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The role of environmental factors and tree injuries in soil carbon respiration response to fire and fuels treatments in pine plantations

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Abstract The need to understand how forest management practices affect soil CO_2 exchange with the atmosphere (soil respiration) has increased with the recognition of a likely feedback effect of climate warming on soil respiration rates. Previous research addressing the mechanisms driving soil respiration has yielded inconsistent and/or conflicting results. This study looked to alternative above-ground forest characteristics to help explain spatial variability in soil respiration in a 30-year-old Sierra Nevada pine plantation. Fire hazard mitigation is one of the predominant management goals in these and other western US forests. Therefore, this analysis examined how fuels treatments, including shredding of understory vegetation (mastication), prescribed fire, and a combination thereof, affected soil respiration and its relationship to environmental factors and post-fire tree injuries. Multiple regression models indicated that mastication had no significant impact on soil respiration, but the roles of soil temperature and forest floor depth (O horizons) in the models increased after the treatment. Burning reduced soil respiration by $\sim$14%, and increased its sensitivity to tree proximity and the exposure of bare mineral soil. Scorch height in burned stands was negatively correlated with soil respiration. Models incorporating only tree injury or tree proximity parameters explained between 63% and 91% of the variability in burned plantations. This work suggests that measures of above-ground forest features can increase understanding of management impacts on soil respiration, and the mechanisms by which these impacts occur. These results are especially applicable in Mediterranean climates, where moisture stress reduces the effectiveness of soil microclimate in explaining soil respiration.

Keywords Soil CO_2 efflux · Prescribed burning · Thinning · Soil moisture · Scorch height

Introduction

Forests are heralded for their sequestration of carbon, and constitute one of world's major terrestrial carbon pools (Tans et al. 1990). The role of intensively managed forests, such as plantations, in global carbon storage was specifically identified in the 1997 Kyoto Protocol on climate change (Murray et al. 2000). The majority of forest carbon is sequestered in their soils, making soil CO_2 evolution to the atmosphere, or soil respiration, one of the major pathways of global carbon flux (Houghton and Woodwell 1989). As soil respiration is positively correlated with mean annual

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temperatures, it is likely that increased respiration rates would result in a positive feedback effect on global climate warming (Jenkinson et al. 1991; Raich and Schlesinger 1992). This has significantly increased concerns throughout the scientific community over how anthropogenic activities impact soil respiration patterns.

The rate at which soil CO_2 is emanated from the soil surface is influenced by both environmental and biological factors. Soil CO_2 efflux is a product of autotrophic (root) and heterotrophic (soil micro- and macro-organisms) respiration sources, which are influenced by the interaction of climate, forest floor attributes, vegetation characteristics, and soil physical and chemical properties. Forest management practices, which throughout the American West are increasingly aimed at fire hazard and fuels reduction, can change the magnitude and/or direction of the drivers of soil carbon respiration. Fire hazard mitigation treatments typically involve a combination of silvicultural and prescribed burning techniques (Stephens and Moghaddas 2005). Depending on the methods and their implementation, treatments can impact both biophysical components and processes and thus influence the loss of soil CO_2 from the soil to the atmosphere (Ma et al. 2004; Concilio et al. 2005). The most commonly employed fuels reduction strategies include thinning, prescribed burning, and combinations thereof, which have each been linked to increases, decreases, and no changes in soil respiration rates in the few studies addressing this topic (Kaye and Hart 1998; Ma et al. 2004; Concilio et al. 2005; Tang et al. 2005). Large-scale implementation of fuels reduction strategies could thereby have significant impacts on ecosystem carbon flux and implications for global climate change.

Although numerous studies have employed upper profile measures of soil moisture and soil temperature as the predominant drivers of both temporal and spatial patterns of soil respiration (Singh and Gupta 1977; Weber 1990; Tang et al. 2005), these microclimate indicators have been less successful in seasonally moisture-stressed ecosystems such as the Sierra Nevada of California (Xu and Qi 2001; Concilio et al. 2005), and in burned forests (O'Neill et al. 2002; Concilio et al. 2005). There is also the confounding factor of differential response of heterotrophic and autotrophic respiration sources to changes in soil temperature, leading researchers to question the assumption of a universal role for soil temperature (Rey et al. 2002; Bhupinderpal-Singh et al. 2003). In many cases, soil physical and chemical properties are not significantly impacted by fuels management practices (Johnson and Curtis 2001). Understanding how forest management affects soil carbon efflux should therefore explore a range of biotic and abiotic forest components to help explain treatment effects. Such an analysis can also be used to identify differential sensitivity of soil respiration to biophysical controls.

