

Short-Term Effects of Experimental Burning and Thinning on Soil Respiration in an Old-Growth, Mixed-Conifer Forest

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ABSTRACT / To understand the roles of forest management practices in meeting the goals of forest sustainability and CO₂ sequestration, we evaluated the effects of burning and thin-

ning treatments on soil respiration and soil environments in an old-growth, mixed-conifer forest in California's southern Sierra Nevada. Six experimental treatments with two levels of burning and three levels of thinning were implemented across three dominant patch types: closed canopy (CC), *Ceanothus* shrub (CECO), and open canopy (OC). We measured soil respiration rate (SRR), soil temperature (T_{10}), moisture (M_s), and litter depth (LD), in the summers of 2000 and 2002. Soil total C and total N were measured in 2002. SRR was significantly different among the three patch types. In 2000, SRR was 0.75, 0.86, and 0.26 g CO₂ m⁻² hr⁻¹ in CC, CECO, and OC, respectively. In 2002, SRR was 0.79, 0.97, and 0.44 g CO₂ m⁻² hr⁻¹ in CC, CECO, and OC, respectively. The analysis of variance indicated that burning and thinning significantly affected soil respiration and soil environments. In particular, SRR significantly decreased in burned CECO patches but increased in unburned and thinned CECO. SRR in CC and OC did not significantly change. T_{10} and M_s increased, whereas LD and soil C decreased in treated patches. We also developed pre- and posttreatment exponential models to predict SRR using soil environmental variables. The effects of burning and thinning on soil CO₂ efflux and soil environments imply that forest carbon pools would be reorganized with widespread application of these forest management practices.

Soil respiration, including autotrophic and heterotrophic respiration, plays an important role in global carbon cycling (Schlesinger and Andrews 2000). While it is well known that soil CO₂ efflux is sensitive to soil environmental variables, such as soil temperature and moisture, texture, pH, total C, and total N (Singh and Gupta 1977, Orchard and Cook 1983, Raich and Schlesinger 1992), forest management activities, such as burning and thinning, can also change soil environments and significantly affect soil CO₂ efflux (Raich and Schlesinger 1992, McGuire and others 1995, Schlesinger and Andrews 2000). Subsequently, sound scientific evidence is necessary to understand the im-

pacts of forest management activities on soil respiration and soil environments (Wildung and others 1975, Parker and others 1983, Raich and Schlesinger 1992, McGuire and others 1995, Klopatek and others 1998).

In the Sierra Nevada Mountains, prescribed burning and thinning are applied often to restore historical forest structure and composition (North and others 2002). Prescribed burning impacts soil environments by consuming accumulated litter and soil organic matter, whereas mechanical thinning compacts soil, causing a decrease in soil aeration and restricting root growth and microbial activities (Poff 1996). These forest management activities could significantly alter soil CO₂ efflux. However, the effects of burning and thinning on soil CO₂ efflux is not well known in this area.

Our study was designed to understand the effects of prescribed burning and thinning on soil respiration and soil environments based on two-year field measure-

KEY WORDS: Soil respiration; Prescribed burning; Thinning; Soil temperature; Soil moisture; Mixed conifer

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ments in an old-growth mixed-conifer forest in the Sierra Nevada mountains. Our specific objectives were to: (1) quantify soil respiration rate before and after prescribed burning and thinning treatments, (2) estimate the effects of prescribed burning and thinning on soil respiration and soil environments, and (3) compare empirical models of the pre- and posttreatment relationships between soil respiration rate and soil environmental variables.

Methodology

Study Site

The study site is Teakettle Experimental Forest (TEF), located at 36°58'N, 119°2'W between 1880 and 2485 m elevation in the Sierra National Forest, California, USA. The Sierra Nevada is typified by a Mediterranean climate, which has hot, dry summers and cool, wet winters. Accordingly, soils experience seasonal drought during the summer (Dallman 1998). The average annual precipitation in this area is 1250 mm. Most of the precipitation falls during intense snowstorms between November and April. The depth of the snowpack is an important influence on the soil water conditions of the forest during the following summer. The mean air temperature in July is 14.5°C, whereas the mean air temperature in January is 1.0°C. Soils are generally Xerumbrepts and Xeropsamments typical of southwestern slopes of the Sierra Nevada. The granite-based soils have a coarse sandy loam texture throughout the relatively shallow profile (75–100 cm) with approximately 18%–20% volumetric soil water holding capacity. Soil bulk density at 20–25 cm depth is 1.09 g cm⁻³. Duff and litter comprise 90.5% of soil cover, bare soil 5.8%, and large woody debris 3.7%. Organic matter content within the 0–10 cm depth of the mineral soil is 6.35% (North and others 2002).

The TEF consists of 1300 ha of old-growth, mixed-conifer forest. The major conifer species include white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and red fir (*Abies magnifica*). The mixed-conifer forest is a matrix of tree clusters punctuated with gaps averaging 5–20 m in diameter. Bare ground and several shrubs occupy gaps. The most dominant shrub is whitethorn ceanothus (*Ceanothus cordulatus*) (North and others 2002). Extensive analysis of vegetation conditions at the TEF was made to identify different forest communities and intensively analyze mixed-conifer conditions to appropriately size and locate permanent plots for burning and thinning treatments (North and others 2002). Within several of the plots, we located 54

sampling points equally divided among the three dominant patch types: closed canopy tree groups (CC, characterized by > 80% canopy cover and a thick litter layer), patches of *Ceanothus* shrub (CECO, *Ceanothus* cover > 60%), and open canopy (OC, herb, shrub and tree cover < 20%).

