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Wildfire reduces carbon dioxide efflux and increases methane uptake in ponderosa pine forest soils of the southwestern USA

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Abstract Severe wildfire may cause long-term changes in the soil-atmosphere exchange of carbon dioxide and methane, two gases known to force atmospheric warming. We examined the effect of a severe wildfire 10 years after burning to determine decadal-scale changes in soil gas fluxes following fire, and explored mechanisms responsible for these dynamics. We compared soil carbon dioxide efflux, methane uptake, soil temperature, soil water content, soil O horizon mass, fine root mass, and microbial biomass between a burned site and an unburned site that had similar stand conditions to the burned site before the fire. Compared to the unburned site, soil carbon dioxide efflux was 40% lower and methane uptake was 49% higher at the burned site over the 427-day measurement period. Soil O horizon mass, microbial biomass, fine root mass, and surface soil water content were lower at the burned site than the unburned site, but soil temperature was higher. A regression model showed soil carbon dioxide efflux was more sensitive to changes in soil temperature at the burned site than the unburned site. The relative importance of methane uptake to carbon dioxide efflux was higher at the burned site than the unburned site, but methane uptake compensated for only 1.5% of the warming potential of soil carbon dioxide efflux at the burned site. Our results suggest there was less carbon available at the burned site for respiration by plants and microbes, and the loss of the soil O horizon increased methane uptake in soil at the burned site.

Keywords Carbon · Methane uptake · Microbial biomass · *Pinus ponderosa* · Soil CO_2 efflux · Wildfire

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Introduction

Fire regimes in ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) forests of the semi-arid southwestern USA have shifted from

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high-frequency low-severity fires to low-frequency high-severity fires (Covington et al. 1994, 1997). This shift in fire regimes has increased tree density and decreased the herbaceous understory (Cooper 1960; Covington and Moore 1994). The resulting high fuel loads have combined with drought and warmer temperatures to increase the size and frequency of wildfires (Westerling et al. 2006). Anthropogenic emissions of the greenhouse gases carbon dioxide (CO_2) and methane (CH_4) are partly responsible for warmer temperatures (IPCC 2007; Shine and Sturges 2007).

Severe fire produces feedbacks with the atmosphere that may increase the likelihood of further wildfires. In the short term, burning of vegetation and the soil O horizon releases a pulse of carbon (C) to the atmosphere, largely as CO_2. Long-term effects of wildfire on CO_2 and CH_4 fluxes are unclear; however, recent studies suggest that impacts of severe fire on CO_2, energy, and water fluxes between ponderosa pine forests and the atmosphere extend for at least a decade after severe burning (Dore et al. 2008; Montes-Helu et al. 2009). The sparse grassland ecosystem that replaced the ponderosa pine forest in these studies is still a net source of C to the atmosphere 10 years after burning because total ecosystem respiration is greater than gross primary production (Dore et al. 2008). Understanding the magnitude and direction of the effect of fire on the components of total ecosystem respiration is critical to understanding the interaction between burned ecosystems and the atmosphere. The movement of CO_2 out of soil into the atmosphere (soil CO_2 efflux) is a major component of total ecosystem respiration (Goulden et al. 1996; Law et al. 1999; Janssens et al. 2001; Irvine et al. 2007). Severe fire has been shown to reduce soil CO_2 efflux in a variety of forest ecosystems (Litton et al. 2003; Bergner et al. 2004; Michelsen et al. 2004; Czimczik et al. 2006). However, severe fire has previously been shown to have little effect on soil CO_2 efflux in ponderosa pine forests over both shorter (<2 years; Irvine et al. 2007) and longer ($\sim$10 years; Grady and Hart 2006) time scales.

The mechanisms by which burning may reduce soil CO_2 efflux are unclear. Soil CO_2 efflux results from plant metabolic activity (autotrophic respiration) and the decomposition of organic material by microbes (heterotrophic respiration), and may be influenced by site productivity, live root mass, soil temperature, or soil water content (Janssens et al. 2001; O'Neill et al. 2002; Campbell et al. 2004; Luo and Zhou 2006; Curiel Yuste et al. 2007). Severe fire has been suggested to change the balance between autotrophic and heterotrophic respiration (Czimczik et al. 2006; Irvine et al. 2007), alter fine root dynamics (Hart et al. 2005a), and change the soil heterotrophic community (Bergner et al. 2004).

Methane is the second-most important gas forcing climate change (Shine and Sturges 2007), with a global warming potential that is 25 times greater than CO_2 per molecule (Forster et al. 2007). The only known biological sink of CH_4 occurs in soil as the result of oxidation of atmospheric CH_4 by methanotrophic bacteria (Bédard and Knowles 1989). The impact of severe fire on CH_4 uptake in forests has received little study. In forests, soil CH_4 uptake is primarily limited by the diffusion of the substrates necessary for CH_4 uptake, CH_4 and O_2, into the mineral soil (Born et al. 1990; Adamsen and King 1993; Castro et al. 2000). Burning may alter the diffusion of CH_4 into soil by changing soil water content and removing the soil O horizon (Striegl et al. 1992; King 1997; Saari et al. 1998; Steinkamp et al. 2001; Borken et al. 2006). Severe fire has the potential to change the importance of CH_4 uptake relative to soil CO_2 efflux.

At the same study sites in a northern Arizona ponderosa pine ecosystem that were used for assessments of ecosystem-level CO_2 (Dore et al. 2008) and water and energy (Montes-Helu et al. 2009) balances, we addressed the following questions about the cycling of C between forest soils and the atmosphere after severe fire: (1) Does severe fire have long term effects on CO_2 and CH_4 fluxes between soil and the atmosphere? (2) If so, is this due to changes in soil temperature and soil water content associated with the fire, or due to other effects of the fire?; and (3) Does fire change the relative importance of CH_4 uptake relative to soil CO_2 efflux? We evaluated these questions by intensively sampling CO_2 and CH_4 fluxes at a burned site and unburned site. We also evaluated the potential mechanisms by which burning may alter CO_2 efflux and CH_4 uptake by measuring soil temperature, soil water content, soil O horizon mass, fine root mass, and microbial C.

Methods

Study sites

We selected two study sites in northern Arizona, USA for measurements of soil CO_2 efflux and CH_4 uptake in ecosystems currently or formerly dominated by ponderosa pine. The soil measurements in our study occurred within the "footprint" of an eddy covariance tower that measured fluxes of C, water, and energy (Dore et al. 2008; Montes-Helu et al. 2009). The sites consisted of an unburned ponderosa pine forest site and a former ponderosa pine forest that burned in a high severity fire in 1996, resulting in 100% tree mortality and consuming the entire soil O horizon (burned site).

