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Thinning reduces soil carbon dioxide but not methane flux from southwestern USA ponderosa pine forests

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ABSTRACT

Forest soils are important components of the global carbon cycle because they both store and release carbon. Carbon dioxide is released from soil to the atmosphere as a result of plant root and microbial respiration. Additionally, soils in dry forests are often sinks of methane from the atmosphere. Both carbon dioxide and methane are greenhouse gases whose increasing concentration in the atmosphere contributes to climate warming. Thinning treatments are being implemented in ponderosa pine forests across the southwestern United States to restore historic forest structure and reduce the risk of severe wildfire. This study addresses how thinning alters fluxes of carbon dioxide and methane in ponderosa pine forest soils within one year of management and examines mechanisms of change. Carbon dioxide and methane fluxes, soil temperature, soil water content, forest floor mass, root mass, understory plant biomass, and soil microbial biomass carbon were measured before and after the implementation of a thinning and in an unthinned forest. Carbon dioxide efflux from soil decreased as a result of thinning in two of three summer months. Average summer carbon dioxide efflux declined by an average of $34 \, \text{mg C m}^{-2} \, \text{hr}^{-1}$ in the first year after thinning. Methane oxidation did not change in response to thinning. Thinning had no significant short-term effect on total forest floor mass, total root biomass, or microbial biomass carbon in the mineral soil. Understory plant biomass increased after thinning. Thinning increased carbon available for decomposition by killing tree roots, but our results suggest that thinning reduced carbon dioxide emissions from the soil because the reduction in belowground autotrophic respiration was larger than the stimulation of heterotrophic respiration. Methane oxidation was probably not affected by thinning because thinning did not alter the forest floor mass enough to affect methane diffusion from the atmosphere into the soil.

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1. Introduction

The net carbon (C) flux between ecosystems and the atmosphere is important to the global C cycle (Chapin et al., 2002). The C flux is primarily the result of the difference between gross photosynthesis and the respiration of carbon dioxide (CO_2) from ecosystems. Ecosystem disturbances can alter the balance of gross photosynthesis and respiration and hence may change the C source or sink strength of an ecosystem (e.g., Law et al., 2004; Misson et al., 2005; Dore et al., 2008). Carbon dioxide efflux from soil (CO_2 efflux) is the largest terrestrial source of C to the atmosphere, contributing 75 Pg C yr^{-1} (1 Pg = 10^{15} g; Schlesinger and Andrews, 2000). Soil CO_2 efflux is tightly coupled with net primary productivity (NPP) in ecosystems worldwide (Raich and Schle-singer, 1992; Janssens et al., 2001) and soil CO_2 efflux is expected to increase as a result of higher temperatures (Schlesinger and Andrews, 2000). Two biological processes are responsible for soil CO_2 efflux: root metabolic activity (autotrophic respiration) and the decomposition of organic material by microbes (heterotrophic respiration; Ryan and Law, 2005). Ecosystem disturbance can directly or indirectly alter these two sources of soil CO_2 efflux.

Methane (CH_4) is known to be the second most important gas responsible for recent atmospheric warming (Shine and Sturges, 2007). Levels of CH_4 in the atmosphere have doubled in the last 200 years mostly as a result of agricultural activity (Crutzen, 1991; Whalen, 1993). Despite a much lower atmospheric concentration ($\sim 1.7 \, \mu\text{mol mol}^{-1}$) than CO_2 ($\sim 380 \, \mu\text{mol mol}^{-1}$), CH_4 has a warming potential 21 times greater per mole than CO_2, and accounts for over 30% of the radiative forcing of Earth's energy balance (Lelieveld et al., 1998; Shine and Sturges, 2007). Soils are the only known biological sink of CH_4 due to the oxidation of CH_4 to methanol (CH_3OH) for energy by methanotrophic bacteria (Hanson

and Hanson, 1996). The oxidation of CH_4 is a substrate-limited process that depends on the presence of CH_4 and oxygen diffusing from the atmosphere into soil, or from zones of high to low concentration within soil. Because of its greater atmospheric warming potential than CO_2, CH_4 oxidation in soil may partly offset warming caused by soil CO_2 efflux.

The forests of the southwestern United States have experienced a shift in vegetation cover in the last century from a low density ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) overstory with large grass openings to high density ponderosa pine stands with little herbaceous cover, less herbaceous diversity, and thick forest floors (Cooper, 1960; Covington and Sackett, 1984; Covington and Moore, 1994; Fulé et al., 1997). These dense forests are C sinks, yet are more susceptible to intense stand-replacing fires than forests with historic structure (Covington et al., 1994; Allen et al., 2002; Kaye et al., 2005). In an effort to reduce fuels and fire hazard and to re-create historic forest stand structure, restoration thinning treatments are being implemented in ponderosa pine forests of the southwestern U.S. (e.g., Covington et al., 1997; Skov et al., 2004). Forests are likely to experience increased restoration management given predictions of increased fire frequency associated with climate change (Westerling et al., 2006). Restoration treatments often use mechanical thinning to reduce tree density and harvesting may be followed by prescribed fire. Determining how restoration thinning changes soil C fluxes is necessary to understand potential feedbacks between forest management activities and climate warming.

The removal of trees from ecosystems has had ambiguous effects on soil CO_2 efflux. Soil CO_2 efflux has increased (Kaye and Hart, 1998; Selig and Seiler, 2004; Selmants et al., 2008), decreased (Kaye and Hart, 1998; Tang et al., 2005), or not changed (Toland and Zak, 1994) in response to overstory harvesting. The variability in the response of soil CO_2 efflux to thinning may be because the autotrophic and heterotrophic components of respiration can respond to perturbations independently of each another (Curiel Yuste et al., 2007). For instance, soil CO_2 efflux may be reduced by thinning due to the killing of respiring tree roots (Pypker and Fredeen, 2003; Wiseman and Seiler, 2004; Tang et al., 2005), but could also increase if soil heterotrophs decompose dead roots rapidly after thinning (Curiel Yuste et al., 2007).

