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Evaluation of methods for estimating soil carbon dioxide efflux across a gradient of forest disturbance

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Abstract

Better understanding of variation in soil carbon dioxide (CO_2) efflux caused by measurement techniques is needed, especially over gradients of site disturbance, to accurately estimate the global carbon cycle. We present soil CO_2 efflux data from a gradient of disturbance to ponderosa pine (***Pinus ponderosa*** C. Lawson var. ***scopulorum*** Engelm.) forests in northern Arizona, USA that were obtained using four different techniques: vented static chambers, a Licor 6400-09, and soil CO_2 diffusion profiles using two different models (Moldrup, Millington–Quirk) to estimate soil gas diffusivity. We also compared soil CO_2 efflux measured by the Moldrup and Millington–Quirk diffusion profile methods to nighttime total ecosystem respiration (TER) data from an eddy covariance tower. We addressed four questions: (1) Does the use of a given method to measure soil CO_2 efflux bias results across a disturbance gradient? (2) Does the magnitude of difference between observed and modeled estimates of soil CO_2 differ between methods and across sites? (3) What is the spatial variability of each method at each site? (4) Which method is closest to the estimate of TER measured by the eddy covariance tower? Although soil CO_2 efflux varied significantly among methods the differences were consistent among sites. Measured and modeled total growing season fluxes were generally higher for the Licor 6400-09 and Millington–Quirk diffusion gradient methods compared with static chamber and the Moldrup diffusion gradient methods. A power analysis showed that the larger static chamber was the most efficient method at sampling spatial variation in soil CO_2 efflux. Nighttime measurements of soil CO_2 efflux from the Moldrup diffusion gradient method were most strongly related to nighttime TER assessed with eddy covariance. The use of a single, well-implemented method to measure soil CO_2 efflux is unlikely to create bias in comparisons across a gradient of forest disturbance.

Keywords: disturbance gradient, eddy covariance, *Pinus ponderosa*, soil CO_2 efflux, soil diffusion profile, soil respiration

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Introduction

The release of carbon dioxide (CO_2) from soil (soil CO_2 efflux) is the largest source of carbon (C) to the atmosphere in most terrestrial ecosystems (Schlesinger & Andrews, 2000). Soil CO_2 efflux is the result of both root and microbial respiration and, in temperate forests and grasslands, exhibits large seasonal, diel, and spatial variations. Although accurate prediction of soil CO_2 efflux is important for models of the global C cycle, uncertainties in estimates exist due partly to methodological differences (Raich & Schlesinger, 1992) and variation in substrate availability, soil temperature, and soil moisture (Davidson *et al*., 1998, 2006; Xu & Qi, 2001; Rodeghiero & Cescatti, 2008).

Forest disturbance events such as thinning or fire have been shown to have idiosyncratic effects on soil CO_2 efflux, with such disturbances decreasing (e.g., Litton *et al*., 2003; Tang *et al*., 2005b; Czimczik *et al*., 2006; Sullivan *et al*., 2008), increasing (e.g., Grady & Hart, 2006; Selmants *et al*., 2008), or having no effect on fluxes (e.g., Toland & Zak, 1994; Irvine *et al*., 2007). While these differences among studies may be due to site-specific characteristics, variation in fluxes produced by different methods of measuring soil CO_2 efflux among studies introduces further uncertainty into comparisons across studies and synthesis efforts.

A variety of methods exist to measure soil CO_2 efflux. Widely used methods are static or dynamic chambers placed on the soil surface, and soil CO_2 diffusion gradient profiles. Chamber-based methods, whether static or dynamic, measure soil CO_2 efflux by quantifying the increase of headspace gas concentration within the chamber headspace over a known time (Hutchinson & Mosier, 1981; Jensen *et al*., 1996). Soil CO_2 diffusion gradient profiles measure soil CO_2 efflux by measuring CO_2 concentrations in the soil at different depths by

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inserting tubes in the soil to different depths (de Jong & Schappert, 1972), or by using small, buried infra-red gas analyzers (IRGAs; Tang *et al*., 2003) and then estimating the diffusion of CO_2 through the soil to the surface. The diffusivity of gas in soil can be calculated by models such as those developed by Moldrup *et al*. (1999) and Millington & Quirk (1961).

The ideal system to measure soil CO_2 efflux has been described by Longdoz *et al*. (2000) to meet the following three requirements: (1) it must not disturb the vertical soil CO_2 concentration gradient; (2) it must not disturb the horizontal air velocity above the soil; and (3) it must not disturb the vertical pressure gradient at the soil–atmosphere boundary. However, these requirements do not mention such logistical factors facing investigators such as portability, cost, or sensitivity to changes in soil temperature or soil water content, two soil physical parameters often used to model soil CO_2 efflux.

Nonautomated chamber-based systems are often used to measure soil CO_2 efflux because their portability and low cost make them efficient at capturing spatial variation in soil CO_2 efflux. However, soil CO_2 efflux measurements using non-automated chambers are typically <1 h in duration and diel measurements are labor intensive; repeated measurements are needed to construct diel patterns. Additionally, vegetation should not be present within the sampling areas of chambers, for the aboveground component may photosynthesize and respire within the chamber and thus confound soil CO_2 efflux. Thus, vegetation is usually clipped or removed from the sampling area before measuring soil CO_2 efflux, further altering soil CO_2 efflux (Grogan & Chapin, 1999). Chamber methods may disrupt diffusion of CO_2 out of the soil, or may change the difference in pressure between the atmosphere and the headspace. As the CO_2 concentration increases within the chamber headspace of static chambers, the concentration gradient between the chamber and the soil decreases, and the measured flux may be reduced (Davidson *et al*., 2002). Conversely, dynamic chambers that use chemical CO_2 scrubbers may overestimate fluxes by increasing the diffusion gradient out of the soil when they reduce the CO_2 concentration in the chamber headspace below ambient levels (Davidson *et al*., 2002). Both static and dynamic chambers are susceptible to problems associated with pressure differences between the air inside and outside the chamber (Davidson *et al*., 2002; Dore *et al*., 2003). In unvented chambers, the increase in gas concentration can increase the pressure in the chamber above ambient levels, suppressing fluxes as gas diffuses laterally away from the zone of high concentration. However, Bain *et al*. (2005) have shown that vented chambers may overestimate fluxes as a result of the Venturi effect (Conen & Smith, 1998) when even low wind speeds cause a mass-flow of CO_2 out of the soil profile. Clearly, chamber-based techniques, while efficient, do not meet the three criteria of an ideal soil CO_2 efflux method (Longdoz *et al*., 2000).