Further, the sampling points were located to take advantage of a larger-scale factorial experiment consisting of two levels of burning and three levels of thinning treatments. The two levels of burning treatment included no burn and an understory burn. The understory burn was a controlled surface burn without overstory crown ignition. The three levels of thinning treatments included no thinning, understory thinning, which involved removal of all trees between 25 and 75 cm dbh, and overstory thinning, which left 22, large, evenly spaced trees per hectare as recommended by the California Spotted Owl Report (CASPO) (North and others 2002). As a result, the six treatments were no burn and no thinning (UN), no burn and understory thinning (UC), no burn and overstory thinning (US), burn and no thinning (BN), burn and understory thinning (BC), and burn and overstory thinning (BS). All treatments were implemented in the summer and fall between August 2000 and November 2001.

Data Collection

Prior to treatments (the summer of 2000), we measured soil respiration rate (SRR), soil temperature at 10 cm depth (T_{10}), volumetric soil moisture within 0–15 cm (M_s), and litter depth (LD) at each of the 54 points. These measurements were repeated at the 54 sampling points during the summer of 2002, about 7 months after prescribed burning and 13–15 months after thinning treatments.

SRR was measured monthly using a dynamic chamber connected to an infrared gas analyzer (IRGA, EGM-2, and SRC-1 Soil Respiration System, PP Systems, Hitchin, Herts, UK). At each sample point, a 10-cm-diameter chamber was directly inserted 1 cm into the forest floor or put on a PVC collar to ensure no leakage at the interface between the soil, collar, and chamber rim. The system was calibrated under actual air pressure conditions once a week during the field measurements using a standard compressed gas regulator. To reduce the influences of diurnal fluctuations in SRR, we measured SRR between 09:00 and 17:00 hours. For any sampling point, we measured SRR at different hours throughout the whole summer.

In situ T_{10} was measured simultaneously with SRR using a digital thermometer (Taylor Digital Max/Min, Forestry Suppliers, Inc.). M_s data were collected using Time Domain Reflectometry (TDR, model 6050XI. Soil

Moisture Equipment Corp., Santa Barbara, California, USA). TDR probes were 30 cm long and installed at a 30° angle to sample soil moisture within 0–15 cm depth in mineral soil. LD was defined as the depth of litter from the surface to the top of mineral soil (i.e., the depth of the organic layer). Coarse woody debris and slashes resulting from the thinning were not included in the litter depth measurements.

In addition, we collected soil samples at the 54 points in 2002 to examine the effects of treatment on soil total carbon and nitrogen. At each point, three surface (0–15 cm) mineral horizon soil samples were collected with a 2-cm-diameter corer from an area within 0.5 m of the soil respiration sample collar. The soils from the three cores were composited, passed through a 2-mm sieve, dried at 70°C for 48 hours, and finely grounded with a mortar and pestle. Total C and N were analyzed on a 0.20 g subsample by dry combustion at the Universidad Metropolitana, San Juan, Puerto Rico, on a LECO-CN analyzer (LECO Corporation, St. Joseph, Michigan, USA).

Data Analysis

We calculated means and standard deviations (STD) of SRR, T_{10} , M_s , and LD for the summer of 2000 and 2002. A paired *t* test was used to test the hypothesis that the mean of each variable differed between the two sampling periods. Then, an analysis of variance (ANOVA) was employed to test the hypothesis that year, patch type, and treatment accounted for the differences between the two-year SRRs. The model was derived using procedure ANOVA for balanced data in SAS (Version 8.0, SAS Institute 1999):

$$\text{SRR} = f[\text{Year}, \text{Treatment}(\text{Year}), \text{Patch}(\text{Year}), \text{Patch}(\text{Treatment})] \quad (1)$$

where Year is the measuring period (i.e., 2000 or 2002), Patch is the patch type (i.e., CC, CECO, and OC), and Treatment is the treatment type (i.e., UN, UC, US, BN, BC, and BS). Because the plots were untreated in 2000 and treated in 2002, Treatment should be considered in different years. Patch types were changed by treatments in the two sampling years. As a result, Treatment is nested in Year, and Patch is nested in Year and Treatment.

Because treatments were not implemented equally across all of the plots, the sampling points for each treatment type became unbalanced according to the actual treatments that occurred at each point. For example, a BS plot was supposed to have burning and overstory thinning treatments implemented across entire area. In reality, some areas within the plot did not

receive any treatment because of high spatial variation of prescribed fire and logging. Thus we used the general linear model (GLM) in SAS for unbalanced data. The model was derived:

$$\text{SRR} = f(\text{Patch}, \text{Burn}, \text{Thin}, \text{Burn} * \text{Thin}) \quad (2)$$

where Patch is the three dominant patch types, Burn included two levels of prescribed burning treatments: burned and unburned; Thin included three levels of thinning treatments: unthinned, understory thinned, and overstory thinned. Least-square means were calculated in order to evaluate the effects of burning, thinning, and their interactions with patch types on the variation of SRR in the posttreatment year 2002.

Prior to establishing multiple linear regression pre-treatment and posttreatment models of the relationship between SRR and T_{10} , M_s , and LD, we examined the normality of population distribution of each variable. Pearson correlation coefficients were calculated to examine the correlations between these variables. We also examined the correlations among soil respiration, total soil C, and total N in the posttreatment year. The stepwise selection method was used to develop the best-fit regression models for each patch type. All statistical analyses were performed in SAS (Version 8.0, SAS Institute 1990). Significance was set at 0.1.

