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Soil respiration response to experimental disturbances over 3 years

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Abstract

Soil respiration is a major pathway for carbon cycling in terrestrial ecosystems yet little is known about its response to natural and anthropogenic disturbances. This study examined soil respiration response to prescribed burning and thinning treatments in an old-growth, mixed-conifer forest on the western slope of the Sierra Nevada Mountains. Experimental treatments were applied in 2001 using a full factorial design consisting of two levels of burning and three levels of thinning, and included: unburned–unthinned (UN), unburned–overstory thinned (US), unburned–understory thinned (UC), burned–unthinned (BN), burned–understory thinned (BC), and burned–overstory thinned (BS). We measured soil respiration rate (SRR), soil moisture (M_S), soil temperature (T_S), and litter depth (LD) for three replicates of each of three dominant patch types (closed canopy, open canopy, and ceanothus shrub) within each of the six treatments ($n = 54$). The same sampling points were measured from May to August in 2000 (pre-treatment) and in 2002, 2003, and 2004 (post-treatment). Within our sampling period there was as much as 37% variation ($p = 0.0005$) between years in the undisturbed patches, which appeared to be driven by changes in precipitation. SRR also varied by year in all treated plots (US: $p = 0.0516$; UC: $p = 0.0006$; BN: $p = 0.0158$; and BC: $p = 0.0040$), with the exception of BS ($p = 0.3344$). SRR response to disturbance varied with patch type, year, and treatment type. In most cases, burning and the combination of burning and thinning had less of an effect on mean SRR than thinning alone. Ceanothus patches appear to have recovered fastest, while treatment effects remained 3 years after thinning in closed canopy ($p = 0.0483$ and 0.0333 in UC and US, respectively) and open canopy patches ($p = 0.0191$ in US). Open canopy patches showed no response to any treatment aside from US. Both UC and US increased SRR in closed canopy and ceanothus patches, and US decreased SRR in open canopy patches. BS increased SRR in 2004 in closed canopy patches ($p = 0.0108$), but no significant changes occurred in any patch type in response to BN or BC treatments. Across all treatments, the relationship of SRR with temperature, moisture, and litter depth changed in post-disturbance years. The results of this study can be used to help understand how management of Sierran mixed-conifer forests affects soil carbon sequestration.
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Keywords: Soil CO_2 efflux; Thinning; Burning; CASPO; Shelterwood; Patch type; Management; Interannual variability; Sierra Nevada

1. Introduction

Soils are major carbon pools (Schlesinger, 1995) and management strategies that maximize soil carbon sequestration may help offset predicted increases in atmospheric CO_2 (Chen et al., 2004). The majority of previous studies have focused on soil carbon cycling in undisturbed systems, while disturbance effects are not as well researched. Since much of our current landscape has been modified by natural and anthropogenic disturbances, it is crucial that we understand the consequences on carbon cycling and consider them in management practice. The effects of forest management on carbon cycling are of particular interest because forests cover 747 million acres of land in the U.S. (USDA FS, 2003), much of which is regularly being treated with mechanical thinning and/or prescribed burning.

A limited number of studies have examined the effects of thinning (e.g., Gordon et al., 1987; Kowalski et al., 2003; Scott et al., 2004; Tang et al., 2005) and burning (e.g., Weber, 1985; Pietikäinen and Fritze, 1993; Litton et al., 2003; Hubbard et al., 2004) on soil respiration rate (SRR) in forest ecosystems. However, few have measured SRR at the same sampling points before and after treatments to follow temporal changes while controlling for interannual and spatial variability (i.e. due to climate, vegetation, soils, etc.). In the U.S., thinning and prescribed burning are increasingly being used as restoration

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treatments in fire suppressed forests, such as Sierra Nevada mixed-conifer forests (Sierra Nevada Forest Plan Amendment, 2004; Healthy Forest Initiative, 2004). These forests normally experience prolonged summer droughts during which fire was historically a frequent low-intensity disturbance. Unlike other western forests, stand structure in the mixed-conifer Sierran forest remains patchy with discontinuous canopy cover after more than a century of fire suppression (North et al., 2004). Several studies have suggested that annual differences in precipitation and snow pack depth could have a significant effect on ecosystem processes such as seedling occurrence and establishment (Galen and Stanton, 1999; Hattenschwiler and Smith, 1999), decomposition (Weatherly et al., 2003), and plant phenology and growth (Walker et al., 1995; Wahren et al., 2005). We do not, however, have a good understanding of how interannual climate interacts with widely used restoration treatments to affect carbon flux in these managed forests.

The objectives of this study were to: (1) examine SRR response to various management strategies from 1 to 3 years after treatment and determine whether effects are more pronounced at different times of year, (2) characterize the temporal changes in SRR (seasonal and internannual) and compare how they are affected by treatments, and (3) identify biotic and abiotic factors that may drive spatial variation of SRR during pre- and post-treatment years. In previous research in Sierra Nevada mixed-conifer forests, respiration rates and response to treatments distinctly varied by patch and treatment type for the first 2 years post-disturbance and relationships between SRR and environmental drivers were changed with treatments (Ma et al., 2004; Concilio et al., 2005). Here, we synthesize 4 years of data to examine temporal variation and disturbance effects on SRR from 1 to 3 years after forest management, comparing pre-treatment conditions to each year post-treatment. We have focused on the effects of management strategies that are common to the Sierra Nevada (Sierra Nevada Forest Plan Amendment, 2004; Verner et al., 1992) including prescribed burning, understory fuel reduction (following California spotted owl, or CASPO, guidelines), overstory fuel reduction (shelterwood thinning; up to 40 in. dbh trees), and combinations of fire and thinning.