The climate of the sites consists of cold winters and sunny, dry springs, a "monsoon" type precipitation pattern during July and August (Sheppard et al. 2002), and cool dry fall months. Annual precipitation is divided about evenly between winter, usually as snow, and the summer monsoon season (Sheppard et al. 2002). The 30-year mean precipitation from 1971 to 2000 is 561 mm at the Fort Valley weather station, located between the sites and at about the same elevation (Western Regional Climatic Center, http://www.wrcc.dri.edu/index.html).

The unburned site is located within Northern Arizona University's Centennial Forest, approximately 30 km southwest of Flagstaff, AZ (35°5′20.5″N, 111°45′43.33″W, elevation 2,180 m a.s.l.). The unburned site represents a typical dense ponderosa pine forest in northern Arizona that had not experienced forest management in the previous century. Maximum projected overstory leaf area index (LAI) during the growing season was 2.3 m^2 m^{-2}, and average tree age was 87 years. The forest overstory consisted of ponderosa pine, with scattered Gambel oak (*Quercus gambelii* Nutt.); the understory was dominated by grasses, including *Festuca arizonica* Vasey, *Elymus elymoides* (Raf.) *Swezey*, *Boutelua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths, and *Blepharoneuron tricholepis* (Torr.) Nash. The soil at the unburned site was classified as a complex of Mollic Eutroboralfs and Typic Argiborolls, and the surface soil textural class was a clay loam (Table 1).

The burned site is located on the Coconino National Forest, northwest of Flagstaff, AZ (35°26′43.43″N, 111°46′18.64″W, 2,270 m a.s.l.). In 1996, the burned site was part of the 10,500 ha Horseshoe–Hochderffor

Table 1 Site characteristics of the unburned site and the burned site, which burned in 1996 as part of the Horseshoe–Hochderffor complex fire

Site characteristics	Unburned	Burned
Total leaf area index (m^2 m^{-2})	2.3 (±0.38)	0.60 (±0.17) [2.4 (±0.45) before fire[a]]
Understory leaf area index (m^2 m^{-2})	0.06 (±0.02)	0.60 (±0.17)
Basal area (m^2 ha^{-1})	30 (±4.7)	0 [31 (±6) before fire[a]]
Tree density (trees ha^{-1})	853 (±189)	0 [343 (±49) before fire[a]]
Soil classification	Complex of Mollic Eutroboralf and Typic Argiboroll	Mollic Eutroboralf
% Sand in A horizon	37	30
% Silt in A horizon	39	57
% Clay in A horizon	24	13
2006 mean annual air temperature (°C)[b]	8.8	8.6
2007 mean annual air temperature (°C)[b]	9.1	8.8
2006 precipitation (mm)[b]	692	517
2007 precipitation (mm)[b]	675	551

Both sites are located in northern Arizona, USA. Numbers in parentheses equal ± 1 standard error of the mean

[a] Pre-fire stand structure based on measurements taken in thirteen 0.03 ha plots in an unburned area adjacent to the burned site in 2006

[b] Measured using half-hour averages (for mean annual air temperature) and annual sum (for precipitation) at eddy covariance towers at each site

complex, a stand-replacing wildfire. After the fire, few trees established and none were taller than one meter at the time of measurements. No post-fire management, including seeding or salvage logging, occurred, nor was there any evidence of significant pre-fire forest management. The vegetation consisted of annual and perennial grasses (*Bromus tectorum* L., *Elymus repens* (L.) Gould), shrubs (*Ceanothus fendleri* A. Gray), and forbs (*Oxytropis labertii* Pursh, *Verbascum Thapsus* L., *Linaria dalmatica* L. Mill., *Circium wheeleri* (A. Gray) Petr.). The soil at the burned site was classified as a Mollic Eutroboralf, and the surface soil textural class was a silt loam (Table 1).

At each site, we established three 25 m radius (~0.20 ha) plots 150 m to the west, south, and east of the eddy covariance tower, and two 25 m radius (~0.20 ha) plots 400 m southwest and southeast of the towers. Gas fluxes were measured at three points inside each plot, 0°, 120°, and 240°, and 15 m from plot center. Plots were also used to measure soil characteristics, over- and under-story projected LAI (Dore et al. 2008), microbial C, and soil O horizon mass. Air temperature at the two sites was measured during 2006 at the eddy covariance towers, approximately 3 m above the vegetation canopy, and was similar at each site (Table 1).

Static chamber measures of CO_2 and CH_4

We used vented static-chambers (Hutchinson and Mosier 1981) to simultaneously measure soil CO_2 efflux and CH_4 uptake. In October 2005, we placed three 30-cm diameter, 10-cm tall polyvinylchloride (PVC) pipe "rings" approximately 2 cm into the mineral soil at each of the five plots at each site. Bottom edges were beveled to reduce disturbance to the soil structure during installation. Measurements began 8 months after rings were installed and occurred once a month from June 15th, 2006 to November 1st, 2006, and once every 2 weeks from April 15th, 2007 to August 15th, 2007. All measurements occurred during daylight hours from approximately 07:00 to 15:00 h. Rings ensured that the exact location was measured repeatedly, and prevented lateral diffusion of CO_2 and CH_4 into and out of the ring without severing many plant roots (Wright and Hart 1997). Green plant material growing in the ring was clipped as close to the soil as possible and removed from the ring before each sampling date. To obtain fluxes, we positioned a 15-cm tall, 30-cm diameter vented PVC cap over the ring and sealed the cap to the ring with a 5-cm wide latex band. Chamber headspace volume averaged 15.3 l. A rubber tube, 0.5-cm in diameter and 15-cm long, glued to a hole in the top of the cap, allowed pressure equilibration between the outside atmosphere and the inside chamber headspace. After positioning the cap, 160-ml headspace samples were taken at 0, 15, and 30 min using coated stainless steel evacuated canisters (Silonite Minican, Entech Instruments, Simi Valley, USA).