Results

Comparison Between Pre- and Posttreatment Years

In the summer of 2000, SRR was 0.75, 0.86, and 0.26 g CO₂ m⁻² hr⁻¹ in CC, CECO, and OC, respectively (Table 1). The differences among the patch types were significant ($F = 28.96$, $P < 0.0001$). In the summer of 2002, SRR also differed significantly among patch types ($F = 15.92$, $P < 0.0001$). Compared with SRR measured in 2000, SRR measured in 2002 was 0.11 g CO₂ m⁻² hr⁻¹ higher on average. For each patch type, the mean posttreatment SRR increased by 0.04, 0.11, and 0.18 g CO₂ m⁻² hr⁻¹ in CC, CECO, and OC, respectively, although the increase was only significant for OC (Table 1). Additionally, the variation of SRR after treatments was larger than the variation prior to treatments in all three patch types (Figure 1). Results of ANOVA indicated that years, patch types, and treatments accounted for the differences of SRR between the pre- and post-treatment ($F = 12.19$, $P < 0.0001$). Specifically, the patch types coupled with treatment and year contributed 86% to SRR variation; the treatments coupled with year contributed 12%; year alone contributed 2% (Table 2).

Soil environments of all patch types differed significantly between the pre- and posttreatment (Table 3).

Table 1. Soil respiration rate in summer 2000 and 2002 by three dominant patch types: closed canopy (CC), *Ceanothus* shrub (CECO), and open canopy (OC)

Patch type	Respiration rate (g CO ₂ /m ² /hr)		Difference (2002 – 2000)	N	P > T
	2000 (pretreatment) ^a	2002 (posttreatment) ^a			
CC	0.75 ± 0.46	0.79 ± 0.47	0.04	18	0.6703
CECO	0.86 ± 0.57	0.97 ± 0.65	0.11	18	0.3134
OC	0.26 ± 0.18	0.44 ± 0.30	0.18	18	0.0001
Overall	0.62 ± 0.51	0.73 ± 0.54	0.11	54	0.025

^aValues are means ± SD.

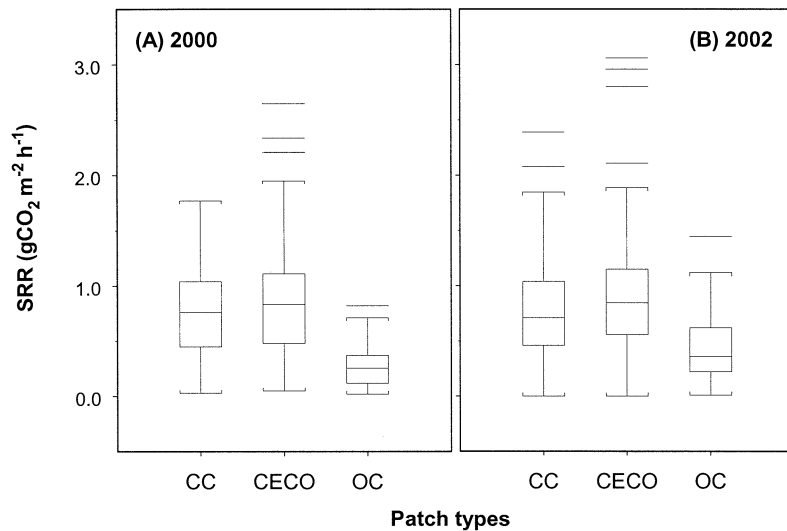


Figure 1. Minima, maxima, medians, and quantiles of soil respiration rate (SRR) in three dominant patch types: CC, closed canopy, CECO, *Ceanothus* shrub, and OC, open canopy ($N = 18$ for each patch type) in the summer of (A) 2000 and (B) 2002.

Table 2. Results of analysis of variance to test hypothesis that soil respiration rate (SRR) differed among years, patch types, and treatments

Source	df	Mean square	F	P > F
Year	1	1.0666	8.11	0.0047
Treatment (year)	10	0.6035	4.59	< 0.0001
Patch (year)	4	4.7321	35.99	< 0.0001
Patch (treatment)	17	1.48716	11.31	< 0.0001

T_{10} and M_s increased, while LD decreased. T_{10} increased 2.7, 3.1, and 1.8°C; M_s increased 3.2, 4.0, and 1.8%; and LD decreased 1.8, 4.5, and 0.5 cm in patch type CC, CECO, and OC, respectively. The sources explained 72% and 43% of the variation of T_{10} and M_s , respectively.

Effects of Burning and Thinning Treatments

Comparing treated points with nontreated points based on the measurements in the posttreatment year

2002, we found that burning and thinning treatments significantly influenced SRR on average ($F = 2.11$, $P = 0.0801$). In particular, burning, which included all of the two levels of burning treatments, significantly decreased SRR in CECO but did not significantly change SRR in CC or OC (Table 4). Thinning, which included all of the three levels of thinning treatments, did not significantly affect SRR in any of the patch types ($P > 0.1$). On the other hand, the interactions of burning and thinning treatments significantly increased SRR in unburned and thinned CECO patch type but did not significantly influence SRR in burned and thinned CECO patches (Table 4, Figure 2).

Burning and thinning treatments significantly changed soil environments (Table 5). Burning significantly increased T_{10} by 4°C but decreased M_s by 3%, LD by 4 cm, and soil total C by 42.6%. Burning did not significantly influence soil total N. Following the combined thinning and burning treatments, M_s significantly increased from 1% to 6%, while other soil environmental variables did not significantly change.