2. Methods

2.1. Study site and field methods

This study was conducted in the Teakettle Experimental Forest (TEF), located within the Sierra National Forest on the western side of the Sierra Nevada mountain range of California (36°58′N, 119°2′W). TEF is 1300 ha, ranges in elevation from 1980 to 2590 m asl, and receives an average of 1250 mm of precipitation a year (mostly from snow). TEF has a Mediterranean climate with hot, dry summers and cold, wet winters (Fig. 1). Soil orders are Inceptisols and Entisols. Soils generally have a course sandy-loam texture, low water-holding capacity, an average bulk density of 1.09 g^{-1} cm^3, and soil depth varies greatly across the stand, ranging from 0 cm on

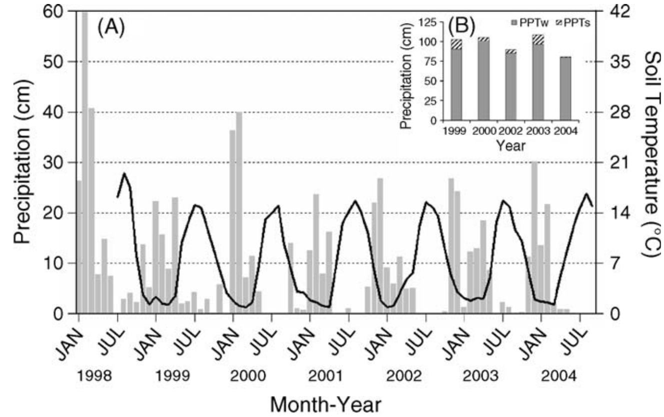

Fig. 1. (A) Monthly precipitation (bars) and mean monthly soil temperature (line) from 1998 to 2004. (B) Winter (previous October to that years' April), spring–summer (May–August) precipitation in the study area by year. Temperature data was recorded at three weather stations at the study site, and precipitation data is from Pacific Gas and Electric Wishon Dam site, located 5 km NE of the study site at 2000 m in elevation (37°0′N, 11°59′W).

exposed boulders to several meters elsewhere (North et al., 2002). Litter depth is also highly variable; gaps exist with little to no litter accumulation while litter can be several feet deep in closed canopy forest patches (North et al., 2002; Ma et al., 2004).

TEF is a patchy ecosystem composed mainly of groups of mixed-conifer trees interspersed with vegetation-free zones and shrub-covered areas dominated by the nitrogen-fixer whitethorn ceanothus (*Ceanothus cordulatus*; North et al., 2002). Three dominant vegetation patch types have been classified using hierarchical clustering analysis: closed canopy (CC), open canopy (OC), and ceanothus shrub (CECO). They occupy 67.7%, 4.7%, and 13.4% of the entire forest area, respectively (North et al., 2002), with the remainder composed mostly of exposed rock. Dominant species in the closed canopy patches include white fir (*Abies concolor* Lindl. ex Hildebr), Jeffrey pine (*Pinus jeffreyii* Grev.and Balf), sugar pine (*Pinus lambertiana* Douglas), red fir (*Abies magnifica* A. Murr), and incense cedar (*Calocedrus decurrens* (Torr.) Florin). Understory herbaceous cover is sparse (at 2.5% on average) but rich (see more details in North et al., 2005b).

Our field measurements were conducted within 18, 4 ha plots, which were scaled and placed based on semi-variance and cluster analysis in order to have equal representative percentages of the three main mixed-conifer patch types (North et al., 2002). Three replicates of each of six treatments were randomly assigned to the 18 experimental plots. Treatments were a full factorial design of burning and no burning crossed with no thinning, understory thinning (following California spotted owl, or CASPO, guidelines), and overstory thinning (shelterwood; up to 40 in. dbh trees). The six treatments that resulted were control (UN), unburned–understory thinned (UC), unburned–overstory thinned (US), unburned–not thinned (BN), burned–understory thinned (BC), and burned–overstory thinned (BS). Mechanical thinning took place in September–October of 2000 for burn–thin treatments (i.e., the BC and BS plots), June–July of 2001 for the thin-only plots (UC and US), and prescribed fire was applied in fall of 2001 for all the burn treatments (BC, BS, and BN). Thinning treatments left much slash on the forest floor and, consequently, burning in combination with thinning was greatly intensified compared to burning alone. Ma et al. (2005) found significant differences in SRR between vegetative patch types within mixed conifer forests. For this reason we stratified our sample points within each treatment by the three dominant pre-treatment patch types. We randomly selected three established gridpoints at least 25 m apart, one of each patch type in each treatment, and replicated this design three times for each treatment type, for a total of 54 points.

Measurements of SRR were taken biweekly from June through August at each sampling point in 2000, 2002, 2003, and 2004 with portable infrared gas analyzers (EGM-2 and EGM-4 Environmental Gas Monitor, PP Systems, UK) and attached SRC-1 Soil Respiration Chambers (PP Systems, UK). In 2004, sampling was expanded until October, but data from September to October was only used for seasonal comparison. SRR measurements were made on 5 cm tall, 10 cm diameter PVC collars, which were inserted 1 cm into the soil surface (including litter layer) at least 1 week before measurements were taken to avoid disturbance effects. The EGM-2 was calibrated weekly with standard, 700 ppm CO_2 gas under ambient air pressure, and barometric pressure readings were taken at the time of sampling to correct for differences in pressure. All SRR measurements were corrected for machine error (Ma et al., 2005) as Butnor and Johnsen (2004) found that the PP Systems EGM overestimates SRR in loose sandy soils, like those present at TEF. Simultaneous to SRR measurements, soil temperature (T_S) was measured at a depth of 10 cm within 30 cm of each PVC collar with handheld thermometers (Taylor Pocket Digital Thermometer). Soil moisture (M_S) from 0 to 15 cm depth was measured using a Time Domain Reflectometry (TDR) unit (Model 6050XI Soil Moisture Equipment Corp., Santa Barbara, California, USA) either at the time of SRR sampling or within 6 days provided that no precipitation events occurred in the interim. TDR measurements were made on 30 cm long steel rods inserted into the ground within 30 cm of each PVC collar at a 30° angle. Litter depth (LD) measurements were made at every sampling point to the nearest 0.5 cm. In 2000 and 2001, litter depth was defined as the depth from the top of the ground surface to the top of the mineral soil (i.e., the entire O horizon). In 2002 and 2003, we measured litter depth as the depth of the O*i* horizon only. No comparisons of litter depth were made between years because LD was only used as an explanatory variable of SRR within each year in this study.

2.2. Statistical analyses

Means, standard deviations, and standard errors were calculated for SRR, T_S, M_S, and LD by treatment, patch type, and year (from June to August). All variables were checked for normal distribution with Shapiro-Wilk tests, and SRR and LD data were log transformed to normalize for statistical analysis. All analyses were conducted using SAS software (V9.1, SAS Institute Inc., Cary, North Carolina, USA) and a p-value of 0.05 was used to determine statistical significance unless otherwise noted.