In the semi-arid southwestern U.S., where ecosystem functions are driven by pulses of precipitation and large variations in temperature, effects of thinning on soil CO_2 efflux in ponderosa pine forests are often confounded by inter-annual climatic variability, which may have contributed to a reduction in CO_2 efflux one year after thinning and an increase in soil CO_2 efflux in the next (Kaye and Hart, 1998). Responses of soil CO_2 efflux to thinning also appear to change over time since tree removal, as ecosystem C pools change. Eight years after thinning at the same site used by Kaye and Hart (1998), Boyle et al. (2005) found higher soil CO_2 efflux in thinned than unthinned plots when soils were dry, and no effect when soil moisture was high. In another study, conducted 6–15 years after thinning, soil CO_2 efflux was generally lower in thinned stands than adjacent unthinned control sites but varied seasonally (Grady and Hart, 2006). No studies in southwestern ponderosa pine forests have examined the effect of thinning on CO_2 efflux within one year after treatment or combined pre- and post-treatment data with an unthinned site to control for the influences of inter-annual variability in temperature and precipitation on CO_2 efflux.

Considering the important role of CH_4 in climate warming and the importance of soil as a sink, the effects of thinning on CH_4 oxidation have not been adequately examined. Forest thinning may alter CH_4 oxidation by changing either the activity of methanotrophic bacteria or the diffusion of substrate into the soil. Methane oxidation is often low at low soil water contents, greatest at intermediate soil water contents, and low at high soil water contents. Low soil water content can result in cellular osmotic stress of methanotrophic bacteria, though the content at which this stress occurs seems to vary among ecosystems (West and Schmidt, 1998; Davidson et al., 2004), whereas high soil water content limits the diffusion of CH_4 from the atmosphere into the soil. Methane oxidation in ponderosa pine soils has not been found to be significantly related to changes in soil water content (Hart, 2006). Methane oxidation is often not associated with changes in soil temperature because temperature only has small impacts on the diffusion of CH_4 in soil (King, 1997), though the only known study of CH_4 oxidation in northern Arizona forest soils found that CH_4 oxidation decreased in high-elevation spruce/fir forest soil transplanted to a warmer low-elevation site.

Rates of CH_4 oxidation have not been measured in thinned ponderosa pine forests of the southwestern U.S. Thinning a slash pine (*Pinus elliottii*) forest in Florida, USA increased soil water content sufficiently to limit substrate availability for oxidation and convert the soil from a net sink of CH_4 to a net source of CH_4 to the atmosphere as a result of methanogenesis (Castro et al., 2000). Disturbance to the forest floor of New Zealand pine plantations increased CH_4 oxidation by as much as 70% (Tate et al., 2006). Reducing forest floor mass increased the diffusion of CH_4 from the atmosphere into the soil, thereby enhancing CH_4 oxidation (Saari et al., 1998; Steinkamp et al., 2001). Thinning has been shown to either decrease (Tate et al., 2006) or increase forest floor density (Kaye and Hart, 1998).

This study addresses the following questions in ponderosa pine forests of northern Arizona: (1) how does forest thinning change fluxes of CO_2 and CH_4 in the first growing season after treatment? and (2) by what mechanisms might thinning alter fluxes of CO_2 and CH_4? We addressed these questions by intensively measuring pre- and post-treatment fluxes of CO_2 and CH_4 in a single large (1 km^2) experimentally thinned forest and a 1 km^2 unthinned "control" forest as a case study of thinning in southwestern US ponderosa pine forests. We monitored soil temperature and soil water content simultaneously with gas flux measurements, and quantified thinning effects on elements of the forest C cycle including forest floor mass, root biomass, understory plant biomass, and soil microbial C.

2. Methods

2.1. Study sites

We measured soil CO_2 efflux and CH_4 oxidation at two sites dominated by ponderosa pine in northern Arizona, USA. The sites consisted of a densely forested, unmanaged site (control) and a similar site that was partially restored to historical conditions using mechanical thinning in September 2006 (restoration). The sites were also used for an eddy covariance study of CO_2 and energy flux from the land to the atmosphere. The control site was the same site used by Dore et al. (2008) and Montes-Helu et al. (in review). Our soil measurements occurred in the 1 km^2 "footprint" of the eddy covariance measurements at both sites.

The control 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 2180 m a.s.l.). The control site represents a typical dense ponderosa pine stand in northern Arizona, and has not experienced forest management in over a century. Tree age averaged 87 years, projected overstory leaf area index (LAI) was 2.3, and peak understory LAI was 0.06 in 2006 (Table 1; Dore et al., 2008). The forest overstory consists of ponderosa pine, with scattered Gambel oak (*Quercus gambelii*); the

Table 1
Site characteristics of the control site and the restoration site which was mechanically thinned during September 2006

Site characteristic	Control	Restoration (pre-thin)	Restoration (post-thin)
Tree density (number ha^{-1})	853	465	154
Basal area (m^2 ha^{-1})	30.0	20.5	12.6
Projected overstory leaf area index (m^2 m^{-2})	2.3	1.5	0.8
Projected understory leaf area index (m^2 m^{-2})	0.06	0.07	0.18
Total 2006 annual precipitation (mm)	696	446	
Mean 2006 air temperature (°C)	8.8	9.8	
Soil classification	Complex of Mollic Eutroboralf and Typic Argiboroll	Typic Eutroboralf	
Surface soil textural class	Clay loam	Silt loam	

understory is dominated by grasses, including *Festuca arizonica*, *Elymus elymoides*, *Boutelua gracilis*, and *Blepharoneuron tricholepsis*. The soil at the control site was a complex of a Mollic Eutroboralf and a Typic Argiboroll, and the surface soil textural class is a clay loam (Table 1).

The restoration site is also located in the Centennial Forest, 10 km southwest of Flagstaff, AZ and 6.7 km from the control site (35°8′35.81″N, 111°43′39.53″W, elevation 2193 m a.s.l.). The site experienced occasional single-tree selection harvesting for saw timber and poles between 1956 and 1991. The dominant tree species is ponderosa pine, with occasional Gambel oak. Understory plants include *Festuca arizonica*, *Elymus elymoides*, *Lupinus argenteus*, and occasionally *Bromus tectorum* L. Soils are classified as a Typic Eutroboralf, with a silt-loam surface texture (Table 1). The site was mechanically thinned in September 2006 using guidelines established by the Ecological Restoration Institute (Covington et al., 1997). Thinning focused on removing dense clusters of small diameter trees; no trees larger than 40 cm diameter at breast height (1.4 m) were cut. Slash generated by the thinning was piled on site and will be burned at a later date. Broadcast prescribed fire, a component of complete restoration management, was not employed in this study. Thinning reduced tree density by 67%, basal area by 39%, and projected overstory LAI by 41% (Table 1).