Concentrations of CO_2 and CH_4 in the samples were measured using gas chromatography within 2 days of sampling. Because samples were overpressurized (160 ml in 100 ml), we knew if a canister had leaked because it had no pressure and we thus discarded that measurement. This occurred rarely (less than twelve times over all sampling dates) because leaky canisters were not used in future sampling efforts. The same headspace gas sample was used to measure the concentration of CO_2 and CH_4. The concentration of CO_2 was measured using a thermal conductivity detector equipped gas chromatograph with a Porapak Q column, and CH_4 was measured using a flame ionization detector equipped gas chromatograph with a Porapak N column (both Shimadzu 8A, Kyoto, Japan). We repeatedly measured gas standards with gas concentrations near sample concentrations (455 μmol mol^{-1} for CO_2; 3.69 μmol mol^{-1} for CH_4) at regular intervals during our sample analyses. Coefficients of variation for check standards for CO_2 and CH_4 were less than 5%.

Soil physical environment

Soil temperature and water content were measured within one meter of the vented static chambers immediately before or during the static chamber measurements on each sampling date. We measured volumetric soil water content in the top 6 cm of the mineral soil at the time of the chamber measurements using a Theta probe with a MLX-2 digital display (Delta T Devices, England). Soil temperature was concurrently measured at the 10-cm mineral soil depth using a soil thermometer (VWR Scientific, Inc., West Chester, PA, USA).

Measurements of C pools

We sampled the soil O horizon at the burned and unburned sites in late September, 2007. Four 30 cm^2 sub-samples were taken in each of the five plots per site and sub-samples were homogenized before being air dried at 20°C. Organic material greater than 6 mm in diameter was considered to be coarse woody debris and was discarded.

We measured fine root mass (<2 mm diameter) in the 0–15 cm mineral soil depth. Three 5.1 cm wide by 15 cm deep soil cores were taken within each of the five plots at both sites in late May, 2006 and again in late May, 2007 using a slide hammer (AMS Core Sampler, American Falls, ID, USA). Samples were taken 3 m distant from the static chambers, away from plot center, in May 2006 and 3 m towards plot center from the static chambers in May 2007. The majority of fine roots are present within the top 15 cm of mineral soil in these forest, and few roots exist in the forest floor (Wright and Hart 1997). Soil and roots within the cores were separated with a hydropneumatic elutriator (Scienceware Bel-Art Products, Pequannock, NJ, USA) and roots were collected on stack sieves of 2 and 0.5 mm diameter (Kaye and Hart 1998). Roots were oven dried at 60°C for 72 h. Live and dead roots were pooled. Any remaining mineral soil attached to roots was accounted for by ashing the sample in a muffle furnace (Stevens and Jones 2006). Mass lost on ignition was used to convert the oven-dry root mass to ash-free oven dry mass (Kaye and Hart 1998).

We measured microbial C at both sites on May 31st, 2007 during the warm, dry spring season and again during the late-summer monsoon season on September 1, 2007. The upper 10 cm of the mineral soil was sampled using a 2-cm diameter Oakfield sampler (Model HC, Oakfield Apparatus Inc., Oakfield, WI, USA). Three cores were taken between 1 and 2 m distant from each static chamber ring and homogenized into a single subsample. Soil microbial C was determined using the chloroform ($CHCl_3$) fumigation-extraction method (Vance et al. 1987; Haubensak et al. 2002). The amount of C extracted from both unfumigated and fumigated soil samples was measured using a TOC-Vcsh total organic carbon analyzer (Shimadzu, Kyoto, Japan). Microbial C was determined by subtracting organic C in the unfumigated samples from the organic C in the fumigated samples, and dividing by an extraction efficiency factor (k_{EC}) of 0.39 (Sparling et al. 1990; Grady and Hart 2006).

Statistical analyses

To determine if the burned site had different rates of soil CO_2 efflux or CH_4 uptake than the unburned site, we used repeated measures analyses of variance (RM ANOVA) to test for differences in gas fluxes between the unburned and burned sites over the 14 sampling dates. Data from each of the 15 rings per site were considered to be independent to allow enough degrees of freedom to include the 14 sampling dates in the analysis. For all other analyses, plot averages were considered to be the experimental unit ($n = 5$). Repeated measures ANOVAs were also used to test differences between the burned and unburned sites for microbial C, understory plant biomass, and fine root mass. A one-way ANOVA was used to test soil O horizon mass differences between sites. Because of unequal variances in soil CO_2 efflux between measurement dates, all CO_2 flux data were ln-transformed before being analyzed by ANOVA, but we present untransformed means and standard errors to facilitate interpretation. We did not ln-transform the CH_4 data because the variances were homogenous and the residuals were normal. We used linear regression to compare soil CO_2 efflux and CH_4 uptake rates with microbial C and fine root biomass. We compared the regressions using bootstrapped estimates of the difference between slopes in the burned and unburned stands (Manly 1997). Relationships were estimated by resampling with replacement 1000 times and calculating differences in slopes and confidence intervals (Resampling Stats 4.0.7, *Resampling Stats Inc.*, Arlington, VA, USA).

To address our second objective, we developed a model in order to assess whether the response of soil CO_2 efflux to soil water content and temperature differed between the unburned and burned sites. We used this model exclusively to investigate whether the relationship of soil CO_2 efflux with soil temperature and water content differed between sites. Thus we report both significant and non-significant model coefficients. We developed the model using pooled data for both sites; the categorical variable "K" represented the fire effect, where $K = 0$ stands for the unburned site and $K = 1$ stands for the burned

site. The model had three continuous variables (soil temperature, water content, and water content squared) similar to Tang et al. (2005). A significant interaction between K and the three continuous variables statistically tested whether soil CO_2 efflux responded to soil temperature and soil water content differently at the unburned and burned sites. The model form was:

$$\ln(F) = \beta_0 + \beta_1 T + \beta_2 \theta + \beta_3 \theta^2 + \beta_4 K + \beta_5 T\theta + \beta_6 T\theta^2 + \beta_7 KT + \beta_8 K\theta + \beta_9 K\theta^2 + \beta_{10} KT\theta + \beta_{11} KT\theta^2 \quad (1)$$

where F (μmol CO_2 m^{-2} s^{-1}) is soil CO_2 efflux, T (°C) is soil temperature at 10 cm mineral soil depth, θ (m^3 m^{-3}) is soil water content integrated over the top 6 cm of the mineral soil, and β represents the coefficient estimate. A similar model construction technique was used for CH_4 uptake, also with the purpose of determining if the relationship between soil CH_4 uptake and soil temperature and soil water content differed between sites. The model had the form:

$$U = \beta_0 + \beta_1 T + \beta_2 \theta + \beta_3 \theta^2 + \beta_4 K + \beta_5 T\theta + \beta_6 T\theta^2 + \beta_7 KT + \beta_8 K\theta + \beta_9 K\theta^2 + \beta_{10} KT\theta + \beta_{11} KT\theta^2 \quad (2)$$

where U (nmol CH_4 m^{-2} s^{-1}) is CH_4 uptake.

