

Contrasting soil respiration in young and old-growth ponderosa pine forests

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Abstract

Three years of fully automated and manual measurements of soil CO₂ efflux, soil moisture and temperature were used to explore the diel, seasonal and inter-annual patterns of soil efflux in an old-growth (250-year-old, *O* site) and recently regenerating (14-year-old, *Y* site) ponderosa pine forest in central Oregon. The data were used in conjunction with empirical models to determine which variables could be used to predict soil efflux in forests of contrasting ages and disturbance histories. Both stands experienced similar meteorological conditions with moderately cold wet winters and hot dry summers. Soil CO₂ efflux at both sites showed large inter-annual variability that could be attributed to soil moisture availability in the deeper soil horizons (*O* site) and the quantity of summer rainfall (*Y* site). Seasonal patterns of soil CO₂ efflux at the *O* site showed a strong positive correlation between diel mean soil CO₂ efflux and soil temperature at 64 cm depth whereas diel mean soil efflux at the *Y* site declined before maximum soil temperature occurred during summer drought. The use of diel mean soil temperature and soil water potential inferred from predawn foliage water potential measurements could account for 80% of the variance of diel mean soil efflux across 3 years at both sites, however, the functional shape of the soil water potential constraint was site-specific. Based on the similarity of the decomposition rates of litter and fine roots between sites, but greater productivity and amount of fine litter detritus available for decomposition at the *O* site, we would expect higher rates of soil CO₂ efflux at the *O* site. However, annual rates were only higher at the *O* site in one of the 3 years (597 ± 45 vs. 427 ± 80 g C m⁻²). Seasonal patterns of soil efflux at both sites showed influences of soil water limitations that were also reflected in patterns of canopy stomatal conductance, suggesting strong linkages between above and below ground processes.

Keywords: *Pinus ponderosa*, soil CO₂ efflux, soil temperature, soil water content

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Introduction

In a recent synthesis of data from a wide range of forest ecosystems across Europe, it was concluded that the observed variation in net ecosystem carbon exchange (NEE) could be explained by the relative importance of ecosystem respiration (Valentini *et al.*, 2000). Further analysis indicated over two-thirds of this respiratory flux could be attributed to soil respiration (Janssens *et al.*, 2001), in general agreement with findings from earlier reports from both deciduous and coniferous forest ecosystems (Davidson *et al.*, 1998; Law *et al.*, 1999a; Longdoz *et al.*,

2000). NEE is the balance between two large fluxes, respiration by autotrophs and heterotrophs and assimilation, which determine the carbon sink or source strength of a forest. In studies of net carbon uptake by vegetation from the atmosphere, contributions from soils have generally received minimal attention, yet soil processes are very difficult to characterize when modeling ecosystem processes compared with quantifying rates of assimilation (e.g. Ryan *et al.*, 1997; Law *et al.*, 2000).

The widely used micrometeorological eddy-covariance method for determining NEE is often subject to substantial error under calm wind conditions at night (Law *et al.*, 1999b; Aubinet *et al.*, 2000; Baldocchi *et al.*, 2000), when soil efflux accounts for the majority of ecosystem carbon exchange (Lavinge *et al.*, 1997). Consequently manually

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based chamber techniques are widely used to determine the respiratory components of NEE. These techniques, although highly valuable, do not readily allow CO₂ fluxes to be measured at similar temporal scales as half-hourly eddy-covariance measurements, and consequently require the use of site-specific models to predict fluxes both spatially and temporally. They are also often limited due to the logistic considerations of collecting sufficient data to develop a detailed understanding of the variables controlling the fluxes under consideration. For example, widely reported Q₁₀ values for soil respiration (the relative increase in soil efflux rate for a 10 °C rise in temperature) are often given without explicit reference to where soil temperature was measured and whether the depth had been determined to be the best correlated with CO₂ efflux throughout the season. In addition, periodic measurements that are used to develop statistical soil CO₂ efflux models over the year may be subject to short-term environmental influences, such as recent rain events (e.g. Kelliher *et al.*, 1999; Law *et al.*, 2001b), which may bias model predictions.

Automated soil chamber systems are capable of providing some of the detailed information needed to help develop more widely applicable mechanistic models of soil CO₂ efflux, and in the process, help generate more accurate estimates of the contribution of soil respired CO₂ to eddy covariance estimates of NEE. Such systems allow continuous measurement of soil CO₂ effluxes on both diel and seasonal time scales, and provide the detail needed to explore the relationships between soil fluxes and key environmental variables. In this paper, we present results from manual and fully automated soil CO₂ efflux systems, together with environmental variables, to explore the patterns of soil efflux in young and old ponderosa pine forests in central Oregon. The study sites were selected from opposite ends of a chronosequence in an effort to improve our understanding of the current and future potential of forests to sequester carbon. We aim to address two questions in particular: (1) Are the diel, seasonal and inter-annual patterns of soil CO₂ efflux in a recently regenerating and an old-growth ponderosa pine forest comparable? and (2) Can soil CO₂ efflux be modeled using the same variables in both forests? These questions are extremely relevant at a time when estimates of carbon balance and storage are being developed across entire regions (Cohen *et al.*, 1996; Schimel *et al.*, 2000; IPCC, 2001).

Methods

Study sites

Both sites are situated in the eastern Cascades, near Sisters, Oregon, USA (Table 1), and are part of the AmeriFlux network of micrometeorological flux

Table 1 Characteristics of O and Y sites. Height data for the O site are given for the two size classes (0–30 cm, > 30 cm diameter breast height) based on survey data covering approximately 1 ha plots of each stand type (50 years: 874 tree ha⁻¹ and 250 years: 76 tree ha⁻¹). Y site characteristics were based on survey data covering 1570 m² ground area (~1200 tree ha⁻¹). Standard deviations where available are given within brackets

	O site	Y site
Latitude	44°30' N	44°26' N
Longitude	121°37' W	121°34' W
Elevation (m)	915	1188
Mean Annual		
Temperature (°C)	8.1	7.5
Annual precipitation (mm)	524	552
Age	50/250	14
Mean height (m)	10 (0.2), 34 (0.8)	2.7 (1.3)
Leaf area index	2.1	1.0
Soil sand/clay fractions (%)	62/8	65/10

measurement sites. The old-growth site (O) is located in the Metolius Research Natural Area and includes old (250 years), young (50 years) and mixed patches of ponderosa pine. Each age class accounts for approximately half the site leaf area index (LAI). The site has never been logged. The understory is sparse with patches of bitterbrush, bracken fern (*Pteridium aquilinum*) and strawberry (*Fragaria vesca*). The young pine site (Y) was previously an old-growth forest that had been clearcut in 1978, and allowed to regenerate naturally. The understory includes manzanita (*Arctostaphylos patula*) and bitterbrush (*Purshia tridentata*) and accounts for approximately 40% of the site LAI.

