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Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California

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Abstract

Soil-surface CO_2 efflux and its spatial and temporal variations were examined in an 8-y-old ponderosa pine plantation in the Sierra Nevada Mountains in California from June 1998 to August 1999. Continuous measurements of soil CO_2 efflux, soil temperatures and moisture were conducted on two 20 × 20 m sampling plots. Microbial biomass, fine root biomass, and the physical and chemical properties of the soil were also measured at each of the 18 sampling locations on the plots. It was found that the mean soil CO_2 efflux in the plantation was 4.43 μmol m^{-2} s^{-1} in the growing season and 3.12 μmol m^{-2} s^{-1} in the nongrowing season. These values are in the upper part of the range of published soil-surface CO_2 efflux data. The annual maximum and minimum CO_2 efflux were 5.87 and 1.67 μmol m^{-2} s^{-1}, respectively, with the maximum occurring between the end of May and early June and the minimum in December. The diurnal fluctuation of CO_2 efflux was relatively small (< 20%) with the minimum appearing around 09.00 hours and the maximum around 14.00 hours. Using daytime measurements of soil CO_2 efflux tends to overestimate the daily mean soil CO_2 efflux by 4–6%. The measurements taken between 09.00 and 11.00 hours (local time) seem to better represent the daily mean with a reduced sampling error of 0.9–1.5%. The spatial variation of soil CO_2 efflux among the 18 sampling points was high, with a coefficient of variation of approximately 30%. Most (84%) of the spatial variation was explained by fine root biomass, microbial biomass, and soil physical and chemical properties. Although soil temperature and moisture explained most of the temporal variations (76–95%) of soil CO_2 efflux, the two variables together explained less than 34% of the spatial variation. Microbial biomass, fine root biomass, soil nitrogen content, organic matter content, and magnesium content were significantly and positively correlated with soil CO_2 efflux, whereas bulk density and pH value were negatively correlated with CO_2 efflux. The relationship between soil CO_2 efflux and soil temperature was significantly controlled by soil moisture with a Q_{10} value of 1.4 when soil moisture was <14% and 1.8 when soil moisture was >14%. Understanding the spatial and temporal variations is essential to accurately assessment of carbon budget at whole ecosystem and landscape scales. Thus, this study bears important implications for the study of large-scale ecosystem dynamics, particularly in response to climatic variations and management regimes.

Keywords: fine root biomass, forest carbon cycle, microbial biomass, soil CO_2 efflux, soil temperature and moisture, spatial and temporal variation

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Introduction

Soil-surface CO_2 efflux, commonly referred to as soil respiration, is a significant component of the global carbon cycle and is likely to be affected by global warming. It is estimated that a global warming of 0.03 °C per year will enhance soil respiration, producing a net release of an additional 60 PgC from soil to the atmosphere between 1990 and 2050. That amount of carbon would be equivalent to a 19% increase in fossil fuel combustion during the same period (Jenkinson *et al*. 1991). Forest ecosystems constitute a major reservoir of the global soil carbon (Houghton *et al*. 1990; Tans *et al*. 1990). Therefore, understanding carbon cycling in forest ecosystems is critical for estimating the future global carbon budget.

Soil CO_2 efflux has been measured in various forest ecosystems all over the world (Crill 1991; Raich & Schlesinger 1992; Joshi 1994; Vose *et al*. 1995; Thierron & Laudelout 1996; Davidson *et al*. 1998; Russell & Voroney 1998; Epron *et al*. 1999a). High spatial and temporal variability of soil CO_2 efflux has been reported (Raich *et al*. 1990; Hanson *et al*. 1993; Thierron & Laudelout 1996). The variability has been attributed to species composition, stand age, management practices, and climatic and edaphic conditions (Edwards & Ross-Todd 1983; Ewel *et al*. 1987; Hanson *et al*. 1993; Toland & Zak 1994; Nakane & Lee 1995). The high spatial variation in soil CO_2 efflux indicates a need for large sample size in order to get a representative value of CO_2 efflux in an ecosystem (Raich *et al*. 1990; Dugas 1993). However, a large sample size requires intensive field sampling in a limited time period because soil CO_2 efflux may change considerably over time. Understanding of the spatial and temporal variations of CO_2 efflux is needed for determining adequate sample size in an ecosystem (Fang *et al*. 1998).

The relationship between the variation of soil CO_2 efflux and the environmental factors may be used to scale up chamber measurements of CO_2 efflux to the ecosystem and larger scales (Fang *et al*. 1998). The present work is intended to bridge some existing gaps in the study of the joint effects of multiple environmental factors on soil CO_2 efflux, particularly in a Mediterranean climate. Specifically, the objectives of the present paper are: (i) to determine soil CO_2 efflux in a young ponderosa pine plantation; (ii) to characterize spatial and temporal variation of soil CO_2 efflux in the plantation; and (iii) to examine the relationships between environmental factors and soil CO_2 efflux.

Materials and methods

Site description

The study site, a part of the Ameriflux network, is in a young ponderosa pine plantation which is located (38°53′42.9″N, 120°37′57.9″W, 1315 m) adjacent to Blodgett Forest Research Station, a research forest of the University of California, Berkeley, CA. The plantation was dominated by 7–8-y-old ponderosa pine (*Pinus ponderosa*). Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), giant sequoia (*Sequoiadendron giganteum*), and California black oak (*Quercus kelloggii*) were occasional inclusions in the overstorey canopy. The plantation had an average diameter at breast height (d.b.h.) of 7.6 cm, an average height (d.b.h. > 3 cm) of 3.4 m, and a density (d.b.h. > 3 cm) of 1213 stems ha^{-1}. Overstorey leaf area index (LAI) was about 4.5 (total needle surface area) in the end of 1998 growing season (Xu 2000). About 58% of the ground area was covered by trees, 24% by shrubs, and the remaining 18% is grass, stumps, and bare soil. The major understorey shrubs were manzanita (*Arctostaphylos* spp.) and *Ceonothus* spp. with an average height of about 80 cm and an LAI of 1.6 (total surface area) in 1998 growing season.

