C in savanna soils than in ponderosa soils (C/N ratios in Table 1). It is well known that N limits enzyme production, microbial biomass and ultimately SOM decomposition (Melillo *et al.*, 1982; Henriksen & Breland, 1999; Allison, 2005), which may partially explain the differences in palatability of SOM between ecosystems. Although F_m was expected to decrease as the fast pool disappeared and SOM stabilized (Townsend *et al.*, 1997; Gaudinski *et al.*, 2000; Holland *et al.*, 2000; Trumbore, 2000), it showed an unexpected late increase in the four soils (Fig. 6). By the end of the incubation its value was close to its initial, indicating that old/recalcitrant OM might not necessarily be associated with lower decomposition rates when normalized by the remaining C.

Decomposition rates observed in the trenched pine soils (Fig. 2a) emphasizes this idea. Soil respiration of the trenched soils accounted roughly for half the respiration recorded at the control plots during 2003 (Misson *et al.*, 2006) but in 2005 respiration rates were similar for both trenched and control soils (Fig. 2a). Soil respiration rates in control soils were similar during both years. The similarity of soil moisture values during summer 2003 and 2006 (compare Fig. 2 with Fig. 1 in Misson *et al.*, 2006) suggest that the observed relative increase in metabolic activity of the trenched respect control soils could not be explained by soil moisture or by incorporation of fine roots to the soil (Table 1). Lab incubations confirmed the field trend observations (Fig. 6a and b), since trenched soil despite the lower

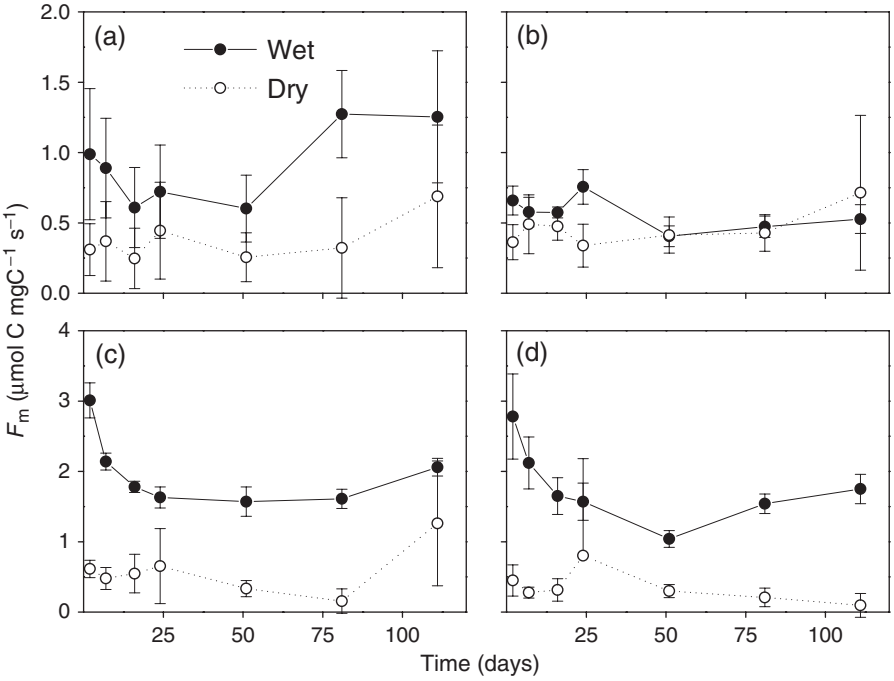

Fig. 6 Temporal evolution of decomposition-derived soil CO_2 fluxes as a function of remaining soil C (F_m, µmol C mg soil C^{-1} s^{-1}) in the wet (closed circles) and dry (open circles) treatments in the four studied soils: ponderosa pine trenched (a), ponderosa pine trenched (b), oak savannah open (c) and oak savannah understorey (d). Error bars represent the standard error of the mean.

C content (Table 1) showed slightly higher F_m rates than nontrenched soils.

We, therefore, hypothesize that microbial community were able to optimize their strategy to transient changes in the quality of SOM, increasing their efficiency. Recent studies have criticized first-order kinetics models because they do not reflect these adjustments of microbial community structure (Schimel, 1995; Stark & Firestone, 1996; Schimel & Gulledge, 1998; Balser *et al*., 2001; Balser & Firestone, 2004; Hawkes *et al*., 2005). Ecophysiological characteristics, such as adjustments of the microbial communities to optimize the oxidation of existing substrates, are not taken into account. More labile C, that is readily decomposable (e.g. at the beginning of the incubation or in the nontrenched plots), would favour opportunistic/cheaters (r-strategic) over enzyme producers (K-strategic) (Allison, 2005; Fontaine & Barot, 2005). Depletion of the labile C in turn favours organism able to produce extracellular enzymes able to break down more stable fractions of SOM (Allison, 2005). It, therefore, might be that SOM decomposition not only depends on the substrate biochemistry but also on the ability of the existing microbial community to decompose the available substrate. Moreover, absence of living roots either in soil cores or trenched soils, and the consequent diminishment of competition for nutrients, may favour SOM decomposition.