The soil CO_2 diffusion gradient method using buried IRGAs satisfies the three requirements of an ideal method to measure soil CO_2 efflux. Once inserted vertically in the soil, these IRGA probes do not disturb the vertical soil CO_2 concentration gradient, the aboveground horizontal air velocity, or the vertical pressure gradient at the soil–atmosphere boundary. Neither does this technique disturb the aboveground or belowground growth of plants. Further, it has the potential to provide excellent temporal resolution of fluxes because measurements are automated, though its cost and energy demands constrain spatial replication. However, the reliance of this approach on an estimate of soil gas diffusivity is problematic. Although soil gas diffusion is largely driven by soil texture and the gas concentration gradient of the profile, soil temperature and water content are continuously acting on the volume of soil air-filled pore space through which the gas may diffuse. *In situ* measures of diffusivity are being developed (Risk *et al*., 2008; von Fischer *et al*., 2009) but until recently, investigators either used existing models [such as those developed by Moldrup *et al*. (1999) and Millington & Quirk (1961)] or estimated diffusivity specifically for their sites (Jassal *et al*., 2004).

Until one method is proven to best minimize artifacts when measuring soil CO_2 efflux, and is efficiently deployable, investigators will have to choose among a variety of available methods. Several studies have shown that different methods of measuring soil CO_2 efflux yield different results (Nay *et al*., 1994; Jensen *et al*., 1996; Bekku *et al*., 1997; King & Harrison, 2002; Liang *et al*., 2004; Pumpanen *et al*., 2004). Of those studies, however, none have determined whether the use of a given method may bias comparisons of soil CO_2 efflux across a gradient of disturbance. To evaluate this possibility, we measured soil CO_2 efflux using four different techniques at one densely forested site, one site that was thinned to reduce the risk of wildfire, and one severely burned site. We desired to determine whether the use of a given method across different sites biases results. Because many investigations of soil CO_2 efflux model their results based on soil physical properties such as soil temperature and soil water content (e.g., Davidson *et al*., 1998, 2006; Epron *et al*., 1999; Tang *et al*., 2005a; Sullivan *et al*., 2008), we also compared the similarity of measured growing season soil CO_2 efflux from different methods across sites to modeled estimates of growing season soil CO_2 efflux. Next, we compared the statistical power, or sample size required to estimate a site mean within 10% or

20% of the true mean, among methods. Lastly, we determined which method most accurately estimated soil CO_2 efflux, represented by nighttime total ecosystem respiration (TER) measured with the eddy covariance technique at a site with little aboveground respiration. To accomplish these objectives, we measured soil CO_2 efflux using static chambers, a Licor LI-6400-09 dynamic chamber (Li-Cor Inc., Lincoln, NE, USA), and a soil CO_2 diffusion gradient profile using two different commonly used estimates of soil gas diffusivity: the Moldrup *et al.* (1999) model and the Millington & Quirk (1961) model. Additionally, we report nighttime eddy covariance data at the burned site, where the measurement of TER at night should be closely related to soil CO_2 efflux because of low aboveground biomass (Dore *et al.*, 2008). We compare these eddy covariance data to concurrent nighttime soil CO_2 efflux measurements from the two soil CO_2 diffusion gradient techniques to further evaluate, *in situ*, the accuracy of methods of measuring soil CO_2 efflux.

Materials and methods

Site description

We measured soil CO_2 efflux, soil temperature, and soil volumetric water content at three sites currently or formerly dominated by ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) near Flagstaff, AZ, USA. The sites consisted of an unburned ponderosa pine forest that has not experienced management in over a century (control), a ponderosa pine forest that was thinned in September 2006 (thinned), and a ponderosa pine forest that burned in a high severity fire in 1996 (burned). All sites are described in further detail by Dore *et al.* (2008), Sullivan *et al.* (2008) and Montes-Helu *et al.* (2009), but the sites are briefly summarized below.

The control site represented a typical dense, fire-prone ponderosa pine forest in northern Arizona. The forest overstory consists of ponderosa pine and scattered Gambel oak (*Quercus gambelii* Nutt.). Tree basal area averaged $30\,m^2\,ha^{-1}$, and the projected leaf area index (LAI) was $2.3\,m^2\,m^{-2}$. The soil at the control site is classified as a complex of Mollic Eutroboralfs and Typic Argiborolls (Miller *et al.*, 1995), and the surface soil textural class is a clay loam.

The thinned site was a dense ponderosa pine forest similar in stand structure to the control site until mechanical harvesting occurred in September 2006 using thinning guidelines established by the Ecological Restoration Institute (Covington *et al.*, 1997). The thinning removed dense clusters of small-diameter trees in an effort to restore the forest to pre-Euro-American settlement stand conditions and reduce the risk of severe wildfire. The thinning reduced tree density from 465 to 154 trees ha^{-1}, basal area from 20.5 to $12.6\,m^2\,ha^{-1}$, and projected LAI from 1.5 to $0.8\,m^2\,m^{-2}$. The soil is classified as a Typic Eutroboralf (Miller *et al.*, 1995) and the surface soil textural class is a silt loam.

The burned site was part of the 10 500 ha Horseshoe–Hochderffer Complex fire, a stand-replacing wildfire that burned in 1996. Prefire ponderosa pine tree density, basal area, and projected LAI (343 trees ha^{-1}, $31\,m^2\,ha^{-1}$, and $2.4\,m^2\,m^2$, respectively) were measured in an unburned area adjacent to the study area, and were similar to the control and thinned sites. The fire killed all the trees within the study area, and the few trees that have established since the fire were shorter than 1 m at the time of our study. Postfire peak-season projected LAI was $0.6\,m^2\,m^{-2}$ in 2006 and was comprised entirely of understory plants. The fire resulted in a vegetation conversion to annual and perennial grasses [*Bromus tectorum* L., *Elymus repens* (L.) Gould], shrubs (*Ceanothus fendleri* A. Gray) and forbs [*Oxytropis lambertii* Pursh, *Verbascum thapsus* L., *Linaria dalmatica* L. Mill., and *Cirsium wheeleri* (A. Gray) Petr.]. The soil at the burned site is classified as a Mollic Eutroboralf (Miller *et al.*, 1995) and the surface soil textural class is a silt loam.

The climate at the sites consists of cold dry winters and sunny, dry springs. A 'monsoon' type precipitation pattern (Sheppard *et al.*, 2002) occurs in July and August and the fall months are typically cool and dry. The 30-year mean precipitation from 1971 to 2000 was 561 mm at the Fort Valley weather station, located between the sites (Western Regional Climatic Center, http://www.wrcc.dri.edu/index.html). Approximately half the annual precipitation occurs during the summer monsoon season (Sheppard *et al.*, 2002).