The site is characterized by a Mediterranean climate with a cold and wet winter and a hot and dry summer. Annual precipitation has averaged 1660 mm since 1961, with the majority of precipitation falling between September and May, and almost no rain in the summer. The average (over 33 years) minimum daily temperature in January was 0.6 °C and the average maximum daily temperature in July was 28.3 °C. The winter is wet and cold with an average of 254 cm snow. Trees generally break bud in May and set bud in late July to early August. The year of 1998, an El Niño year, was an exception, with the new needle elongation starting in June. 1999, a La Niña year, was also an anomalous year, with bud break in late April for the ponderosa pine trees at the site.

The study site is relative flat with slopes < 3° in the present sampling area. The site soil is a fine-loamy, mixed, mesic, ultic haploxeralf in the Cohasset series whose parent material was andesitic lahar. It is relatively uniform and dominated by loam and clay-loam. Coarse woody debris was scattered on the forest floor from the residuals of previous harvesting (clear-cutting). The soil had an average pH value of 5.5, organic matter of 6.9%, and total N of 0.17%.

Field measurements

Two 20 × 20 m sampling plots were established, 40 m apart, to represent the 'footprints' of the tower flux measurements using eddy covariance technique. In each plot, soil CO_2 efflux and soil temperatures were measured on a 3 × 3 matrix with 10 m spacing. Soil CO_2 efflux was measured using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system for data collection and storage. The chamber has a pressure relief valve to keep the pressure inside and outside the chamber in a dynamic equilibrium state. The chamber features no internal fan that may create pressure fluctuations inside the chamber. Norman *et al*. (1992) described the principles of the soil chamber in detail.

A soil collar, with a height of 4.4 cm and a diameter of 11 cm, was inserted into the soil at each sampling point one day prior to the measurements. All soil collars were left on site for the entire period of study. The measurement of soil CO_2 efflux started in June 1998. Data sampling was conducted about every 2 weeks in the summer 1998 and about every month in the fall and early winter of 1998. From late April to June 1999 soil CO_2 efflux was sampled about every 2 weeks and about every month after July 1999. No measurements were taken between late December 1998 and early April 1999 when snow covered the ground. Typically, the measurements started in the early morning and ended in late afternoon. It took 3–4 min to take three replicated readings of the soil CO_2 efflux. It took 1–1.5 h to sample all 18 points at both measurement plots. For each point, 6–10 measurements were normally obtained in one day. In addition, 24-h measurements were conducted each month from June to September 1998 to examine the diurnal pattern of soil CO_2 efflux. The sampling procedure during the night was the same as for the daytime measurements.

Soil temperatures at 10 cm and 20 cm depth were monitored at all 18 points using custom-built thermocouple sensors connected to dataloggers (CR10X and 23X; Campbell Scientific, Inc., Logan, UT, USA). In addition, soil temperature at 0, 5, 15, 30, and 50 cm, air temperature at 1.5 m, and volumetric soil moisture (0–30 cm average) were monitored at a point in the centre of each plot. We used time domain reflectometry (TDR) (Campbell Scientific, Inc.) to measure the soil moisture. Two parallel rods of the TDR were inserted vertically into the top 30 cm of the soil to get the water content of 30 average of the topsoil. Temperature and moisture data were logged every five minutes. Gravimetric soil moisture and soil bulk density were measured in July and August 1998 by coring the soil adjacent to each of the 18 sampling points where CO_2 efflux was measured. Soil water content was determined by oven dry method at 105 °C for 48 h.

In mid-November 1998 the soil collars were relocated to adjacent areas (within 20–30 cm of the original location) and the soil was cored where the soil collars were located previously. A soil sample was obtained every 10 cm to a depth of 50–70 cm using a soil auger with a diameter of 10.4 cm. The soil samples were analysed in the laboratory to determine root biomass, microbial biomass, and soil physical and chemical properties.

Roots were classified into three categories: fine root (⩽ 1 mm), small roots (1–5 mm), and medium roots (> 5 mm). No roots with diameter > 5 cm were found in the present soil samples. Dead roots were distinguished from live roots by their colour and elasticity. Roots were oven-dried at 70 °C for 48 h and weighed with a resolution of 0.1 mg. Twenty grammes of rock-free soil was used to determine soil water content; soil bulk density was determined using intact soil cores. Finally, the soils were sieved (2-mm mesh) for the analyses of nutrients and microbial biomass.

Microbial biomass (C_{mic}) was determined using the chloroform fumigation-extraction method (Vance *et al*. 1987). C_{mic} was calculated as the difference in organic carbon between fumigated and nonfumigated (control) samples. A moist sample was divided into two portions of 20 g each. One portion was fumigated with ethanol-free $CHCl_3$ for 48 h at 25 °C in a sealed desiccator. After fumigant removal, the soil was extracted with 50 mL 0.5 M K_2SO_4 for 30 min at 200 rpm and filtered (Whatman 42). The nonfumigated portion was extracted similarly at the time that fumigation started. Extracts were kept frozen until analysed. The organic C in the extracts was measured using a Total Organic Carbon (TOC-5050 A) Analyser (Shimadzu Scientific Instruments, Columbia, MD). C_{mic} was calculated as follows: $C_{mic} = EC/k_{EC}$, where EC = (organic C extracted from fumigated soil) – (organic C extracted from nonfumigated soil) and $k_{EC} = 0.45$ (Wu *et al*. 1990; Joergensen 1996). C_{mic} was measured for the top two layers of the soil (0–10 cm and 10–20 cm).