To determine the direction and magnitude of the response of soil CO_2 efflux to soil temperature and soil water content between sites, we compared the difference in soil CO_2 efflux between sites by parameterizing our model with values within a range observed during our study for soil water content or temperature and holding the other variable (soil temperature or soil water content, respectively) constant at the mean value.

Fluxes were calculated by linear regression of CO_2 or CH_4 concentration against the sampling interval (e.g. Horz et al. 2002; Hart 2006). Fluxes with an R^2 lower than 0.95 for CO_2 indicated a non-linear flux and were deleted from further analysis. No threshold was imposed on CH_4 fluxes. Ten percent of all CO_2 fluxes were removed.

We calculated cumulative fluxes of CO_2 and CH_4 by multiplying the daily sum (mg CO_2 or CH_4 m^{-2} day^{-1}) by one-half the number of days since the last sample and one half the number of days until the next sample (Kaye and Hart 1998). The sum of these averages provided a cumulative value (g m^{-2}) for the 427 days from the beginning of the sampling on June 15th, 2006 to August 15th, 2007. An annual estimate was also calculated using the same method between June 15th, 2006 and June 14th, 2007.

We show soil CO_2 efflux data using positive values. Rates of CH_4 uptake are expressed as negative values because CH_4 uptake is a sink from the atmosphere. We used JMP software (v 5.0, SAS Institute, Cary, NC USA) in all statistical analyses except for the resampling procedures.

We measured soil CO_2 and CH_4 fluxes, soil C pools, and soil physical properties at one unburned site and one burned site. Both sites were representative of ponderosa pine forests that were susceptible to severe fire. Although we used statistical techniques to assist in interpreting the differences observed between sites, we do not extrapolate our results beyond these two study sites.

Results

Fire reduced soil CO_2 efflux and increased CH_4 uptake

The unburned site had higher mean soil CO_2 efflux than the burned site on all measurement dates except May 1st, 2007 (Fig. 1a). Mean soil CO_2 efflux was 40% higher at the unburned site over the entire measurement period ($p < 0.001$; Table 2). Soil CO_2 efflux was significantly different between sites, and the difference between sites varied by sampling date (time by site interaction, $p < 0.001$). Differences between sites were greater during the late summer of 2006 than during the late summer of 2007 (Fig. 1a). However, soil CO_2 efflux was greater at the unburned site than the burned site during both 2006 ($p < 0.001$) and 2007 ($p < 0.001$). The burned site emitted 270.4 g m^{-2} less C from the soil as CO_2 than the unburned site during our 427 days measurement period (Table 2). The burned site emitted 239.6 g m^{-2} less C from the soil as CO_2 than the unburned site during the year June 15th, 2006 to June 14th, 2007.

Mean CH_4 uptake over all sampling dates was 49% greater at the burned site than the unburned site (Table 2) over the entire measurement period. The difference between sites varied significantly by sample date (time by site interaction, $p = 0.047$). Methane

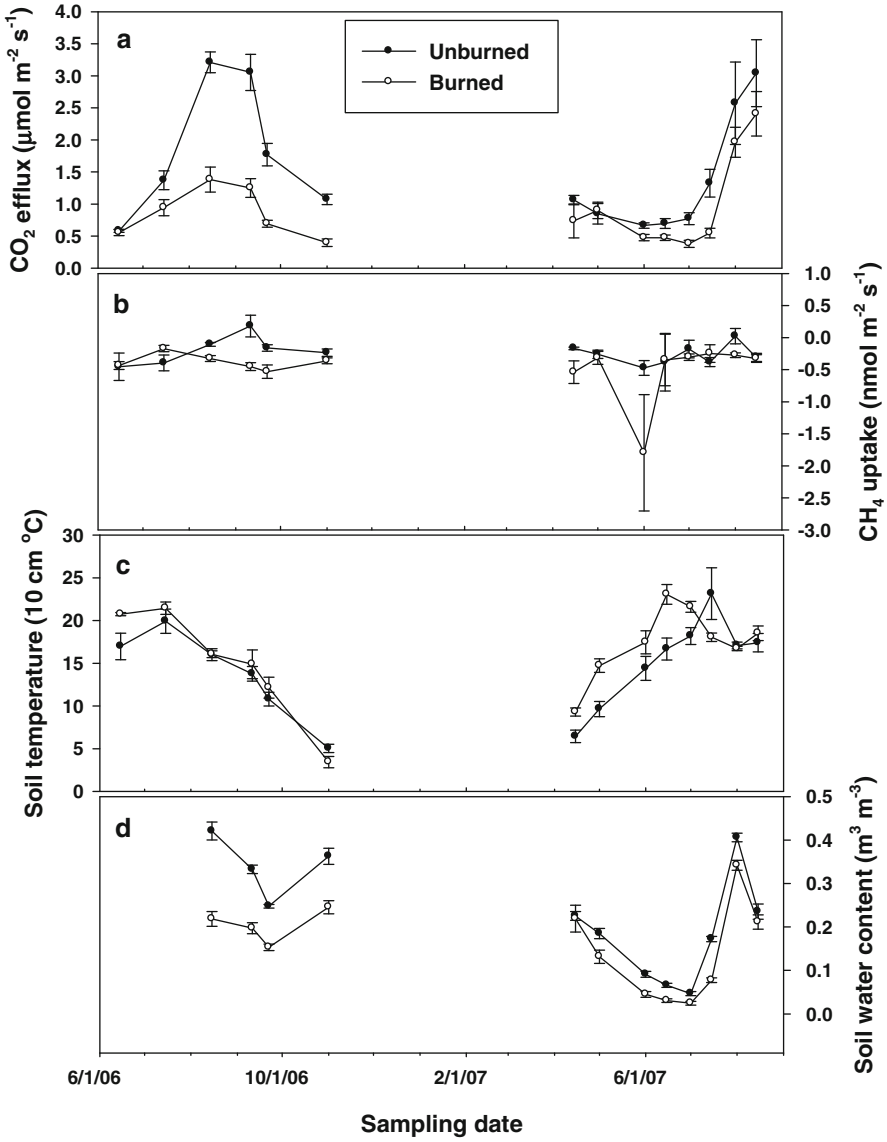

Fig. 1 Soil carbon dioxide efflux (CO_2 efflux; **a**), methane (CH_4) uptake (**b**), soil temperature at the 10 cm mineral soil depth (**c**), and soil water content integrated over the upper 6 cm of mineral soil (**d**) at the unburned and burned sites during the measurement period of June 2006–August 2007. *Error bars* represent ±1 standard error of the mean

uptake was greater at the burned site during 2006 ($p = 0.009$) and but not 2007 ($p = 0.138$). The only sample dates during which the unburned site took up more CH_4 than the burned site were June 15th, 2006, June 15th, 2007 and July 15th, 2007 (Fig. 1b).