Water limitation and organic matter decomposition

Water limitations affected both rates of decomposition and its response to temperature at different time scales. Although soil moisture limited seasonality of soil CO_2 efflux more in the oak savanna than in the pine site (Fig. 4), summer drought decreased substantially the rates of decomposition at both ecosystems (open symbols, Fig. 6). After rewetting, decomposition efficiency experienced a strong increase, especially in oak soils (closed symbols, Fig. 6). This highlights the important role of sporadic rain events during the driest and hottest periods. While labile plant-derived substrate is prevented for decomposition during the extremely dry summer, sporadic rain stimulation of microbial activity may shift the C balance of these ecosystems during dry periods (Xu *et al*., 2004; Misson *et al*., 2005). Our results, therefore, highlight the influence that the combination of water limitation, labile inputs to soil and sporadic summer rain events may have in soil C dynamics of these two Mediterranean ecosystems.

Under moderate summer drought, seasonal Q_{10} decreased when drought-affected data (defined as in Xu & Qi, 2001a, b) were included (dotted lines in Fig. 4a and b). A gradual decrease of soil water content during spring and summer (Fig. 2c) affected both fine roots and microbial metabolic activity because diffusion of

nutrients and substrate occurs in water medium (Belnap *et al.*, 2003). Limitation to soil metabolic activity will therefore increase as soil water content decreases during the season (e.g. Xu & Qi, 2001a, b; Reichstein *et al.*, 2002a, b; Curiel Yuste *et al.*, 2003; Xu *et al.*, 2004). On short-time scales, temperature sensitivity of microbial decomposition was always lower in dry than in wet soils (Fig. 7). SOM decomposition in the relatively dry pine soils showed typically a positive relationship with temperature ($Q_{10} > 1$; Fig. 7a and b), but the relationship between temperature and SOM in the very dry oak soils was typically negative ($Q_{10} < 1$; Fig. 7c and d). Under field conditions we found the same trend during dry periods (Fig. 8), which supported the lab observations. Low values of Q_{10}, were expected for dry soils because microbial activity takes place in the water films (Harris, 1981; Paul & Clark, 1996). Values of Q_{10} below 1 were nonetheless less expected. Because soil water potential is a function of temperature and the relative humidity (*Rh*) of air in the pore space, relatively fast changes in temperature performed in this experiment might have affected soil water potential and soil metabolic activity:

$$\psi = R \times T/M \times (\ln Rh), \qquad (10)$$

where ψ is soil water potential (MPa), R the Universal Gas Constant (8.31×10^{-3} L Mpa mol^{-1} K^{-1}), T the observed soil temperature at measurement time (K), M (18.05×10^{-3} L mol) is the molecular mass of water and Rh is the relative humidity. A reduction in soil water potential is exacerbated by the fact that soil temperature increases more when soil pore space gets drier. Fig. 9 shows that as soils gets both warmer (high T) and drier (low relative humidity), soil water potential can change from -6 to less than -12 MPa in the vicinity of the existing drought-tolerant microbes.

Temperature sensitivity of microbial decomposition

The relatively low values of Q_{10} (typically below the physiological value of 2) found under lab conditions (Fig. 7) were below those reported at the ecosystem level (Raich & Schlesinger, 1992; Xu & Qi, 2001a, b; Janssens & Pilegaard, 2003; Rey & Jarvis, 2006) and in former studies of soil decomposition (Kirschbaum, 1995; Katterer *et al.*, 1998; Holland *et al.*, 2000; Reichstein *et al.*, 2000; Dalias *et al.*, 2001; Fierer *et al.*, 2003, 2005; Fang *et al.*, 2005). Because temperature sensitivity of respiration decreases as temperature increases (Lloyd & Taylor, 1994; Atkin & Tjoelker, 2003; Janssens & Pilegaard, 2003; Price & Sowers, 2004), the relatively high temperatures used in this study may partly explain the low Q_{10} values obtained. Values of Q_{10} expected for the temperature range of the study derived from an Arrhenius-like equation (Lloyd & Taylor, 1994),