Root free soil samples from the top-three layers (0–10, 10–20 and 20–30 cm) were analysed at the DANR Analytical Laboratory, University of California, Davis, CA. Soil pH was measured with a pH meter and soil organic matter was determined by potassium dichromate reduction of organic carbon and subsequent spectrophotometric measurement. Soil nitrogen (total Kjeldahl nitrogen) was determined by the wet oxidation of soil organic matter using standard Kjeldahl procedure with sulphuric acid and digestion catalyst. Extractable phosphate was determined using alkaline extraction by 0.5 normal $NaHCO_3$. Available exchangeable potassium, calcium, and magnesium were determined using 1 normal ammonium acetate (pH 7.0) and subsequent determination by atomic absorption/emission spectrometry.

Data analysis

Soil respiration and microclimate data were processed in an Excel97 spreadsheet. Analysis of variance (ANOVA) was used to test the difference in CO_2 efflux among the 18 sampling locations and regression analysis to examine the relationships between soil CO_2 efflux and environmental factors. Standard deviation and the coefficient of variation were used to represent the spatial variation in CO_2 efflux among the 18 sampling locations. Univariate and bivariate models are used to examine the relationship between soil CO_2 efflux and soil temperature and/or soil moisture. The models are listed below:

$$F = \beta_0 \, e^{\beta_1 T} \tag{1}$$

$$F = \beta_0 + \beta_1 W \tag{2}$$

$$F = \beta_0 \, e^{\beta_1 T} W^{\beta_2} \tag{3}$$

where F is soil CO_2 efflux rate (μmol m^{-2} s^{-1}), W is volumetric soil water content (%), T is soil temperature (°C) at 10 cm depth, and β_0, β_1, and β_2 are constants fitted by the least-square technique. Soil temperature was taken at 10 cm depth because this produces the best fit for the models among all depths where the soil temperature was taken. The Q_{10} values, known as the multiplier to the respiration rate for a 10° increase in temperature were calculated as:

$$Q_{10} = e^{10\,\beta_1} \tag{4}$$

where β_1 is taken from (1). The relationships between soil CO_2 efflux and fine root biomass, microbial biomass, and soil nutrients were also examined using linear and nonlinear (natural log of soil CO_2 efflux vs. the environmental factor) regressions. All the statistical analyses were performed in an Excel97 spreadsheet.

A further examination was made of the relationship between soil CO_2 efflux and either soil temperature or soil moisture when one of the two variables is held constant. Partial correlation analysis was used to detect the possible confounding effect of soil temperature on the relationship between soil CO_2 efflux and soil moisture, and vice versa. The coefficient of partial correlation was calculated as (Neter *et al*. 1996):

$$r_{Y2,1} = \frac{r_{Y2} - r_{12} r_{Y1}}{\sqrt{(1 - r_2^2)(1 - r_{Y1}^2)}} \tag{5}$$

where: $r_{Y2,1}$ is the coefficient of partial correlation between dependent variable Y and independent variable X_2 when the other independent variable X_1 is fixed; r_{Y1} denotes the coefficient of simple correlation between Y (soil CO_2 efflux) and X_1 (e.g. soil moisture); r_{Y2} denotes the coefficient of simple correlation between Y and X_2 (e.g. soil temperature); and r_{12} is the coefficient of simple correlation between X_1 and X_2.

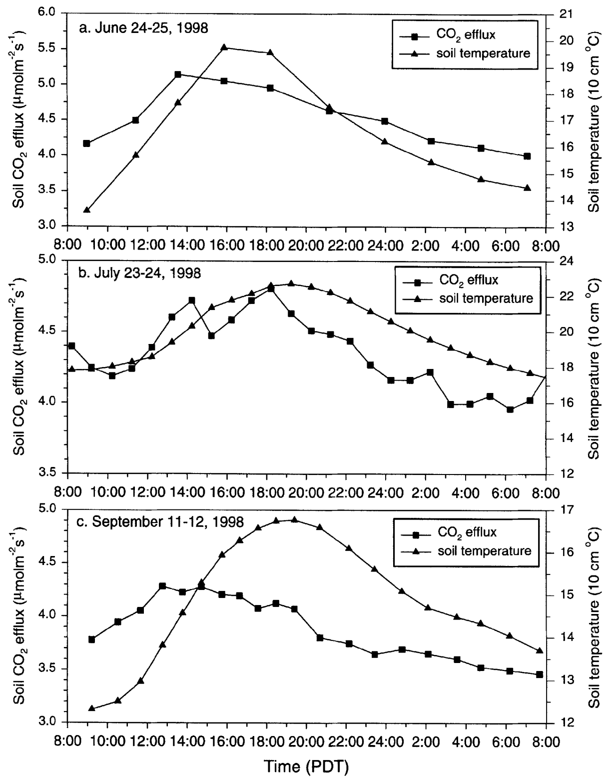

Fig. 1 Diurnal trend of soil CO_2 efflux and soil temperature (10 cm) in mid, late, and post growing season of 1998. Each datum represents the average of measurements over all 18 locations.

Results

The diurnal and seasonal variations of the soil CO_2 efflux

Soil CO_2 efflux showed an asymmetric diurnal pattern, with the minimum appearing around 08.00 hours (local time) and the maximum around early afternoon (13.00–15.00 hours) (Fig. 1). The diurnal range was normally less than 1 μmol m^{-2} s^{-1}, or about 20% of its mean value. Soil CO_2 efflux followed the increasing trend of soil temperature in the morning, but then leveled off with slight fluctuations while soil temperature kept increasing in the afternoon (Fig. 2). From evening to early morning of the next day, soil CO_2 efflux followed the declining trend of soil temperature with little fluctuations (Fig. 1). In midsummer, when soil moisture was near its annual minimum, the soil CO_2 efflux appeared to have smaller diurnal fluctuation and a later trough, in comparison with June and September measurements (Fig. 1a,b,c).