Table 3. Soil temperature (T_{10}), moisture (M_s), and litter depth (LD) in summer 2000 and 2002 by three dominant patch types: closed canopy (CC), *Ceanothus* shrub (CECO), open canopy (OC)

Variable and patch type	2000	2002	Difference	<i>N</i>	<i>P</i> > <i>T</i>
	(pretreatment)	(posttreatment)	(2002 – 2000)		
T_{10} (°C)					
CC	13.1 (1.9)	15.8 (4.0)	2.7	18	< 0.0001
CECO	15.0 (2.9)	18.1 (4.6)	3.1	18	< 0.0001
OC	19.8 (4.4)	21.6 (6.5)	1.8	18	0.0678
M_s (%)					
CC	7.1 (3.0)	10.3 (3.5)	3.2	18	< 0.0001
CECO	6.4 (2.5)	10.4 (3.5)	4.0	18	< 0.0001
OC	7.4 (2.6)	9.2 (2.6)	1.8	18	< 0.0001
LD (cm)					
CC	11.6 (5.1)	9.8 (7.5)	–1.8	18	0.1322
CECO	8.4 (7.8)	3.9 (5.4)	–4.5	18	< 0.0001
OC	0.6 (1.0)	0.1 (0.2)	–0.5	18	< 0.0001

Table 4. Results of analysis of variance to test effects of burning and thinning treatments on soil respiration rate (SRR) in three dominant patch types: closed canopy (CC), *Ceanothus* shrub (CECO), and open canopy (OC)

Patch type and source	<i>df</i>	Mean square	<i>F</i>	<i>P</i> > <i>F</i>
CC				
Burn	1	0.0448	0.22	0.6436
Thin	2	0.0496	0.25	0.7835
Interactions of burn and thin	1	0.0003	0	0.9705
CECO				
Burn	1	3.9788	9.61	0.0092
Thin	2	0.1537	0.37	0.6975
Interactions of burn and thin	2	1.5290	3.69	0.0562
OC				
Burn	1	0.0141	0.16	0.6939
Thin	2	0.0976	1.12	0.3544
Interactions of burn and thin	—	—	—	—

Empirical Models

The relationships between SRR and soil environmental variables differed before and after treatments. Prior to burning and thinning treatments, there was a negative relationship between SRR and T_{10} and between SRR and M_s , but SRR was positively correlated to LD (Figure 3). After treatments, SRR was not correlated strongly to T_{10} and LD, but it was correlated positively to M_s . T_{10} decreased with increasing litter depth before and after treatments (Figure 4). M_s was correlated negatively to LD prior to treatments, but no longer correlated to LD following treatments. T_{10} and M_s did not have significant correlation. Soil total C and N were correlated strongly to each other ($r = 0.92$), but neither was significantly correlated to SRR (Figure 5).

The combined effects of T_{10} and LD, M_s and LD, and T_{10} and M_s produced different effects on SRR before and after treatments (Figure 6). SRR increased

as T_{10} and LD increased preceding treatments (Figure 6A), but this pattern was not observed following treatments (Figure 6B). Prior to treatments, SRR did not increase as M_s and LD increased (Figure 6C). Following treatments, SRR was increased with an increase in M_s . SRR also increased with increases in LD when LD was less than ~15 cm, and then decreased as LD increased (Figure 6D). SRR generally increased with increases in T_{10} and M_s in spite of several exceptional cases in pre-treatment data (Figure 6E and F).

The exponential models were developed between SRR and T_{10} , M_s , and LD before and after treatment (Table 6). SRR depended on T_{10} and LD prior to treatments. The negative relationship between SRR and T_{10} in this ecosystem was confirmed by the model. The pretreatment model explained 62% of the SRR variation (Figure 7A). After treatments, M_s played a central