Both sites have a similar climate with typically cold winters, warm and dry springs, a "monsoon" type precipitation pattern during July and August (Sheppard et al., 2002), and cool and dry fall months. About half the annual precipitation falls in the form of snow during the winter months, and the remainder falls as rain during the summer monsoon season (Sheppard et al., 2002). The 30-year mean precipitation from 1971 to 2000 is 581 mm at the Flagstaff Airport (Flagstaff WSO AP) weather station, located an average of 7.1 km from our sites (Western Regional Climatic Center, http://www.wrcc.dri.edu/index.html).

At each site, we established five 25-m diameter circular plots. The plot locations were selected to be representative sources of the fluxes measured by the eddy covariance tower, which samples air from the south-southwesterly winds that prevail during the growing season. Three plots were 150 m to the west, south, and east of the eddy covariance towers, and two plots were 400 m southwest and southeast of the tower. Soil gas fluxes were sampled at three locations within each plot, 0°, 120°, and 240° and 15 m from plot center. The plots were also used to measure over- and under-story LAI (Dore et al., 2008), understory plant biomass, litterfall rates, soil characteristics, and soil microbial C. Air temperature and precipitation at the two sites were measured at the eddy covariance towers (Table 1).

2.2. Soil CO$_2$ and CH$_4$ fluxes

We measured net fluxes of CO$_2$ and CH$_4$ between soil and the atmosphere simultaneously using vented static chambers (Hutchinson and Mosier, 1981). Measurements were taken approximately

each month from June 15th 2006 to May 1st, 2007; fluxes were measured twice monthly from June 1st 2007 to August 15th, 2007. The control site was inaccessible because of snow between December 2006 and March 2007. No measurements were made at the restoration site during the thinning in September 2006.

In October 2005, 30-cm diameter, 1-cm thick, and 10-cm tall polyvinylchloride (PVC) "rings" were inserted approximately 2 cm into the mineral soil at the three locations within each of the five plots. Edges were beveled to minimize soil disturbance during insertion. Eight months passed before measurements began to allow vegetation to adjust to the presence of the rings. Rings prevented lateral diffusion of CO$_2$ and CH$_4$ into and out of the ring without severing many plant roots. They also marked the sampling location so the same soil area was measured repeatedly. Rings were removed during thinning at the restoration site and ring centers were marked with surveying "whiskers" (Presco, Sherman, TX, USA). The ring locations were exposed to harvesting and skidding activity during the thinning like the rest of the soil at the restoration site. Rings were reinstalled at the restoration site in early October 2006, immediately after thinning.

We measured fluxes by securing a 15-cm tall, 30-cm diameter vented PVC cap over the ring with a 5-cm wide latex band. Chamber headspace volume averaged 15.3 L. Caps were vented with a 0.5 cm diameter, 15 cm long rubber tube glued to a hole in the top of the cap. The vent allowed pressure equilibration between the outside atmosphere and the chamber headspace. Headspace samples (160 mL) were taken 0, 15, and 30 min after placing the chamber cap on the ring using coated stainless steel evacuated canisters (Silonite Minican, Entech Instruments, Simi Valley, CA, USA).

We used gas chromatography to measure CO$_2$ and CH$_4$ concentrations of the sampled headspace gas. The same headspace gas sample was injected into two different gas chromatographs. We used a thermal conductivity detector-equipped gas chromatograph with a Porapak Q column (Shimadzu 8A, Kyoto, Japan) to measure CO$_2$ concentrations. Methane concentrations were measured using a flame ionization detector-equipped gas chromatograph with a Porapak N column (Shimadzu 8A). Check standards for CO$_2$ and CH$_4$ had coefficients of variation less than 5%. Fluxes were calculated using linear regression of CO$_2$ and CH$_4$ concentration against the sampling interval and were adjusted for temperature and pressure using the ideal gas law (Saggar et al., 2004). Fluxes that had an r^2 lower than 0.95 for CO$_2$ and 0.90 for CH$_4$ were indicative of erratic changes in headspace gas concentrations over time and were removed from further analysis. Ten percent of CO$_2$ fluxes and 45% of CH$_4$ fluxes were rejected. Using an r^2 of 0.95 for CH$_4$ would have caused most CH$_4$ fluxes to be rejected, and applying an exponential decay function to match the first-order uptake rate of CH$_4$ (e.g. Paul and Clark, 1996; Jaatinen et al., 2004) would have resulted in the rejection of more data than the use of linear regression (e.g. Horz et al., 2002; Hart, 2006). The greater rejection rate of CH$_4$ fluxes than CO$_2$ fluxes may have been due to temporal variation in the activity of the relatively small

methanotrophic microbial community, or may have been due to the lower concentrations and fluxes of CH_4 than CO_2.

2.3. Soil physical environment

We measured the 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 10 cm mineral soil depth using a soil thermometer (VWR Scientific, Inc., West Chester, PA, USA). Soil temperature and soil water content were measured within 1 m of the vented static chambers.

2.4. Measurements of C cycle elements

We sampled the entire forest floor (O horizon) to the mineral soil at the restoration site in May of 2005 and again in September of 2007 to obtain pre- and post-thinning values. The forest floor was sampled at the control site in September 2007. Four 30 cm^2 sub-samples of the forest floor were taken in each of the five plots per site and sub-samples were homogenized before being air dried at 20 °C.

We measured fine (<2 mm diameter) root density by taking three soil cores from the 0 to 15 cm mineral soil depth within each of the five plots per site. The vast majority of fine roots are present within the top 15 cm of mineral soil in northern Arizona ponderosa pine forests, and few roots exist in the forest floor (Wright and Hart, 1997). Cores were taken in late May 2006 (pre-thinning), and in late May 2007 (post-thinning) at both sites using a 5.1 cm diameter slide hammer (AMS Core Sampler, American Falls, ID, USA). Samples were taken 3 m distal of the static chambers in 2006 and 3 m proximal of the static chambers in 2007, relative to plot center. Roots were separated from soil within the cores with a hydropnuematic elutriator (Scienceware Bel-Art Products, Pequannock, NJ, USA) and roots were collected on stack sieves of 2 mm and 0.5 mm diameter. Roots were oven dried at 60 °C for 72 h. Live and dead roots were pooled. Any mineral soil remaining on the roots was accounted for by ashing the sample in a muffle furnace at 500 °C for 10 min (Stevens and Jones, 2006). Root mass lost on ignition was used to convert the oven-dry root mass to ash-free oven-dry mass (Kaye and Hart, 1998).