Soils are freely draining sandy loams, and classified as alfic vitrixerands and ultic haploxeralfs at the O and Y sites, respectively. Both sites experience warm dry summers and cool wet winters. Eddy covariance and periodic manual chamber based flux measurements of the components of NEE have been made at the O site since 1996 (Anthoni *et al.*, 1999; Law *et al.*, 1999b) and the Y site since 1998 (Law *et al.*, 2001a; Anthoni *et al.*, 2002).

Manual measurements of soil CO₂ efflux

Soil CO₂ efflux was measured on a monthly basis during 1999 and 2000 at each site using a LI-6400 with LI-6000-9 soil chamber (LI-COR inc, Lincoln, NE, USA). Measurements were made using PVC collars that had been placed in the soil the previous day to minimize disturbance effects. At the O site, 18 collars (10.7 cm diameter, 13 cm high) were installed leaving 2.5 cm protruding above the soil surface. They were randomly

distributed with six collars in each of three stand types; areas previously designated as pure old growth, areas of mixed age trees and areas of young trees. On nearly all occasions, collars were placed at points that did not include vegetation, however, occasionally shoots of *Fragaria* were removed before measurements were taken. At the Y site, due to the lack of a significant litter layer, collars 5 cm high were used, and 18 collars were placed randomly along a 60 m transect.

Automated measurements of soil CO₂ efflux

An automated, multiplexing, non-steady-state chamber system based on the design of Goulden & Crill (1997) was employed at each site and operated from 1999 through 2001. Twelve chambers with dimensions of 0.46 m side length, 0.15 m height, 0.21 m² sampling area and 0.032 m³ volume were fabricated from aluminium sheet. At each site, six chambers were installed permanently during the early summer of 1999. Chambers were selectively placed at points covering the range of conditions that were suspected to drive the spatial variability of soil CO₂ efflux, i.e. both close to and distant from surrounding trees and shrubs, under heavy shade and in open areas. Comparisons between spatially dynamic manual measurements and spatially fixed automated chamber measurements were used to ascertain spatial bias between the two techniques. Minimal alteration of temperature and moisture conditions was achieved by mounting the automated chamber lids on a frame that allowed each to be pivoted vertically and held clear from the soil surface when not in use (89% of the time). The chambers were actuated pneumatically using compressed nitrogen. The lower edge of each chamber, constructed of aluminium angle, was permanently installed 2.5 cm into the soil surface. This arrangement allowed unrestricted root growth below the chamber. We tested the impact of pressure equilibration tubes on efflux measurements by adding tubes suitable for the chamber volume (Hutchinson & Mosier, 1981). We were unable to detect any differences in soil efflux measurements with the addition of such tubes, and consequently they were not used during this study. Chambers were connected to a central box containing an infrared gas analyser (LI-6262), a pump, solenoids, and logging and control equipment (Campbell Scientific, Logan, Utah, USA). The single control box was moved between sites at approximately 2-week intervals. Measurements were made on each chamber sequentially, all six chambers being measured within a 1.5 h period, the process being repeated 16 times per day. During a measurement, the chamber lid was lowered for 10 min and the concentration of CO₂ was recorded at minute intervals (2 s averaging). A 5-min period was left between measurements on chambers.

The linear increase in CO₂ concentration over the final 9 min of this 10-min measurement period was used to determine the rate of soil efflux. Data invariably showed a high coefficient of determination (r^2) and data with r^2 of 0.98 or less were discarded as they were considered to be the consequence of leaks. At the time of a measurement, soil temperature was automatically recorded at 2, 8 and 15 cm depths and soil moisture at 10 cm and 30 cm depths below each chamber (CS615, Campbell Scientific). The automated chamber system determined soil CO₂ efflux rate as CO₂ concentration increased above ambient resulting in a small reduction in the natural diffusion gradient. This artifact is a widely recognized trait of non-steady-state chamber soil efflux systems (Livingston & Hutchinson, 1995) and was quantified in this study. For approximately 1 week at each site the system was run in a mode whereby chamber headspace CO₂ concentration was reduced 15 $\mu\text{mol mol}^{-1}$ below ambient CO₂ concentration at the beginning of each measurement and the rate of soil efflux determined both as the chamber headspace CO₂ concentration passed through ambient concentration, and as chamber headspace CO₂ concentration increased above ambient during the remaining cycle of the measurement. It was found that on average the rate of soil CO₂ efflux was underestimated by 14 and 8%, at the O and Y site, respectively, when using the automated chamber in the normal mode of operation. Consequently all data collected with the automated soil chamber system were corrected accordingly.

Separation of autotrophic and heterotrophic respiration

A simple technique to determine the relative contributions of autotrophic (root) and heterotrophic respiration to soil surface CO₂ effluxes was applied at both sites. Measurements were made in June (day 153), July (day 201), and October (day 278) 2000. Total soil surface CO₂ efflux was measured with a LI-6000-9 soil chamber using PVC soil collars that had been placed 1 cm into the Oa horizon at least 24 h earlier to minimize disturbance effects. Litter was then removed and placed within a capped LI-6000-9 soil chamber for measurement of litter respiration. Root respiration was measured the next morning at the same time of day. Fine and coarse roots were sifted from 30 cm deep cores taken from directly beneath the soil collars and measured in the capped LI-6000-9 soil chamber. Timing has been refined to minimize change in soil temperature and moisture during the measurements (Law *et al.*, 2001a, 2001b).

Subsidiary measurements

Soil moisture and soil temperature profile measurements were made continuously below each automated soil

respiration chamber. In addition, soil moisture was measured at one location at each site at 3 cm depth to detect transient soil surface rewetting due to summer rainfall events (CS615). Soil temperature was measured half-hourly at two locations at the O site at 32 cm and 64 cm depths, and one location at the Y site at 32 cm depth. Rooting zone soil water potential was determined approximately monthly from predawn needle water potential measurements made with a pressure chamber. Previous-year needles were sampled from 10 trees per site and soil water potential inferred from foliage values after accounting for gravitational potential (-0.1 MPa per 10 m of measurement height above ground).