Soil's inherently high spatial variability has confounded interpretation of the mechanisms responsible for spatial variability in forest soil respiration rates (Kaye and Hart 1998; Xu and Qi 2001; Tang et al. 2005). Standard errors typically exceed 10% of the mean soil respiration value (Raich and Schlesinger 1992). In two Sierra Nevada studies, microclimate (soil temperature and soil water) proved less than or equally important to biological (i.e., vegetation cover) or physical (i.e., litter depth) factors in explaining spatial variability of soil respiration (Xu and Qi 2001; Concilio et al. 2005). In this study, the relative importance of forest floor components, vegetation, microclimate, and treatment effects on these variables in explaining soil respiration were explored. The analysis took place in a managed ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws)/Jeffrey pine (*Pinus jeffreyi*, Grev. & Balf.) plantation in the central Sierra Nevada of California. The goals were to examine (1) if forest floor characteristics, vegetation type coverage, and microclimate were linked to spatial variability in soil respiration, (2) how fuels treatments influenced these relationships, and (3) how fire-induced tree injuries and forest floor consumption related to soil respiration rates.

Methods

Site description

In the Groveland Ranger District of the Stanislaus National Forest in the central Sierra Nevada, over 1,820 ha of ponderosa and Jeffrey pine plantation forest were planted to replace second-growth mixed onifer stands destroyed during the 1973 Granite Fire. Since the plantations have developed fire-hazardous structures and fuel load build-up over the last 25–30 years, fuels reduction treatments were prescribed for the Granite plantations. The treatments were aimed at reducing potential fire behavior and competition between trees and understory vegetation, and increasing forest health and resistance to disturbance. The project area was deemed a Demonstration Site by the US Department of the Interior/Department of Agriculture Joint Fire Science Program, because plantations are common throughout the nation as the most effective means of reforestation after fire or harvest.

The plantation units sampled in this study were all located within 10 km west of Cherry Lake (37° 58′ 33″, 119° 54′ 47″), in the Stanislaus National Forest of CA within the central Sierra Nevada mountain range, and included two control units, one Burn only unit, and two Mastication + Burn units. Logistical challenges limited prescribed burning opportunities, and prevented the replication of the Burn treatment. The units were chosen at random from structurally similar plantation stands stratified by the particular fuels reduction treatment assigned to them (Table 1). All units faced south or south to southeast, with gentle slopes ranging from 3% to 15%. Elevations ranged from 1,500 to 1,800 m. While the area sampled within each unit was the same (400 m^2), total unit sizes ranged from 14 to 82 ha.

Tree species found in the plantation units included Jeffrey pine, sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* Gord. & Glend), incense-cedar (*Calocedrus decurrens* [Torr.] Floren.), and infrequent giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh). Ponderosa and Jeffrey pine comprised more than 90% of the pre-treatment and over 95% of the post-mastication tree composition in all units. The understory was largely composed of whitethorn (*Ceanothus cordulatus* Kellogg), and greenleaf manzanita (*Arctostaphylos patula* E. Greene), with less abundant species including gayophytum (*Gayophytum diffusum* Torrey & A. Gray), Sierra current (*Ribes nevadense* Kellog.), Sierra gooseberry (*Ribes roezlii* Regel.) and bracken fern (*Pteridium aquilinum* (L.) Kuhn).

The Granite plantations are influenced by a Mediterranean climate where summer drought conditions are common. Average summer and winter temperatures are 21°C and 4°C (based on 50 years of data; WRCC 2005). Total annual precipitation averages ~120 cm, largely comprised of snowfall (~80%), which can at times linger through June. The soil respiration sampling period for this study extended from June of 2003 to November of 2005. Excepting the unusual amount of precipitation in late October of 2004 (33 cm versus a 50 years average of 6.5 cm), total precipitation before and during the sampling period was similar between the 3 years. Soils are Incepticols in the Pachic Xerumbrepts class, developed from either metasedimentary or granitic rock, and belong to the Fiddletown series (USDA 1981). They are

Table 1 Forest characteristics during each treatment stage (year) in five Stanislaus National Forest plantation units, CA