We clipped four subplots (each of 0.5 m^2 area) in the five plots where gas fluxes were measured to estimate peak annual understory biomass. All clippings were conducted in September of 2006 and 2007 before the first frost. In 2006, the restoration site was clipped before thinning commenced. We sampled different but adjacent subplots in the first and second years. Samples were dried at 70 °C for 24 h and weighed to obtain dry mass.

We sampled the mineral soil for microbial C at both sites on September 1, 2006, immediately before thinning began and again one year after thinning on September 1, 2007. Microbial C was sampled from the top 10 cm of the mineral soil using a 2 cm diameter Oakfield sampler (Model HC, Oakfield Apparatus Inc., Oakfield, WI, USA). Three cores were taken 1 m adjacent to each static chamber ring and homogenized, for a total of three subsamples per plot. Microbial C was extracted from soil samples using the chloroform ($CHCl_3$) fumigation-extraction method (Brookes et al., 1985; Vance et al., 1987; Haubensak et al., 2002). Both unfumigated and fumigation-extracted samples were analyzed on 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 quotient (k_{EC}) of 0.39 (Sparling et al., 1990; Grady and Hart, 2006).

2.5. Statistical analyses

We used one control and one thinned site in a before-after-control-impact (BACI) statistical design (Eberhardt and Thomas, 1991), and at each site used the five plots described above as our experimental units. Both sites were representative of ponderosa pine forests in northern Arizona, USA in both stand structure and climate, and the plots were selected from each site without bias towards stand characteristics. Therefore, we used statistical techniques to interpret the magnitude and consistency of differences between sites. We do not extrapolate our results beyond the study sites.

We used repeated measures analyses of variance to identify the effects of thinning on all measurements except forest floor mass. The year by site interaction tested the effect of thinning because it assessed whether the difference between the control and thinned sites changed from 2006 (before thinning) to 2007 (after thinning). To test for differences in forest floor mass, two one-way analyses of variance were used to compare: (1) pre- and post-thinning forest floor mass at the restoration site; and (2) 2007 forest floor mass between the control and restoration sites.

We developed a model to evaluate the impact of changes in soil water content and soil temperature following thinning on soil CO_2 efflux. For this model, we used all data from the control site and only post-thinning data from the restoration site. Not enough pre-thinning soil water content data existed for a sufficiently powerful regression, and the restoration site may have had different responses to soil water content and temperature before and after thinning. Soil water content and soil temperatures are known to be important drivers of soil CO_2 efflux and they may change as a result of thinning (Kaye and Hart, 1998; Conant et al., 2004; Tang et al., 2005; Simonin et al., 2007; Selmants et al., 2008). We used both soil water content and soil water content squared in our model similar to Tang et al. (2005). To measure the effect of thinning on our model, we used one model for pooled data over both sites with three continuous variables (soil temperature, water content, and water content squared) and one categorical variable (e.g. Tang et al., 2005). We used the categorical variable "R" to represent restoration thinning, where $R = 0$ stands for the control site and $R = 1$ stands for the restoration site. The interactions between the categorical variable and the continuous variables were used to statistically test whether the response of soil CO_2 efflux to temperature and soil water content differed between the control and thinned sites. Our model took the form:

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

where F (mg m^{-2} hr^{-1}) is soil CO_2 efflux, β_n represents the coefficient, T (°C) is soil temperature at 10 cm mineral soil depth, and θ (m^3 m^{-3}) is soil water content integrated over the top 6 cm of the mineral soil.

A similar model construction technique was used for CH_4 oxidation, though CH_4 oxidation was not ln-transformed, because fluxes were at times either negative or positive. The model had the form:

$$O = \beta_0 + \beta_1 R + \beta_2 T + \beta_3 \theta + \beta_4 \theta^2 + \beta_5 RT + \beta_6 R\theta + \beta_7 R\theta^2 + \beta_8 T\theta \\ + \beta_9 T\theta^2 + \beta_{10} RT\theta + \beta_{11} RT\theta^2$$

where O (mg m^{-2} hr^{-1}) is CH_4 oxidation.