Measurements of soil CO_2 efflux

We used three different methods to measure soil CO_2 efflux at each site between April 2007 and September 2007.

(1) *Static chambers*:

We measured soil CO_2 efflux with vented static chambers as described by Hutchinson & Mosier (1981) and Sullivan *et al.* (2008). Soil CO_2 efflux was measured by placing a series of 15 cm tall, 30 cm diameter vented polyvinyl chloride (PVC) caps over 30 cm diameter PVC collars inserted approximately 2 cm into the mineral soil. Green plant material was clipped and removed before sampling. Headspace gas samples were taken 0, 15, and 30 min after placing the chamber cap on the collar. Samples were then analyzed using a thermal conductivity detector-equipped gas chromatograph with a Porapak Q column (Shimadzu 8A, Kyoto, Japan) to measure CO_2 concentrations.

(2) *Licor LI-6400-09 dynamic chamber*:

We used a LI-6400 infrared gas analyzer (IRGA) equipped with a LI-6400-09 soil CO_2 efflux chamber to obtain instantaneous soil CO_2 efflux measurements (see Liang *et al.*, 2004). The LI-6400-09 soil chamber was placed on collars fitted 2 cm into the mineral soil to minimize disturbance to the surface soil and ensure repeated sampling of the same soil area. As with the static chamber, any green plant material growing within the collar was clipped and removed before each measurement.

(3) *Soil CO_2 gradient profile using two diffusion calculations*:

We used buried sets of solid-state IRGA probes (GMM 222; Vaisala Inc., Helsinki, Finland) to obtain continuous measurements of soil CO_2 efflux during the growing season. The GMM 222 is a small IRGA that can be buried vertically in the soil to measure soil CO_2 concentrations at different depths (Tang *et al.*, 2003). The probes were connected to a datalogger (CR-10xTD, Campbell Scientific Inc., Logan, UT, USA) and a multiplexer (AM25 T, Campbell Scientific Inc.). The system was powered by solar panels. At each profile, three probes were inserted 2, 10, and 20 cm into the mineral soil by removing a soil core precisely the diameter of the IRGA probe plus its soil adapter. The IRGA probes were run continuously to minimize condensation buildup. The IRGA probes measured soil CO_2 concentrations every 20 s and the CR10X-TD datalogger averaged the measurements into 30 min intervals.

We estimated soil CO_2 efflux every 30 min by applying the measured CO_2 profile concentrations and an estimate of soil diffusivity from Fick's first law:

$$\mathrm{FC} = -D\frac{\partial c}{\partial z}, \tag{1}$$

where FC is soil CO_2 efflux, D is the soil gas diffusion coefficient ($\mathrm{m^2\,s^{-1}}$), c is the CO_2 concentration at a known soil depth, ($\mu\mathrm{mol\,m^{-3}}$), and z is the depth (m). We applied two different, commonly used models of soil gas diffusivity. The first model was developed by Moldrup *et al.* (1999) as described by Tang *et al.* (2005a) and is hereafter referred to as the Moldrup method:

$$D = D_{\mathrm{m}}\phi^2\left(\frac{\varepsilon}{\phi}\right)^{\beta S}, \tag{2}$$

where D_{m} is the molecular diffusivity of CO_2 in air, ε is the soil air-filled porosity, Φ is the total porosity, S is the mineral soil fraction smaller than 2 μm, and β is a parameter, which in this case is a constant, 2.9. The second model, we applied was developed by Millington & Quirk (1961) and is hereafter referred to as the Millington–Quirk method:

$$D = D_{\mathrm{m}}\frac{\varepsilon^{\frac{10}{3}}}{\phi^{\frac{2}{3}}}. \tag{3}$$

Measurements of soil temperature and soil water content

Soil temperature was measured within 1 m of the LI-6400-09 and static chamber collars at the 10 cm mineral soil depth during the measurement period using a soil thermometer (VWR Scientific Inc., West Chester, PA, USA). Soil temperature was measured within 20 cm of the Vaisala GMM 222 probes at 2, 10, and 20 cm depths in the mineral soil using a thermocouple and CR10X-TD datalogger. As with the GMM 222, measurements were taken every 20 s and recorded as 30 min averages.

Soil water content was measured during LI-6400-09 and static chamber measurements with a θ-probe attached to an MLX-2 digital display (Delta T Devices, Cambridge, UK). The θ-probe measured the integrated volumetric soil water content over the top 6 cm of the mineral soil. Volumetric soil water content was measured within 20 cm of the IRGA probes at 2, 10, and 20 cm depths in the mineral soil using horizontally buried ECH_2O probes (Decagon Devices, Pullman, WA, USA). We developed site-specific calibrations of the ECH_2O probes to accurately estimate soil water content (Montes-Helu *et al.*, 2009).

Eddy covariance measurements

The eddy covariance technique (Baldocchi,, 2003) was used to measure CO_2 fluxes at the burned site (Dore *et al.*, 2008). Eddy covariance has been used previously to measure soil respiration in different ecosystems (e.g., Janssens *et al.*, 2000; Baldocchi *et al.*, 2006; Richardson *et al.*, 2006; Jassal *et al.*, 2007). To avoid confounding soil respiration with aboveground plant respiration and photosynthesis, the eddy covariance instruments in these previous studies were used below the forest canopy or on sites with little vegetation and only nighttime data were used. We present nighttime eddy covariance data from the burned site only, where the instrument tower was low (2.5 m) and vegetation was sparse (maximum LAI was 0.6 $\mathrm{m^2\,m^{-2}}$). We only compare the eddy covariance data to the nighttime soil CO_2 efflux data obtained from the soil CO_2 gradient techniques which produced continuous 30 min averages at night. Soil CO_2 efflux data measured with the static chamber and LI-6400-09 methods were not compared with the eddy covariance data because we did not use these methods at night. Eddy covariance data used in the comparison were only high quality, 30 min night data above the u* threshold of 0.2 $\mathrm{m\,s^{-1}}$. We computed nighttime means only for nights with more than 10 high-quality records. For additional details on the eddy covariance measurements and instrumentation, see Dore *et al.* (2008) and Montes-Helu *et al.* (2009).