The mean annual soil CO_2 efflux (excluding January through March) was 3.82 μmol m^{-2} s^{-1} with growing season (May through July) of 4.43 μmol m^{-2} s^{-1} and nongrowing season (April and August through November) of 3.12 μmol m^{-2} s^{-1}. The seasonal trend of soil CO_2 efflux followed that of soil moisture during the summers of 1998 and 1999 when volumetric soil moisture was low. From October 1998 to May 1999, when soil moisture was relatively high, soil CO_2 efflux followed the trend of soil temperature rather than moisture. September and May were transition periods when both soil moisture and temperature controlled CO_2 efflux (Fig. 2). In 1998 soil CO_2 efflux decreased from 4.7 μmol m^{-2} s^{-1} in June to about 3.4 μmol m^{-2} s^{-1} at the end of August, and then increased to 4.2 μmol m^{-2} s^{-1} in September followed by a rapid decline to the annual minimum in early November. Soil CO_2 efflux in the winter (measured when there was no snow cover) was only about 38% of the value in early summer (Fig. 2). In 1999, soil CO_2 efflux increased rapidly from about 2.7 μmol m^{-2} s^{-1} at the end of April to the annual maximum of 5.7 μmol m^{-2} s^{-1} in early June, followed by rapid decrease to 4.2 μmol m^{-2} s^{-1} in mid-June and then to 2.9 μmol m^{-2} s^{-1} in late August. Soil CO_2 efflux had a higher peak value in June in 1999 when compared to 1998 (Fig. 2).

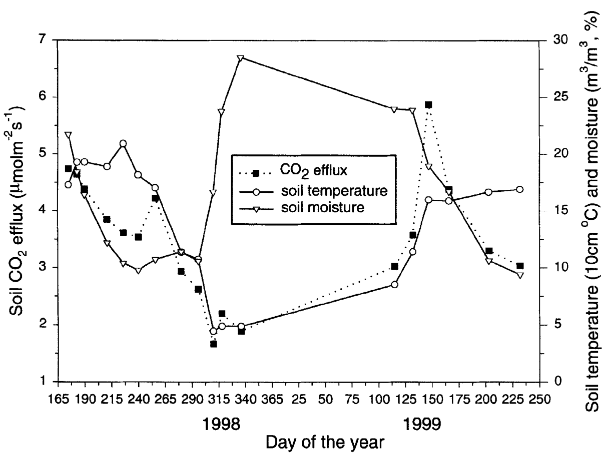

Fig. 2 Seasonal trend of soil CO_2 efflux, soil temperature (10 cm in depth), and soil volumetric moisture (average of top 30 cm) in a young ponderosa pine plantation from June 1998 to August 1999 (no data between late December 1998 to April 1999 when snow covered the ground). Each datum represents daytime mean over all measurements of 18 locations.

The spatial variation of the soil CO_2 efflux

The spatial variation of soil CO_2 efflux was high in the plantation (Table 1). The ratio of maximum to minimum was 2.5 and 2.8 for growing season and nongrowing season, respectively. The differences in CO_2 efflux among the 18 sampling locations were significant ($P < 0.01$). The standard deviation of CO_2 efflux was higher in the growing seasons than in the nongrowing seasons. However, the coefficient of variation of growing season was smaller than that of nongrowing season, suggesting a relatively higher spatial variation for nongrowing season. The standard deviation of CO_2 efflux was also positively correlated with this mean value and their relationship can be described by a simple linear regression equation. For nongrowing season measurements:

$$SD = -1.10 + 1.07\,MEF \qquad (r^2 = 0.85). \qquad (6)$$

For growing season measurements:

$$SD = -1.64 + 0.79\,MEF \qquad (r^2 = 0.87), \qquad (7)$$

where SD is the standard deviation of CO_2 efflux among the 18 sampling locations, MEF is the mean CO_2 efflux of the 18 locations. Equation (6) has a larger slope than (7), which means that the spatial variation of CO_2 efflux increases more dramatically during the nongrowing season than the growing season given the same increase of the mean CO_2 efflux.

Soil CO_2 efflux and belowground properties

The spatial correlations between soil CO_2 efflux and 10 variables describing soil properties are summarized in Table 2. (Note: the soil collars were relocated after the

Table 1 Summary statistics of CO_2 efflux, soil temperature and soil moisture of the 18 sampling locations

	Growing season (May–July)			Non-growing season (August–April)			All seasons		
	CO_2 efflux μmolm^{-2} s^{-1}	Ts10 (°C)	soil moisture (gravimetric%)	CO_2 efflux μmolm^{-2} s^{-1}	Ts10 (°C)	soil moisture[a] (gravimetric%)	CO_2 efflux μmolm^{-2} s^{-1}	Ts10 (°C)	soil moisture (gravimetric%)
Mean	4.43	16.08	19.57	3.12	14.09	10.21	3.82	15.16	14.89
SD	1.35	1.98	2.64	1.09	1.59	1.92	1.17	1.63	1.94
CV(%)	30.37	12.33	13.51	34.88	11.32	18.83	30.70	10.72	13.05

[a]Including August, September and October.
Ts, soil temperature at 10cm in depth; SD, standard deviation; CV, coefficient of variation.