Treatment effects were quantified by comparing SRR in treated plots to those in the control. In preliminary analysis, we used a one-way repeated measures analysis of variance (ANOVA) to test differences between the plots by year (SRR = f(plot)) and found that SRR was significantly different between plots before treatments were applied ($F_{[5,140]} = 3.18$, $p = 0.0095$). To compensate for spatial heterogeneity in the forest ecosystem and interannual variation, we calculated the percent difference in SRR between each treatment plot (TRT) and the control (CTL) by patch type and date: $\%\Delta\mathrm{SRR} = [(\mathrm{SRR}_{\mathrm{TRT}} - \mathrm{SRR}_{\mathrm{CTL}})/\mathrm{SRR}_{\mathrm{CTL}}] \times 100$. The standardized dataset was used to determine whether differences in SRR by year were due to treatment effects with a one-way repeated measures analysis of variance with contrast statements: %ΔSRR = f(year). Percent data was transformed before analysis by calculating the square root of the arcsine of each value. In addition, SRR data was transformed by calculating the difference of each mean value in SRR by treatment, patch, and sampling date from treatment ($\mathrm{SRR}_{\mathrm{TRT}i}$) to the pre-treatment control ($\mathrm{SRR}_{\mathrm{CTL}o}$): $\mathrm{SRR}_{\mathrm{D}} = \mathrm{SRR}_{\mathrm{CTL}o} - \mathrm{SRR}_{\mathrm{TRT}i}$. In the control, $\mathrm{SRR}_{\mathrm{D}}$ was 0 in 2000, and positive or negative over subsequent years depending on its relationship to corresponding sites in 2000. $\mathrm{SRR}_{\mathrm{D}}$ data were normalized with a log transformation and the corrected values were then compared with a repeated measures ANOVA: $\mathrm{SRR}_{\mathrm{D}} = f(\mathrm{TRT\ year} \times \mathrm{TRT})$. SRR response to disturbance by time of year was tested in 2004 to determine whether response was more pronounced during certain months. A one-way ANOVA was performed by month, from June to October: SRR = f(TRT). SRR was log transformed before analysis. Post-disturbance seasonal variation in SRR was examined by each patch-treatment combination from June to October in 2004 with one-way repeated measures ANOVA using orthogonal contrast statements that made direct comparisons between months: SRR = f(month). To determine how SRR varied by year, we examined variation in the UN treatment by year using a one-way repeated measures analysis of variance (ANOVA) with contrast statements to compare each combination of years: SRR = f(year). Data from treated plots (BN, UC, BC, US, BS) were analyzed in the same way to determine how treatments affected interannual patterns.

Relationships between SRR and T_S, M_S, and LD were examined by year using stepwise regression: SRR = $f(T_S, M_S, \mathrm{LD})$. Although SRR usually increases exponentially with T_S (e.g., Singh and Gupta, 1977), this relationship has only been found at TEF when volumetric soil moisture is greater than 10% (Ma et al., 2005). It was clear through graphical observation that there was no obvious exponential trend between SRR and T_S in these data. We, therefore, used simple linear regression to explore the relationship between SRR and T_S by year: SRR = $f(T_S)$. Untransformed means of SRR, T_S, M_S, and LD by sampling date, patch, and treatment type were used in regression analyses. The best model was chosen in each case based on partial R^2 values, p-values, and model $C(p)$. The $C(p)$ statistic, similar to Akaike's Information Criteria, is a measure of total squared error of a model and used as a criterion for model selection (Mallows, 1973).

3. Results

3.1. Disturbance effects on SRR

We found that SRR was significantly different by year across all treatments ($F = 3.65$, $p = 0.0136$) and by the combined effect of year and treatment ($F = 0.0245$, $p = 0.0145$) after correcting for spatial variability between plots. However, differences in SRR were only apparent within some patch-treatment combinations (Fig. 2). In closed canopy patches, UC, US, and BS produced an increase in SRR (Fig. 2A). UC and US also increased SRR in ceanothus patches (Fig. 2B). Mean SRR in open canopy patches was only affected significantly by the US treatment, which caused a decrease (Fig. 2C). BN and BC treatments had no significant effect on SRR in any patch type.

SRR response over the three subsequent years varied by patch type and treatment (Fig. 2). In closed canopy patches, UC significantly increased mean SRR all 3 years post-treatment ($p = 0.0154$, 0.0200, and 0.0483 in 2002, 2003, and 2004, respectively) and US and BS significantly increased mean SRR in 2004 ($p = 0.0333$ and 0.0108, respectively; Fig. 2A). In ceanothus patches, peak SRR response to thinning treatments (UC and US) occurred in 2002 and 2003 and rates returned to pre-treatment levels by 2004 (Fig. 2B). Within unburned open canopy patches in US treatments, mean SRR decreased each year and was significantly lower in 2003 ($p = 0.0068$) and 2004 ($p = 0.0191$; Fig. 2C).