We show soil CO_2 efflux data using positive numbers because soil CO_2 efflux is a source to the atmosphere. Rates of CH_4 oxidation are expressed as negative numbers because CH_4 oxidation is a sink from the atmosphere. We used JMP software (v. 5.1, SAS Institute,
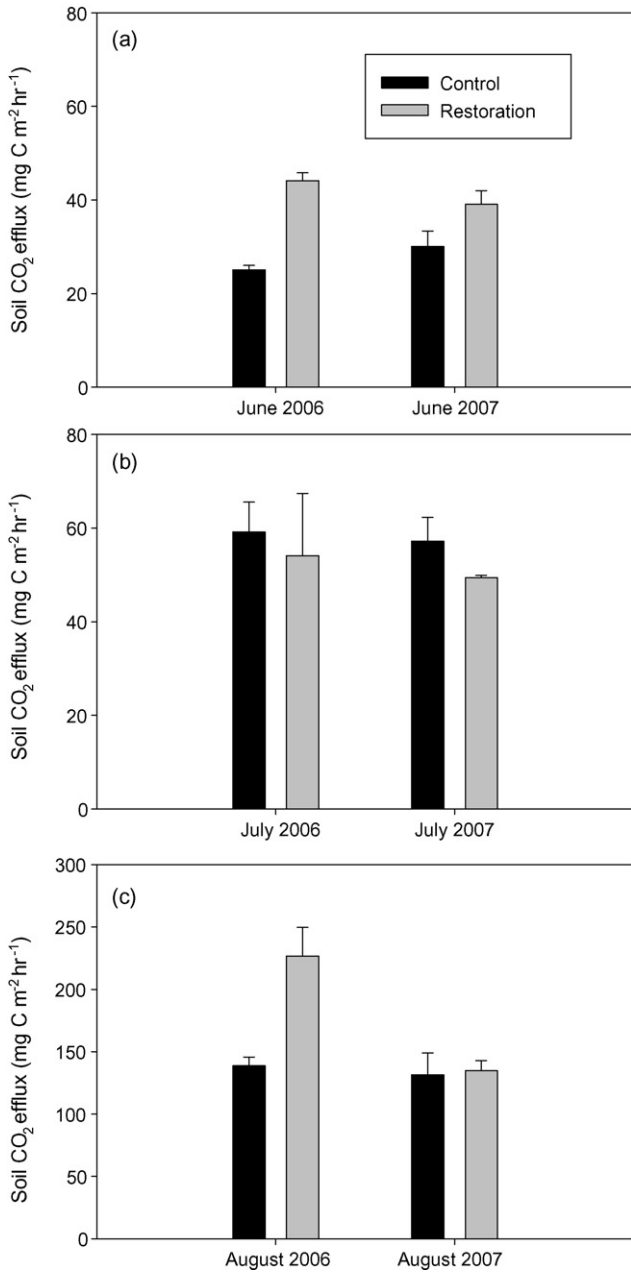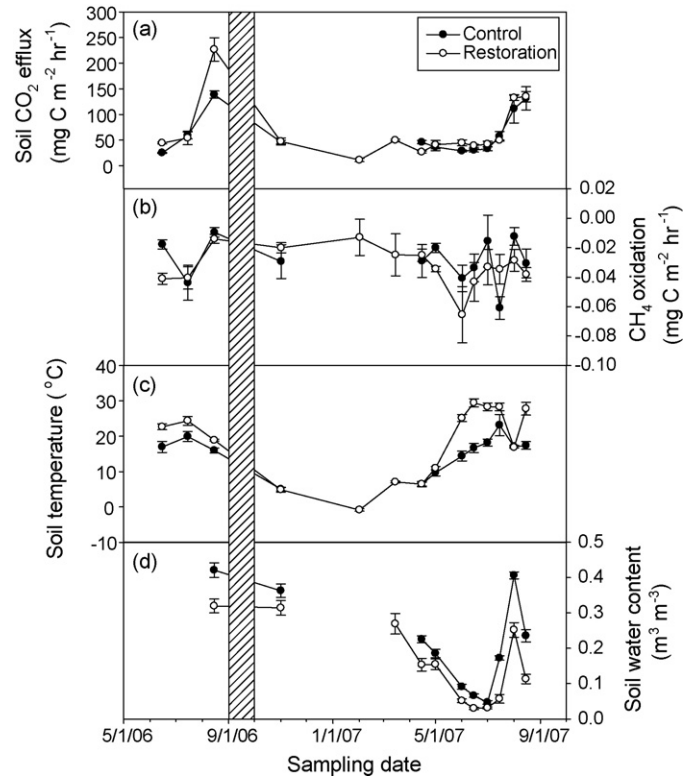
Fig. 1. Soil carbon dioxide (CO_2) efflux during June (a), July (b), and August (c) at the control and restoration sites before (2006) and after (2007) thinning at the restoration site. *P* values for the site by year interaction are 0.066 in June, 0.851 in July, and 0.032 in August. Error bars represent ±1 standard error; *n* = 5.


Fig. 2. Soil carbon dioxide (CO_2) efflux (a), methane (CH_4) oxidation (b), soil temperature at 10 cm mineral soil depth (c), and volumetric soil water content (0–6 cm mineral soil depth; d) at the control and restoration sites during the measurement period June 2006 to August 2007. Error bars represent ±1 standard error; *n* = 5. Vertical, cross-hatched box represents dates of thinning at the restoration site in September 2006.

Cary, NC USA) in all analyses. Statistical significance for all analyses was set, *a priori*, at $p < 0.05$.

3. Results

3.1. Effects of thinning on CO_2 efflux and CH_4 oxidation

The response of soil CO_2 efflux to thinning changed monthly during the summer (Fig. 1). The restoration site had lower soil CO_2 efflux after thinning than before thinning when compared to the control site in June of 2006 and 2007 but the differences were only weakly significant (Fig. 1a; site by year interaction $p = 0.066$). Between July 2006 and July 2007, soil CO_2 efflux changed the same at each site (Fig. 1b; site by year interaction $p = 0.851$). In contrast,

soil CO_2 efflux decreased more between August 2006 and August 2007 at the restoration site than at the control site (Fig. 1c; site by year interaction $p = 0.032$). Soil CO_2 efflux at both sites varied during the measurement period and was highest during the late-summer monsoon season in both years (Fig. 2a). The restoration site had higher mean soil CO_2 efflux during June, July, and August than the control site in 2006 (109.0 mg C m^{-2} h^{-1} to 74.9 mg C m^{-2} h^{-1}, respectively) and 2007 (74.8 mg C m^{-2} h^{-1} to 73.37 mg C m^{-2} h^{-1}, respectively).

Thinning had no significant effect on CH_4 oxidation for any of the three months measured (Fig. 3). The year by site interaction in June ($p = 0.346$), July ($p = 0.193$), and August ($p = 0.770$) indicate similar differences in CH_4 oxidation between sites before (2006) and after (2007) thinning. Methane oxidation at the control site was greatest during the late summer of 2007, and at the restoration site was greatest during the late spring and early summer of 2007 (Fig. 2b). Methane oxidation during winter was lower than in summer (Fig. 2b). Rates of CH_4 oxidation at the restoration site maintained a constant average of −0.03 mg C m^{-2} h^{-1} during the summers of 2006 and 2007, while CH_4 oxidation at the control site increased from −0.02 mg C m^{-2} h^{-1} during the summer of 2006 to −0.04 mg C m^{-2} h^{-1} during the summer of 2007.