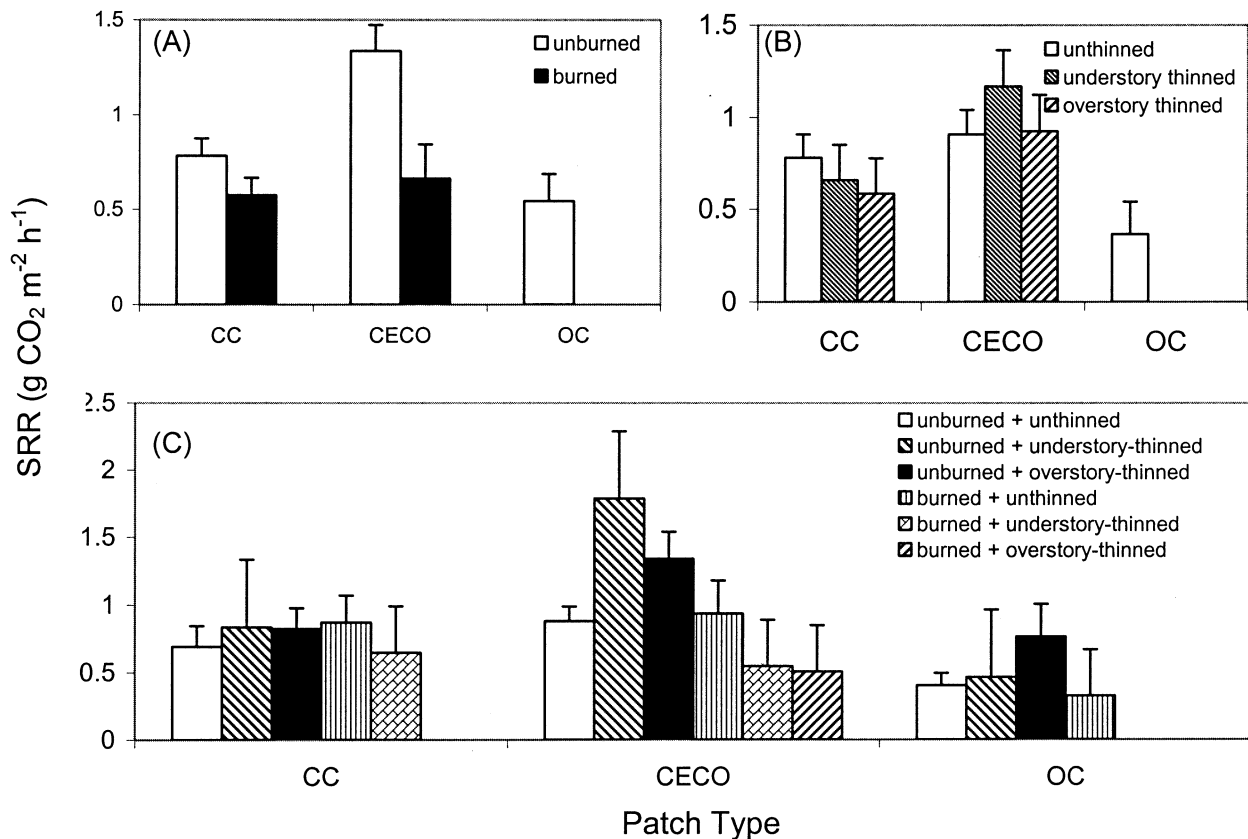


Figure 2. Least-square means and errors of soil respiration rate (SRR) for the effects of (A) burning, (B) thinning, and (C) their combinations in three dominant patch types: CC, closed canopy, CECO, *Ceanothus* shrub, and OC, open canopy in the summer of 2002. Least-square means of burned OC in (A), understory-thinned and overstory-thinned OC in (B), and burned-overstory-thinned CC and burned-understory-thinned and burned-overstory-thinned OC in (C) were not estimated due to the lack of sampling points in these treatments.

role in the model. The post-treatment model explained 48% SRR variation (Figure 7B).

Discussion

We found that thinning treatments did not significantly influence soil respiration approximately one year after thinning, likely because thinning can act to both enhance and inhibit root and microbial respiration. For example, thinning may directly reduce living root biomass (and root respiration) by removing trees and other vegetation. However, thinning also reduces competition for soil moisture and nutrients, which may stimulate growth in the surviving trees resulting in increased living root activity. Thinning can also reduce soil microbial biomass by disturbing the humus layer (Mallik and Hu 1997). Alternatively, the logging slash and organic matter that is mixed into the mineral soil would increase substrate availability, thereby potentially increasing microbial activity and accelerating litter and

soil organic matter decomposition (Mallik and Hu 1997, Ohashi and others 1999, DeLuca and Zouhar 2000, Siira-Pietikäinen and others 2001, Carter and others 2002). If several of these processes operate simultaneously after thinning, the net effect could be no observable change in CO_2 efflux although the sources of the CO_2 might differ dramatically from unthinned forests.

Soil respiration increased in the unburned and thinned CECO patches but decreased in burned and thinned CECO points. Although the exact reason for the differences in soil respiration between the two treatments are not well understood, fire behavior may influence the variation of burned area. Fire behavior depends on multiple factors such as fuel loading, fuel moisture, and fuel bed bulk density (Miller and Urban 2000, Sparks and others 2002). The input of logging slash following thinning helped the prescribed surface fire in the combination treatment to spread more evenly, and possibly hotter, than in the single burning

Table 5. Results of analysis of variance to test effects of burning and thinning treatments on soil environmental variables: soil temperature (T_{10}), soil moisture (M_s), litter depth (LD), soil total carbon (C), and soil total nitrogen (N)

Variable and source	<i>df</i>	Mean Square	F	<i>P</i> > F
T_{10}				
Burn	1	113.3826	5.57	0.0226
Thin	2	19.3023	0.95	0.3949
Interaction of burn and thin	2	0.9819	0.05	0.9530
M_s				
Burn	1	40.1226	6.15	0.0169
Thin	2	26.2010	4.02	0.0247
Interaction of burn and thin	2	23.9576	3.67	0.0331
LD				
Burn	1	91.1912	3.54	0.0663
Thin	2	33.8845	1.32	0.2783
Interaction of burn and thin	2	4.2708	0.17	0.8477
C				
Burn	1	12.6410	4.62	0.0371
Thin	2	0.6931	0.25	0.7772
Interaction of burn and thin	2	0.1449	0.05	0.9485
N				
Burn	1	0.0088	1.92	0.1724
Thin	2	0.0027	0.59	0.5566
Interaction of burn and thin	2	0.0005	0.11	0.8969