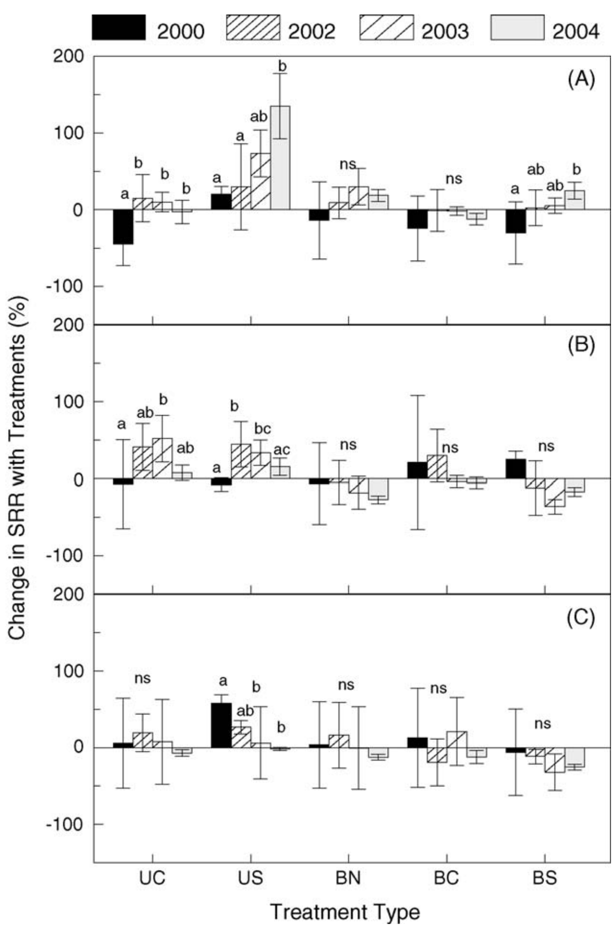

Fig. 2. Percent change in soil respiration rate (SRR, g CO_2 m^{-2} h^{-1}) from treatment (UC, US, BN, BC, and BS) to control (UN) during pre-treatment (2000) and post-treatment (2002–2004) years within three patch types: (A) closed canopy, (B) ceanothus shrub, and (C) open canopy. Treatments include unburned–understory thinned (UC), unburned–overstory thinned (US), burned–unthinned (BN), burned–understory thinned (BC), and burned–overstory thinned (BS). Error bars represent one standard deviation from the mean and different letters represent significantly different means ($p \leq 0.05$).

3.2. Seasonal and interannual variability in SRR

Three years post-disturbance (i.e., 2004), treatment effects on SRR appear to be most pronounced in the early summer (June and July), where significant differences existed at a 99% confidence level ($p = 0.0002$ and 0.0045, respectively). SRR differed marginally by treatment in September ($p = 0.0529$), while in August and October no differences were apparent (p, = 0.3797 and $p = 0.301$, respectively).

SRR decreased from peak levels in June and July throughout the summer and fall within most patch-treatment combinations in 2004 (Fig. 3). There were significant differences in SRR between at least 2 months (generally June or July and October) in both closed canopy and ceanothus patch types (respectively) within the UN (Fig. 3A, $p = 0.0144$ and 0.0039), BN (Fig. 3B, $p = 0.0012$ and 0.0077), UC (Fig. 3C, $p = 0.0019$ and 0.0039), BC (Fig. 3D, $p = 0.0049$ and 0.0180), and US (Fig. 3E, $p = 0.0003$ and 0.0005) treatments. In the BS treatment (Fig. 3F), there was a difference in SRR by month within ceanothus patches ($p = 0.0001$), but none in the closed canopy ($p = 0.3697$). Within open canopy patches, there was at least one significant difference in SRR by month (again, mostly between June or July and October) within the UN (Fig. 3A, $p = 0.0035$), UC (Fig. 3C, $p < 0.0001$), and the BC (Fig. 3D, $p = 0.0015$) treatments; but not after BN (Fig. 3B; $p = 0.1402$), US (Fig. 3E; $p = 0.2916$), or BS (Fig. 3F; $p = 0.3158$) treatments.

SRR varied by year within most treatments (Fig. 4). Mean summer SRR was highest in 2000 and 2003 in the control, with a 37% difference between the highest and lowest year ($p = 0.0005$; Fig. 4A). Previous winter's precipitation was also greatest in 2000 and 2003 (Fig. 1B). Thus, precipitation appeared to be a driver of interannual SRR variability. Within each patch type in the UN treatment, interannual percent differences between the highest year (CC: 0.62 g CO_2 h^{-1} m^{-2}, CECO: 0.65 g CO_2 h^{-1} m^{-2}, and OC: 0.51 g CO_2 h^{-1} m^{-2}) and lowest year (CC: 0.37 g CO_2 h^{-1} m^{-2}, CECO: 0.45 g CO_2 h^{-1} m^{-2}, and OC: 0.27 g CO_2 h^{-1} m^{-2}) were 40%, 31%, and 47% in closed canopy ($p = 0.0010$), ceanothus ($p = 0.0026$), and open canopy ($p = 0.0309$), respectively.

Interannual variation in SRR in treated plots depended on treatment type (Fig. 4B–F). Within the BN and BC treatments (Fig. 4B and D), there was no change in mean SRR from 2000 to 2003, but it decreased significantly in 2004 ($p = 0.0464$ and 0.0265, respectively). Post-treatment patterns were similar between the different thinning levels, peaking in 2003 with a 31% and 17% increase over 2000 after UC ($p = 0.0011$;

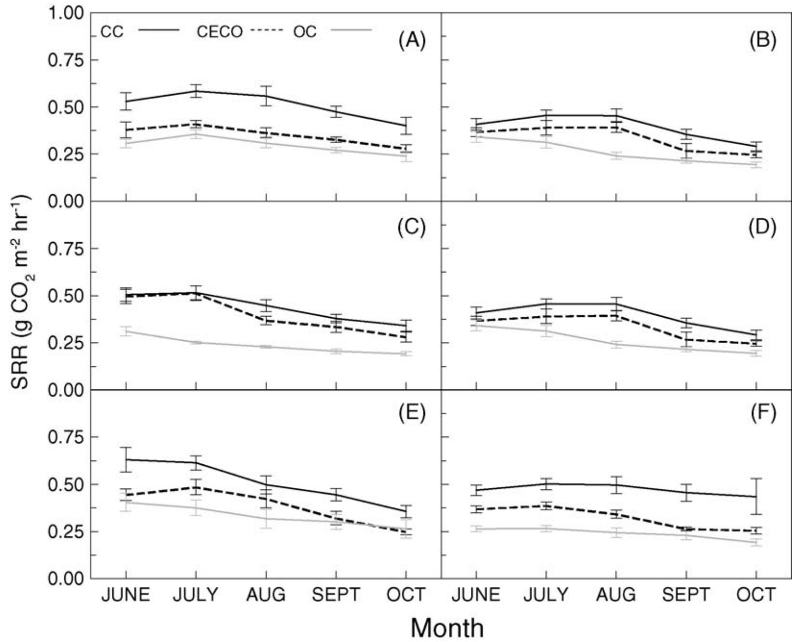

Fig. 3. Mean monthly soil respiration rate (SRR, g CO_2 m^{-2} h^{-1}) from June to October in 2004 in (A) control (UN), (B) burned–unthinned (BN), (C) unburned–understory thinned (UC), (D) burned–understory thinned (BC), (E) unburned–overstory thinned (US), and (F) burned–overstory thinned (BS) treatments. Bars represent one standard error.