3.2. Effects of thinning on soil temperature and water content

Soil temperature (10 cm mineral soil depth) was often greater at the restoration site than the control site both before and after thinning (Fig. 2c). The year by site interactions suggested that thinning increased average soil temperature in June ($p = 0.006$) and August ($p < 0.001$), but not in July ($p = 0.629$).
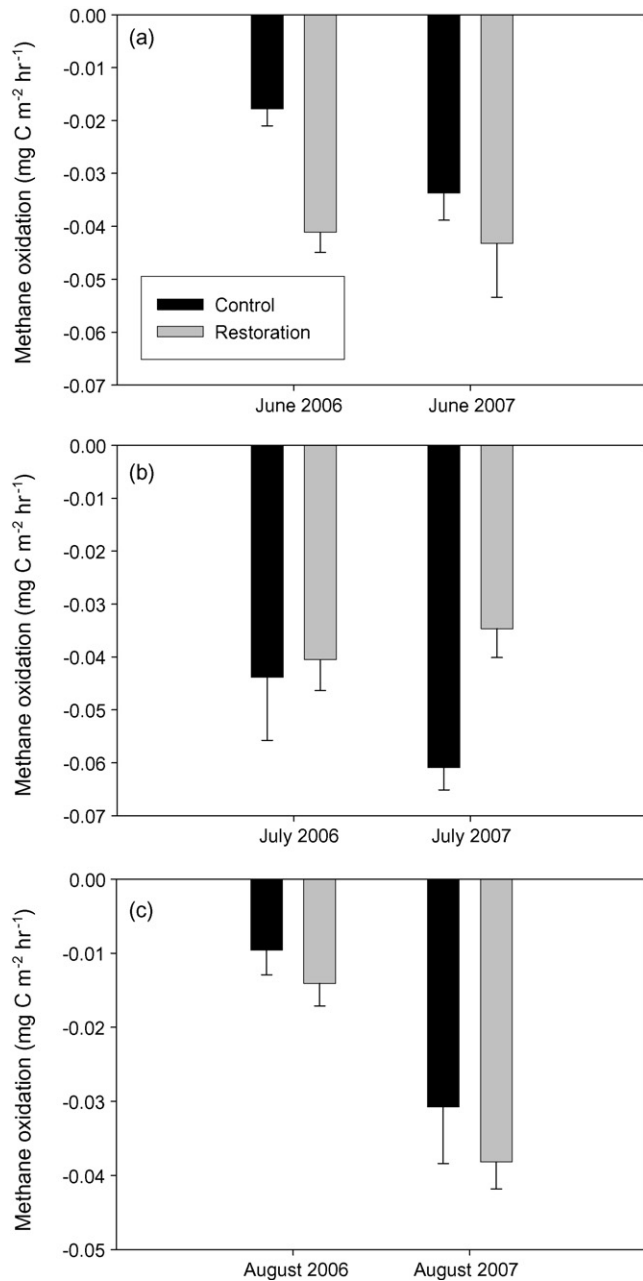
Fig. 3. Methane oxidation rates during June (a), July (b), and August (c) at the control and restoration sites before (2006) and after (2007) thinning at the restoration site. *P* values for the site by year interaction are 0.346 in June, 0.193 in July, and 0.770 in August. Error bars represent ±1 standard error; *n* = 5.

The volumetric water content of the surface soil (0–6 cm mineral soil depth) was consistently lower at the restoration site than the control site before and after thinning (Fig. 2d). Differences in soil water content between sites in August, the only month in which pre- and post-thinning water content data were available, were similar before and after thinning (year by site interaction *p* = 0.450).

3.3. Effect of thinning, soil temperature, and soil water content on gas fluxes

The regression model described variation in soil CO_2 efflux well (R^2 = 0.650; *p* < 0.001; *n* = 99). Soil CO_2 efflux was positively related to soil temperature and water content (Table 2). However, the

Table 2
Coefficients, estimates, standard errors, and probabilities for models relating carbon dioxide efflux and methane oxidation to changes in soil temperature and soil water content at the control site and the thinned restoration site

Flux/coefficient	Estimate	Standard error	Probability
Carbon dioxide efflux (R^2 = 0.650, *p* < 0.001, *n* = 99)			
β_0 intercept	1.94	0.29	<0.001
$\beta_1 R$	0.22	0.20	0.271
$\beta_2 T$	0.05	0.01	<0.001
$\beta_3 \theta$	9.21	2.41	<0.001
$\beta_4 \theta^2$	−11.08	6.20	0.078
$\beta_5 RT$	0.03	0.02	0.183
$\beta_6 R\theta$	0.48	5.31	0.928
$\beta_7 R\theta^2$	−2.32	13.92	0.868
$\beta_8 T\theta$	0.18	0.31	0.560
$\beta_9 T\theta^2$	−0.08	0.64	0.903
$\beta_{10} RT\theta$	0.54	0.59	0.361
$\beta_{11} RT\theta^2$	−1.13	1.27	0.372
Methane oxidation (R^2 = 0.248, *p* = 0.020, *n* = 87)			
β_0 intercept	−0.03	0.02	0.070
$\beta_1 R$	−0.003	0.01	0.840
$\beta_2 T$	0.0003	0.0007	0.704
$\beta_3 \theta$	−0.09	0.15	0.548
$\beta_4 \theta^2$	0.34	0.39	0.378
$\beta_5 RT$	−0.001	0.001	0.386
$\beta_6 R\theta$	0.09	0.32	0.782
$\beta_7 R\theta^2$	−0.13	0.85	0.877
$\beta_8 T\theta$	−0.04	0.02	0.055
$\beta_9 T\theta^2$	0.09	0.32	0.039
$\beta_{10} RT\theta$	0.05	0.04	0.142
$\beta_{11} RT\theta^2$	−0.11	0.08	0.141

R is a categorical variable representing the control (*R* = 0) and restoration (*R* = 1) sites. θ is the volumetric soil water content (0–6 cm mineral soil depth); *T* is soil temperature (10 cm mineral soil depth).

response of soil CO_2 efflux to soil temperature and water content was similar between sites, as shown by the non-significant interactions between the categorical site variable and the continuous variables (Table 2).