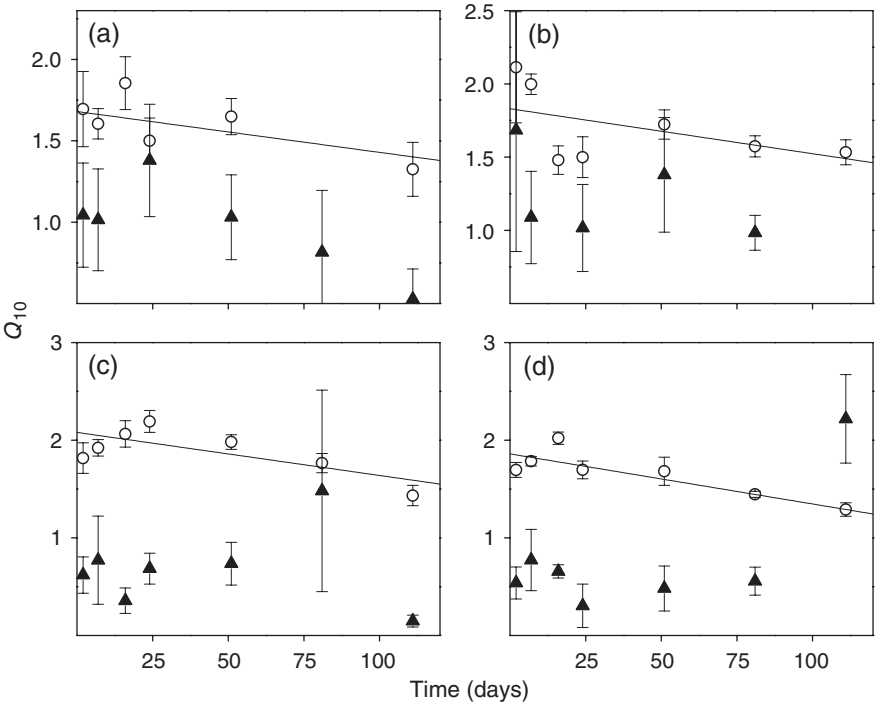

Fig. 7 Temporal evolution of the sensitive to temperature of microbial decomposition (expressed as Q_{10}) in the wet (open circles) and dry (closed triangles) treatments in the four studied soils: ponderosa pine trenched (a), ponderosa pine control (b), oak savanna open (c) and oak savanna understorey (d). Error bars represent the standard error of the mean. Statistics of the linear fit are given in Table 3.

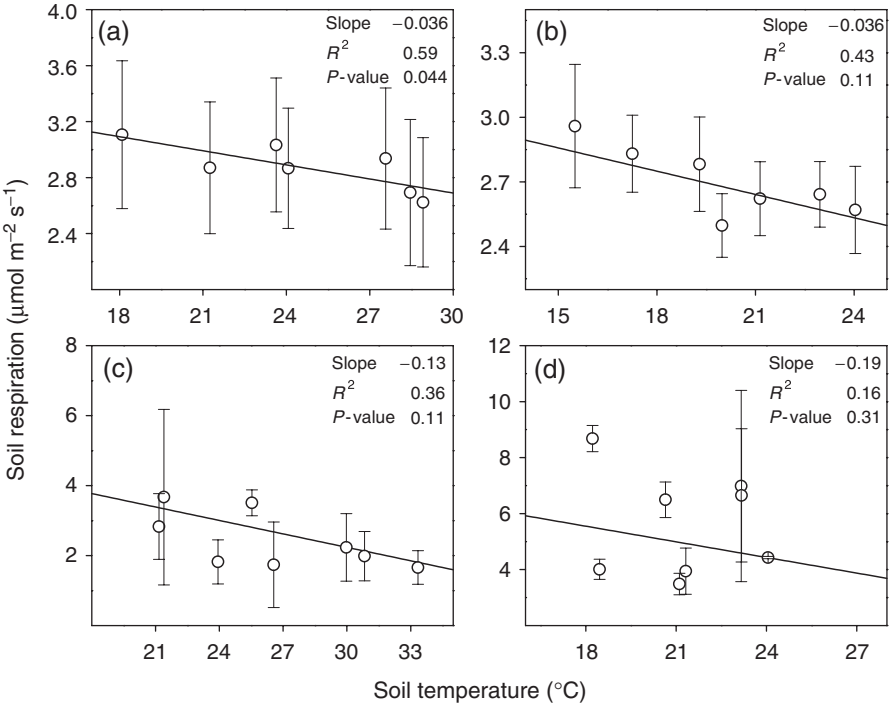

Fig. 8 Diurnal variations in soil respiration measured in the field during dry events as a function of soil temperature in: ponderosa pine trenched (a), ponderosa pine control (b), oak savanna open (c) and oak savanna understorey (d). Error bars represent the standard deviation.

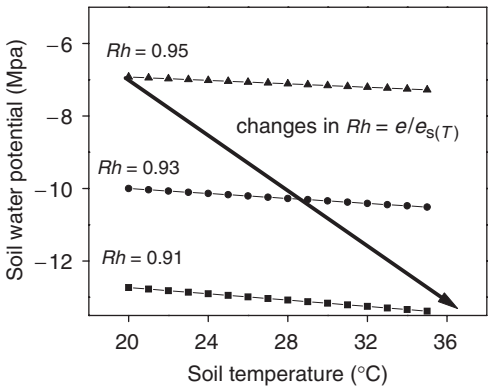

Fig. 9 Modeled fluctuations of soil water potential as a function of soil temperature for three different relative humidities. Soil water potential was inferred from our soil moisture values and existing water retention curves for these soils (data not shown). Assuming a temperature of 25 °C and using Eqn (10), *Rh* was estimated as 0.93 for the oak savanna soils.

using a constant E_a of 51 kJ mol^{-1} (the typical value for enzyme kinetics performed in laboratory; Van't Hoff, 1898), would be 1.94. This value resembles those observed in the early stages of the incubation for the wet soils (Fig. 7).