Results

Chamber comparisons

Comparison of manual and automated soil CO₂ efflux measurements at both sites indicated good agreement between techniques (Fig. 1). On 14 out of the 19 occasions when data were available from both systems over the same measurement period, there were no significant differences ($P < 0.05$) between effluxes measured by the different techniques. On this basis, we considered no significant spatial bias was detected between the two measurement techniques, and consequently the degree

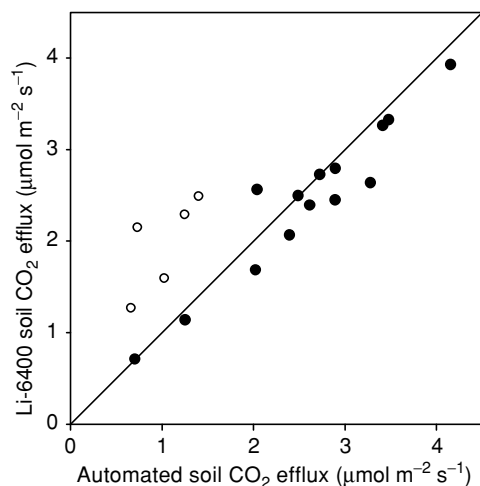


Fig. 1 Comparison of manual and automated soil CO₂ efflux measurements at both sites. Each point is the mean of 18 manual measurements (Li-6400 with Li-6000-9 chamber) and 6 automated chamber measurements made over the same 90-minute period. Comparisons were made at various points across the season. Manual measurements were taken at different locations on all occasions but automated chambers were spatially fixed. Closed symbols indicate no significant differences between measurement techniques ($P < 0.05$). The one-to-one relationship is shown (fine line).

of accuracy (i.e. closeness to the true population mean) of the mean soil efflux as determined by the manual measurements was assumed representative of the accuracy of the mean soil efflux measured by the automated chambers. At the O site, the mean soil CO₂ efflux would be on average within 20% of the population mean ($P = 0.10$). At the Y site, the mean soil CO₂ efflux would be on average within 15% of the population mean ($P = 0.10$). The five open points (Fig. 1) showed significant differences between techniques; four out of five of these points were from comparisons made at the O site and each was associated with rain events on the day of soil collar installation or soil efflux measurement. On such occasions we speculate the manual efflux technique may overestimate soil efflux due to litter disturbance caused by the installation of relatively deep soil collars in conjunction with rewetting the litter due to rainfall.

Seasonal patterns of soil variables and CO₂ efflux

The seasonal pattern of soil moisture depletion and associated soil temperatures were representative of the continental type climatic conditions on the east side of the Cascades (Fig. 2). Soil moisture deficit developed between April and October followed by recharge by late season rain and snowfall. Winter precipitation during 2000 was substantially lower than the previous 2 years at both sites (Table 3) and resulted in a more rapid decline in soil water potential during the following summer (2001) than compared to the previous years (Fig. 2). The soil water potential at 30 cm depth, computed from soil texture and moisture measurements (Saxton *et al.*, 1986), reached values below -3 MPa during the latter summer months across all years at both sites. The difference in maximum soil moisture between sites was in part attributed to higher soil porosity at the O site, with bulk densities of 1.14 g cm⁻³ at the O site and 1.35 g cm⁻³ at the Y site as measured over 100 cm depth. There were no substantial differences in sand and clay fractions averaged over the same depth, 62% sand and 8% clay at the Y site and 65% sand and 10% clay at the O site. Diel mean soil temperatures at 15 cm depth peaked in early August at both sites, however, between days 100 and 300, values at the Y site remained on average 2.0 °C higher than those at the O site (Fig. 2).

The range of diel mean soil CO₂ efflux measured by the automated chambers was similar between sites (0.4 – 4.0 μmol m⁻² s⁻¹) although each site exhibited markedly different seasonal patterns (Fig. 2). At the O site, soil efflux showed a strong positive seasonal correlation with soil temperature (Fig. 3). At the Y site, a much weaker relationship between soil efflux and soil temperature was observed (Fig. 3); soil efflux peaked in late May approximately 2 months before maximal soil temperatures

Fig. 2 Seasonal variation of diel mean soil CO₂ efflux measured with the automated chambers at both sites across three seasons. Overlaid lines refer to the site-specific models fitted to the data (see modeling section for details) and extrapolated using entire annual course of driving variables. For clarity, modeled flux is only shown for 2000 (both sites, heavy line) and 2001 (O site only, fine line). Also shown are diel mean soil temperature at 15 cm depth (10 day average), diel mean soil volumetric moisture content (VMC) at 10 cm horizon (10 day average) and soil water potential inferred from predawn foliage water potential (bars indicate ± 1 SE).

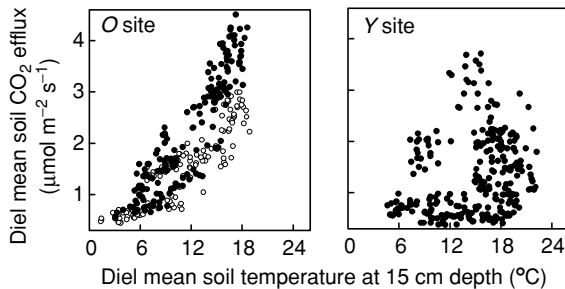
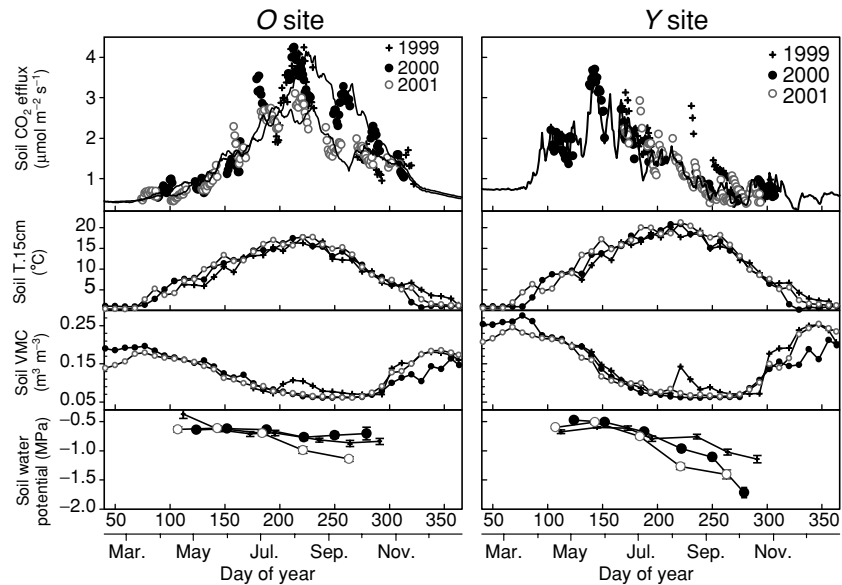