The model relating CH_4 oxidation to soil temperature and water content was statistically significant but did not predict variation in CH_4 oxidation well (R^2 = 0.248; *p* = 0.020; *n* = 87). As with soil CO_2 efflux, thinning did not change responses of CH_4 oxidation to soil temperature or water content because all interactions between the categorical site variable and the continuous variables were non-

Table 3
Mean (±1 standard error) pre- and post-thinning biomass and carbon pools at the control and restoration sites

Variable/year	Control	Restoration
Forest floor mass (g m^{-2})		
2005	Not sampled	2344 (685)
2007	3146 (685)	3302 (842)
Fine root biomass[a] (g m^{-2})		
2006	254.5 (32.3)	186.7 (3.7)
2007	226.7 (15.2)	125.8 (7.5)
Understory aboveground plant biomass (g m^{-2})*		
2006	15.6 (6.5)	11.7 (2.6)
2007	15.2 (5.8)	26.1 (3.4)
Microbial biomass carbon (mg C kg^{-1})		
2006	627 (40)	405 (40)
2007	800 (60)	516 (60)

Thinning occurred at the restoration site in September 2006 after all 2006 measurements were made. Fine root biomass was measured within the top 15 cm mineral soil, while microbial carbon was measured within the top 10 cm mineral soil. For all variables, *n* = 5; * indicates a significant time by site interaction (*p* < 0.05).
[a] Includes live and dead roots.

significant (Table 2). The interaction of soil temperature and soil water content squared was significantly related to CH_4 oxidation ($p = 0.039$), and the interaction of soil temperature and soil water content on CH_4 oxidation was nearly significant ($p = 0.055$; Table 2).

3.4. Effects of thinning on forest C pools

Thinning did not significantly alter forest floor mass within one year of thinning. Mean forest floor mass increased by 29% from 2005 (pre-thinning) to 2007 (post-thinning) at the restoration site, but due to the large spatial variation within the site, this difference was non-significant (one-way ANOVA $p = 0.339$; Table 3). Forest floor masses at the restoration and control sites were statistically similar after thinning in 2007 ($p = 0.899$).

Similarly, fine root biomass did not change significantly in the first year after thinning. The restoration site had less fine root biomass during 2006 and 2007 than the control site (site main effect $p = 0.008$), and in 2006 both sites had more fine roots than in 2007 (year main effect $p = 0.002$; Table 3). Mean fine root biomass decreased between 2006 and 2007 proportionally more at the restoration site (33%) than the control site (11%), but the absolute change in root mass between years was similar between sites (year by site interaction $p = 0.142$; Table 3).

Thinning increased aboveground understory plant biomass at the restoration site one year after thinning (year by site interaction $p = 0.028$). Between 2006 and 2007, understory plant biomass increased by 220% at the restoration site, but decreased by 3% at the control site (Table 3).

Microbial C did not change in response to thinning (year by site interaction $p = 0.590$). Microbial C was lower at the restoration site than the control site during both 2006 and 2007, and there was more microbial C in 2007 than in 2006. Microbial C increased between 2006 and 2007 about the same amount at each site (Table 3).

4. Discussion

4.1. Effects of thinning on CO_2 efflux

Thinning appears to have reduced soil CO_2 efflux during two out of three months in the first summer after treatment. Evidence for a decline in soil CO_2 efflux after thinning was strongest in August ($p = 0.032$) and marginal in June ($p = 0.066$). June, with its high temperatures and low precipitation, and August, with its cooler temperatures and monsoonal precipitation patterns, represent two distinctly different periods during the growing season. Given the large spatial and temporal variation in soil CO_2 efflux, we observed that thinning may cause a seasonal decrease of soil CO_2 efflux within one year after thinning (Fig. 1). Our experimental design, which used both before- and after-treatment measurements at the restoration and control sites, was necessary to detect these changes as soil CO_2 efflux was higher at the restoration site than the control site during many of the sampling dates and varied seasonally at both sites. Even though our findings only represent a case study of the effects of thinning on soil gas fluxes in ponderosa pine, our evidence that thinning decreases soil CO_2 efflux immediately after treatment is consistent with other reports for ponderosa pine forests (Kaye and Hart, 1998; Tang et al., 2005).

4.2. Mechanisms by which thinning reduced CO_2 efflux

Thinning may reduce soil CO_2 efflux by killing trees, by altering the soil environment, or by changing amounts and sources of belowground C for microbial metabolism. The thinning in our study reduced tree density by ~67% and basal area and projected LAI by ~40%. Removal of trees by thinning likely decreased both photosynthesis (on a per area basis) and the amount of respiring roots in the first post-treatment growing season. Increases in understory biomass did not compensate for the lost photosynthesis due to tree removal during thinning.

Thinning altered the soil environment by increasing soil temperature during June and August. This increase in soil temperature occurred during the same months when thinning reduced soil CO_2 efflux. Higher soil temperatures commonly cause higher soil CO_2 efflux in an exponential, "Q_{10}" relationship (Luo and Zhou, 2006). Therefore, the observed reduction in soil CO_2 efflux during June and August as a result of thinning occurred despite higher soil temperatures at the restoration site. The restoration site had consistently drier surface soil conditions than the control site both before and after treatment. However, thinning did not appear to have impacted soil water content in August when pre- and post-treatment data allowed a statistical comparison. The lower volumetric soil water content observed at the restoration site may have been caused by lower precipitation at the restoration site in 2006 (Table 1) or higher soil temperature and greater evaporation from the surface soil after thinning (e.g., Simonin et al., 2007).

The relationship between soil CO_2 efflux and soil temperature and water content was not significantly different between the restoration site after thinning and the control site (Table 2). The similar effects of soil temperature and water content on soil CO_2 efflux at the two sites suggest that although thinning may change the soil physical environment, it does not change the response of soil CO_2 efflux to variation in soil temperature and water content under the conditions of our study. The response of CO_2 efflux to soil temperature and soil water content observed in our study is consistent with reports for a ponderosa pine plantation in the Sierra Nevada Mountains, California, USA, where thinning did not alter the response of soil CO_2 efflux to either soil temperature or soil water content (Tang et al., 2005). The similar results reported by Tang et al. (2005) and this study suggest that a model of soil CO_2 efflux based upon soil temperature and soil water content may adequately predict soil CO_2 efflux in both unthinned and thinned ponderosa pine forests, at least in the first summer after thinning.

The amount of C available in an ecosystem may determine soil CO_2 efflux (Janssens et al., 2001; Law et al., 2001; Tang et al., 2005; Selmants et al., 2008). Our results are consistent with emerging evidence (Kaye et al., 2005) that mechanical thinning in ponderosa pine forests of Northern Arizona often has few short-term effects on forest floor C pools, whereas restoration treatments that combine thinning with prescribed burning often alter C pools (Hart et al., 2006; Selmants et al., 2008). The small difference in forest floor mass between thinned and unthinned stands suggests that with the exception of road building, the mechanical thinning and slash piling implemented for this study did not dramatically change the amount of biomass in the forest floor. This finding is similar to previous reports of forest floor mass after mechanical thinning in northern Arizona (Kaye and Hart, 1998).