Depletion of the fast C pool influenced differently both ecosystems (Fig. 10). Temperature sensitivity of decomposition expressed as Q_{10} increased in oak soils while C_f was gradually depleted but decreased in pine control soils (Fig. 10b, Table 3). Theory states that temperature sensitivity of the organic matter should increase as the quality of the substrate decreases (Bosatta & Ågren, 1998), which supports the increase in Q_{10} found in oak savannah soils (Fig. 10b). This theory has been supported recently by experimental evidence (Fierer *et al*., 2003, 2005). However, the decrease in Q_{10} in pine soils (Fig. 10b), the consistent decrease in Q_{10} in all four soils by the incubation end (Fig. 7), or the low values of seasonal Q_{10} of the older/more recalcitrant trenched soils (Fig. 4a) could not be explained by this theory.

A number of observational 'deviations' from the kinetic theory recently reported (Liski *et al*., 1999; Giardina & Ryan, 2000; Fang *et al*., 2005) suggest that the complexity of the process transcend the single theory (Davidson & Janssens, 2006). Other factors such as physical or biochemical accessibility to substrate by microbes (Davidson *et al*., 2006), water availability and substrate diffusion (Davidson & Janssens, 2006) or microbial population dynamics (Monson *et al*., 2006) also affect the response to temperature of SOM decomposition. Temperature sensitivity for most enzymatic kinetics correspond to a Q_{10} around 2, which resembles the initial Q_{10} values of nontrenched plots under no

 Global Change Biology, doi: 10.1111/j.1365-2486.2007.01415.x

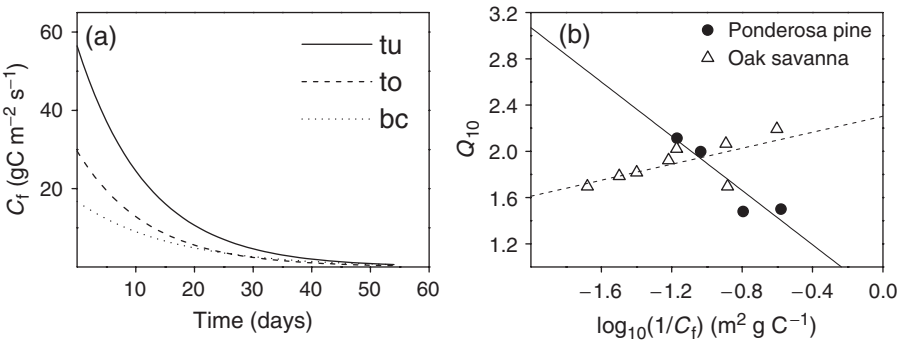

Fig. 10 (a) Simulated depletion of C_f based on the initial C_f values (g C m^{-2}) and the constant rate k_f (day^{-1}) for the three soils with initial values of C_f (see Table 2); (b) Q_{10} against the Log transformed inverse of the remaining C_f at each incubation measurement date. Lines represent the linear fit for ponderosa pine control soils (solid line) and oak savannah soils (dotted line).

Table 3 Slopes of the linear fit of Q_{10} vs. time for the wet treatment (Fig. 8)

	Slope	SEM	R^2	*P*-value
bt	−0.00251	0.00164	0.37	0.2017
bc	−0.00307	0.00185	0.35	0.15815
to	−0.00441	0.00177	0.55	0.05514
tu	−0.00513	0.00111	0.81	0.00565

Statistics of the fit are also given: standard error of the mean (SEM), correlation coefficient (R^2) and *P*-value. The treatments are ponderosa pine trenched (bt), ponderosa pine control (bc), oak savanna open area (to) and oak savanna understorey (tu).

water limitation in this study (Fig. 7). The subsequent decrease in Q_{10} might be explained by a decrease in access to substrate of the enzymatic machinery, independently of a hypothetical increase in temperature sensitivity (Davidson *et al.*, 2006). However, our calculations suggest that decomposition rates of recalcitrant organic matter were not necessarily lower in this study (see Fig. 6). As suggested above possible shifts in microbial community composition from fast-growing r-strategic to slow-growing K-strategic dominated community may have also included microbial biomass as a confounding factor in Q_{10} calculations. Therefore, though decomposition of more recalcitrant organic matter may be more dependent on temperature, other mechanisms such as SOM stabilization or decreases in growth rates of the microbial community may counteract this effect.

Conceptual model of decomposition

Based on our observations, the scheme in Fig. 11 offers a guideline for modelling both microbial decomposition rates and temperature sensitivity of the process. We defined six factors as potential sources of variability on SOM decomposition: (1) labile C inputs from active root plants (*GPP*); (2) quality of SOM associated with the intrinsic biochemical properties of vegetation (q); (3) degree of physical, chemical and/or biochemical protection of the substrate ([S]); (4) rate of microbial respiration (μ); (5) Soil moisture (θ) and (6) soil temperature (T).