Soil gas flux was related to soil temperature and water content

Soil temperature was higher during most sampling dates at the burned site than the unburned site (Fig. 1c), despite similar mean annual air temperatures at both sites in 2006 and 2007 (Table 1). Mean soil water content in the surface soil was higher on all sampling dates at the unburned site than the burned site (Fig. 1d). Peak soil water content was lower at the burned site in 2006 than in 2007. Annual precipitation measured at the eddy covariance towers was greater in 2006 at the unburned site than the burned site (Table 1), but the seasonal pattern of precipitation was similar at each site (Dore et al. 2008).

The regression model predicted soil CO_2 efflux well ($R^2 = 0.753$; $p < 0.001$; $n = 115$). Soil CO_2 efflux was significantly and positively related to soil temperature and water content (Table 3). The

Table 2 Mean, total cumulative (427 days), and annual rates of carbon dioxide (CO_2) efflux from soil and methane (CH_4) uptake in soil at the unburned and burned sites

Variable/unit	Unburned	Burned
Mean		
CO_2 efflux (μmol CO_2 m^{-2} s^{-1})	1.54	0.92
CH_4 uptake (nmol CH_4 m^{-2} s^{-1})	−0.24	−0.45
Total (g C m^{-2} 427-day^{-1})		
CO_2 efflux	610.25	339.80
CH_4 uptake	−0.10	−0.21
Annual (g C m^{-2} $year^{-1}$)		
CO_2 efflux	510.72	271.15
CH_4 uptake	−0.08	−0.19

response of soil CO_2 efflux to soil water content was similar between sites, as shown by the non-significant p-value for the categorical (K) and continuous variable (θ, θ^2) interactions (Table 3). The model predicted lower soil CO_2 efflux at the burned site than the unburned site at any given value of soil water content (Fig. 2). In contrast, soil temperature had different effects on soil CO_2 efflux at the burned site than the unburned site ($K * T$ interaction, $p = 0.018$; Table 3). The model predicted lower soil CO_2 efflux at the burned site than the unburned site at low (<20°C) soil temperatures, but at higher soil temperatures (>20°C), soil CO_2 efflux was predicted to be greater at the burned site than the unburned site (Fig. 3).

The regression model failed to explain a significant amount of variation in CH_4 uptake ($R^2 = 0.132$; $p = 0.195$; $n = 112$; Table 3). All continuous, categorical, and interaction terms in the model were non-significant when considered separately (Table 3). Therefore, the response of CH_4 uptake to soil water content and soil temperature was indistinguishable between the burned and unburned sites.

Fire reduced soil C pools

Severe fire significantly affected all C pools measured 10 years after burning. Soil O horizon mass was ~10-fold lower at the burned site than the unburned site ($p = 0.004$; Table 4). The burned site had lower fine root biomass in the top 15 cm of the mineral soil than the unburned site during both 2006 and 2007 ($p = 0.001$; Table 4), and the site difference was consistent over years (site × year interaction $p = 0.124$). Mean fine root mass did not differ between years within a site ($p = 0.719$).

Table 3 Coefficients, estimates, standard errors, and probabilities for models relating carbon dioxide efflux and methane uptake to soil temperature and soil water content at the unburned site and the burned site

Gas flux/coefficient	Estimate	Standard error	Probability
Carbon dioxide efflux ($R^2 = 0.753$, $p < 0.001$, $n = 115$)			
β_0 intercept	1.84	0.28	<0.001
β_1 T	0.07	0.01	<0.001
β_2 θ	9.32	1.75	<0.001
β_3 θ^2	−12.94	4.14	0.002
β_4 K	−0.33	0.10	0.001
β_5 $T * \theta$	0.19	0.34	0.581
β_6 $T * \theta^2$	0.36	0.89	0.687
β_7 $K * T$	0.05	0.02	0.018
β_8 $K * \theta$	0.48	3.47	0.890
β_9 $K * \theta^2$	−4.55	8.16	0.578
β_{10} $K * T * \theta$	0.47	0.68	0.489
β_{11} $K * T * \theta^2$	−0.11	1.75	0.950
Methane uptake ($R^2 = 0.132$, $p = 0.120$, $n = 112$)			
β_0 intercept	−0.96	0.43	0.021
β_1 T	0.02	0.02	0.319
β_2 θ	2.79	2.47	0.261
β_3 θ^2	−3.47	5.85	0.555
β_4 K	0.09	0.07	0.178
β_5 $T * \theta$	−0.68	0.49	0.167
β_6 $T * \theta^2$	1.44	1.26	0.256
β_7 $K * T$	−0.0002	0.02	0.990
β_8 $K * \theta$	−1.16	2.46	0.639
β_9 $K * \theta^2$	2.38	5.85	0.685
β_{10} $K * T * \theta$	−0.19	0.49	0.690
β_{11} $K * T * \theta^2$	0.29	1.26	0.818

K is the categorical variable representing the unburned ($K = 0$) and burned ($K = 1$) sites. θ is the volumetric soil water content (0–6 cm mineral soil depth); T is soil temperature (10 cm mineral soil depth)

The unburned site had greater microbial C than the burned site during both May 31st, 2007 and September 1st, 2007 (Table 4). Both the burned and unburned sites had lower microbial C in May than September, and the unburned site had a greater increase in microbial C between May and September than the burned site (time by site interaction $p = 0.030$). Soil CO_2 efflux was significantly and positively correlated to microbial C at both sites (Fig. 4a). The slope of this

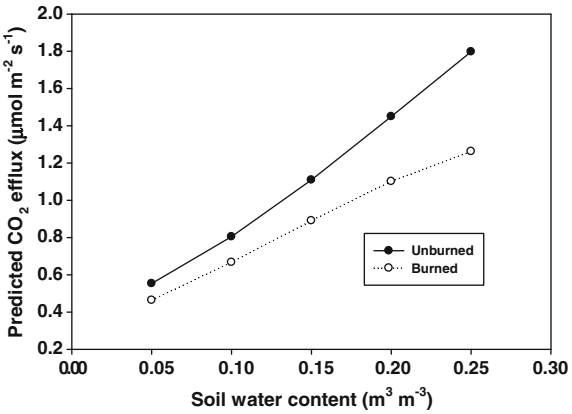

Fig. 2 Model-predicted soil carbon dioxide (CO_2) efflux as a function of water content (see "Methods") at a range of soil water contents observed at the unburned and burned sites. Soil temperature was held constant