Table 2 Summary statistics of fine root biomass, microbial biomass, and soil perperties and coefficients of correlation among themselves and between them and the soil CO_2 efflux for the sampling locations

	pH	bulk density (g/cm^3)	root(<5mm) biomass(g)	microbial C gC g^{-1}	OM %	TKN %	P-Olsen ppm	K meq/100g	Ca	Mg
Mean	5.48	0.73	2.00	0.22	7.89	0.17	12.94	0.56	4.39	0.45
SD	0.29	0.18	0.91	0.12	3.69	0.07	12.52	0.11	2.37	0.27
pH	1.00									
bulk density	0.53	1.00								
root (<5mm)	–0.36	–0.33	1.00							
microbial C	–0.33	–0.67	0.57	1.00						
OM	–0.66	–0.78	0.15	0.69	1.00					
TKN	–0.56	–0.89	0.22	0.70	0.93	1.00				
P-Olsen	–0.62	–0.48	0.07	0.37	0.81	0.72	1.00			
K	0.01	–0.60	0.45	0.54	0.26	0.49	0.01	1.00		
Ca	0.13	–0.52	0.26	0.72	0.50	0.59	0.23	0.51	1.00	
Mg	–0.21	–0.68	0.40	0.76	0.66	0.76	0.49	0.60	0.83	1.00
6/24/98	–0.66	–0.64	0.50	0.70	0.80	0.79	0.61	0.33	0.49	0.67
6/25/98	–0.63	–0.59	0.53	0.71	0.77	0.76	0.59	0.30	0.49	0.68
7/2/98	–0.65	–0.68	0.37	0.67	0.84	0.83	0.65	0.33	0.48	0.67
7/9/98	–0.45	–0.50	0.65	0.68	0.47	0.56	0.23	0.51	0.43	0.59
7/30/98	–0.59	–0.57	0.55	0.65	0.68	0.74	0.60	0.49	0.35	0.57
8/14/98	–0.57	–0.63	0.59	0.58	0.61	0.69	0.58	0.47	0.32	0.58
8/28/98	–0.44	–0.60	0.56	0.50	0.43	0.55	0.36	0.63	0.24	0.41
9/13/98	–0.47	–0.72	0.58	0.65	0.60	0.68	0.51	0.56	0.42	0.61
10/7/98	–0.51	–0.68	0.62	0.57	0.51	0.62	0.51	0.51	0.32	0.60
10/23/98	–0.12	–0.44	0.48	0.33	0.19	0.27	0.28	0.37	0.22	0.34
10/24/98	–0.27	–0.52	0.53	0.43	0.34	0.40	0.41	0.39	0.25	0.43
11/6/98	–0.32	–0.41	0.59	0.41	0.29	0.43	0.39	0.33	0.28	0.55
11/14/98	-0.47	–0.44	0.32	0.12	0.34	0.43	0.45	0.12	–0.01	0.31
Grow98	–0.63	–0.63	0.53	0.72	0.76	0.78	0.57	0.40	0.48	0.67
NonGrow98	–0.44	–0.65	0.61	0.52	0.47	0.58	0.49	0.50	0.30	0.54
Annual98	–0.58	–0.70	0.63	0.67	0.66	0.74	0.58	0.49	0.42	0.66

SD, standard deviation; CV, coefficient of variation; OM, organic matter; TKN, total Kjeldahl nitrogen; Grow98, growing season in 1998, including June and July; NonGrow98, non-growing season in 1998, including August through November. The absolute value >0.46 indicates that correlation is significant.

measurements of soil CO_2 efflux on 14 November 1998, any data obtained after that day were omitted for this correlation analysis.) First, when the CO_2 efflux averaged over a period from 24 June to 14 November 1998 are correlated with soil property variables, it is found that total Kjeldahl nitrogen, bulk density, microbial biomass, organic matter content, and exchangeable magnesium have relatively high correlation coefficients. A single variable from this group can explain 44–55% of the variance in the CO_2 efflux of the 18 points. However, the correlation with calcium is insignificant ($P = 0.12$). Second, soil pH value and bulk density in the top 10 cm are negatively correlated with soil CO_2 efflux. Soil bulk density explained about 49% of the variance of CO_2 efflux and pH explained 34%. Third, significant correlation is also found for fine root biomass and phosphorus. We divided the growing and nongrowing season, using the end of July as cut-off date. When CO_2 efflux was averaged separately for growing and nongrowing seasons and then correlated with the soil property variables, an apparent distinction was found between the correlation coefficients for the group of variables that have higher correlation with annual average of CO_2 efflux. This group consists of total Kjeldahl nitrogen, bulk density, microbial biomass, organic matter content, and exchangeable magnesium. These variables all have a much higher correlation with CO_2 efflux during the growing season, while the correlation during the non-growing season is almost insignificant for all the variables (Table 2). This contrast in correlations for growing and nongrowing seasons is also shown when daily CO_2 efflux data were correlated with the soil property variables (Table 2). All of the environmental variables listed in Table 2 explained 84% of the spatial variations in annual CO_2 efflux in 1998 when a multiple regression analysis was applied.

Table 3 The spatial variations of soil temperature and moisture in explaining the variance of CO_2 efflux in growing, non-growing and whole season (sample size is 18 for all the analyses)

	Growing season[a]		Non-growing season[b]		All seasons[c]	
Model	R^2	P	R^2	P	R^2	P
Equation 1	0.01	0.89	0.24	0.04	0.05	0.38
Equation 2[d]	0.17	0.09	0.21	0.05	0.18	0.08
Equation 3	0.15	0.30	0.34	0.04	0.21	0.17

[a]May–July. [b]August–April (except snow covered periods). [c]Excluding snow covered periods. [d]Gravimetric water content.

Effects of soil temperature and moisture on soil CO_2 efflux

The spatial variation of soil CO_2 efflux was poorly explained by the spatial variations of soil temperature and moisture (gravimetric). For growing season and all seasons, none of the models (Eqns 1, 2, and 3) are significant ($\alpha = 0.05$) in explaining the spatial variation of CO_2 efflux (Table 3). For nongrowing season, the models are only marginally significant ($\alpha = 0.05$) and explain no more than 35% of the variance in CO_2 efflux (Table 3).