Sample design of soil CO_2 efflux measurements

We measured soil CO_2 efflux at three locations within five 25 m diameter plots at each of the three sites as described in Sullivan *et al.* (2008) and Dore *et al.* (2008). The collars for the LI-6400-09 and static chambers were within 1 m of each other and were approximately 0°, 120°, and 240° and 15 m from plot center. The soil CO_2 diffusion gradient profiles were arrayed 0°, 120°, and 240° and 10 m from plot center, and were 5 m from the chambers.

We measured soil CO_2 efflux using the LI-6400-09 and static chamber methods nine times between April 1, 2007 and September 30, 2007 at all three sites. These measurements were taken between 7:00 and 13:00 hours on 3 consecutive days, though for simplicity we only present the mean date of measurement.

We used each paired sample point within a plot as a sample unit. This allowed us to compare soil CO_2 efflux measurements taken as proximately as possible in both time and space. The LI-6400-09 and static chamber measurements were taken at the same time at each sampling point. Soil CO_2 efflux measured with the profile methods was compared with data obtained with the chamber methods at the nearest location (~ 5 m distant) during the measurement period. When comparing the chamber methods to the Moldrup and Millington–Quirk methods, we only used Moldrup and Millington–Quirk data from the same date and time during which the chamber methods were used (between 7:00 and 13:00 hours). Comparing our measurements in this way minimized bias from diel variation in soil CO_2 efflux.

Statistical analyses

The overall goal of our statistical analysis was to evaluate the influence of different methods on comparisons of soil CO_2 efflux among sites. Because our study included one control site, one thinned site, and one burned site, the levels of disturbance were not spatially replicated, and thus the sites should be considered as case studies within a gradient of disturbance. All three sites were representative of ponderosa pine forests in northern Arizona, USA in both predisturbance stand structure and climate, and the plots were systematically selected within each site without bias (see Dore *et al.*, 2008; Sullivan *et al.*, 2008).

To determine if the use of different soil CO_2 efflux methods might bias results, we used a two-factor repeated measures analysis of variance (ANOVA). A significant site × method interaction or time × site × method interaction would indicate that the difference among sites depended on the method used. To further explore the statistical relationship among methods within sites and among sites within methods, we used a one-factor ANOVA and a Tukey's HSD posthoc test. We ln-transformed all data before analysis in order to normalize the distribution of the data and homogenize the variances. All statistical analyses were performed using JMP software (v. 5.1; SAS Institute, Cary, NC, USA). We set statistical significance, *a priori*, at $P \leq 0.05$.

Total measured growing season soil CO_2 efflux for the static chambers and LI-6400-09 was estimated using the same interpolation technique as Kaye & Hart (1998), where each measurement date was a mid-point of a measurement period. We assigned the measured soil CO_2 efflux value to all the dates within that measurement period, which equaled one half the days before the measurement and one half the days after the measurement date. We calculated total measured growing season soil CO_2 efflux for the probe-based methods by adding all the half-hour averages recorded within the growing season. This approach therefore included diel variation in total growing season estimates using the Moldrup and Millington–Quirk methods and excluded diel variation in total growing season estimates using the chamber methods. However, as previously stated, one of the advantages of the Moldrup and Millington–Quirk methods over the LI-6400-09 and static chamber methods is its ability to better estimate temporal patterns in soil CO_2 efflux.

We also predicted total growing season soil CO_2 efflux for all the methods based on a series of regression models incorporating soil temperature and soil water content. The best model for each method was evaluated using Akaike's Information Criterion with a second-order bias correction (AICc) and a weighted Akaike score (Akaike, 1973; Anderson, 2008). AICc selects the best-fitting and most-parsimonious model. The models were based on those published by Tang *et al.* (2005a) and Sullivan *et al.* (2008) and are as follows:

$$\ln(\mathrm{FC}) = \beta_0 + \beta_1 \mathrm{T}, \tag{4}$$

$$\ln(\mathrm{FC}) = \beta_0 + \beta_1 \theta, \tag{5}$$

$$\ln(\mathrm{FC}) = \beta_0 + \beta_1 \theta + \beta_2 \theta^2, \tag{6}$$

$$\ln(\mathrm{FC}) = \beta_0 + \beta_1 \mathrm{T} + \beta_2 \theta + \beta_3 \theta^2, \tag{7}$$

$$\ln(\mathrm{FC}) = \beta_0 + \beta_1 \mathrm{T} + \beta_2 \theta + \beta_3 \theta^2 + \beta_4 \mathrm{T}\theta + \beta_4 \mathrm{T}\theta^2, \tag{8}$$

where β_n is the parameter coefficient, T is soil temperature (°C), and θ is soil water content ($m^3\,m^{-3}$). Based on the AICc, we determined that the best-fitting model form for the static chamber method was Eqn (7), while the preferred model form for the LI-6400-09, Moldrup, and Millington–Quirk methods was Eqn (8) (data not shown).

We used the respective best-fitting model for each technique to predict growing season (April 1, 2007 to September 30, 2007) soil CO_2 efflux for each measurement method using independent measurements of soil water content and temperature on the half-hour time scale at the nearby eddy covariance tower. Independent measurements of soil temperature (CS 107; Campbell Scientific Inc.) and soil water content (CS 616; Campbell Scientific Inc.) were recorded at the base of the eddy covariance tower at depths of 2 and 10 cm. We averaged the 2–10 cm depths to calculate the models for the chamber-based techniques because the models were generated using soil water content integrated over 0–6 cm.

We performed a *posthoc* power analysis of our results to determine the number of samples needed to accurately estimate the site mean soil CO_2 efflux based on measured spatial variation in our study. To do this, we applied the following equation:

$$n = \frac{t^2 \sigma^2}{A^2}, \tag{9}$$

where n is the number of sample points required, t is the t-statistic at a desired confidence level and degrees of freedom, σ is the standard deviation of the mean of the measurements, and A is the maximum allowable difference between the estimate of soil CO_2 efflux and the true value (Thompson, 2002).

Results and discussion

Our results suggest that methods did not bias comparisons of CO_2 efflux across the forest disturbance gradient. This is the first study of which we are aware to compare soil CO_2 efflux among dynamic and static chambers and soil diffusion methods across a forest disturbance gradient. The site × method, time-method, and time × site × method interactions in the two-way repeated measures ANOVA were not significant (Table 1). The methods varied when averaged over sites (Table 1). Similarly, one-factor ANOVAs showed that the four methods measured significantly different soil CO_2 effluxes at each site (Table 2). The one-factor ANOVAs indicated that, for each method, sites were significantly different from each other (Table 2). All methods measured the lowest mean daily growing season soil CO_2 efflux at the burned site and significantly higher fluxes at the thinned site.