Fig. 3 Correlation between diel mean soil CO₂ efflux from the automated chamber system and diel mean soil temperature at 15 cm depth. Three seasons of data are shown. For the O site, data from 2001 is indicated by open symbols (season with reduced soil water availability).

occurred, and thereafter declined with increasing soil water deficit (Fig. 2). Soil CO₂ efflux at the O site showed a stronger seasonal decline during 2001 in comparison to previous years that was correlated with lower values of soil water potential as determined from predawn foliage water potential. Small summer rainfall events (Fig. 4) have a transient impact on the seasonal patterns of soil efflux relative to the influence of the underlying seasonality in soil temperature (both sites) and soil moisture deficit (principally Y site). Between mid-August and mid-October (Fig. 4) approximately one-third of the 43 g C m⁻² that was respired from the soil at the Y site could be attributed to these rain events. However, we predict that if there had been no soil moisture deficit, approximately 317 g C m⁻² would have been respired during the same period (see modeling section, predicted using model 7), illustrating that soil moisture availability primarily controlled soil CO₂ efflux during this period.

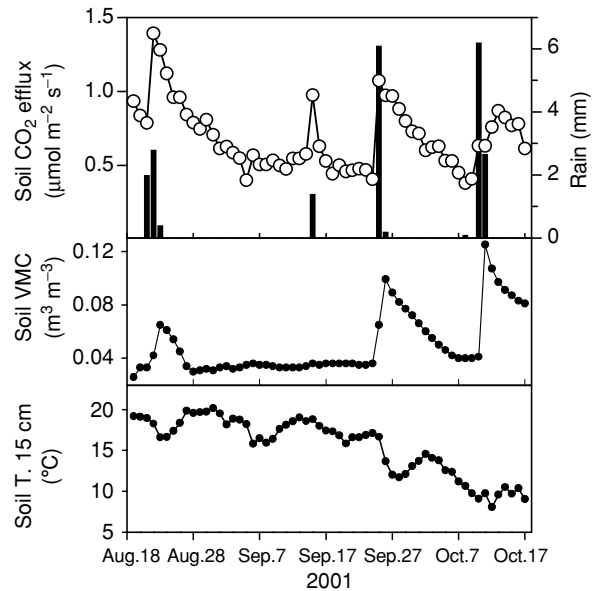


Fig. 4 Influence of rainfall events (vertical bars) on diel mean soil CO₂ efflux (open symbols) over a 2-month period at the Y site. Data shown is the mean of six automated chambers. Also shown is diel mean soil moisture at 3 cm depth and soil temperature at 15 cm depth.

The coefficient of variation (CV) of diel mean soil efflux measured with the automated chambers showed a distinct pattern at both sites (Fig. 5), and was generally lowest in mid-summer. A bimodal distribution with maximum variation at days 135 and 260 was evident at the O site. At the Y site, the CV decreased from the start of measurements on day 103 to day 170 then increased to a second maximum by day 250.

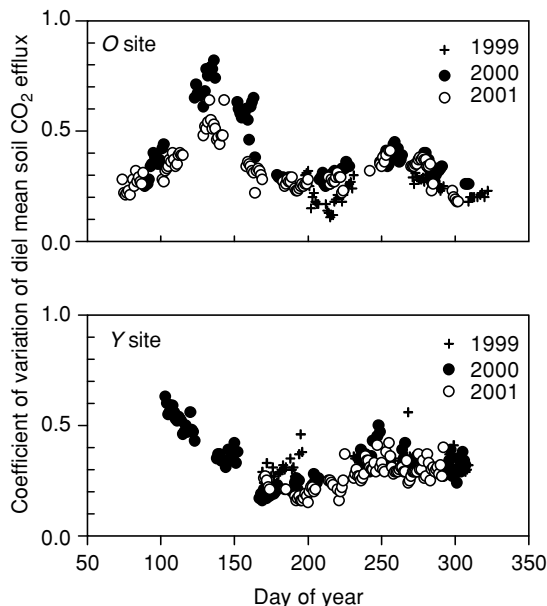


Fig. 5 Coefficient of variation between diel mean soil effluxes measured by the automated chambers at both sites across three seasons.

Separation of autotrophic and heterotrophic respiration showed that at the O site, roots accounted for 43% of soil surface CO₂ efflux in June, 53% in July, and 42% in October. At the Y site, roots accounted for 49% of soil surface CO₂ efflux in June, and 53% in July and October. The standard error was 8% in most cases, indicating no significant difference in fraction of total soil efflux that was from roots among sample periods. Thus, roots accounted for about half of total soil surface CO₂ efflux through the growing season. Fine root biomass in the 30 cm deep soil cores was lowest in June at both sites (141 g C m⁻² at Y site, SE 33; 159 g C m⁻² at O site, SE 29), and peaked in July at the Y site (753 g C m⁻², SE 96) and October at the O site (807 g C m⁻², SE 156). Litter was scant and often dry, and accounted for only 4–6% of the total soil surface CO₂ efflux at both sites in spring 2000, and 12–17% in spring of 2001 when litter moisture was greatest. During the dry summer, CO₂ efflux from litter was undetectable.