The subjectivity of SOM decomposition to most of these factors has been described in semimechanistically models such as CENTURY (e.g. Parton *et al.*, 1987). However, there exists lot of uncertainties regarding the mechanisms of photosynthetic control of SOM decomposition and its role in temporal and spatial variation of heterotrophic activity.

Aggregation formation (physical protection), adsorption onto mineral surfaces (chemical protection) or biochemical transformation of SOM towards more complex substrates (biochemical protection) are the three mechanisms responsible for SOM protection (Δ[S]) (Sollins *et al.*, 1996; Thornley & Cannell, 2001; Six *et al.*, 2002). Although some evidence suggests saturation levels in SOM stabilization (Six *et al.*, 2002), it is not clear at which extent increasing temperatures may increase the degree of physical and physico-chemical stabilization of SOM (Thornley & Cannell, 2001).

Changes in microbial respiration caused by changes in the intrinsic respiration of the existing microbes (low efficiency) or changes in the microbial community composition (adaptation and higher efficiency) may affect SOM decomposition and its response to temperature. Questions to be answered are the time scale and time line of microbial community adaptation to climatic changes and how this will affect the turnover time of different C pools.

The net temperature sensitivity can be altered by a number of factors too (see right part of scheme). Those factors can obscure the intrinsic and direct temperature

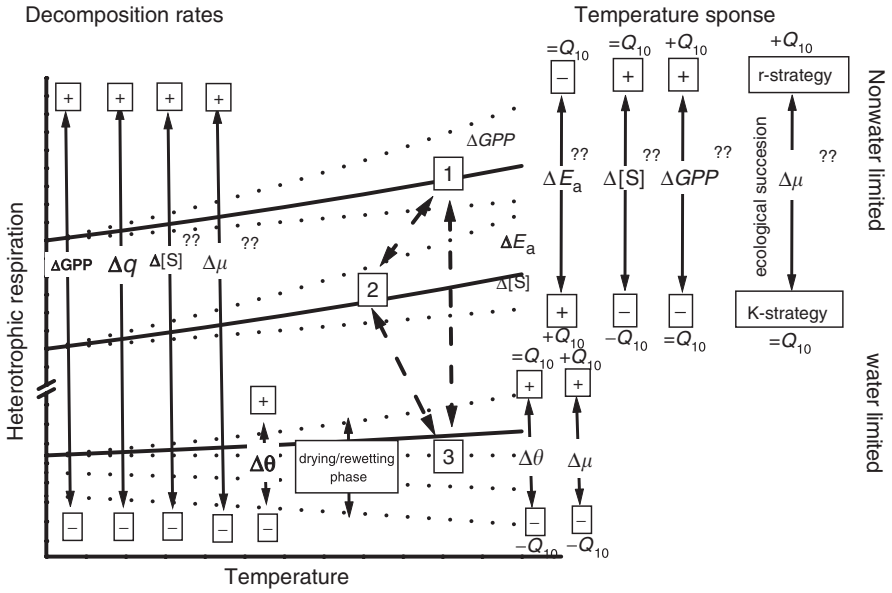

Fig. 11 Schematic representation of the influence exerted by several environmental factors on the rate of SOM decomposition and its temperature sensitivity. On the left axis, we represent factors involved in the magnitude of the decomposition-derived flux and on the right side, we depict factors involved in the temperature sensitivity of the decomposition-derived flux. The upper half of the scheme accounts for factors affecting SOM decomposition under no water limitation (nonwater limited) and the lower portion depicts effects of water limitation (water limited). Except for temperature, the influence of each environmental factor is assessed in the vertical axis, specifying the sign of the influence as negative (−), positive (+) or no influence (=) over decomposition rates and temperature sensitivity. Question marks are added to those factors whose influence needs further study. Solid lines represent the changes in decomposition rate as a function of temperature that corresponds to a Q_{10} of 2. Dotted lines represent deviations from the expected Q_{10} relationship of 2 (typical sensitivity of most enzymatic processes). SOM, soil organic matter.

sensitivity of the process ($Q_{10} \approx 2$). Three different scenarios were defined in the scheme. Dashed arrows indicate the possibility of transition among scenarios in case of deviations from the conditions in which one scenario was defined (e.g. an increase in photosynthetic activity $-\Delta GPP$ – during spring may probably increase root exudation), causing a transition from scenario 2 to 1.

Scenario number 1 represents soils under conditions with no water limitation, high plant activity and exudates production, or high exposure to labile C, such as snow melting ($+\Delta GPP$). Under these conditions it is likely that values of Q_{10} will approach the physiological value of 2. Changes in fine root activity (ΔGPP) via exudates production and SOM decomposition priming will be a confounding factor on calculations of Q_{10} at seasonal time scales. On shorter time scales, successional changes in microbial community structure from r- to K-strategic dominated communities ($\Delta\mu$) may also act as a confounding factor. Because these microbial populations exhibit different growth rates (Fontaine & Barot, 2005), elevated Q_{10}'s may respond to fast increases in the biomass respiring (r-strategy) when root exudation increases.