The sites in our study experienced strong seasonal variation in precipitation and soil water content caused by the abrupt transition from the late spring and early summer dry season to the late summer wet season. Soil temperature and water content both reflected seasonal climatic patterns at the three sites. After snow melt, the soil water content gradually decreased to its lowest level in early July, when the monsoon rains began (Fig. 1). Soil temperature generally increased to a maximum in early July, and trended downward for the second half of the growing season (Fig. 1). The burned site had a higher average soil temperature (10 cm depth) than the other sites (Fig. 1c).

All methods documented temporal variation in soil CO_2 efflux. The two-factor repeated measures ANOVA showed soil CO_2 efflux to vary significantly by time (Table 1). The significant time × site interaction indicated that site differences in soil CO_2 efflux depended on measurement date (Table 1). However, the time-by-method interaction was not significant, suggesting that differences in soil CO_2 efflux among methods were similar over measurement dates. During the dry season all four methods measured low soil CO_2 efflux (Fig. 2). In contrast, the LI-6400-09 and Millington–Quirk methods measured larger increases in soil CO_2 efflux in response to the late-summer monsoon rains than the static chamber and Moldrup methods at the two forested sites (Fig. 2a and b). This pattern held for the Millington–Quirk method, but not the LI-6400-09 method, at the burned site (Fig. 2c). However, at all sites, the LI-6400-09 consistently measured greater soil CO_2 efflux than the static chamber, and the Millington–Quirk method consistently measured greater soil CO_2 efflux than the Moldrup technique (Fig. 2).

Observed total growing season soil CO_2 effluxes (Fig. 3a) reflected the patterns of mean growing season soil CO_2 effluxes (Fig. 2). At the control site, where power outages limited the use of the Moldrup and Millington–Quirk methods after August 1, 2007, the LI-6400-09 method measured the highest total soil CO_2 efflux, followed by the Millington–Quirk method; the Moldrup and static chamber methods measured lower total soil CO_2 efflux. At the thinned site, the Millington–Quirk method had slightly higher total soil CO_2 efflux than the LI-6400-09, but both were substantially higher than either the static chamber or Moldrup methods. At the burned site, the Millington–Quirk method again measured the highest soil CO_2 efflux during the growing season of all the methods. The Moldrup and LI-6400-09 methods had similar total growing season soil CO_2 efflux at the burned site, while efflux was lowest for the static chamber method.

The predicted values of total growing season soil CO_2 efflux obtained using the best-fitting regression model determined by AICc for each method applied to the same independently measured soil temperature and water content data (Fig. 3b) tended to reflect the observed values of total growing season soil CO_2 efflux across sites (Fig. 3a). The LI-6400-09 and Millington–Quirk methods had greater predicted total growing season soil CO_2 efflux than the static chamber and Moldrup methods (Fig. 3b). At the burned site, the predicted value of LI-6400-09 total soil CO_2 efflux was greater than the observed value of total growing season soil CO_2 efflux. As with the observed values, sites had little influence on the magnitude of the difference of predicted values of soil CO_2 efflux among methods. Thus, the models were accurate enough to estimate total growing season soil CO_2 efflux while maintaining the observed difference among methods.

Soil CO_2 efflux is known to have substantial spatial variation at even the centimeter scale (Davidson *et al.*, 2002; Liang *et al.*, 2004; Rodeghiero & Cescatti, 2008). The results of the power analysis suggest that there was large spatial heterogeneity in soil CO_2 efflux between our sample units within a site (Table 3). The burned site required fewer samples than either the control or

Table 1 Results of a two-way repeated measures analysis of variance comparing mean daily ln-transformed soil CO_2 efflux measured simultaneously using four different methods with site (control, thinned, and burned), method (static chamber, LI-6400-09, Moldrup, and Millington-Quirk), time, and their interactions as factors

Source	Test	*F*/approx *F*-value	*P*-value
Between subjects			
Overall	*F*-test	1.44	0.2712
Intercept	*F*-test	7.97	< 0.0154
Site	*F*-test	1.34	0.2990
Method	*F*-test	3.40	0.0534
Site × method	*F*-test	0.10	0.9955
Within subjects			
Overall	Pillai's trace	1.38	0.0905
Time	*F*-test	15.64	0.0010
Time × site	Pillai's trace	2.98	0.0219
Time × method	Pillai's trace	1.24	0.3027
Time × site × method	Pillai's trace	0.95	0.5515

Table 2 Results of three separate one-way analyses of variance (one for each site) testing differences in mean daily growing season soil CO_2 efflux among four different methods (static chamber, Licor 6400-09, Moldrup, and Millington-Quirk)

	Mean soil CO_2 efflux ($\mu mol\,m^{-2}\,s^{-1}$)					
Site	Static chamber	Licor 6400-09	Moldrup model	Millington-Quirk model	*F*-value	*P*-value
Control	1.56 ± 0.25^{b1}	3.62 ± 0.25^{a1}	1.44 ± 0.57^{b12}	2.48 ± 0.57^{ab12}	21.31	< 0.0001
Thinned	1.77 ± 0.17^{c1}	2.86 ± 0.16^{ab1}	1.76 ± 0.34^{bc1}	3.42 ± 0.34^{a1}	10.10	< 0.0001
Burned	1.06 ± 0.14^{b2}	1.52 ± 0.14^{a2}	1.28 ± 0.27^{ab2}	2.41 ± 0.27^{a2}	4.59	0.0038
F-value	15.94	31.08	3.12	3.44		
P-value	<0.0001	<0.0001	0.0508	0.0376		

The *F*-values, *P*-values, and Tukey's HSD comparison of means are based on ln-transformed data, but the means ± standard error are reported as untransformed values. Different superscripted letters in the same row represent statistical differences ($P \leq 0.05$) among methods within a site. Different superscripted numbers in the same column represent statistical differences among sites within a method. The number of spatially independent samples in the analysis was 15 for the static chamber and Licor-6400-09 methods and three for the Moldrup and Millington-Quirk methods.

thinned sites to capture the spatial heterogeneity within a site, perhaps due to the lack of an overstory canopy which would introduce heterogeneity in litter quality, light penetration, and soil microclimate. Both chamber methods generally required fewer samples to estimate soil CO_2 efflux within 10% or 20% of the mean than the two methods based on CO_2 gradient profiles (Table 3). Of the chamber-based methods, the static chamber consistently required fewer samples than the LI-6400-09 to estimate soil CO_2 efflux within 10% or 20% of the mean. Of the methods based on CO_2 gradient profiles, the Moldrup method required fewer samples than the Millington–Quirk method to estimate soil CO_2 efflux within 10% or 20% of the mean.