Our results for fine root biomass are consistent with a study in ponderosa pine forests in northern Arizona that reported no change in total root biomass one year after thinning (Kaye and Hart, 1998). Our measurements of fine root biomass did not separate live and dead roots, and, due to slow fine root decomposition rates in northern Arizona ponderosa pine forests (Hart et al., 2005a), dead fine roots were likely still present in our samples eight months after thinning. It is also possible that as dead fine roots decomposed, the remaining trees grew new live roots, and the two effects mitigated each other.

In our study, understory aboveground herbaceous biomass increased after thinning consistently with previous reports for

ponderosa pine forests of northern Arizona (Moore et al., 2006; Laughlin et al., 2006). Herbaceous understory biomass provides higher quality (i.e., lower carbon to nitrogen ratio) litter inputs to the soil than pine litter (Hart et al., 2005b). Because of the increase in understory biomass, thinning should increase the quantity of high-quality C available for microbial decomposition and respiration (Hart et al., 2005b). However, because our study only examined the short-term effect of thinning, it is likely that this source of C was not yet available for decomposition. Our results of lower soil CO_2 efflux after thinning can be explained by the decline in live tree root respiration being greater than the possible increase in soil CO_2 efflux resulting from an increase in production of roots by surviving trees and herbaceous plants and possible increased heterotrophic respiration associated with the decomposition of newly dead roots and understory plant litter.

Microbial C did not change within one year of thinning in our study. Though we sampled on only a single date during the late summer monsoon season before and after thinning, our short-term results are consistent with a long-term study in thinned ponderosa pine forests. Ten to fifteen years after thinning, Grady and Hart (2006) reported no change in microbial C between thinned and control stands during the warm, wet monsoon season in northern Arizona. The lack of a difference in microbial C between thinned and unthinned stands suggests little change in the population of soil microbes as a result of increased substrate from dead roots. Our results are not consistent with Curiel Yuste et al.'s (2007) hypothesis that soil heterotrophs respond rapidly to changes in C substrate as a result of root death in ponderosa pine forests. Their study was conducted at a site in the Sierra Nevada Mountains of California that is wetter (1290 mm mean annual precipitation) than our study area in northern Arizona (561 mm mean annual precipitation). Northern Arizona may lack adequate precipitation in most years for rapid decomposition of the dead roots produced by thinning.

Our finding of a small immediate decrease of soil CO_2 efflux after thinning is likely the net effect of several mitigating factors. Tree root respiration decreased as a result of thinning while understory plant root respiration increased after thinning in response to the increase in understory plant biomass. The effect of thinning on heterotrophic respiration is unclear: though thinning resulted in more dead roots and high-quality understory litter, there appeared to be no change in the amount of C stored in the microbial biomass pool. Either heterotrophic respiration may have increased slightly and the microbial biomass has high C turnover and little storage of C, or heterotrophic respiration was unchanged because decomposition was not elevated within one year of thinning. Higher soil temperatures after thinning during June and August would have likely increased both decomposition and soil CO_2 efflux. The loss of tree-root respiration is likely responsible for the observed decline in soil CO_2 efflux, but this decline was not more pronounced due to changes in understory plant root respiration, soil temperature, and possibly heterotrophic respiration. Our finding that plant biomass exerts strong control on soil CO_2 efflux in thinned or harvested forests is consistent with previous studies in loblolly pine (Selig and Seiler, 2004; Wiseman and Seiler, 2004), boreal (Pypker and Fredeen, 2003), and ponderosa pine forests (Tang et al., 2005; Grady and Hart, 2006).

4.3. Thinning does not change CH_4 oxidation in the short-term

Thinning did not significantly change CH_4 oxidation rates during any of the three months measured (Fig. 3). Though the regression model showed that CH_4 oxidation is influenced by interactive effects of soil temperature and water content, CH_4 oxidation responded similarly to changes in soil temperature and

water content at the control and restoration sites. The interactive effect of soil temperature in our study and the results reported by Hart (2006), who found a decrease in CH_4 oxidation with increasing temperature in northern Arizona high-elevation spruce-fir forest soil transplanted to a down-slope ponderosa pine forest, suggest that soil temperature may be an important regulator of CH_4 oxidation in northern Arizona soils despite the common belief that soil temperature is unrelated to CH_4 oxidation (King, 1997). Despite extremely low soil water content in the dry months of June (<0.05 m^3 m^{-3}), we did not observe a decrease in CH_4 oxidation consistent with cellular osmotic stress to methanotrophic bacteria caused by desiccation, as has been observed in other ecosystems (West and Schmidt, 1998; Davidson et al., 2004). In fact, the greatest rates of CH_4 oxidation at the restoration site occurred during periods of low soil moisture content, suggesting that higher air-filled-porosity during those periods allowed greater diffusion of CH_4 into the soil for metabolism by soil methanotrophs. The lack of a significant change in forest floor mass with thinning is likely the main reason CH_4 oxidation did not change in response to thinning. Removal of the forest floor has increased CH_4 oxidation in other forests (Saari et al., 1998; Steinkamp et al., 2001).

5. Conclusion

Restoration thinning is likely to continue or accelerate in southwestern U.S. ponderosa pine forests given the prediction of an increase in the frequency of large wildfires associated with climate warming (Westerling et al., 2006). Our results suggest that thinning can reduce soil CO_2 efflux during the first post-thinning summer because the decrease in soil autotrophic respiration is larger than the expected increase in soil heterotrophic respiration. Thinning had little immediate impact on other potential sources of soil CO_2 efflux, including forest floor mass, total fine root biomass, and microbial C. We conclude that the soil is too dry and C cycling too slow at our study sites in northern Arizona, USA for thinning to greatly stimulate soil heterotrophic respiration one year after thinning. Mechanical thinning with slash piling has no effect on CH_4 oxidation likely because the forest floor density is not substantially altered during thinning under the conditions of our study. Although thinning reduced soil CO_2 efflux in our study, the overall C source or sink strength of a thinned forest is also influenced by other components of ecosystem carbon balance, such as gross primary production and respiration of above-ground plant tissues.

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