Scenario 2 represents soils receiving little or no labile C ($-\Delta GPP$), therefore less quality of SOM ($-\Delta q$). Under conditions with no water limitation, the kinetic theory predicts an increase in the temperature dependency of substrate oxidation. We suggest that other factors, specially the accessibility to substrate (Δ[S]) by microbes, may counteract the increase in energy dependence of decomposition of recalcitrant substrates (Davidson *et al*., 2006).

Scenario 3 represents water limited the soils ($\Delta\theta$) subjected to temperature and water fluctuations (summer drying/rewetting or spring snow melts). In this scenario, sporadic rain events will eventually bring the flux to predrought values and temperature sensitivity to Q_{10} values close to 2. The magnitude of the increase will depend primarily on the amount of labile C stored in soils after drought-induced microbial mortality and secondarily on the quality of SOM. Successional changes on microbial community ($\Delta\mu$) may act as a confounding factor too. The negative slope of the variation of decomposition as a function of temperature in the dry soils could not be explained and future experiments should be designed to understand this effect.

 Global Change Biology, doi: 10.1111/j.1365-2486.2007.01415.x

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References

Allison SD (2005) Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters*, **8**, 626–635.

Alvarez R, Alvarez CR (2000) Soil organic matter pools and their associations with carbon mineralization kinetics. *Soil Science Society of America Journal*, **64**, 184–189.

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, **8**, 343–351.

Baldocchi DD, Tang J, Xu L (2006) How switches and lags in biophysical regulators affect spatio-temporal variation of soil respiration in an oak-grass Savanna. *Journal Geophysical Research, Biogeosciences*, **111**, G02008, doi: 10.1029/2005JG000063.

Baldocchi DD, Xu LK, Kiang N (2004) How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland. *Agricultural and Forest Meteorology*, **123**, 13–39.

Balser TC, Firestone MK (2004) Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. *Biogeochemistry 2005*, **73**, 395–415.

Balser TC, Kinzig AP, Firestone MK (2001) Linking soil microbial communities and ecosystem functioning. In: *The Functional Consequences of Biodiversity* (eds Kinzig AP, Pacala S, Tilman GD), pp. 265–295. Princeton University Press, Princeton, NJ.

Belnap J, Hawkes CV, Firestone MK (2003) Boundaries in miniature: two examples from soil. *Bioscience*, **53**, 739–749.

Bernal MP, Navarro AF, Sánchez-Monedero MA, Roig A, Cegarra J (1998) Influence of sewage sludge compost stability and maturity on carbon and nitrogen mineralization in soil. *Soil Biology and Biochemistry*, **30**, 305–313.

Bosatta E, Ågren GI (1998) Soil organic matter quality interpreted thermodynamically. *Soil Biology and Biochemistry*, **31**, 1889–1891.

Bowling DR, McDowell NG, Bond BJ, Law BE, Ehleringer JR (2002) 13C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. *Oecologia*, **131**, 113–124.

Breland TA (1994) Enhanced mineralization and denitrification as a result of heterogeneous distribution of clover residues in soil. *Plant and Soil*, **166**, 1–12.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.

Curiel Yuste J, Janssens IA, Carrara A, Ceulemans R (2004) Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology*, **10**, 161–169.

Curiel Yuste J, Janssens IA, Carrara A, Meiresonne L, Ceulemans R (2003) Interactive effects of temperature and precipitation on soil respiration in a temperate maritime pine forest. *Tree Physiology*, **23**, 1263–1270.

Dalias P, Anderson JM, Bottner P, Couteaux MM (2001) Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. *Global Change Biology*, **7**, 181–192.

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217–227.

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.

Davidson EA, Janssens IA, Luo YQ (2006) On the variability of respiration in terrestrial ecosystems, moving beyond Q_{10}. *Global Change Biology*, **12**, 154–164.

Fang CM, Smith P, Moncrieff JB, Smith JU (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature*, **436**, 881–881.

Fierer N, Allen AS, Schimel JP, Holden PA (2003) Controls on microbial CO_2 production, a comparison of surface and subsurface soil horizons. *Global Change Biology*, **9**, 1322–1332.

Fierer N, Craine JM, McLauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. *Ecology*, **86**, 320–326.

Fontaine S, Barot S (2005) Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecology Letters*, **8**, 1075–1087.

Franzluebbers K, Weaver RW, Juo ASR, Franzluebbers AJ (1994) Carbon and nitrogen mineralization from cowpea plants part decomposing in moist and in repeatedly dried and wetted soil. *Soil Biology and Biochemistry*, **26**, 1379–1687.

Gaudinski JB, Trumbore SE, Davidson EA, Zheng SH (2000) Soil carbon cycling in a temperate forest, radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry*, **51**, 33–69.

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.

Gibelin AL, Deque M (2003) Anthropogenic climate change over the Mediterranean region simulated by a global variable resolution model. *Climate Dynamics*, **20**, 327–339.