However, the temporal variation of soil CO_2 efflux can be explained well by the temporal variation of soil temperature and moisture (volumetric). Fitting (3) with all the data collected from June 1998 to August 1999 (averaged over 18 measurement locations) showed that soil temperature and moisture combined explained 70% of the temporal variation of soil CO_2 efflux, although a direct univariate regression based on (1) and (2) failed to achieve a high value of R^2 (data are shown in Fig. 3). The relationship between soil CO_2 efflux and soil temperature (Eqn 1) was affected by soil moisture. For those measurements where soil moisture was lower than 14%, soil temperature explained about 60% of the variance of CO_2 efflux. When soil moisture was higher than 14%, soil temperature explained 73% of the variance of CO_2 efflux (Fig. 3). The relationship between CO_2 efflux and soil moisture (Eqn 2) depends also on the magnitude of soil moisture. When soil moisture was below 19%, soil moisture and CO_2 efflux was positively correlated ($R^2 = 0.54$, $P \approx 0$, $N = 59$). When soil moisture was above 19%, soil moisture and CO_2 efflux was negatively correlated ($R^2 = 0.74$, $P \approx 0$, $N = 21$) (Fig. 4). Regrouping the data based on moisture can significantly improve the model result for predicting soil CO_2 efflux. For soil moisture below 19%, the relationship between CO_2 efflux and soil temperature and moisture can be empirically fitted as:

$$F = 0.33W^{0.69}e^{0.042T} \quad (R^2 = 0.76, P \approx 0, N = 59). \quad (8)$$

When soil moisture is above 19% the relationship can be fitted as:

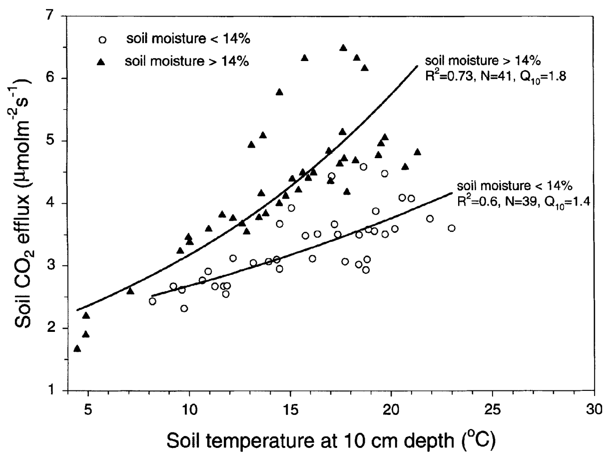

Fig. 3 The effect of soil moisture on the relationship between soil CO_2 efflux and soil temperature. High Q_{10} value corresponds to high soil moisture. Each datum represents the average over 18 measurement locations.

$$F = 26.17W^{-0.82}e^{0.047T} \quad (R^2 = 0.95, P \approx 0, N = 21). \quad (9)$$

Note that in the bivariate model, soil moisture positively contributes to soil CO_2 efflux when soil moisture < 19% (Eqn 8) and turns to the opposite when soil moisture > 19% (Eqn 9).

Discussion

Soil CO_2 efflux and its variation

The measurements of soil CO_2 efflux (2.43–6.03 μmol m^{-2} s^{-1}) presented herein fall right in the range of 1.0–6.5 μmol m^{-2} s^{-1} reported by Law *et al.* (1999) for a ponderosa pine plantation in central Oregon with a similar climate pattern to the present study site. These results also agree well with those of Davidson *et al.* (1998), who reported a range of 0.44–6.97 μmol m^{-2} s^{-1} for a temperate mixed hardwood forest in Massachusetts. Compared to other measurements of soil-surface CO_2 efflux, in France Epron *et al.* (1999a) found a range of 0.4–4.0 μmol m^{-2} s^{-1} for a beech forest and Thierron &

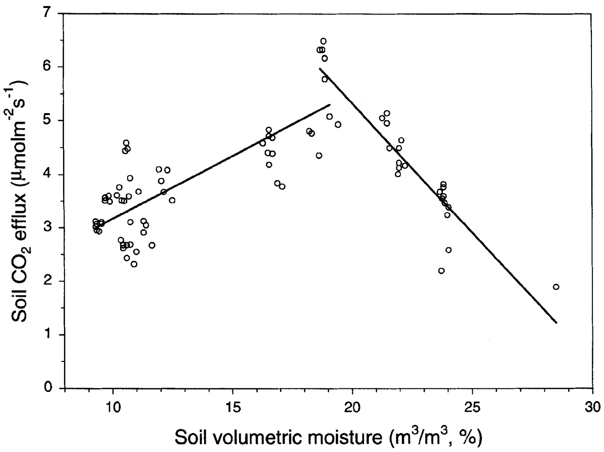

Fig. 4 The relationship between soil CO_2 efflux and soil moisture: soil CO_2 efflux and soil moisture are positively correlated when soil volumetric moisture < 19% and negatively correlated when soil volumetric moisture > 19%. Each datum represents the average over 18 measurement locations.

Laudelout (1996) measured the daily average CO_2 efflux varied from 3.2 to 10.7 μmol m^{-2} s^{-1} in June in a French deciduous forest. While multiple factors contribute to the differences in the measurement results, the generally low soil moisture, high soil temperature and soil organic matter content from the residuals of previous harvest at our site are believed to be the three major factors that determine the magnitude of the soil CO_2 efflux at the present study site.