Diel patterns of soil CO₂ efflux

To explore the degree of hysteresis or lag between hour-by-hour patterns of soil warming (or cooling) at one of several depths and hour-by-hour patterns of efflux from the soil surface, the product moment correlation coefficient (r) was computed each day between the mean soil efflux from the six automated chambers (over a 1.5-h period) and soil temperature measured at 2, 8 and 15 cm depth (Fig. 6). Before correlations were calculated, values

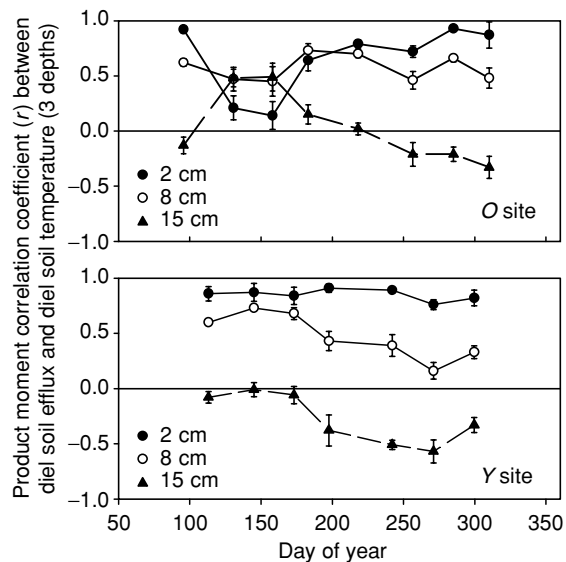


Fig. 6 Correlation between diel pattern of soil CO₂ efflux and diel patterns of soil temperature measured at 2, 8 and 15 cm depth at both sites during 2000. Correlation coefficients were averaged over approximately 2-week periods at each site to generate each point. Bars indicate ± 1 SE.

of efflux and temperature within each day were normalized (between 0 and 1) to remove bias associated with smaller ranges of diel temperature at greater soil depth. A strong positive correlation indicates a small lag between soil warming at that depth and soil efflux, whilst a negative and weaker correlation indicates substantial lag between soil warming at that depth and soil efflux. The average correlation coefficient was calculated for each 2-week period that the automated soil efflux system was running at each site during 2000. At both sites, diel patterns of soil efflux were most positively correlated with diel patterns of soil temperature measured at 2 cm depth when viewed across the season as a whole. The exception was between approximately day 125 and day 165 at the O site, when soil efflux was better correlated with soil temperature at either 8 cm or 15 cm depth. Outside this period, soil efflux at both sites almost exclusively showed a weak negative correlation with soil temperature at 15 cm depth. At both sites, the degree of correlation between soil efflux and temperature at either 8 cm or 15 cm depth decreased after approximately day 165, providing evidence for a greater lag between soil efflux and soil temperature at this depth during the latter half of the season.

Conceptually it is useful to consider soil CO₂ efflux as the sum of two (or more) components being generated on different time scales; (a) an underlying flux which appears correlated with diel mean soil temperatures and (b) an efflux superimposed on this that shows a diel oscillation which is highly correlated with diel

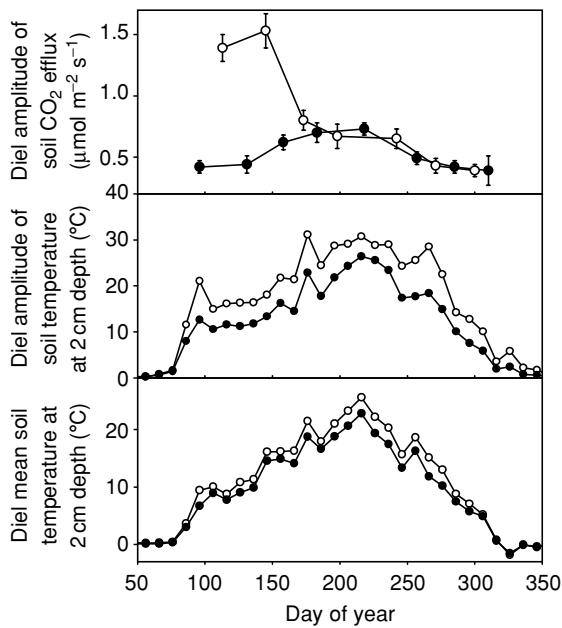


Fig. 7 Diel amplitude of soil CO₂ efflux at each site during 2000. Values were averaged over approximately 2-week periods to generate each point. Diel amplitude of soil temperature at 2 cm depth (10 day average) and diel mean soil temperature at 2 cm depth (10 day average) are also shown. Bars indicate ± 1 SE.

patterns of soil temperature close to the surface. To further investigate these superimposed diel oscillations of soil CO₂ efflux we examined the diel oscillations of efflux in relation to diel patterns of soil temperature at 2 cm depth (Fig. 7). The diel amplitude of soil efflux at both sites was substantial. At the O site, the diel amplitude of soil efflux showed a unimodal pattern across the season with the greatest amplitude in soil efflux corresponding to the time of greatest diel amplitude in soil temperature. At the Y site, when soil water availability was high (prior to day 160), there was substantially greater diel amplitude in soil efflux than the rest of the year. Data beyond day 160 showed similar values, and followed a similar pattern to that at the O site.

Modeling seasonal soil CO₂ efflux

Empirical models of a multiplicative form were used to describe the correlation of diel mean soil efflux to soil temperature and soil moisture (Table 2). As a consequence of the highly contrasting seasonal patterns of soil efflux at O and Y sites in spite of similar seasonal patterns of soil temperature and soil moisture depletion within the upper soil profile, no single empirical model using temperature and moisture at a specified depth fit the data well at both sites. At the O site, diel mean soil CO₂ efflux showed a non-linear relationship with diel mean soil temperature (Fig. 3). The use of soil

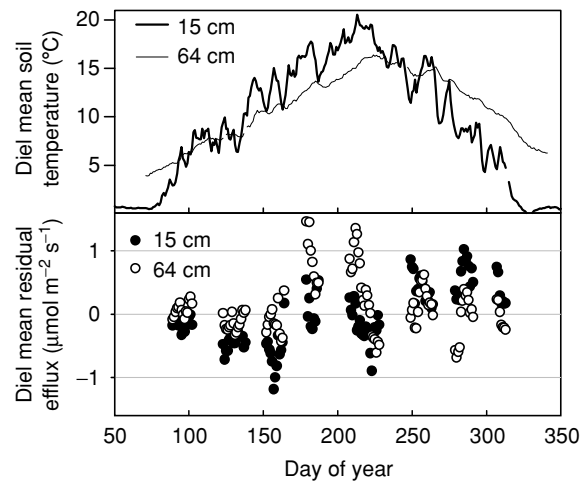


Fig. 8 Diel mean soil temperature at O site at 15 cm (heavy line) and 64 cm (fine line) depth during 2000. Modeled residual soil CO₂ efflux based on models of soil efflux driven by soil temperature at 15 cm (●, model 1) and 64 cm (○, model 2) depth (see modeling section for details).