Fig. 4C) and US ($p = 0.0936$; Fig. 4E) treatments, respectively. BS treatments showed no variation in SRR by year ($p = 0.3344$; Fig. 4F).

3.3. Biophysical influences on SRR

A shift in environmental factors associated with SRR occurred with treatments. Soil temperature was an important explanatory variable of SRR pre-treatment, but not post-treatment. This was found both through simple linear and multivariate regression analysis. With simple linear regression, we found that temperature explained 16% of SRR variation in 2003 ($p = 0.0992$), and even less in 2002 ($R^2 = 0.04$, $p = 0.4449$) and 2004 ($R^2 = 0.14$, $p = 0.1261$). Through multivariate analysis (Table 1), we found that litter depth was an important driver of SRR in post-treatment years, explaining increasingly more variation in SRR each year from 16% to 56%. Soil moisture played a secondary role in 2004 (partial $R^2 = 0.18$) and a primary role in 2002 (partial $R^2 = 0.25$).

4. Discussion

Treatment effects on SRR varied by year, treatment type, and patch type in this mixed-conifer old-growth forest. Treatment responses were more pronounced within the most intensively thinned and/or burned plots in at least some patches, suggesting that SRR response may be proportional to treatment intensity. This finding is consistent with other studies that have measured soil environmental variables (i.e., SRR, microbial biomass and productivity, fungal hyphae) after various treatments and found response proportional to intensity (Ahlgren and Ahlgren, 1965; Messina et al., 1997; Pietikäinen et al., 2000). In our study, US affected mean SRR in all patch types while UC only affected mean SRR in ceanothus shrub and closed canopy patches. Thus, it appeared that the more intensive thinning treatment, US, had a greater impact on SRR than the less intensive UC treatment. The only change in mean SRR that came with burning was within the closed canopy BS treatment, which was the most intensive burning treatment (i.e.,

Table 1
Multiple regression results for SRR = $f(T_S, M_S, \text{LD})$

Year	Equation	Partial R^2			Model		
		T_S	M_S	LD	p-Value	C_p	R^2
2000	SRR = 1.20 − 0.043T_s	0.55	ns	ns	0.0005	0.13	0.55
2002	SRR = 0.015 + 0.04M_s + 0.012LD	ns	0.25	0.16	0.0197	2.09	0.41
2003	SRR = 0.43 + 0.067LD	ns	ns	0.31	0.0156	0.05	0.31
2004	SRR = −0.15 + 0.059M_s + 0.048LD	ns	0.18	0.56	<0.0001	2.03	0.74

Partial R^2 values are given for each of the independent variables: soil temperature at 10 cm depth (T_S), soil moisture from 0 to 15 cm depth (M_{S},), and litter depth (LD). The model R^2 and C_p values are given for the best model by year pre-treatment (2000) and post-treatment (2002, 2003, and 2004). ns = not significant at the $\alpha = 0.10$ level.

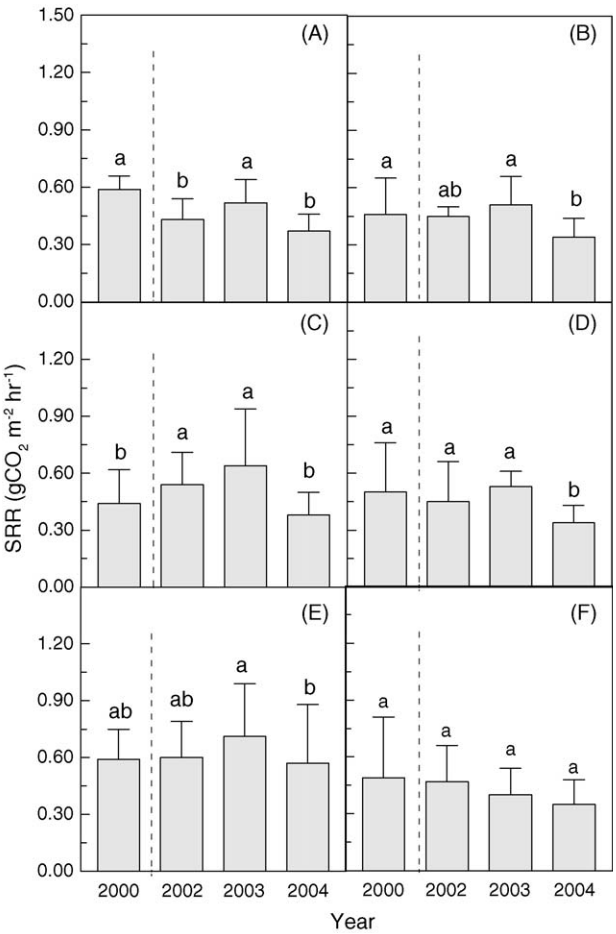

Fig. 4. Mean soil respiration rate (SRR, g CO_2 m^{-2} h^{-1}) in pre-treatment (2000) and post-treatment (2002–2004) years across all patch types by treatment type: (A) control (UN), (B) burned–unthinned (BN), (C) unburned–understory thinned (UC), (D) burned–understory thinned (BC), (E) unburned–overstory thinned (US), and (F) burned–overstory thinned (BS). Error bars represent one standard deviation from the mean and different letters represent significantly different means ($p \leq 0.05$).

the forest floor was most completely burned). Thinning alone had more of an impact on SRR than burning.

Research has been conducted in other forests to assess the legacy effects following disturbance on SRR (Weber, 1990; Ohashi et al., 1999), ecosystem carbon flux (Amiro, 2001), and soil chemical and physical properties (Ziemer, 1964; DeLuca and Zouhar, 2000). Recovery time can vary from a few years (Weber, 1990; Fritze et al., 1993; Messina et al., 1997) to much longer (Ziemer, 1964; Fritze et al., 1993) depending on the site, variable of interest, and type of disturbance. In our study, many patch-treatment combinations showed no response in mean SRR, making it difficult to conclude much about recovery time (i.e., ecosystem resilience). However, of those treatments that did produce a response, recovery time appears to depend heavily on patch type. Mean SRR recovered to pre-treatment levels in ceanothus patches (UC, US) by the 3rd year post-disturbance, but an increasing trend remained in closed canopy (UC, US, BS) and a decreasing trend in open canopy patches (US). Thinning probably produces longer-lasting effects on closed canopy patches because they are more directly affected by removal of tree biomass, and subsequent physical and biological changes. Open canopy gaps may have been highly affected by logging activities (i.e. landings and roads), leading to greater compaction and soil textural changes.