Although the soil CO_2 diffusion gradient (Moldrup and Millington–Quirk) techniques provide excellent temporal resolution, they are difficult to spatially replicate due to their cost and semipermanent installation in the soil. The chamber methods (static chamber and LI-6400-09) are portable, allowing for more samples within a study area. The static chamber we used sampled a soil area of $706.8\,cm^2$, whereas the LI-6400-09 sampled a soil area of only $71.6\,cm^2$. Therefore, we expected the static chamber method to most efficiently sample spatial variation of soil CO_2 efflux, followed by the LI-6400-09, and then the Moldrup and Millington–Quirk methods. While our expectation that the static chamber would require the least number of samples to accurately estimate site mean soil CO_2 efflux was correct, we discovered that a large number of samples would be required to accurately estimate soil CO_2 efflux at the forested sites with any method. The sample sizes we report here for the LI-6400-09 (Table 3) bracket the 355 (within ± 10%) and 89 (within ± 20%) samples reported for a one-site power analysis of three methods by Liang *et al*. (2004). Our finding that the burned site, which lacked forest cover, would have required fewer samples and the forested sites more samples to accurately estimate site CO_2 efflux may assist other investigators in planning sampling designs.

Soil CO_2 efflux estimated with the Moldrup method was more similar to TER at the burned site (Fig. 4a) than the Millington–Quirk method (Fig. 4b). The relationship between TER and nighttime soil CO_2 efflux from the Moldrup model was nearly 1 : 1, with a slope of 1.095 (Fig. 4a). TER below $1.5\,\mu mol\,m^{-2}\,s^{-1}$ was well correlated to soil CO_2 efflux using the Millington–Quirk model (Fig. 4b), but the apparent high sensitivity of the Millington–Quirk model to changes in soil water caused Millington–Quirk to measure much higher soil CO_2 efflux than the eddy covariance method when nighttime TER was greater than $1.5\,\mu mol\,m^{-2}\,s^{-1}$. We could not make this comparison for the static chamber or LI-6400-09 because they were not deployed at night when TER was estimated by eddy covariance. In the semi-arid, pulse-precipitation-driven ecosystem of this study, the Moldrup model accurately measured soil CO_2 efflux during both dry and wet seasons, whereas the Millington–Quirk model accurately measured low values of soil CO_2 efflux during the dry season, but overestimated soil CO_2 efflux during the wet season.

The results of our study are consistent with other studies that show dynamic chambers such as the LI-6400-09 measure higher fluxes than static chambers (Jensen *et al*., 1996; Pumpanen *et al*., 2004). This result could be due to the buildup of CO_2 over time within the static chamber headspace that may reduce soil CO_2 efflux by reducing the diffusion gradient of CO_2 between the soil and the headspace. However, dynamic chambers may create a slight suction on the soil by 'scrubbing' the CO_2 concentration below ambient concentrations, thereby increasing the movement of CO_2

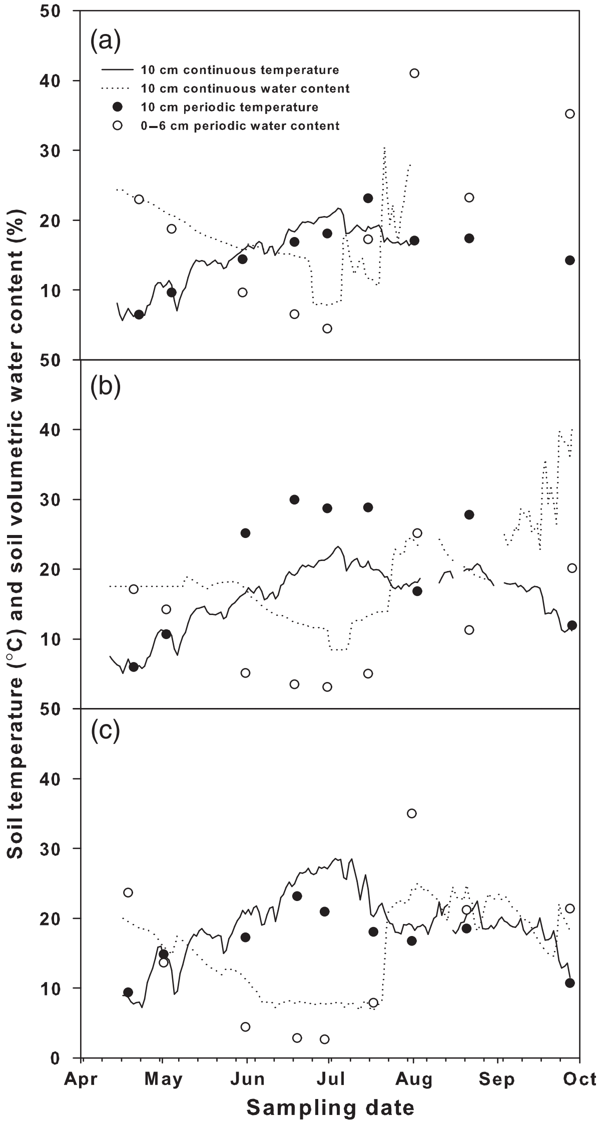

Fig. 1 Mean daily soil temperature and soil volumetric water content at the unmanaged control site (a), thinned site (b), and burned site (c) from April 1 to September 30, 2007. The number of spatially independent replicates at each site was three for the continuous temperature and soil water content measurements used with the Moldrup and Millington-Quirk techniques of measuring soil CO_2 efflux. The number of spatially independent locations sampled was 15 for the periodic temperature and soil volumetric water content measurements, recorded during the static chamber and LI-6400-09 methods, $n = 15$.