Gleixner G, Kramer C, Hahn V, Sachse D (2005) The effect of biodiversity on carbon storage in soils. In: *Forest Diversity an Function: Temperate and Boreal Systems* (eds Scherer-Lorenzen M, Korner C, Schulze E-D), pp. 165–183. Springer-Verlag, Berlin, Germany.

Goldstein AH, Hultman NE, Fracheboud JM *et al.* (2000) Effects of climate variability on the carbon dioxide, water, and sen-

sible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). *Agricultural and Forest Meteorology*, **101**, 113–129.

Grayston SJ, Vaughan D, Jones D (1997) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. *Applied Soil Ecology*, **5**, 29–56.

Harris RF (1981) Effect of water potential on microbial growth and activity. In: *Water Potential Relations in Soil Microbiology* (eds Parr JF, Gardner WR, Elliott LF), pp. 23–95. ASA, Madison, WI.

Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters*, **8**, 976–985.

Henriksen TM, Breland TA (1999) Nitrogen availability effects on carbon mineralization, fungal and bacterial growth, and enzyme activities during decomposition of wheat straw in soil. *Soil Biology and Biochemistry*, **31**, 1121–1134.

Högberg P, Nordgren A, Buchmann N *et al*. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411**, 789–792.

Holland EA, Neff JC, Townsend AR, McKeown B (2000) Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems, implications for models. *Global Biogeochemical Cycles*, **14**, 1137–1151.

Howard DM, Howard PJA (1999) Relationships between CO_2 evolution, moisture-content and temperature for a range of soil types. *Soil Biology and Biochemistry*, **25**, 1537–1546.

Hyvonen R, Ågren GI, Dalias P (2005) Analysing temperature response of decomposition of organic matter. *Global Change Biology*, **11**, 770–778.

Janssens IA, Kowalski AS, Ceulemans R (2001) Forest floor CO_2 fluxes estimated by eddy covariance and chamber-based model. *Agricultural and Forest Meteorology*, **106**, 61–69.

Janssens IA, Pilegaard K (2003) Large seasonal changes in Q_{10} of soil respiration in a beech forest. *Global Change Biology*, **9**, 911–918.

Katterer T, Reichstein M, Andren O, Lomander A (1998) Temperature dependence of organic matter decomposition, a critical review using literature data analyzed with different models. *Biology and Fertility of Soils*, **27**, 258–262.

Kirschbaum MUF (1995) The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. *Soil Biology and Biochemistry*, **27**, 753–760.

Kueppers LM, Snyder MA, Sloan LC, Zavaleta ES, Fulfrost B (2005) Modeled regional climate change and California enaemic oak ranges. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 16281–16286.

Kuzyakov Y, Cheng W (2001) Photosynthesis controls of rhizosphere respiration and organic matter decomposition. *Soil Biology and Biochemistry*, **33**, 1915–1925.

Kuzyakov Y, Cheng W (2004) Photosynthesis controls of CO_2 efflux from maize Rhizosphere. *Plant and Soil*, **263**, 85–99.

Liski J, Ilvesniemi H, Makela A, Westman CJ (1999) CO_2 emissions from soil in response to climatic warming are overestimated – The decomposition of old soil organic matter is tolerant of temperature. *Ambio*, **28**, 171–174.

Livingston GP, Hutchinson GL (1995) Enclosure-based measurement of trace gas exchange: applications and sources of error. In: *Biogenic Trace Gases: Measuring Emissions from Soil and Water* (eds Matson PA, Harriss RC), pp. 14–51. Blackwell Science, Oxford.

Lloyd J, Taylor JA (1994) On the temperature-dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Lynch JM, Whipps JM (1990) Substrate flow in the Rhizosphere. *Plant and Soil*, **129**, 1–10.

McDowell NG, Bowling DR, Bond BJ *et al*. (2004) Response of the carbon isotopic content of ecosystem, leaf, and soil respiration to meteorological and physiological driving factors in a Pinus ponderosa ecosystem. *Global Biogeochemical Cycles*, **18**, 12.

McLauchlan KK, Hobbie SE (2004) Comparison of labile soil organic matter fractionation techniques. *Soil Science Society Of America Journal*, **68**, 1616–1625.

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Misson L, Gershenson A, Tang JW, McKay M, Cheng WX, Goldstein A (2006) Influences of canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a young ponderosa pine forest. *Tree Physiology*, **26**, 833–844.

Misson L, Tang JW, Xu M, McKay M, Goldstein A (2005) Influences of recovery from clear-cut, climate variability, and thinning on the carbon balance of a young ponderosa pine plantation. *Agricultural and Forest Meteorology*, **130**, 207–222.

Monson RK, Lipson DL, Burns SP *et al*. (2006) Winter forest soil respiration controlled by climate and microbial community composition. *Nature*, **439**, 711–714.

Norton JM, Firestone MK (1991) Metabolic status of bacteria and fungi in the Rhizosphere of ponderosa pine-seedlings. *Applied and Environmental Microbiology*, **57**, 1161–1167.