There was an increase in mean SRR with thinning within closed canopy and ceanothus patches. SRR has also been elevated after thinning in other forests (Gordon et al., 1987; Hendrickson et al., 1989; Messina et al., 1997; Ohashi et al., 1999; Kowalski et al., 2003), possibly due to microclimatic or vegetative changes (including belowground biomass, microbial activity, etc.) brought about by the disturbance (see Ma et al., 2004; Concilio et al., 2005). In closed canopy patches, especially in unburned plots, fresh inputs of logging slash probably increased litter quality, contributing to increased microbial activity. At TEF, open canopy patches generally have little vegetative growth or litter layer (North et al., 2002) and most CO_2 production probably stems from tree roots that spread into the open gaps. SRR may have been reduced due to decreased rates of root respiration in open canopy areas when trees are removed from adjacent closed canopy patches. Disturbance of soil surface and texture by logging machinery could also have been responsible. Other studies have documented an increase in soil compaction with harvesting activities (Gomez et al., 2002; Powers, 2002). This could lead to a decrease in diffusion rates of CO_2 (i.e., decreasing SRR). Open canopy patches may be particularly susceptible to compaction because forest gaps would be the easiest places to execute logging activities.

Although burning was found to decrease SRR 1 year after treatment at TEF (Ma et al., 2004) and at other sites (Weber, 1990; Rhoades et al., 2002; Hubbard et al., 2004; Michelsen et al., 2004), we found no change in SRR after prescribed burning with or without thinning, with the single exception of an increase in SRR in closed canopy patches after the BS treatment. This increase may be due to an increase in root and/or microbial respiration with vegetative regrowth and nutrient inputs (North et al., 2004). We have observed that the nitrogen-fixing ceanothus shrub has begun to dominate areas that were once closed canopy in these plots.

Even without disturbance (in the control plot), SRR was highly variable from year to year, and appeared to correspond with variation in winter precipitation. High snowfall years were followed by increased mean summer SRR. In the Sierra mountains, fluctuations in precipitation can be great from 1 year to the next (North et al., 2005a) and SRR are expected to be correspondingly variable because its major sources – autotrophic and heterotrophic respiration – are regulated by water conditions (Ma et al., 2005). Furthermore, several other studies have shown that ecosystem processes that contribute to changes in soil respiration (i.e., plant phenology and decomposition) are affected by annual differences in precipitation and snow pack (Walker et al., 1995; Wahren et al., 2005; Weatherly et al., 2003). Burning treatments tended to dampen or eliminate (in the case of BS) the amount of interannual variation in SRR, and thinning treatments caused a change in the pattern from the control.

We found that seasonal changes in SRR in 2004 were similar in all patch types and after all treatments, with the exception of the BS treatment in closed canopy and open canopy patches. Seasonal patterns in SRR at TEF are driven by dynamics of temperature and moisture (Ma et al., 2005). The Sierra Nevada mixed-conifer ecosystem is moisture limited, experiencing a summer drought and receiving most precipitation in the form of winter snow (North et al., 2002; Fig. 1A and B). Tree physiological processes and microbial decomposition depend on sufficient soil moisture levels during the growing season (Royce and Barbour, 2001). SRR in Sierran old-growth, mixed conifer forests generally peaks shortly after snowmelt (in May, June and/or July) and decreases as moisture becomes limiting (Ma et al., 2005). The fact that most treated plots showed similar patterns to control indicates that temperature and moisture dynamics probably continue to influence seasonal changes in SRR even after disturbance.

Treatment effects on SRR were most pronounced during June and July, which is the peak of the growing season at TEF. Buchman (2000) also found higher within-site variability in *Picea abies* stands in the summer months during peak SRR, and other studies have shown that SRR response to treatment is more pronounced at certain times of year (Knapp et al., 1998) or during different years depending on interannual climatic variation (Kaye and Hart, 1998). Understanding how treatment effects vary with time of year is important for identifying times of priority for sampling and for determining whether scaling treatment differences up from one time scale to another is appropriate. For example, our results suggested that to adequately capture treatment effects in Sierran mixed conifer forests, SRR should be sampled in the early spring. In addition, SRR differences in June or July should not be extrapolated to annual or seasonal levels as they would exaggerate the effect of the disturbances.

One of the most striking findings of the study was the lack of fluctuation with both season (in 2004) and year in the closed canopy patches of the BS plot. Although the mechanisms behind these changes are difficult to infer without further investigation, it may be that treatment effects outweigh climatic influences. Thinning and burning may homogenize abiotic conditions or produce extreme conditions (with increased canopy openness and decreased litter depth), which could reduce the influence of climatic drivers on SRR. Ma et al. (2005) reported that temporal patterns in SRR were more dynamic in closed canopy and ceanothus patches than in open canopy patches at TEF. Our results also show less variation in open canopy patches; there was no change in SRR by month in open canopy patches of burned–unthinned, unburned–overstory thinned and burned–overstory thinned treatments. The lack of seasonal SRR fluctuation in 2004 in closed canopy patches of the BS treatment may occur because the treatment produced open canopy-like conditions in these patches. These results suggested that severe disturbance could have a great effect on soil biological activity and future research should focus on the mechanistic changes caused by this disturbance and the long-term response of the soil processes.

Since vegetative cover, root biomass, soil chemistry, litter quantity and quality, microclimate, and forest structure can all change with forest management practices (e.g., Ziemer, 1964; Covington, 1981; Chen et al., 1999; Zheng et al., 2000; Carter et al., 2002), we expect that environmental influences driving SRR may also be altered. In this study, the most important explanatory variable of SRR variation shifted from temperature in the pre-treatment year to litter depth in post-treatment years (Table 1).