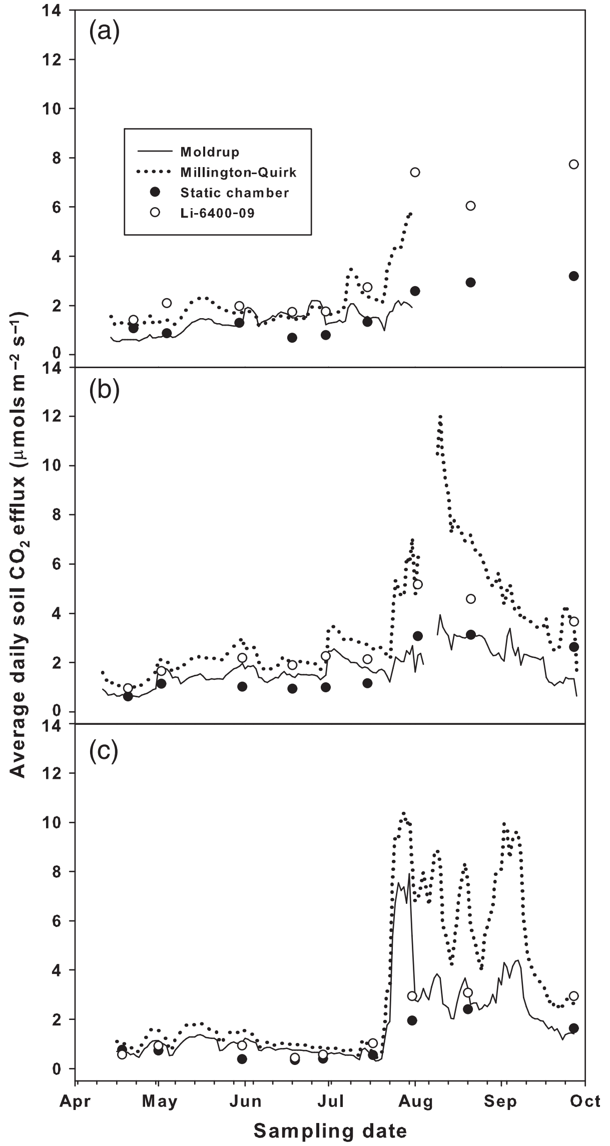

Fig. 2 Mean daily soil CO_2 efflux between April 1 and September 30, 2007 measured using four different methods at the unmanaged control site (a), the thinned site (b), and the burned site (c) from April 1 to September 30, 2007. The number of spatially independent locations sampled was 15 for the static chamber and LI-6400-09 methods, and three for the Moldrup and Millington-Quirk methods. Missing Moldrup and Millington-Quirk data were caused by power failures.

out of the soil via lateral diffusion from within the soil profile. Because both the static chamber and LI-6400-09 methods were vented, mass flow of CO_2 out of the soil profile and into the chamber headspace should have been consistent between the methods, and is unlikely to account for the differences we report (Bain *et al.*, 2005).

We know of no other field comparison of two diffusivity models used in methods of measuring soil CO_2 efflux based on CO_2 gradient profiles across a gradient of disturbance. The only methodological difference between the Moldrup and Millington–Quirk methods is the model used to predict the diffusivity of gas in the soil; soil CO_2 concentration, soil temperature, and soil water content data used for both methods were the same. The Millington–Quirk model was more sensitive to changes in soil water content than the Moldrup model. The highest values of soil CO_2 efflux measured

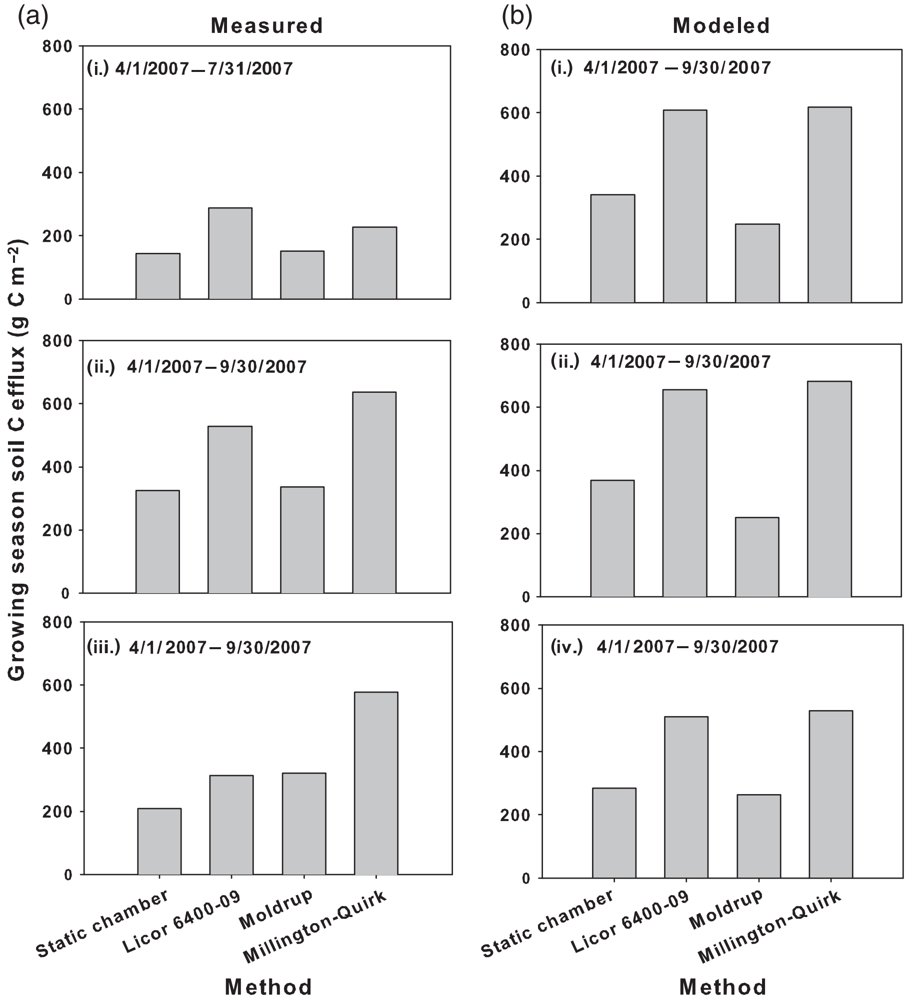

Fig. 3 Total observed (a) and predicted (b) growing season soil CO_2 efflux at the unmanaged control, thinned, and burned sites using four different methods of measuring soil CO_2 efflux. Observed total values were the sum of all half-hour values for the Moldrup and Millington-Quirk methods, and the sum of interpolated values (see 'Materials and methods') based on daily totals for the static chamber and Licor 6400-09 methods. Predicted total growing season soil CO_2 efflux was predicted from regression models for the four methods using the same values of soil temperature and soil water content at each site, which were obtained from the nearby Eddy covariance towers. The total measured growing season soil CO_2 efflux at the control site only includes data from April 1 to July 31, 2007 due to a power failure. All other panels include data from April 1 to September 30 2007.

by any method during the measurement period occurred during the wet season. The high values of soil CO_2 efflux measured by the Millington–Quirk method (Fig. 1b and c) overestimated nighttime TER measured at the burned site (Fig. 4b). A previous analysis of this model (see Jassal *et al*., 2005) suggested that at low soil air-filled porosities (high soil water contents) the Moldrup and Millington–Quirk models predict similar diffusivities, and at high soil air-filled porosities the Moldrup model estimates a lower diffusivity than the Millington–Quirk model. Our results differ from this suggestion because the Moldrup and Millington–Quirk models measured similar soil CO_2 efflux at low water contents (high soil air-filled porosities), yet the Millington–Quirk model measured greater soil CO_2 efflux than the Moldrup model at high water contents. The physical factors that underlie the better performance of the Moldrup model than the Millington–Quirk model for measuring soil CO_2 efflux at our sites requires more investigation.