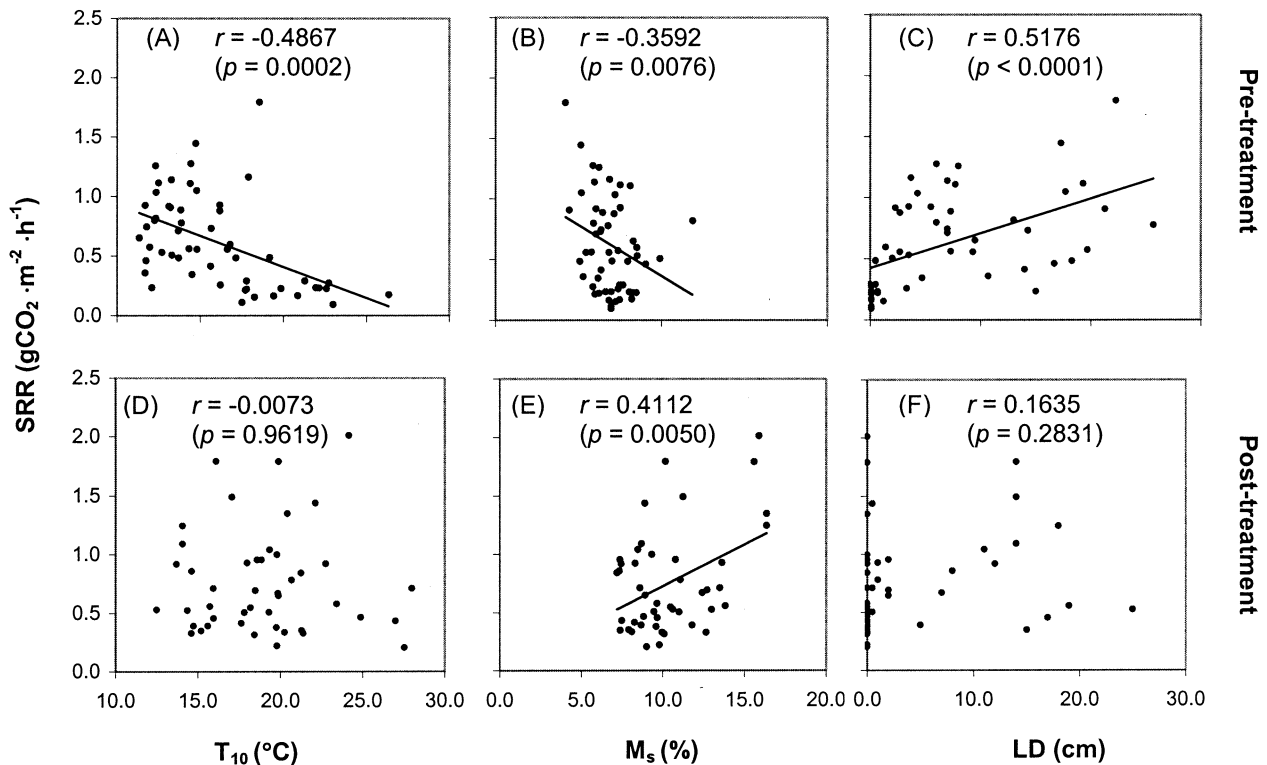


Figure 3. Comparisons between the pre- and post-treatment relationships of soil respiration rate (SRR) to soil temperature (T_{10}), soil moisture (M_s), and litter depth (LD) across patch types. Each dot on the figures is the grand mean of the monthly measurements from each sampling point across patch types ($N = 54$).

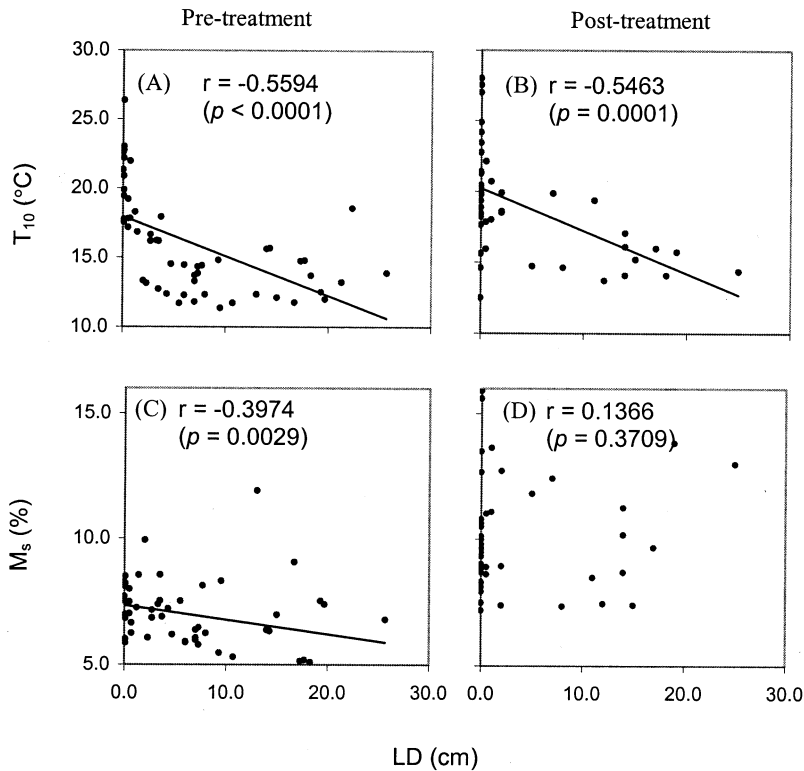


Figure 4. Comparisons between the pre- and post treatment correlations between litter depth (LD) and soil temperature (T_{10}), and between LD and soil moisture (M_s) across patch types. Each dot on the figures is the grand mean of the monthly measurements from each sampling point ($N = 54$).

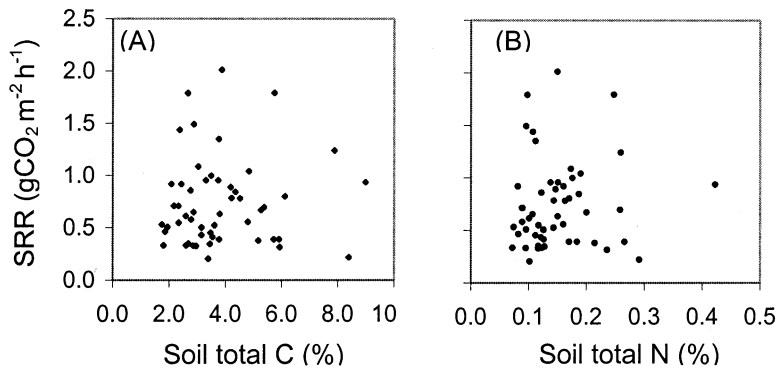


Figure 5. Relationships among soil respiration (SRR) and soil total carbon (C) and nitrogen (N). Each dot on the figures is the grand mean of the monthly SRR measurements from each sampling point ($N = 54$).

treatment. Thus, the result of the higher temperatures could have been to reduce microbial activity.