Litter may become increasingly important in post-disturbance SRR models due to increased patchiness, increased quality, a shift in the ratio of autotrophic to heterotrophic respiration to total SRR, or a combination of these or other factors. It is clear that organic matter is important to soil processes in the TEF ecosystem, where it is patchily distributed and responsible for great differences in moisture and nutrient holding capacity of the forest's young, sandy soils (North et al., 2002). TEFs soils are highly permeable and have a low water holding capacity (North et al., 2002). During the summer drought, the presence of litter allows longer retention of soil moisture, which may contribute to increased tree and microbial respiration. Litter depth influences SRR in undisturbed areas of TEF as well (Ma et al., 2005) but disturbance may have increased its influence on SRR by increasing the spatially heterogeneity of litter depth. Litter depth was greatly reduced in all burning treatments (by 63%, 84%, and 95% from 2000 to 2002 in BN, BC, and BS, respectively), but fire was sometimes patchy (especially in BN) leaving the litter layer untouched in some areas. Alternatively, a change in litter quality could have occurred with disturbance. Increased rates of decomposition due to increased temperature, moisture, and nutrient levels have been found immediately following harvest at other forests (i.e., Covington, 1981). This may have also occurred in thinned plots at TEF, where moisture and temperature were significantly increased 2 years post-disturbance (Concilio et al., 2005). Increased decomposition could result in a shift in the ratio of autotrophic and heterotrophic respiration to total SRR, and explain the change in post-disturbance drivers. It has been found that root and microbial respiration respond to microclimatic drivers differently (Boone et al., 1998) and, therefore, any shift in the ratio of these two major components to total SRR can result in differences in predictive abilities of explanatory variables. Regardless of the cause, this shift in SRR response to environmental influences indicates that even if mean SRR does not change with treatments, the mechanisms driving carbon soil cycling may change. This could result in a difference in carbon efflux over the long term.

5. Conclusions

We measured SRR in an old-growth, mixed-conifer forest for 3 years after burning and thinning treatments and found that response varied with treatment type, patch type, and time-since-disturbance. Thinning alone impacted mean levels of SRR the most; SRR remained increased in the closed canopy patches and decreased in open canopy patches 3 years after treatments. Within the same treatment class (i.e., burning or thinning), more intense levels of disturbance had a greater effect on SRR in closed canopy patches. Closed canopy and open canopy patches showed longer recovery times to thinning treatments than ceanothus shrub. The system appeared to be relatively resistant to changes in mean SRR in the years immediately following burning treatments, with or without thinning. Thus, some of the treatments used in this experiment, which mimic current forest management and restoration techniques, may not cause dramatic changes in terms of soil carbon emission if treatment intensity is controlled. However, relationships of environmental drivers with SRR were changed with treatments. We expect to see continuing changes as vegetative regrowth proceeds with accompanying shifts in microclimate and litter quality and quantity. This study will provide important baseline data for comparison in future years to assess long term changes in SRR after thinning and prescribed burning.

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References

Ahlgren, I.F., Ahlgren, C.E., 1965. Effects of prescribed burning on soil microorganisms in a Minnesota jack pine forest. Ecology 46, 304–310.

Amiro, B.D., 2001. Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. Global Change Biol. 7, 253–268.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Buchman, N., 2000. Biotic factors controlling soil respiration rates in *Picea abies* stands. Soil Biol. Biochem. 32, 1625–1635.

Butnor, J., Johnsen, K., 2004. Calibrating soil respiration measures with a dynamic flux apparatus using artificial soil media of varying porosity. Eur. J. Soil Sci. 55, 639–647.

Carter, M.C., Dean, T.J., Zhou, M., Messina, M.G., Wang, Z., 2002. Short-term changes in soil C, N, and biota following harvesting and regeneration of loblolly pine (*Pinus taeda* L). For. Ecol. Manage. 164, 67–88.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. Variations in local climate can be used to monitor and compare the effects of different management regimes. BioScience 49, 288–297.

Chen, J., Brosofske, K.D., Noormets, A., Crow, T.R., Bresee, M.K., LeMoine, J.M., Euskirchen, E.S., Mather, S.V., Zheng, D., 2004. A working framework for quantifying carbon sequestration in disturbed land mosaics. Environ. Manage. 34, S210–S221.

Concilio, A., Ma, S., Li, Q., LeMoine, J., Chen, J., North, M., Moorhead, D., Jensen, R., 2005. Soil respiration response to prescribed burning and thinning in mixed conifer and hardwood forests. Can. J. For. Res. 35, 1581–1591.

Covington, W.W., 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. Ecology 62, 41–48.

DeLuca, T.H., Zouhar, K.L., 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. For. Ecol. Manage. 138, 263–271.

Fritze, H., Pennanen, T., Pietikäinen, J., 1993. Recovery of soil microbial biomass and activity from prescribed burning. Can. J. For. Res. 23, 1286–1290.

Galen, C., Stanton, M., 1999. Seedling establishment in alpine buttercups under experimental manipulations of growing-season length. Ecology 80, 2033–2044.

Gomez, G.A., Singer, M.J., Powers, R.F., Horwath, W.R., 2002. Soil compaction effects on water status of ponderosa pine assessed through 13C/12C composition. Tree Physiol. 22, 459–467.

Gordon, A.M., Schlenter, R.E., Van Cleve, K., 1987. Seasonal patterns of soil respiration and CO_2 evolution following harvesting in the white spruce forests of interior Alaska. Can. J. For. Res. 17, 304–310.

Hattenschwiler, S., Smith, W., 1999. Seedling occurrence in alpine treeline conifers: a case study from the central Rocky Mountains, USA. Acta Oecol. 20, 219–224.

Healthy Forest Initiative, 2004, http://agriculture.senate.gov/forest/forhxadt-sec.pdf.

Hendrickson, O.Q., Chatarpaul, L., Burgess, D., 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Can. J. For. Res. 19, 725–735.

Hubbard, R., Vose, J., Clinton, B., Elliott, K., Knoepp, J., 2004. Stand restoration burning in oak-pine forests in the southern Appalachians: effects on aboveground biomass and carbon and nitrogen cycling. For. Ecol. Manage. 190, 311–321.

Kaye, J., Hart, S., 1998. Restoration and canopy-type effects on soil respiration in a ponderosa pine–bunchgrass ecosystem. Soil Sci. Soc. Am. J. 62, 1062–1072.

Knapp, A.K., Conard, S.L., Blair, J.M., 1998. Determinants of soil CO_2 flux from a sub-humid grassland: effect of fire and fire history. Ecol. Appl. 8, 760–770.

Kowalski, S., Sartore, M., Burlett, R., Berbigier, P., Loustau, D., 2003. The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. Global Change Biol. 9, 1051–1065.