Jensen *et al*. (1996) measured soil-surface CO_2 efflux over two days with 8 data points in a *Pinus radiata* D. Don forest in New Zealand using a dynamic chamber method (portable infra-red CO_2 analyser). Their results showed no apparent diurnal pattern in CO_2 efflux, which may be a consequence of the lack of variation in soil temperature (at 15 cm depth) and the high soil moisture (close to field capacity during the measurements). Davidson *et al*. (1998) reported a diurnal trend resembling the temperature pattern. Kutsch & Kappen's (1997) measurements at crop fields showed a diurnal trend of CO_2 efflux similar to ours, except that their diurnal maximum occurred later (about 16.00 hours). The asymmetric diurnal pattern obtained in the present paper (Fig. 1) suggests that using daytime measurements to represent daily mean soil CO_2 efflux will tend to overestimate daily average CO_2 efflux. Thus, it is not appropriate to scale-up soil CO_2 efflux to a longer temporal scale based on daytime measurements of CO_2 efflux and daily soil temperature. Larionova *et al*. (1989) suggested that soil respiration measured between 09.00 and 11.00 hours can be used to estimate the daily mean CO_2 efflux rate; by this method in the present data, it was found that the sampling error in estimates the daily mean soil CO_2 efflux could be reduced to 0.9–1.5%.

Soil CO_2 efflux in the young ponderosa pine plantation studied herein appears to have smaller seasonal variation than those obtained in previous studies of various forest ecosystems. Specifically, greater values were obtained for early summer (June) and early winter (November and December), but smaller values for midsummer. Fang *et al*. (1998) measured soil CO_2 efflux in a 26-y-old slash pine plantation in Florida and found the efflux rate was about 4.9 μmol m^{-2} s^{-1} in October and about 2 μmol m^{-2} s^{-1} in January. Billings *et al*.'s (1998) study of a mature boreal forest showed that soil CO_2 efflux was only 1.3 μmol m^{-2} s^{-1} in early June but about 5.7 μmol m^{-2} s^{-1} in August. The differences in seasonal variation may be attributed to the differences in seasonal changes of soil temperature and moisture. Summer drought at the present study site effectively limited soil CO_2 evolution and offset the temperature effect that would enhance CO_2 production during the summer. The constraints on soil CO_2 efflux in mid-summer may have resulted from reduced microbial activity owing to low soil moisture. Raison *et al*. (1986) suggested that a minimum soil moisture content might be required for microbial activity in the decomposition processes. In Billings *et al*.'s (1998) study, the soil did not experience apparent moisture stresses, so the soil CO_2 efflux more or less followed the temporal variation of the soil temperature. In addition to moisture and temperature effects, the high rate of CO_2 efflux in late May and early June at the present site may be related to the root phenology of shrubs and trees (Singh & Gupta 1977). Root respiration has been estimated to account for 30–90% of the total soil-surface CO_2 efflux (Bowden *et al*. 1993; Thierron & Laudelout 1996; Epron *et al*. 1999b). The seasonal pattern found in this study resembles the one found by Law *et al*. (1999) at a ponderosa pine plantation in Oregon; in addition to the general trend, Law *et al*. also found an abrupt 'jump' in soil CO_2 efflux in early June. The similarity is expected because the vegetation and climate conditions are comparable at the two sites.

The coefficient of variation of CO_2 efflux at the present study site is about 30%, which is lower than the value of 55% reported by Fang *et al*. (1998) in a slash pine plantation in Florida. In addition, Russell & Voroney (1998) found a coefficient of variation of CO_2 efflux between 16 and 45% along a 40-m transect, with 2–4 m sampling interval, in a mature aspen boreal forest. Understanding the spatial variability of CO_2 efflux within an ecosystem is critical to estimate the mean CO_2 efflux from the soil surface of the ecosystem. The estimation accuracy will generally improve with an increase in the number of sampling locations. The present study indicates that a sample size of 7 and 27 is large enough to estimate the mean soil respiration within 20% and 10% of the truth, respectively, at a confidence level of 90% in the plantation. Russell & Voroney (1998) suggested that a mean sample size of 40 could estimate the population mean soil CO_2 efflux within 10% and a sample size of 10 would estimate it within 20%. Stratified sampling techniques can be used to further improve the estimation accuracy and reduce the sample size, especially in a highly heterogeneous ecosystem (Fang *et al*. 1998).

The results presented herein also indicate that the spatial variation of CO_2 efflux is highly related to root and microbial biomass, soil physical and chemical properties, and soil temperature and moisture, which may provide clues to the design of stratified sampling in the field. For example, classifying the ecosystem into gaps and vegetation-covered areas would be appropriate because fine root biomass and soil CO_2 efflux are normally lower in gaps than under canopies (Brumme 1995). Additional categorization could include stratifying the study area into high and low nitrogen content zones according to soil maps or differentiating the ecosystem into north-facing vs. south-facing slopes, and flat vs. steep areas because soil temperature and moisture are often different among these topographic categories (Xu *et al*. 1997).

Relationships among soil CO_2 efflux, soil temperature, and soil moisture

Soil temperature and moisture, as well as their interaction, show significant effects on the temporal change of soil CO_2 efflux. Soil CO_2 efflux and soil temperature are exponentially related and their relationship is modified by volumetric soil moisture. Results presented herein support previous studies where low soil moisture constrains soil CO_2 efflux (Linn & Doran 1984; Doran *et al*. 1990; Bowden *et al*. 1998; Davidson *et al*. 1998). They also reveal Q_{10} decreases with the decline of soil moisture; the Q_{10} value was 1.4 and 1.8 for volumetric soil moistures of < 14% and > 14%, respectively (Fig. 3). This suggests that soil CO_2 efflux is less sensitive to soil temperature under lower soil moisture conditions. Dörr & Münnich (1987) conducted a multiyear study in a grassland and a beech–spruce forest in Germany, and found that yearly Q_{10} values varied from 1.4 to 3.1, with the low values occurring mostly in the wet years and the high values mostly in the dry years. The discrepancy may be a consequence of the wetter, finer-textured soil at their study sites. However, the present study supports Davidson *et al*.'s (1998) result showing low Q_{10} values at well-drained sites and the high values at wetter sites. Q_{10} values in a variety of forest soils have been reported in a range 1.4–5.6 (Schlesinger 1977; Dörr & Münnich 1987; Crill 1991; Kicklighter *et al*. 1994; Davidson *et al*. 1998). The Q_{10} values for the present study are in the lower part of the range because of the severe soil water stresses during the summer at the study site.