Unit number	Treatment type	Trees/ha	BA (m^2/ha)	Avg. DBH (cm)	Avg. height (m)	Avg. Ht. to LC (m)	Canopy cover (%)
185	None	363	25.67	27.75	11.96	2.00	57.14
	Mastication	272	28.95	35.54	14.84	3.25	71.43
	Burn	272	29.78	37.26	15.41	5.28	66.00
106	None	363	22.37	26.74	12.03	2.58	35.71
	Mastication	222	20.61	33.97	14.82	3.73	39.30
	Burn	222	22.29	35.34	14.80	7.45	39.30
132	None	368	28.54	30.84	14.47	3.86	53.57
	Burn	368	28.54	35.02	17.31	9.30	54.10
184	Control	236	12.25	24.68	9.93	1.51	14.29
150	Control	550	26.63	23.17	11.34	3.73	75.00

DBH is diameter at 1.4 m height, Ht. to LC is height to live crown, BA is basal area, PIPO is ponderosa pine, PIJE is Jeffery pine moderately deep to deep (50–100 cm) with a gravelly sandy loam texture in the upper horizons and pH ranging from 5.6 to 6.6 (USDA 1981). Soils are generally dry from July to October (USDA 1981).

Mastication and burning treatments

Mastication in the Mastication + Burn units was completed by mid-June of 2004, and all soil respiration sampling began in early July. Small trees (≤23 cm in diameter) and understory vegetation were mechanically shredded and all resulting materials were distributed and left on site, resulting in a 5 m × 5 m spacing of residual conifers. Density was decreased from 363 to 272 trees/ha in one unit and from 363 to 222 trees/ha in the other unit, and resulting average basal areas were not significantly different between the two units. Understory herbaceous and shrub vegetation was also masticated, along with diseased and suppressed trees. Prescribed burning was conducted in the masticated and Burn units on June 28, 2005 between 10:00 AM and 11:00 PM using a combination of backing and strip-head firing techniques (Martin and Dell 1978). Nearly 2 cm of rain fell on June 17th, which enabled prescribed burning during what would typically be within the summer drought season. Desired environmental parameters for the burns included: relative humidity between 25% and 65%; wind speed below 8 km/h; temperature between 0 and 24°C; and 10 h fuel moisture between 7% and 15% throughout the day.

Soil respiration, temperature, and moisture measurements

Due to logistical constraints and access limitations during the winter, early spring, and late fall seasons, all five units were consistently measured July and late October of 2003–2005. Typically once each month, soil carbon respiration rates (SRR) in each unit were measured from early morning to evening in order to capture diurnal fluctuations. In 2004, measurements were taken during the last and first weeks of September and October, respectively.

The Li-Cor 6400-09 soil chamber coupled with a Li-Cor 6400 photosynthesis system (Li-Cor, Lincoln, NE) was used to measure CO_2 emissions. In each of the five units, nine soil CO_2 efflux sampling points were established and their locations permanently marked to ensure that the location was identical following the treatments ($N = 45$ total). The sampling points were spaced 10 m apart on a 3 × 3 matrix with a randomized starting point. At each point, a 4.4 cm tall soil collar with a diameter of 11 cm was inserted ~1 cm into the soil. As no alterations to the vegetation, litter, or soil within the soil collar were made, site disturbance was limited. Percent soil moisture (M_s) on a dry weight basis was assessed by extracting soil cores adjacent to the soil collars, then oven-drying the samples for 48 h at 105°C. Using a temperature probe connected to the Li-Cor photosynthesis unit, soil temperature was measured at 10 cm depths within 10 cm of each sampling point. These depths have been shown to provide soil temperatures that are closely related to variation in

Table 2 Mean (±standard error) soil respiration rate (SRR), soil temperatue (T_s), and soil moisture (M_s) for each year and three different fuels reduction treatments in the Stanislaus National Forest pine plantations, CA

Year	Treatment type	SRR (μmol m^{-2} s^{-1})	T_s (°C)	M_s (%)
2003 (pre-treatment)	Control	3.46 (0.35)	18.94 (0.26)	10.91 (0.52)
	Mastication + Burn	4.54 (0.54)	16.69 (0.21)	12.00 (0.37)
	Burn	4.55 (0.44)	18.83 (0.31)	8.30 (0.56)
2004 (post-mastication)	Control	2.37 (0.22)	13.40 (1.99)	10.89 (1.72)
	Mastication + Burn	3.42 (0.45)	12.79 (0.25)	9.78 (0.42)
	Burn	3.41 (0.56)	13.77 (0.36)	8.24 (0.29)
2005 (post-burning)	Control	3.25 (0.32)	14.09 (0.22)	11.47 (0.81)
	Mastication + Burn	2.68 (0.41)	12.26 (0.22)	15.10 (0.79)
	Burn	3.83 (0.58)	14.94 (0.30)	8.46 (0.36)

soil carbon respiration rates (Xu and Qi 2001). Concurrently with SRR measures every hour, soil temperatures (T_s) were recorded and a daily measure of soil moisture was conducted. Average sampling season values are shown for each treatment type in Table 2.