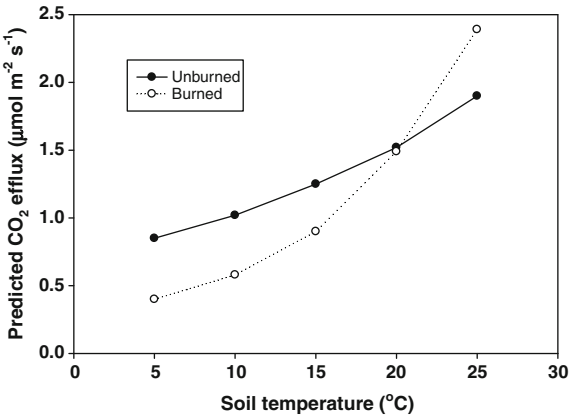

Fig. 3 Model-predicted soil carbon dioxide (CO_2) efflux as a function of temperature (see "Methods") at a range of soil temperatures observed at the unburned and burned sites. Soil water content was held constant

relationship was two-fold higher at the burned site than the unburned site, and the coefficient of determination was also higher at the burned site ($R^2 = 0.729$, $p = 0.003$) than at the unburned site ($R^2 = 0.548$, $p = 0.023$). The slopes were different at the bootstrapped 85% confidence interval, with a mean slope difference of 0.010 μmol CO_2 m^{-2} s^{-1} mg C^{-1} kg $soil^{-1}$, a lower slope confidence limit of 0.00004 μmol CO_2 m^{-2} s^{-1} mg C^{-1} kg $soil^{-1}$, and an upper slope confidence limit of 0.018 μmol CO_2 m^{-2} s^{-1} mg C^{-1} kg $soil^{-1}$. Soil CO_2 flux was not significantly related to fine root biomass at either site ($p = 0.611$, 0.555 at the unburned at burned sites, respectively).

Table 4 Mean values (±1 standard error; $n = 5$) of carbon pools at the unburned and burned sites

Variable/date sampled	Unburned	Burned
Soil O horizon mass (g m^{-2})		
2007	314.6 (68.5)	31.2 (7.7)
Fine root biomass (g m^{-2})		
2006	254.5 (32.3)	79.68 (22.5)
2007	226.7 (15.2)	122.93 (25.2)
Microbial carbon (mg kg^{-1})		
May 31, 2007	245 (41)	157 (17)
September 1, 2007	800 (60)	339 (39)

There was no correlation between CH_4 uptake and microbial C at either the unburned or burned sites ($p = 0.814$, $p = 0.080$ respectively; Fig. 4b).

Fire increased the importance of CH_4 uptake relative to soil CO_2 efflux

By reducing soil CO_2 efflux and increasing CH_4 uptake, severe fire increased the relative importance of CH_4 uptake to radiative forcing from soil gas exchange in the burned forest. We evaluated the net change in warming potential of CO_2 and CH_4 by comparing the two gases to a standard warming potential known as a "CO_2 equivalent" (CO_{2e}). Carbon dioxide has a CO_{2e} of 1 mol CO_2 mol^{-1} CO_2; a recent estimate suggests that over 100 years' time CH_4 has a CO_{2e} equal to 25 mol CH_4 mol^{-1} CO_2 (Forster et al. 2007). After multiplying CH_4 molar uptake rates by 25 to convert CH_4 to CO_{2e}, we estimated that a reduction of 1.5% of the CO_{2e} emitted by soil CO_2 efflux occurred due to CH_4 uptake at the burned site over the 427-day measurement period. At the unburned site, soil CH_4 uptake reduced the CO_{2e} released to the atmosphere from soil CO_2 efflux by only 0.40%.

Discussion

Our results show that 10 years after a severe wildfire killed all the trees in a ponderosa pine forest, soil CO_2 efflux was lower and CH_4 uptake was higher during much of the year when compared to an unburned site (Fig. 1a). We attribute this difference to the effects of the fire. Though we have no measurements of forest

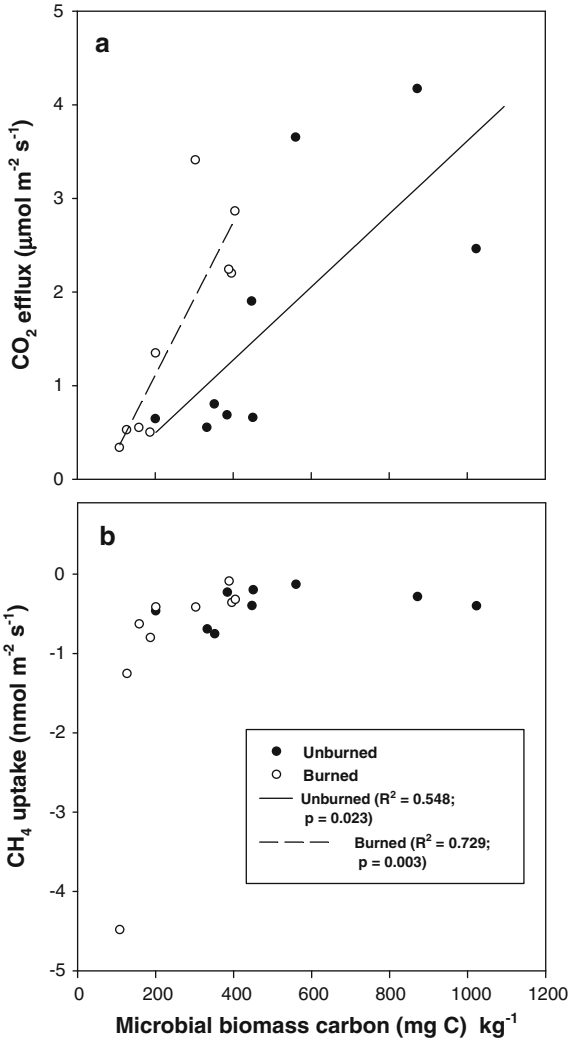

Fig. 4 Relationship between soil carbon dioxide (CO_2) efflux (**a**), methane (CH_4) uptake (**b**), and microbial carbon at the unburned and burned sites. Flux data from June 1st, 2007 and August 15th, 2007 are paired with microbial biomass carbon values obtained on May 31st, 2007 and September 1st, 2007, respectively. *Regression lines* are shown only for significant ($p < 0.05$) relationships

structure or soil gas fluxes before the fire, we have evidence that the burned and unburned sites were similar before the fire. Unburned forests located within 1 km of the burned site had nearly identical tree basal area and projected LAI as the unburned site. Furthermore, soils at both sites are classified as Mollic Eutroboralfs or the very similar Typic Argiboroll. Finally, data from the eddy covariance towers show similar vapor pressure deficit, maximum air temperature, and total solar radiation above the vegetation canopy at the two sites during 2006 (Montes-Helu et al. 2009). These data suggest that differences in our results between the sites examined here can be attributed to the fire disturbance and subsequent vegetation shift, and are not likely due to a pre-existing condition or climatic differences between the sites.