Litton, C.M., Ryan, M.G., Knight, D.H., Stahl, P.D., 2003. Soil-surface carbon dioxide efflux and microbial biomass in relation to tree density 13 years after a stand replacing fire in a lodgepole pine ecosystem. Global Change Biol. 9, 680–696.

Ma, S., Chen, J., North, M., Erikson, H., Bresee, M., LeMoine, J., 2004. Short-term effects of experimental burning and thinning on soil respiration in an old-growth, mixed conifer forest. Environ. Manage. 33, S148–S159.

Ma, S., Chen, J., Butnor, J.R., North, M., Euskirchen, E.S., Oakley, B., 2005. Biophysical controls on soil respiration in dominant patch types of an old growth mixed conifer forest. For. Sci. 51, 221–232.

Mallows, C.L., 1973. Some comments on C–P. Technometrics 42, 87–94.

Messina, M.G., Schoenholtz, S.H., Lowe, M.W., Ziyin, W., Gunter, D.K., Londo, A.J., 1997. Initial responses of woody vegetation, water quality, and soils to harvesting intensity in a Texas bottomland hardwood ecosystem. For. Ecol. Manage. 90, 201–215.

Michelsen, A., Andersson, M., Jensen, M., Kjoller, A., Gashew, M., 2004. Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems. Soil Biol. Biochem. 36, 1707–1717.

North, M., Oakley, B., Chen, J., Erikson, H., Gray, A., Izzo, A., Johnson, D., Ma, S., Marra, J., Meyer, M., Purcell, K., Rambo, T., Roath, B., Rizzo, T., Schowalter, T., 2002. Vegetation and ecological characteristics of mixed-conifer and red-fir forests at the teakettle experimental forest. UDSA For. Serv. Gen. Tech. Rep. PSW-186. Pacific Southwest Research Station, Albany, CA.

North, M., Chen, J., Oakley, B., Song, B., Rudnicki, M., Gray, A., 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forests. For. Sci. 50, 299–311.

North, M., Hurteau, M., Friegener, R., Barbour, M., 2005a. Influence of fire and El Nino on tree recruitment varies by species in Sierran mixed conifer. For. Sci. 51, 187–197.

North, M., Oakley, B., Fiegener, R., Gray, A., Barbour, M., 2005b. Influence of light and soil moisture on Sierran mixed-conifer understory communities. Plant Ecol. 177, 13–24.

Ohashi, M., Gyokusen, K., Saito, A., 1999. Measurement of carbon dioxide evolution from a Japanese cedar (*Cryptomeria japonica* D Don) forest floor using an open-flow chamber method. For. Ecol. Manage. 123, 105–114.

Pietikäinen, J., Fritze, H., 1993. Microbial biomass and activity in the humus layer following burning: short-term effects of two different fires. Can. J. For. Res. 23, 1275–1285.

Pietikäinen, J., Hiukka, R., Fritze, H., 2000. Does short-term heating of forest humus change its properties as a substrate for microbes? Soil Biol Biochem. 32, 277–288.

Powers, R.F., 2002. Effects of soil disturbance on fundamental, sustainable productivity of managed forests. In: Verner, J. (comp.). The Kings River Sustainable Ecosystem, Project, USDA Forest Serv. Gen. Tech. Rep. PSW-GTR-183. Pacific Southwest Research Station, Albany, CA, pp. 63–82.

Rhoades, C., Barnes, T., Washburn, B., 2002. Prescribed fire and herbicide effects on soil processes during barrens restoration. Restor. Ecol. 10, 656–664.

Royce, E., Barbour, M., 2001. Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone. Am. J. Bot. 88, 919–932.

Schlesinger, W.H., 1995. Soil respiration and changes in soil carbon stocks. In: Woodwell, G.M., Mackenzie, F.T. (Eds.), Biotic Feedbacks from the Warming of the Earth. Oxford University Press, Inc., pp. 159–168.

Scott, N.A., Rodrigues, C.A., Hughes, H., Lee, J.T., Davidson, E.A., Dail, D.B., Malerba, P., Hollinger, D.Y., 2004. Changes in carbon storage and net carbon exchange one year after an initial shelterwood harvest at Howland Forest, ME. Environ. Manage. 33, S9–S22.

Sierra Nevada Forest Plan Amendment, 2004. Sierra Nevada Forest Plan Admendment: Final Environmental Impact Statement, vols. 1–6. USDA Forest Service, Pacific Southwest Region, Vallejo, CA.

Singh, J.S., Gupta, S.R., 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43, 449–528.

Tang, J., Qi, Y., Xu, M., Mission, L., Goldstein, A.H., 2005. Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada. Tree Physiol. 25, 57–66.

USDA Forest Service, 2003. America's Forests: 2003 Health Update, http://www.fs.fed.us/publications/documents/forest-health-update2003.pdf.

Verner, J., McKelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould, Jr., G.I., Beck, T.W., 1992. The California spotted owl: a technical assessment of its current status. USDA Forest Service General Technical Report No. PSW 133, vi. Pacific Southwest Research Station, USDA For. Serv. Berkeley, CA.

Wahren, C., Walker, M., Bret-Harte, M., 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Global Change Biol. 11, 537–552.

Walker, M.D., Ingersoll, R.C., Webber, P.J., 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. Ecology 76, 1067–1083.

Weatherly, H., Zitzer, S., Coleman, J., Arnone, J., 2003. In situ litter decomposition and litter quality in a Mojave Desert ecosystem: effects of elevated atmospheric CO_2 and interannual climate variability. Global Change Biol. 9, 1223–1233.

Weber, M.G., 1985. Forest soil respiration in eastern Ontario jack pine ecosystems. Can. J. For. Res. 15, 1069–1073.

Weber, M.G., 1990. Forest soil respiration after cutting and burning in immature aspen ecosystems. For. Ecol. Manage. 31, 1–14.

Zheng, D., Chen, J., Song, B., Xu, M., Sneed, P., Jensen, R., 2000. Effects of silvicultural treatments on summer forest microclimate in southeastern Missouri Ozarks. Climate Res. 15, 45–59.

Ziemer, R.R., 1964. Summer evapotranspiration trends as related to time after logging of forests in Sierra Nevada. J. Geophys. Res. 69, 615–620.