Plot variables and tree injuries

The percent coverage of shrub, herbaceous and grassy species, and tree boles were based on ocular estimates made for a 1-m plot surrounding each soil plot (diameter = 1.13 m). Also in these plots, litter, bare mineral soil, and rock cover were estimated. Average litter (O_i horizon) and duff (O_a and O_e horizons) depths were measured at five random locations within a few cm of the soil collars so as to avoid disturbance inside the collar itself. These measures were taken each year.

After burning, the percent of the 1-m plot burned was estimated, based on residual evidence of incomplete combustion such as ash and charred litter or downed woody debris. Cover in the 1-m plots following the burns was measured within a month of the fire, then re-measured at the end of the summer season to document any significant changes.

Post-fire tree injuries for the three trees closest to each soil plot were measured within 2 months of the burning to ensure that the difference between foliage consumption and seasonal needle cast did not confound results. Assessments of mortality could not be accurately made within the 3 months following the burn before the sampling season ended. Rather than measuring the percent of crown length scorched, the percent of crown volume scorched was visually estimated. This has been shown to be a more accurate measure of fire damage than scorch height alone (Peterson 1985) and has been linked to tree mortality in numerous models (Ryan et al. 1988; Saveland and Neuenschwander 1990; Stephens and Finney 2002). For each tree, the percent crown volume scorched (PCVS, including bud and foliage killed but not consumed), and the maximum and opposite-maximum crown scorch heights were documented. Total crown damage (TCD) was calculated as PCVS plus the percent of crown volume consumed (McHugh and Kolb 2003).

In addition to tree diameter and distance from the soil plots, direct measures of stem damage were taken, including bole char heights, percent of bole circumference charred, percent of char below DBH (1.37 m from the ground), and bole char severity ratings (CSR). Bole char severity was rated at maximum char height, below 30.5 cm on the side of maximum char, at the side opposite the maximum bole char height, and below 30.5 cm on the side opposite where maximum bole char occurred. Bole char severity was defined as 1 = bark is black but not consumed, fissures not blackened, 2 = entire bark and fissures blackened, but not consumed, and 3 = entire bark and fissures blackened, with significant consumption of bark evident (Ganz et al. 2003). Bark beetles (*Dendroctonous valens* (LeConte)) in the burned units were detected within days of the fire, although beetles had not yet established colonies. Profuse resin exudates were identified on some trees, and were also recorded. Bark beetle attacks were documented when observed.

Data analysis

For all analyses, SRR, T_s, and M_s values were averaged over the four sampling months per year in each unit, resulting in 45 values per year total (18 Control, 18 Mastication + Burn, and 9 Burn Only plots). The parameters explored in relation to treatment effects and SRR patterns, including microclimate, forest floor, and vegetation measures will hereafter be referred to as ''plot variables'', as described in Table 3.

Analysis of covariance (ANCOVA) was used to determine whether changes in environmental, vegetation, and forest floor variables following treatments were significant in relation to those documented in the control plots due to inter-annual differences in precipitation and air temperature. For each pair of years compared, representing the effects of mastication and fire in untreated units (2003–2005), of mastication in masticated units (2003–2004), and of burning in untreated and masticated units (2004–2005), the previous year's data was used as a covariate along with treatment type.

Initial correlation analysis was used to explore which plot variables were significantly ($P < 0.05$) related to log-transformed soil respiration rates for each treatment stage (pretreatment, post-mastication, and post-burning). Plot variables that were correlated with SRR for any of the years were further

Table 3 Parameters measured for each soil plot for use in multiple regression analysis of each variable's influence on soil respiration rates following mastication, burning and mastication plus burning in Stanislaus National Forest pine plantations, CA