By reducing plant biomass and leaf area, the fire likely caused the higher soil temperatures we measured. The reduction in leaf area would be accompanied by a reduction in transpiration, and increased flux of solar energy to the soil surface. Greater soil heat flux at the burned site than the unburned site and lower evapotranspiration at the burned site than the unburned site limited the cooling effect of latent energy at the burned site (Montes-Helu et al. 2009). Though Montes-Helu et al. (2009) reported greater soil water storage at the burned site than the unburned site over a depth of 65 cm, we observed lower surface (0–6 cm) soil water content at the burned site than the unburned site. This result may have been because the burned site received less precipitation than the unburned site, or more likely because the higher soil surface temperature of the burned site increased evaporation from the surface soil (O'Neill et al. 2002).

The differences in soil temperature and soil water content do not, by themselves, explain the lower soil CO_2 efflux at the burned than the unburned site. By modeling soil CO_2 efflux as a function of soil temperature and water content we determined that the relationship between soil temperature and soil CO_2 efflux differed between the burned and unburned sites (Table 3), but the relationship between soil water content and soil CO_2 efflux did not differ. Soil CO_2 efflux was more sensitive to changes in soil temperature at the burned site than the unburned site. At temperatures lower than 20°C the model predicted lower soil CO_2 efflux at the burned site than the unburned site; at temperatures higher than 20°C, the model predicted higher soil CO_2 efflux at the burned site. During our measurement period, the burned site had mean soil temperatures greater than or equal to 20°C on twice as many occasions as the unburned site. This indicates that if soil temperatures were causing a difference in soil CO_2 efflux between the burned and unburned sites, the burned site might be expected to have higher soil CO_2 efflux than the unburned site, contrary to what we found.

It is possible that though both sites had a similar response of soil CO_2 efflux to soil water content, the absolute differences in water content between the sites resulted in the lower rates of soil CO_2 efflux at the burned site. The unburned site had higher predicted soil CO_2 efflux than the burned site at the same soil water contents when soil temperature was held constant. Similarly, soil CO_2 efflux at the burned site was more similar to soil CO_2 efflux at the unburned site during the 2007 monsoon season, when soil water content was similar for each site, than during the 2006 monsoon season, when soil water content was lower at the burned site. However, the unburned site had higher soil CO_2 efflux even when the soil water contents were similar, including sampling dates on April 15th, July 1st, and August 15th, 2007. The combination of these results suggests that something other than fire-caused differences in soil temperature or soil water content caused a difference in soil CO_2 efflux between sites.

Recent studies in southwestern ponderosa pine forests have shown that disturbance to forests changes the amount of C available for soil CO_2 efflux (Hart et al. 2005b; Grady and Hart 2006; Selmants et al. 2008; Sullivan et al. 2008). Specifically, burning often reduced the amount of C available for soil CO_2 efflux (Hart et al. 2005b; Grady and Hart 2006). Our data support the C-limitation hypothesis described by Hart et al. (2005b) and observed in a variety of ecosystems (Litton et al. 2003; Michelsen et al. 2004; Irvine et al. 2007), which suggests that changes in the quantity and quality of organic inputs from vegetation as a result of fire can alter soil C cycling.

Trees have not re-established on the burned site even 10 years after burning (Dore et al. 2008). The lower LAI at the burned site than the unburned site was accompanied by lower gross primary production (Dore et al. 2008) and likely a concomitant reduction in the amount of photosynthate allocated to belowground autotrophic respiration. Soil CO_2 efflux has been positively correlated with both aboveground and belowground net primary productivity in ponderosa pine forests (Campbell et al. 2004; Irvine et al. 2007). The removal of trees from an ecosystem may reduce the amount of live respiring tree roots, and subsequently reduce total soil CO_2 efflux (Sullivan et al. 2008), and fire in ponderosa pine forests has been reported to reduce both fine root and mycorrhizal biomass (Hart et al. 2005a). The burned site in this study was no exception: fine root biomass was an average of 58% lower at the burned site than the unburned site during the 2 years of this study. Based on other research in ponderosa pine forests in northern Arizona, it appears reasonable to assume that most fine tree roots have decomposed 10 years after fire. Hart et al. (2005a) report that approximately 25% of the mass of fine ponderosa pine roots decomposed within 154 days.

The size of the soil microbial community was lower at the burned site than the unburned site. This finding is consistent with Grady and Hart (2006) who measured microbial C several years earlier in the same fire complex as the one in this study and report that microbial C was lower in burned forests than unburned forests throughout the summer. Lower microbial biomass in the burned compared to the unburned site suggests a reduced heterotrophic contribution to total soil respiration. Yet, microbial C explained a greater proportion of the variation in soil CO_2 flux at the burned site (73%) than at the unburned site (55%), and the slope of the relationship between microbial C and soil CO_2 efflux was two-fold higher at the burned than unburned site. Though it is possible that the lower microbial biomass at the burned site than the unburned site was due to the lower amount of soil water available, the soil microbial biomass was likely also limited by the amount of labile C available for assimilation into microbial biomass (C.S. Ross, unpublished data). This explanation is supported by the increased sensitivity of soil CO_2 efflux to changes in the microbial biomass at the burned site. The microbial biomass at the burned site, though smaller in absolute mass than the unburned site, contributed proportionally more to total soil CO_2 efflux. Our results suggest that by using the assumption that heterotrophic respiration is approximately 50% of total soil CO_2 efflux (Hanson et al. 2000), net ecosystem production (NEP) would be overestimated in burned forests using the formula $NEP = NPP - Rh$ (Ehman et al. 2002; Howard et al. 2004), where NPP is net primary productivity and Rh is heterotrophic respiration.