temperature at 15 cm depth in an exponential function accounted for 73% of the variance of soil efflux when fitted to data for all three seasons (Table 2; model 1). However, even during 2000 (year with no detectable water limitations), the residuals were unevenly distributed with overestimation of soil efflux in the first half of the year and underestimation of efflux in the latter half of the year (Fig. 8). Soil temperature at 64 cm depth provided a more even distribution of residuals across the year due to the seasonal lag in soil warming at this depth (Fig. 8, Table 2; model 2). Soil efflux data collected during 2001 fell below this underlying soil temperature relationship due to soil water limitations (Fig. 3), and the addition of a soil moisture function based on entire rooting zone soil water potential (Ψ_{soil}), inferred from predawn foliage water potential, could account for approximately 80% of the variance of diel mean soil efflux across the 3 years (Fig. 9; panel A, Table 2; models 3 & 4). Soil efflux normalized to a common temperature at the O site showed a weak relationship with soil water content at 10 cm depth (Fig. 9; panel B), and this measure of soil moisture was not used to generate a soil efflux model at the O site. To estimate annual soil effluxes at the O site, efflux model 4 (Table 2) was employed. We assumed that during early spring and fall, the periods during which predawn foliage water potentials were unavailable but soil moistures were high, that soil water potentials did not limit soil CO₂ efflux. The model predicted annual carbon losses at the O site of between 483 and 597 g C m⁻² yr⁻¹ over the 3 years (Table 3).

At the Y site, diel mean soil efflux showed a less tightly defined relationship with diel mean soil temperature than

Table 2 Selected models that were fitted across three seasons of diel mean soil CO₂ efflux data collected at both sites (F_s , $\mu\text{mol m}^{-2} \text{s}^{-1}$). Models describe the trends exhibited between F_s and diel mean soil temperature at 15 or 64 cm depth (T_{15} , T_{64} , respectively) and two measures of soil water deficit ($\delta\theta_{10\text{cm}}$ and $\delta\Psi_{\text{soil}}$), where $\theta_{10\text{cm}}$ is soil volumetric water content at 10 cm depth ($\text{m}^3 \text{m}^{-3}$) and Ψ_{soil} is soil water potential determined from predawn foliage water potential (MPa). Each measure of soil water deficit (δ) was expressed relatively between 0 and 1 (minimum and maximum water deficit, respectively) using $\delta M = (M_{\text{max}} - M)/(M_{\text{max}} - M_{\text{min}})$ where M refers to either $\theta_{10\text{cm}}$ or Ψ_{soil} and subscripts max and min refer to the maximum and the minimum values of the variable across the three seasons. Daily values of Ψ_{soil} were estimated by linear interpolation between periodic measurements

Model #	Model and fitted parameters	n	r^2
O site			
1	$F_s = 0.523 \cdot \exp(0.105 \cdot T_{15})$	298	0.73
2	$F_s = 0.268 \cdot \exp(0.158 \cdot T_{64})$	300	0.67
3	$F_s = 0.478 \cdot \exp(0.115 \cdot T_{15}) \cdot (1 - (0.0011 \cdot \exp(6.185 \cdot \delta\Psi_{\text{soil}})))$	271	0.78
4	$F_s = 0.285 \cdot \exp(0.189 \cdot T_{64}) \cdot (1 - (0.156 \cdot \exp(1.504 \cdot \delta\Psi_{\text{soil}})))$	271	0.81
Y site			
5	$F_s = 0.877 \cdot \exp(0.028 \cdot T_{15})$	271	0.05
6	$F_s = 0.857 \cdot \exp(0.109 \cdot T_{15}) \cdot (1 - (0.063 \cdot \exp(2.685 \cdot \delta\theta_{10\text{cm}})))$	268	0.80
7	$F_s = 6.100 \cdot \exp(0.050 \cdot T_{15}) \cdot (0.023 \cdot \exp(2.223 \cdot (1 - (\delta\Psi_{\text{soil}}))))$	255	0.81

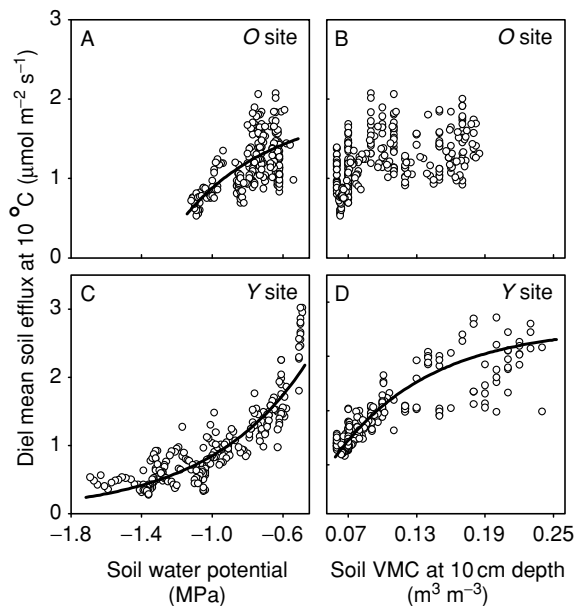


Fig. 9 Diel mean soil CO₂ efflux normalized to constant soil temperature (10°C) using temperature responses functions from soil CO₂ efflux models (Table 2). Overlaid lines are the fitted models. Models shown are # 4, 7 and 6 (panels A, C and D, respectively).

at the O site due to the influence of soil moisture deficit (Fig. 3). The use of soil temperature at 15 cm depth in an exponential function accounted for only 5% of the variance of soil efflux when fitted to data from all three seasons (Table 2; model 5). The addition of a soil moisture constraint based on either soil water content measured at 10 cm depth (Fig. 9; panel D, Table 2; model 6) or soil water potential inferred from predawn foliage water potential

(Fig. 9; panel C, Table 2; model 7) could account for approximately 80% of the variance of soil efflux across the 3 years. It should be noted that the functional forms for the soil water constraint using soil water potential at O and Y sites are contrary in nature; at the O site, the function employed is most sensitive to changes in water potential at the most negative water potentials (driest values) whereas the function employed at the Y site is most sensitive to changes in water potential at the values closest to zero (wettest values). Based on the sensitivity of soil efflux at the Y site to summer rain events (Fig. 4) the model using soil moisture at 10 cm depth (Table 2; model 6) was employed to determine annual carbon losses at this site. Such losses varied between 427 and 519 g C m⁻² yr⁻¹ over the 3 years (Table 3, Fig. 2 overlaid line).