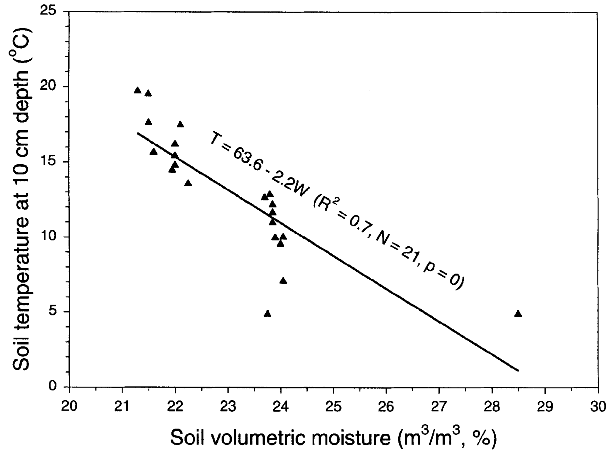

Fig. 5 Soil temperature (10 cm) and soil moisture are negatively correlated at high soil moisture conditions. Data points are averages across all measurement locations.

In contrast to the exponential relationship reported by Keith *et al*. (1997), a bimodal relationship was found herein, which showed that soil CO_2 efflux and soil moisture were positively correlated at low soil moisture contents (< 19%) and negatively correlated at high soil moisture contents (> 19%) (Fig. 4). This result agrees with that of Davidson *et al*. (1998), who studied a temperate mixed hardwood forest, but is based on a splitting point of soil moisture of 19% rather than the 12% reported by these authors. When soil moisture is greater than 19%, which mostly occurred during the winter and spring at the present site, soil temperature and moisture are negatively correlated ($R^2 = 0.7$, $N = 21$, $P = 0$) (Fig. 5). Therefore, the negative correlation between soil CO_2 efflux and soil moisture at high soil moisture is confounded by soil temperature. This negative effect at high soil moisture may also be related to the availability of O_2 in the soil pore space, which affects microbial activity. From laboratory and theoretical studies some researchers have found that high water content can impede diffusion of O_2 into the soil, which impedes decomposition and CO_2 production (Linn & Doran 1984; Doran *et al*. 1990).

Effects of roots, microbes, and soil properties on the spatial variation of soil CO_2 efflux

The results from this study showing increased soil CO_2 efflux in response to the increase in total N, P, organic matter, and fine root biomass are consistent with Joshi's (1994) study in broadleaf and conifer forest in Central

Himalaya. Total N augments soil CO_2 efflux rate by providing a source of protein for microbial growth (Tewary *et al*. 1982) and P availability may limit microbial biomass in mineral soils (Gallardo & Schlesinger 1994). The negative correlation between soil CO_2 efflux and bulk density indicates the importance of pore space for microbial activity (Elliot *et al*. 1980; Doran *et al*. 1990). The present results also show that the soil magnesium content (0–10 cm) is highly correlated with soil CO_2 efflux, especially in the growing season. The present authors have not seen any other studies that address the relationship between soil CO_2 efflux and soil magnesium content. It is speculated that Mg may affect soil microbial activity because soil microbial biomass and Mg are strongly correlated (R^2 = 0.58, N = 18, P = 0) (Table 2). However, it should be noted that the effect of each of these factors may not be individually explained because these factors are often strongly intercorrelated and covary with soil organic matter content and root respiration, major sources for soil-surface CO_2 efflux.

Conclusion

Soil-surface CO_2 efflux in a young ponderosa pine plantation ranges from 3.12 μmol m^{-2} s^{-1} in the non-growing season to 4.43 μmol m^{-2} s^{-1} in the growing season. Soil moisture and its interaction with soil temperature have a strong influence on the temporal variation of soil CO_2 efflux, especially during the summer when soil moisture is low. A nonlinear regression model including soil temperature and moisture explained 76% and 95% of the variation in soil CO_2 efflux for soil volumetric moistures of $<19\%$ and $>19\%$, respectively. Whereas soil temperature and moisture are good predictors of the temporal variation of CO_2 efflux, they are inadequate to explain the spatial variations of soil CO_2 efflux. Soil properties, especially the total Kjeldahl nitrogen, bulk density, microbial biomass, organic matter content, and exchangeable magnesium, seem to be better predictors of the spatial variation. This result that climatic variables control the temporal variation of soil CO_2 efflux and biological and soil processes dominate the spatial variation of CO_2 efflux, is useful for designing field experiments and selecting sampling techniques to improve the estimation of soil CO_2 emission from an ecosystem. However, it should be noted that this result is obtained from two 20×20 m plots. Physical and biological controls on CO_2 efflux may be different for ecosystems at larger scales. For example, soil moisture can be an important factor affecting the spatial variation of soil CO_2 efflux at large scales where soil drainage class varies over the landscape.

In order to scale-up the chamber measurements of soil CO_2 efflux to ecosystem level, it is necessary to incorporate into the model both temporal and spatial variations of CO_2 efflux. Spatially continuous measurements in soil temperature and moisture can be used to estimate soil CO_2 efflux along temporal scales such as daily, monthly, and annual soil CO_2 emission. Measurements and analyses such as these are of great importance for understanding how various ecosystem processes respond to the shifts in climate patterns and management regimes.

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