The different responses of soil respiration to burning and thinning treatment in the CECO patches may also result from either altered microbial activities or microbial biomass. We measured microbial carbon at the TEF outside of our sampling points in 2002 and found that microbial carbon was greater in the CECO patches than those of CC patches regardless of treatments (H. Erickson, unpublished data). Possibly, the changes in SRR in the CECO patch types were due to changes in microbial activity rather than changes in microbial carbon. Previous studies have reported that

microbial carbon typically remains stable or decreases following a prescribed burn and thinning. Wüthrich and others (2002) reported that fire intensities increased soil respiration while the soil microbial biomass remained relatively stable. Alternatively, in a Mediterranean pine forest, microbial biomass C decreased in burned soil nine months after the fire (Hernández and others 1997). Microbial biomass also decreased in the site with prescribed burning following clear-cutting (Pietikäinen and Fritze 1995).

Higher soil respiration in forest ecosystems may also be associated with more available N (Lu and others 1998). For example, as mentioned previously, micro-

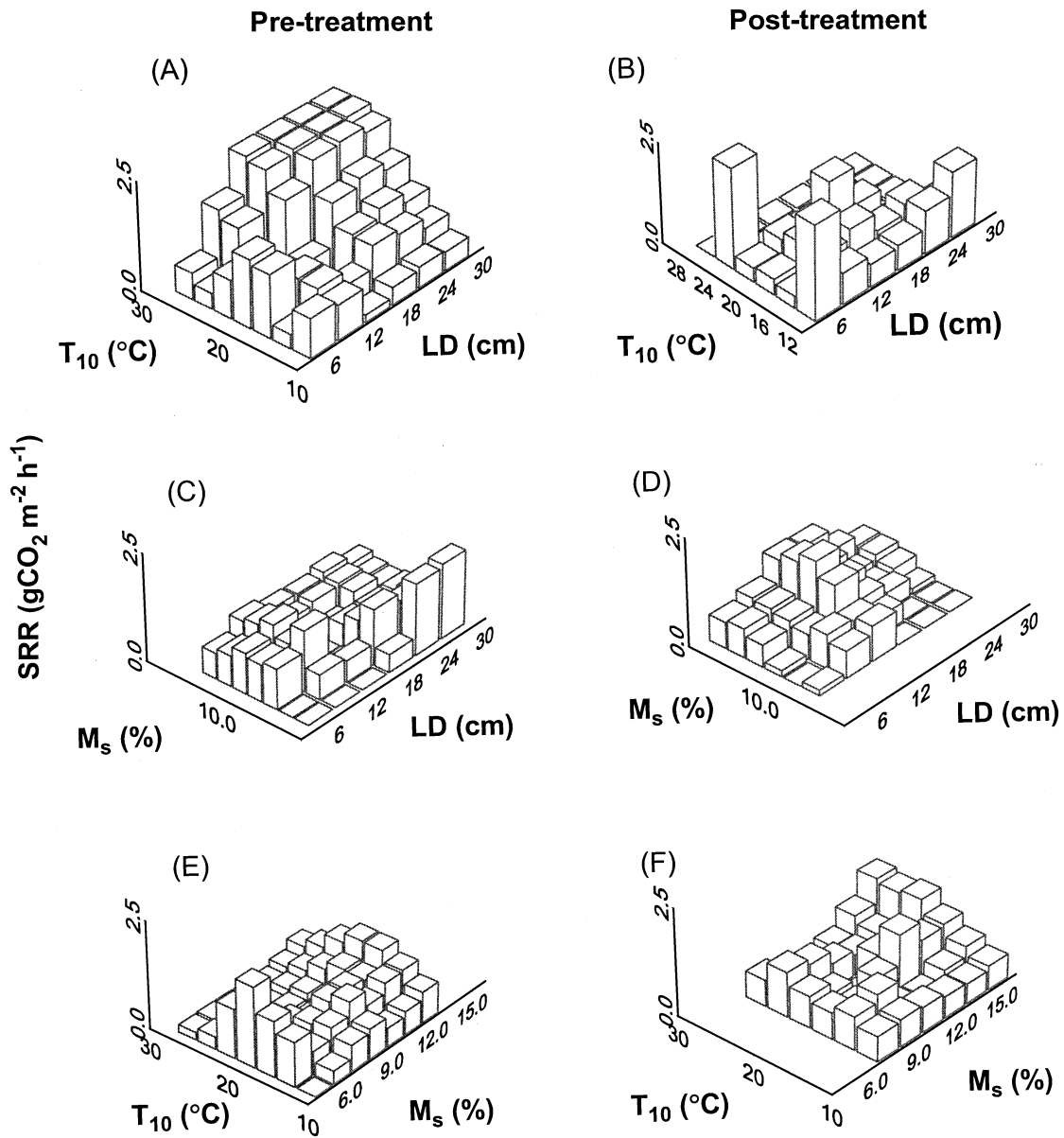


Figure 6. Comparisons between the pre- and post treatment relationships among soil respiration (SRR) and soil temperature (T_{10}), soil moisture (M_s), and litter depth (LD) across patch types ($N = 54$).