Parameter category	Plot variable	Abbreviation	Measured	Measurement location
Microclimate	Soil moisture	M_s (%)	Daily	5–15 cm from soil plot
	Soil temperature	T_s (°C)	Hourly	5 cm from soil plot
Forest floor	Bare mineral soil	BS (%)	Seasonally	1-m plot
	Duff depth	DD (cm)	Seasonally	Soil plot
	Litter cover	LC (%)	Seasonally	1-m plot around soil plot
	Litter depth	LD (cm)	Seasonally	Soil plot
	Rock cover	RC (%)	Seasonally	1-m plot
Vegetation coverage	Herbaceous/grass spp.	HC (%)	Seasonally	1-m plot
	Shrub spp.	SC (%)	Seasonally	1-m plot
	Tree cover	TC (%)	Seasonally	1-m plot
Tree measures	Closest trees	CT (m)	Seasonally	Avg. dist. three closest trees
	Diameter of closest trees (Avg.)	DBH CT (cm)	Seasonally	Avg. dist. three closest trees

investigated for their predictive capacity using stepwise multiple linear regression analysis.

Multiple regression analysis was used to explore the influence of plot variables on SRR response to mastication, burning, and the combination thereof. All model coefficients were optimized using the least-squares technique, and significance probabilities for the whole-model *F*-ratio were <0.05. To avoid multi-collinearity, plots variables with correlations >0.80 were not used in the same model. For each resulting model, the residual plots were checked for homoscedasticity.

In order to further analyze the effects of the treatments, while simultaneously taking into account the influence of independent variables, multivariate models were developed incorporating both continuous and categorical variables (e.g., Tang et al. 2005). Categorical indicator variables (''dummy'' variables; 0 or 1) were assigned to each treatment and to each year. For example, to test whether mastication influenced SRR, all measurements in Mastication + Burn plots were given the indicator ''MA = 1'', while all non-masticated plots were assigned ''MA = 0''. Categorical terms were linked with the continuous independent variables using interaction terms for each possible combination of treatment type and independent variable to assess the influence of treatments on the relationship between SRR and independent variables.

The following general model form was explored for each treatment type and year as well as including the treatments as categorical indicators (all variables are defined in Table 3):

$$\mathrm{Ln\,SRR} = f(T_s M_s \mathrm{BS\,CT\,HC\,RC\,LC\,SC\,LD}) \quad (1)$$

First, all plot variables and interaction terms were included in the multivariate linear regression model. Then, a backward elimination procedure was used to identify significant predictor variables for log-transformed SRR based on *t*- and *F*-tests ($\alpha = 0.05$). After significant variables were thus identified, models were finalized by estimating the coefficients for each retained variable using the least-squares estimation technique.

Log-transformed soil respiration rates following prescribed burning (in 2005 only) were also regressed against tree injury and plot litter and duff consumption variables. The multiple linear regression methodology was identical to that used to analyze treatment effects and the influence of plot variables as described above. All tree injury measures were weighted by the distances between the trees and soil plots, based on the assumption that closer trees would have a greater influence on SRR. Burn units and Mastication + Burn units were modeled both separately and pooled.

Results

Environmental, vegetation, and forest floor characteristics

Mastication increased litter and duff depths in soil plots, and although mastication reduced shrub and

Table 4 Analysis of covariance (ANCOVA) of treatment effects on mean plot variables (SE) and analysis of variance (ANOVA) of treatment type differences between means in Control, Mastication + Burn, and Burn treatments in pine plantations of the Stanislaus National Forest, CA