Papendick RI, Campbell GS (1981) Theory and measurement of water potential. In: *Water Potential Relations in Soil Microbiology. SSSA Special Publication No. 9* (ed. Parr JF), pp. 1–22. SSSA, Madison.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Paul PA, Clark FE (1996) In: *Soil Biology and Biochemistry*, 2nd edn. Academic Press, San Diego, CA.

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature*, **298**, 156–159.

Pregitzer KS, Laskowski MJ, Burto AJ, Lessard C, Zak DR (1998) Variation in sugar maple root respiration with root diameter and depth. *Tree Physiology*, **18**, 665–670.

Price PB, Sowers T (2004) Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proceedings of The National Academy of Sciences of The United States of America*, **101**, 4631–4636.

Pumpanen J, Kolari P, Ilvesniemi H *et al*. (2004) Comparison of different chamber techniques for measuring soil CO_2 efflux. *Agricultural and Forest Meteorology*, **123**, 159–176.

Raich JW, Schlesinger WH (1992) The global carbon-dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Series B-Chemical and Physical Meteorology*, **44**, 81–99.

  doi: 10.1111/j.1365-2486.2007.01415.x

Raich JW, Tufekciogul A (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry*, **48**, 71–90.

Reichstein M, Bednorz F, Broll G, Katterer T (2000) Temperature dependence of carbon mineralisation, conclusions from a long-term incubation of subalpine soil samples. *Soil Biology and Biochemistry*, **32**, 947–958.

Reichstein M, Katterer T, Andren O *et al*. (2005) Temperature sensitivity of decomposition in relation to soil organic matter pools, critique and outlook. *Biogeosciences*, **2**, 317–321.

Reichstein M, Tenhunen JD, Roupsard O *et al*. (2002a) Ecosystem respiration in two Mediterranean evergreen Holm Oak forests, drought effects and decomposition dynamics. *Functional Ecology*, **16**, 27–39.

Reichstein M, Tenhunen JD, Roupsard O *et al*. (2002b) Severe drought effects on ecosystem CO_2 and H_2O fluxes at three Mediterranean evergreen sites, revision of current hypotheses? *Global Change Biology*, **8**, 999–1017.

Rey A, Jarvis P (2006) Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). *Global Change Biology*, **12**, 1894–1908.

Robertson GP, Klingensmith KM, Klug MJ, Paul EA, Crum JR, Ellis BG (1997) Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecological Applications*, **7**, 158–170.

Sampson DA, Janssens IA, Curiel Yuste J, Ceulemans R (2007) Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. *Global Change Biology*, In press.

Schimel J (1995) Ecosystem consequences of microbial diversity and community structure. In: *Arctic and Alpine Biodiversity: Patterns, Causes, and Ecosystem Consequences* (eds Chapin FS, Korner C), pp. 239–254. Springer, Berlin.

Schimel JP, Gulledge J (1998) Microbial community structure and global trace gases. *Global Change Biology*, **4**, 745–758.

Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter, Implications for C-saturation of soils. *Plant and Soil*, **241**, 155–176.

Sleutel S, De Neve S, Roibas MRP, Hofman G (2005) The influence of model type and incubation time on the estimation of stable organic carbon in organic materials. *European Journal of Soil Science*, **56**, 505–514.

Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma*, **74**, 65–105.

Stark JM, Firestone MK (1996) Kinetic characteristics of ammonium-oxidizer communities in a California oak woodland-annual grassland. *Soil Biology and Biochemistry*, **28**, 1307–1317.

Tang JW, Baldocchi DD (2005) Spatial-temporal variation in soil respiration in an oak-grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components. *Biogeochemistry*, **73**, 183–207.

Tang JW, Baldocchi DD, Xu L (2005a) Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biology*, **11**, 1298–1304.

Tang JW, Qi Y, Xu M, Misson L, Goldstein AH (2005b) Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada. *Tree Physiology*, **25**, 57–66.

Thornley JHM, Cannell MGR (2001) Soil carbon storage response to temperature: an hypothesis. *Annals of Botany*, **87**, 591–598.

Townsend AR, Vitousek PM, Desmarais DJ, Tharpe A (1997) Soil carbon pool structure and temperature sensitivity inferred using CO_2 and $^{13}CO_2$ incubation fluxes from five Hawaiian soils. *Biogeochemistry*, **38**, 1–17.

Trumbore S (2000) Age of soil organic matter and soil respiration, Radiocarbon constraints on belowground C dynamics. *Ecological Applications*, **10**, 399–411.

Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric, carbon dioxide driven by temperature change. *Science*, **272**, 393–396.

Van't Hoff JH (1898) Lectures on theoretical and physical chemistry. In: *Chemical Dynamics Part I* (translated by Lehfeldt RA), pp. 224–229. Edward Arnold, London, UK.

Xu LK, Baldocchi DD, Tang JW (2004) How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochemical Cycles*, **18**, GB4002, doi: 10.1029/2004GB002281.

Xu M, Qi Y (2001a) Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biology.*, **7**, 667–677.

Xu M, Qi Y (2001b) Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevadan forest. *Global Biogeochemical Cycles*, **15**, 687–696.