Discussion

Highly contrasting inter-annual and seasonal patterns of soil CO₂ efflux were observed in old-growth and recently regenerating ponderosa pine forests in central Oregon. The majority of the variability could be explained by soil water limitations at both sites, although at each site these limitations acted in differing ways and degrees of intensity, over differing time scales. At the O site, soil water limitation to soil CO₂ efflux was discernable only in 2001 and diel mean soil efflux showed a strong positive seasonal correlation with soil temperature. At the Y site, soil water limitation to soil CO₂ efflux was detected across all 3 years with seasonal patterns of diel mean soil efflux declining before maximum seasonal soil temperature occurred.

The most suitable variable to describe water limitations on soil CO₂ efflux at the O site was the entire rooting zone

Table 3 Total summer (May through October) and winter (November through April) rainfall at O and Y sites together with modeled annual soil CO₂ effluxes, SE given within parentheses (error estimation is based on the assumption that the diel average standard error of the measured effluxes across all chambers can be used to represent degree of confidence in the modeled annual estimate)

Year	SUMMER				WINTER		Modeled annual soil	
	Precipitation (mm)		Days with Precipitation		Precipitation (mm)		CO ₂ efflux (g C m ⁻² y ⁻¹)	
	O site	Y site	O site	Y site	O site	Y site	O site	Y site
1998	172	–	39	–	554	–	–	–
1999	125	141	28	38	404	397	499 (32)	519 (68)
2000	65	65	40	42	200	199	597 (45)	427 (80)
2001	103	108	35	44	–	–	483 (68)	505 (38)

soil water potential as determined from predawn foliage water potential measurements. At this site, soil water potential fell below -0.9 MPa only during the latter part of the summer of 2001, corresponding with a decline in soil efflux (Fig. 2). Predawn foliage water potential is widely used to determine the degree of water stress being experienced by vegetation and is often correlated with reductions in carbon assimilation through declines in stomatal conductance. Canopy stomatal conductance measured at the O site during 1999 and 2000 (Irvine *et al.*, 2002) showed no declines in conductance attributed to soil water limitations. However, preliminary analysis of transpiration data for 2001 suggests a small summer decline in canopy conductance. The availability of soil water during the summer months at these sites is primarily driven by the degree of soil water recharge by winter rainfall. The total winter rainfall during 2000 was approximately half that during the previous winter and a small degree of water stress was observed during 2001 together with a reduction in soil CO₂ efflux.

At the Y site, both the entire rooting zone soil water potential and the soil water content measured at 10 cm depth were suitable variables to describe water limitations on soil CO₂ efflux (Table 2). However, to model seasonal patterns of diel mean soil efflux, using soil water potential required a function that showed high sensitivity at high potential (i.e. close to zero, wetter soils), and low sensitivity at the lower potentials (drier) soil. Such a pattern of sensitivity of soil efflux to soil moisture availability is counter intuitive. In addition, seasonal patterns of soil CO₂ efflux at the Y site showed perturbations due to rainfall events that are not reflected in predawn foliage water potential measurements but were reflected in soil moisture measurements close to the soil surface. Consequently soil moisture at 10 cm depth was the most suitable variable to describe seasonal water limitations on soil CO₂ efflux at this site. Measurements of tree transpiration made at the Y site

indicated strong declines in canopy stomatal conductance from mid-June onwards over all 3 years that could be attributed to soil water limitations (Irvine *et al.*, 2002). Annual estimates of soil efflux at this site were positively correlated to total summer rainfall (Table 3). In 2000, the drier summer was responsible for a 17% decrease in annual soil CO₂ efflux compared to 1999 and 2001. Based on the annual variability of summer rainfall measured over the last 16 years in Sisters (Oregon Climate Service, <http://www.ocs.orst.edu/>), we would expect such a reduction in soil CO₂ efflux to occur at the Y site approximately 1 year in eight.

At both sites, the majority of fine root biomass was found within the upper 30 cm of the soil profile (O. J. Sun, pers. comm.), and fine root respiration directly contributed approximately half of the total soil surface CO₂ efflux. Thus, the upper 30 cm of the soil profile likely accounts for the majority of soil surface CO₂ efflux. The insensitivity of soil CO₂ efflux at the O site to soil moisture depletion over much of the range of soil water content within this zone (Fig. 9; panel B) is therefore counter-intuitive and warrants further investigation. One recent study at the O site suggested that hydraulic redistribution of water from deep in the soil profile to shallow lateral roots occurs overnight (Brooks *et al.*, 2002). It is conceivable that such a mechanism could allow fine roots to maintain a favorable water status in an otherwise dry soil layer, facilitating respiratory activity. Measurements of soil moisture using TDR perhaps only reflect the moisture status of the bulk soil and not that of the fine roots. At the Y site, soil water content below 1 m depth showed little seasonal depletion (J. R. Brooks pers. comm.), indicating little rooting to this depth at this site.

The high spatial variability of soil CO₂ efflux in May and September (Fig. 5) was not correlated with patterns of fine root biomass at both sites (i.e. low root biomass in spring at both sites, high in summer at Y site and high in

fall at *O* site). The bimodal peaks of this pattern at the *O* site were however correlated with times when large changes in the rate of root production were observed (C. Andersen, pers. comm.).