Table 6. Parameters of empirical models^a

	Patch type	a	b	c	d
Pretreatment	CC	0.906	-0.156	0.012	-1.005
SRR = $e^a + b^{LD} + c^{LD-T_{10}} + d$	CECO	1.048	-0.156	0.012	-1.005
	OC	0.535	-0.156	0.012	-1.005
	Posttreatment	CC	0.362	6.504	—
SRR = $a e^{bM_s}$	CECO	0.465	6.504	—	—
	OC	0.220	6.504	—	—

^aSRR - soil respiration rate; LD - litter depth; T_{10} - soil temperature at 10 cm depth; M_s - volumetric soil moisture content; a, b, c, d - parameters; CC - closed canopy; CECO - *Ceanothus* shrub dominant; OC - open canopy.

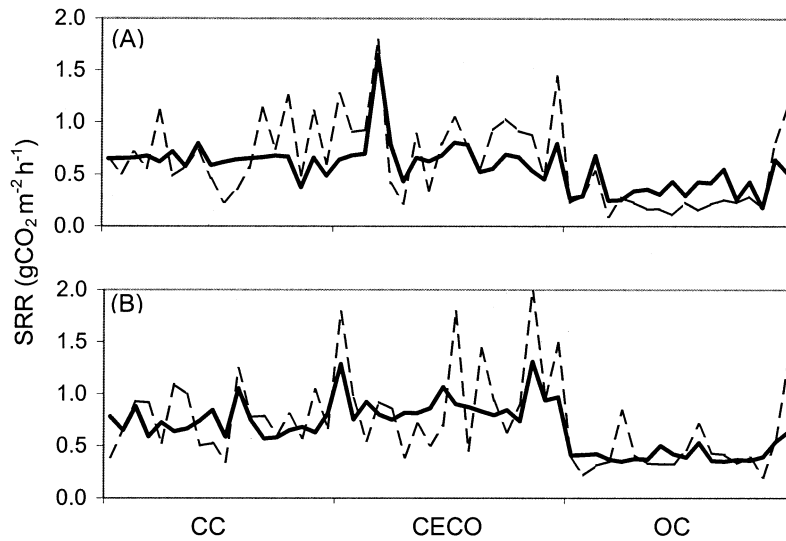


Figure 7. Comparisons between measured (dashed line) and simulated (solid line) soil respiration (SRR) at a single sampling point before and after treatments in three patch types: CC, closed canopy, CECO, *Ceanothus* shrub, and OC, open canopy.

bial carbon was greater in the CECO patches than that of the CC patches despite the treatments (H. Erickson, unpublished data). Soil respiration was also higher in the CECO patches. High availability of nitrogen in the CECO was probably related to the symbiotic *Frankia* spp., a type of N-fixing bacteria (North and others 2002). Our data indicate that thinning treatments played an important role in determining the effects of treatments on soil respiration. Thinning produced logging debris and potentially many dead roots of *Ceanothus* that would provide substrate for decomposition. As a result, microbial activities may be simulated with an increase in N availability (Mallik and Hu 1997). Increased soil respiration in the unburned but thinned CECO patches suggested that *Ceanothus* is critical to the nutrient dynamics in these fire-dependent forests.

In mixed-conifer forests, the spatial variation in litter properties may be a critical influence on soil respiration (Gärdenäs 2000). Changes in the humus layer have been related to decreased soil respiration (Mallik and Hu 1997). Alteration of the litter layer, however, may enhance soil respiration by modifying soil temperature and moisture, aeration, pH, and nutrient availability due to enhanced microbial activity and litter decomposition. It is well known that soil temperature and moisture are two most important soil microclimatic variables influencing soil respiration (Wildung and others 1975, Gordon and others 1987, Hanson and others 1993, Lloyd and Taylor 1994, Davidson and others 1998, Russell and Voroney 1998). Our pretreatment model suggests that litter depth is also critical in determining soil respiration. However, litter depth may not be the best measure of litter properties since moisture, chemical

composition, and age of the litter influence organic matter decomposition, soil temperature, and soil moisture.

The increase in soil moisture following burning and thinning treatments is critical in the Sierra Nevada old-growth, mixed-conifer forest. Increased soil moisture along with high temperature in the summer increases soil organic matter decomposition and stimulates root growth, which results in an increase in soil respiration. However, soil respiration may decrease several years after burning and thinning (Pietikäinen and Fritze 1995, Ohashi and others 1999, Wüthrich and others 2002). With global climate change, the Sierra Nevada forests are predicted to have drier and hotter summers, and wetter and warmer winters (Field and others 1999). If predictions are correct, soil respiration may be restricted by soil moisture during the summer and enhanced during the winter. The forest management practices that we evaluated in this study may serve to offset, at least in the short term, some of these expected changes. Thus, forest management practices and their impacts on soil CO₂ efflux seemed to be relevant within the context of the global climate change.

Conclusion

Prescribed burning and thinning treatment significantly changed soil respiration rate and soil environment variables (i.e., soil temperature, moisture, litter depth, and soil total carbon). In particular, SRR was reduced significantly in the burned CECO patch types but increased in the unburned but thinned CECO

patch types. Thinning did not significantly affect SRR in any patch type across all levels of burning treatments. T_{10} and M_s generally increased, whereas LD and soil C decreased following treatments. The relationships between soil respiration and soil environmental variables also varied between pre- and post treatment measurements. Prior to the treatments, soil respiration was more influenced by soil temperature and confounded with changes in the depth of the litter layer. Following treatments, soil moisture appeared to have a stronger influence on soil respiration. As a result, soil respiration and its microenvironment responded to the prescribed burning and thinning treatments in this old-growth, mixed conifer forest. Our findings should be useful for forest managers charged with assessing and predicting the consequences of alternative forest management on functional attributes (e.g., soil respiration) of mixed-conifer forest ecosystems of the Sierra Nevada.

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