By combusting the soil O horizon, the fire at the burned site reduced the amount of decomposable C available for soil CO_2 efflux (C.S. Ross, unpublished data), and directly reduced a substantial source of soil CO_2 efflux. Other work at nearby sites in northern Arizona ponderosa pine forests has shown that

between 15 and 45% of total soil CO_2 efflux comes from the soil O horizon at unburned sites, depending on the time of year (Grady 2006).

This research adds to a growing quantity of evidence that severe wildfire reduces soil CO_2 efflux by reducing the amount of C substrate available, rather than by altering soil temperature or soil water content. For instance, soil temperature and water content did not explain lower soil CO_2 efflux 13 years after a severe fire in lodgepole pine (*Pinus contorta*) in Yellowstone National Park, USA (Litton et al. 2003) where trees were re-establishing, but not yet mature. However, at large scales, the effects of fire on soil CO_2 efflux appear idiosyncratic. An Oregon ponderosa pine forest experienced a rapid (<2 year) recovery of tree seedlings (>1,200 seedlings ha^{-1}) and autotrophic respiration after a severe fire, and soil CO_2 efflux was the same at burned and unburned forests within 2 years of burning (Irvine et al. 2007). This rapid recovery post-fire in Oregon likely resulted in more C available for soil CO_2 efflux than in the sites we studied in Arizona. Differences in soil quality and climate between Arizona and Oregon may influence the vegetative recovery of the two regions, and explain the difference between our results and those of Irvine et al. (2007). In a boreal forest ecosystem that is cooler and wetter than the semi-arid forest ecosystem we studied, severe burning increased soil temperature and caused a switch from temperature-limited soil CO_2 efflux to moisture-limited soil CO_2 efflux (O'Neill et al. 2002). Low-severity prescribed fire in a ponderosa pine forest in California increased the sensitivity of soil CO_2 efflux to changes in soil temperature and water content (Kobziar and Stephens 2006). The effect of fire on the relationship of soil CO_2 efflux to soil temperature and water content likely depends on climate, pre-fire stand conditions, fire severity, and post-fire vegetative recovery.

Considering the importance of CH_4 to climate change, little is known regarding the effects of fire on CH_4 uptake in ecosystems other than boreal forests. A laboratory study of burned and unburned boreal spruce (*Picea abies*) forest soils showed both short- and long-term increases in CH_4 uptake after burning (Jaatinen et al. 2004). Both burned jack pine (*Pinus banksiana*) and burned black spruce (*Picea mariana*) boreal forests were slightly stronger sinks of CH_4 than unburned forests, even several years after burning (Burke et al. 1997). To our knowledge, we provide the first report of an effect of severe fire on soil CH_4 uptake in semi-arid or ponderosa pine forests. Our results suggests that burned areas have higher rates of CH_4 uptake in soil; as fires in the western USA grow in size and severity (Westerling et al. 2006), this finding may have important consequences on predictions of the global CH_4 sink.

There were slight textural differences between the unburned and burned sites (Table 1). The unburned site had more sand and less clay relative to the unburned site. The effect of this on CH_4 uptake is not clear. Air-filled macropores (>0.06 mm) are an important means by which CH_4 diffuses from the atmosphere into the soil. The greater amount of sand at the unburned site suggests that there is a greater volume of potentially air-filled macropores through which CH_4 could diffuse from the atmosphere. This would suggest that the unburned site, rather than the burned site as we observed, would be more likely to have greater rates of CH_4 uptake.

Because severe wildfire did not change the response of CH_4 uptake to soil temperature or water content, and because CH_4 uptake is independent of other sources of C, the increase in CH_4 uptake we observed after fire may be due to the loss of the soil O horizon. The loss of the soil O horizon may have increased diffusion of CH_4 from the atmosphere to the soil profile. The importance of substrate availability to CH_4 uptake in soils at our study sites is supported by the increased CH_4 uptake during the dry June 2007 sampling dates at the burned site. Methane diffuses from the atmosphere into the mineral soil of dry soils with greater air-filled-porosity more easily than wet soils with less air-filled-porosity. Stimulation of CH_4 uptake resulting from the removal of the soil O horizon has been found in other ecosystems (Saari et al. 1998; Steinkamp et al. 2001). Most methanotrophs live within the A horizon of forest soil (Conrad 1996); however, in a northern hardwood forest, substantial CH_4 uptake was observed in the soil O horizon (Yavitt et al. 1995). That forest was much wetter than the ponderosa pine forests in our study and the soil O horizon was comprised of different litter types. Though we cannot discount the possibility that the fire event caused higher populations of methanotrophic bacteria, we show evidence that fire may increase CH_4 uptake by removing the soil O horizon which acts as a barrier to diffusion.

Any loss after fire of CH_4 uptake that occurred in the soil O horizon was overwhelmed by the increase in the CH_4 uptake activity within the mineral soil.

The relative importance of the soil CH_4 sink was greater at the burned site than the unburned site because CH_4 uptake at the burned site offset a greater percentage of soil CO_2 efflux. In 2006, the burned site was a net source of 109 g C m^{-2} $year^{-1}$ to the atmosphere (Dore et al. 2008). This includes the cumulative effect of aboveground plant respiration, soil CO_2 efflux, and photosynthesis. The 0.19 g CH_4–C m^{-2} $year^{-1}$ taken up by the soil, when multiplied by its warming factor of 25 (Forster et al. 2007), offset 4.4% of the total net ecosystem exchange at the burned site. Methane, though a smaller component of soil gas flux than CO_2, partly mitigates the atmospheric warming potential of the post-fire ecosystem.

Conclusion

Severe fire can have lasting, decadal-scale impacts on soil gas fluxes in ponderosa pine forests of northern Arizona. By killing the overstory and converting the vegetation to a sparse grassland, fire changed the amount and sources of C available for soil CO_2 efflux. Both temperature and soil water content may limit soil CO_2 efflux in these forest soils, but during warm and wet periods, the burned site still had lower soil CO_2 efflux than the unburned site, further supporting the hypothesis that C limitation of soil CO_2 efflux occurs in severely burned semi-arid forest soils. By burning the soil O horizon and converting the plant community to a less-productive grassland, severe fire may have reduced the barrier to diffusion represented by the soil O horizon and increased CH_4 uptake. Though CH_4 uptake was a small portion of total gas flux at either site, CH_4 uptake had a greater relative significance at the burned site than the unburned site because CH_4 uptake rates were higher and CO_2 effluxes were lower at the burned site.

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