Quantification of site-level CO_2 efflux measured with the Moldrup diffusion gradient method would benefit from the addition of a chamber-based method that is more easily spatially replicated. At the burned site, the Moldrup method was similar to the LI-6400-09 and static chamber methods in both seasonal patterns of soil CO_2 efflux (Fig. 1c) and total growing season soil CO_2 efflux (Fig. 3a). However, at the forested sites, the

Table 3 Number of sample points actually measured compared with the number of sample points required for each method at each site to estimate mean soil CO_2 efflux within ± 10% or ± 20% precision with 95% confidence interval

Site/method	Number of sampling points measured	Soil CO_2 efflux (mean ± 1 SD) (μmol m^{-2} s^{-1})	Number of sampling points required for measurements	
			Within ± 10%	Within ± 20%
Control				
Static chamber	15	1.57 ± 0.49	108	27
LI-6400-09	15	3.76 ± 1.29	762	190
Moldrup	3	1.34 ± 0.58	625	156
Millington-Quirk	3	2.01 ± 0.95	1669	417
Thinned				
Static chamber	15	1.79 ± 0.74	249	62
LI-6400-09	15	2.86 ± 0.97	436	109
Moldrup	3	1.85 ± 0.63	725	181
Millington-Quirk	3	3.38 ± 1.04	2015	503
Burned				
Static chamber	15	1.07 ± 0.29	37	9
LI-6400-09	15	1.18 ± 1.55	147	37
Moldrup	3	1.64 ± 0.37	253	63
Millington-Quirk	3	2.86 ± 1.21	2710	678

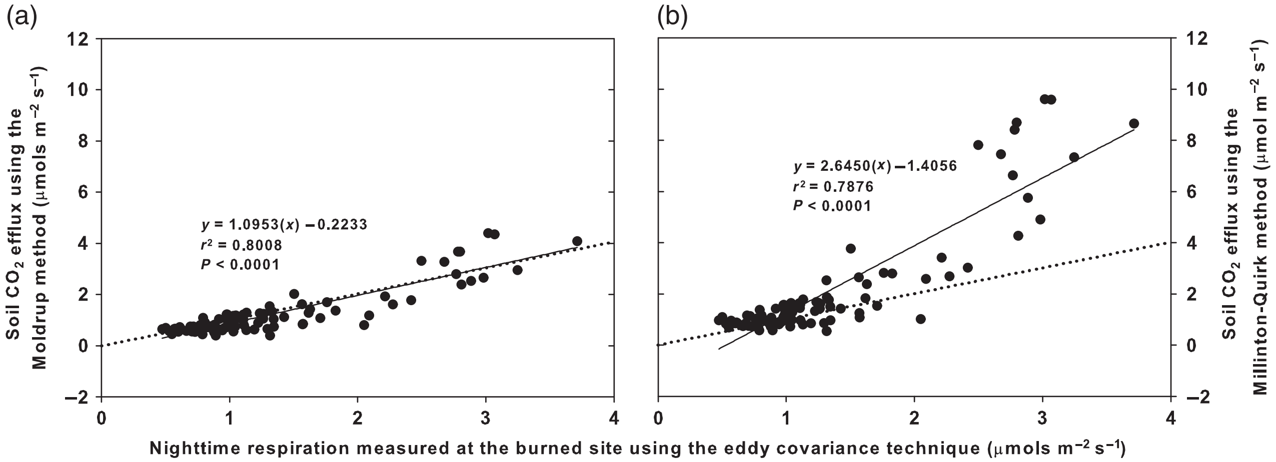

Fig. 4 Nighttime half-hour mean soil CO_2 efflux using the Moldrup (a) and Millington-Quirk (b) methods as compared with nighttime measurements of ecosystem respiration using only high-quality data obtained by the Eddy covariance technique at the burned site. The one-to-one relationship is represented by the dotted lines; $n = 100$ for both panels.

LI-6400-09 measured greater rates of soil CO_2 efflux than the Moldrup method across most sampling dates (Fig. 1a and b), and measured more total growing season soil CO_2 efflux than the Moldrup method (Fig. 3a). At the forested sites, measurement of soil CO_2 efflux with the static chamber was more closely associated with soil CO_2 efflux measured by the Moldrup method. Thus, our results for ponderosa pine forests support the use of a combination of the static chamber method and the Moldrup method to provide the most detailed information on temporal and spatial variation in sites similar to those measured in our study.

Conclusion

Most studies must choose one method to measure soil CO_2 efflux. Our experience with multiple methods suggests all of the methods we studied (static chamber, dynamic chamber, Moldrup and Millington–Quirk CO_2 diffusion profiles) can be used to compare soil CO_2 efflux across forest disturbance gradients similar to the unmanaged, thinned, and burned sites in our study. However, the different methods produced different estimates of mean and total growing season soil CO_2 efflux, which complicates efforts to calculate and compare the contribution of soil CO_2 efflux to whole-ecosystem C budgets among studies that use different methods (e.g. Curtis *et al*., 2002; Kominami *et al*., 2008, Gough *et al*., 2008, Dore *et al*., in press). The methods we studied differed in capacity to accurately sample spatial and temporal variability of soil CO_2 efflux. Ultimately, the method selected to measure soil CO_2 efflux must be the one most appropriate for answering the research question. For studies aimed at quantifying temporal patterns of soil CO_2 efflux (such as those interested in transient responses to precipitation, photosynthetic activity, or microbial activity), an automated method such as the CO_2 diffusion profiles is appropriate, despite limited spatial replication. For studies focused on describing spatial variation of soil CO_2 efflux, intensely replicated measurements with chamber-based methods may be appropriate. For studies that estimate ecosystem C pools or budgets we recommend a combination of at least two methods: one that estimates temporal variability, and one that estimates spatial variability. Similar to comparisons of net ecosystem exchange of CO_2 between eddy covariance measurements and predictions from process models (Amthor *et al*., 2001; Hanson *et al*., 2004), the most accurate estimates of soil CO_2 efflux may be produced by averaging results over different methods and models (Dore *et al*., in press), as all are currently imperfect.

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