At both sites, the diel amplitude of soil efflux (Fig. 7) in relation to the diel mean efflux (Fig. 2) was substantial. The diel amplitude of soil efflux was 59% and 33% of the diel mean efflux at the *Y* and *O* sites, respectively, when averaged across the season. At both sites, the diel amplitude of efflux in relation to the diel mean efflux was greater in spring when soil moisture was available in upper soil layers than in summer in spite of the greater amplitude in soil temperature at this time of year. Other studies report relatively stable diel soil CO₂ effluxes and soil temperatures (e.g. Buchmann, 2000; Davidson *et al.*, 2000). This source of variability may be a significant issue at some sites when using periodic manual measurements to estimate diel mean soil efflux, especially if information about any seasonality in the timing of diel maximum and minimum efflux is unavailable (Fig. 6). For example, in this study, the two times of day chosen at the *Y* site to measure soil efflux with the manual system were initially made without benefit of the diurnal soil efflux information generated by the automated system. As a consequence, estimates of diel mean efflux generated by the manual technique were approximately 7% greater than if the two measurement times had better coincided with diel maximum and minimum efflux, an error easily propagated into annual soil efflux estimates. Diel patterns of soil efflux were most correlated with soil temperature at 2 cm depth except during late spring at the *O* site (Fig. 6). The extremely high soil temperatures and low moisture of soil in this surface layer in summer likely precludes it from being a significant source of respired CO₂. Considering that the soil temperature at 8 cm depth is lagged by approximately 3 h compared to soil temperature at 2 cm depth, and yet it is more likely that the hourly component of soil efflux is being generated closer to this depth than at 2 cm during the summer, it remains to be resolved why patterns of soil efflux within each day are not better correlated with soil temperature at some greater depth. One possibility is that soil CO₂ effluxes are closely coupled with canopy photosynthesis, which would be correlated with incident radiation (and thus air temperature, which is similar in amplitude and timing with soil temperature at 2 cm depth).

Although small rain events during the summer months resulted in brief periods of high soil CO₂ efflux (Fig. 4), these events did not appreciably rewet the soil profile, and the influence on annual soil efflux was insignificant. However, the intensity of rain events was important in determining inter-annual variability in soil efflux. Although there were a similar number of days with rainfall during summer 2000 compared with other years

(Table 3), approximately half the total amount of rainfall was recorded, which resulted in a substantially lower total annual soil efflux estimate. The influence of such rain events should be of concern to those using manual based soil efflux techniques to generate statistical seasonal models of efflux; measurements may be unknowingly made subsequent to such rain events and significantly bias the model predictions over the period between consecutive manual measurements.

In this study, we could not differentiate between the direct effect of soil drought on soil respiratory processes, and that of soil drought on the supply of photosynthates to the roots, due to reduced carbon assimilation. However, a recent study at the *O* site suggested that an appreciable fraction of the carbon detected in soil CO₂ efflux measurements was assimilated as few as 5 days previously (Bowling *et al.*, 2002); this confirms findings of Högberg *et al.* (2001) who suggest that such assimilates could account for at least 65% of total soil respiration. These results suggest that to adequately model soil CO₂ efflux, both above- and below-ground processes must be considered concurrently. To develop more generally applicable models of soil efflux, a better mechanistic interpretation of soil efflux is required. Information is needed on the contributions from autotrophic and heterotrophic sources, and how phenological changes in plants and microbial response to substrate availability through the soil profile influences soil CO₂ efflux. For models to be useful on fine temporal scales, they must be dynamic and consider soil water balance and the movement of drying and rewetting fronts across the soil profile.

Recent studies by Craine *et al.* (1999) and Janssens *et al.* (2001) also suggest that aboveground processes have a major impact on soil respiration, and soil processes should not be viewed in isolation from aboveground productivity. Annual aboveground productivity at the *O* site was more than twice that of the *Y* site (173 vs. 76 g C m⁻² y⁻¹), and annual foliage litter inputs were 40% higher at the *O* site, but both sites had similar inputs of fine root detritus and similar rates of fine root and litter decomposition (Law *et al.*, 2001a). These facts may lead us to believe that the *O* site should have substantially greater rates of soil CO₂ efflux compared to the *Y* site. However, modeled soil efflux at the *O* site was only higher than the *Y* site in one of 3 years. The relatively small differences between annual soil efflux estimates at the two sites do not reflect the substantial differences in aboveground productivity measured at both sites and would not support the hypothesis that productivity rather than specific environmental variables controls soil effluxes when making comparisons among sites (Janssens *et al.*, 2001).

The influence of forest age on soil efflux remains an important area of research. There seems a consensus that

rates of soil efflux directly after felling depend upon the quantities of debris left on site and the degree of site disturbance. Some studies indicate substantial increases in efflux soon after clear-cutting (e.g. Ewel *et al.*, 1986) whilst others report declines in efflux (e.g. Weber, 1990). Several years after felling however, there is no clear pattern in the literature as to whether soil efflux is consistently greater or smaller compared to efflux from the mature forest. Gordon *et al.* (1987) report greater soil effluxes in a spruce forest 4–5 years after being clear felled in comparison with mature uncut forest in Alaska. Ewel *et al.* (1986) on the other hand report lower soil effluxes in a 9-year-old pine stand compared to a mature stand in Florida. Our study suggests year-to-year climatic variability will likely determine whether an old-growth or 14-year-old forest will exhibit the highest soil efflux rates in this semiarid temperate region, where decomposition and turnover rates are much slower than for example, the warm temperate region of Florida.

Conclusions

This study demonstrates the wealth of information that can be gained from automated soil chamber efflux systems to determine those variables that are best related to soil respiration. The results suggest that in seasonally water limited ecosystems, soil CO₂ efflux should be scrutinized in the light of soil moisture availability to vegetation, which may not be closely related to soil moisture content determined by direct measurements in the upper soil profile. It appears that a younger ponderosa pine forest, was unable to utilize soil water from lower regions of the soil profile, and showed seasonally reduced rates of soil CO₂ efflux in comparison to an old growth forest with a well-established rooting system. Such disparity in the patterns of soil respiration between an old-growth and recently regenerating ponderosa pine forest, prevented the use of one simplified relationship to predict seasonal soil CO₂ efflux in the forests of highly contrasting ages. Soil CO₂ effluxes estimated from site-specific models suggested that inter-annual climate variability played a significant role in determining which site showed the highest annual soil CO₂ efflux rates. The regenerating ponderosa pine forest was sensitive to the quantity of summer rainfall whereas the old growth forests was sensitive to soil moisture availability in the deeper soil layers. Site productivity, as represented by aboveground production, appeared to play a less significant role than environmental variables in controlling soil CO₂ effluxes at these two highly contrasting aged forests. We recommend the use of automated soil chamber systems and profile measurements of soil properties, especially when used as part of larger studies that can further investigate how plant processes may influence

root respiration and turnover, detritus inputs and quality, and subsequently, heterotrophic respiration.

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