Plot variable[a]		Treatment type	Values of plot variables: Pre-treatment 2003	Post-mastication 2004	Post-burn 2005	Burn, and mastication + burn effects (2003–2005)	Mastication effect (2003–2004)	Burn effect (2004–2005)
Microclimate	T_s (°C)	Control	18.94 (0.26) a	13.40 (1.99) a	14.09 (0.22) a	a	a	a
		Mastication + Burn	16.69 (0.21) b	12.79 (0.25) a	12.26 (0.22) b	a	b	b
		Burn	18.83 (0.31) a	13.77 (0.36) a	14.94 (0.30) a	b	n/a	a
	M_s (%)	Control	10.91 (0.52) a	10.89 (1.72) a	11.47 (0.81) a	a	a	a
		Mastication + Burn	12.00 (0.37) a	9.78 (0.42) ab	15.10 (0.79) b	b	a	b
		Burn	8.30 (0.56) b	8.24 (0.29) b	8.46 (0.36) c	ab	n/a	a
Forest floor	BS (%)	Control	4.17 (2.27) ab	5.61 (2.09) a	9.78 (3.20) a	a	a	a
		Mastication + Burn	0.78 (0.38) a	2.28 (1.12) a	2.28 (3.20) a	a	a	a
		Burn	17.89 (10.12) b	9.56 (5.00) a	10.89 (7.26) a	a	n/a	a
	DD (cm)	Control	1.08 (0.64) a	1.97 (0.42) a	1.71 (0.47) a	a	a	a
		Mastication + Burn	0.82 (0.15) a	2.37 (0.54) a	0.25 (0.10) b	b	b	b
		Burn	1.69 (0.64) a	2.94 (0.91) a	1.63 (0.72) a	ab	n/a	ab
	LD (cm)	Control	1.48 (0.33) ab	2.75 (0.38) a	2.11 (0.40) a	a	a	a
		Mastication + Burn	1.06 (0.19) a	4.41 (0.66) b	1.16 (0.28) b	a	b	b
		Burn	2.82 (1.06) b	3.39 (0.46) ab	0.39 (0.10) b	b	n/a	c
	LC (%)	Control	67.0 (7.87) a	66.50 (8.09) a	68.9 (7.80) a	a	a	a
		Mastication + Burn	63.7 (4.50) a	67.39 (5.88) a	87.10 (5.11) a	b	a	ab
		Burn	65.9 (10.40) a	76.83 (5.08) a	82.67 (7.63) a	ab	n/a	b
	RC (%)	Control	0.78 (0.55) a	1.50 (1.12) a	1.61 (1.12) a	a	a	a
		Mastication + Burn	0.00 (0) a	0.00 (0) a	0.11 (0.11) a	a	a	ab
		Burn	0.33 (0.24) a	1.56 (1.32) a	3.67 (2.70) a	a	n/a	b
Vegetation coverage	HC (%)	Control	20.56 (5.28) a	15.28 (4.34) a	7.94 (3.39) a	a	a	a
		Mastication + Burn	18.83 (5.24) a	17.94 (4.95) a	8.89 (3.93) a	a	a	a
		Burn	9.44 (5.51) a	6.83 (3.98) a	0.00 (0) a	a	n/a	a
	SC (%)	Control	7.22 (4.84) a	10.67 (5.13) a	10.17 (5.16) a	a	a	a
		Mastication + Burn	13.4 (4.41) a	10.67 (5.32) a	0 b	b	a	b
		Burn	3.67 (2.15) a	3.0 (2.20) a	0 ab	ab	n/a	ab
	TC (%)	Control	0.28 (0.16) a	0.44 (0.22) a	0.50 (0.29) a	a	a	a
		Mastication + Burn	3.28 (1.77) a	1.72 (1.21) a	1.11 (1.11) a	a	a	a
		Burn	2.8 (2.78) a	2.22 (2.22) a	2.78 (2.78) a	a	n/a	a
Tree measures	CT (m)	Control	4.30 (0.79) a	4.30 (0.78) a	4.30 (0.78) a	a	a	a
		Mastication + Burn	3.08 (0.24) a	3.58 (0.21) a	3.58 (0.21) a	a	a	a
		Burn	3.83 (0.45) a	3.39 (0.21) a	3.39 (0.21) a	a	n/a	a

Note: Different lower case letters following values for each variable within columns denote significant differences identified using the Tukey HSD test $\alpha\beta = 0.05$

[a] Abbreviations in Table 3

herbaceous cover in general throughout the units, the impact within the 1 m inventory plots surrounding the soil plots was not detectable when compared with year-to-year changes in the controls (Table 4). The decrease by nearly half of herbaceous cover in controls between 2004 and 2005 was most likely a result of increased grazing pressure in these stands, corroborated by the increase in shrub cover (generally unpalatable) over the 3 years (Table 4). The impact of grazing on the controls is further evidenced by increases in bare mineral soil exposure over the 3 years.

In relation to 2004 values, prescribed fire resulted in a significant decrease in litter and duff depths in the Mastication + Burn unit, a statistical increase in litter cover, and a reduction of litter depth in the Burn unit when compared with the controls (Table 4). The percent of the 1-m plot occupied by litter increased in Mastication + Burn units between 2003 and 2005, while shrub coverage decreased (Table 4). Burning eliminated shrub cover from the 1-m plots in both Burn and Mastication + Burn units, and increased exposure of rocks in the Burn unit.

Log-transformed SRR was significantly correlated with plot variables in each year of sampling. Pre-treatment and 2004 SRR was lower where rock and herbaceous species coverage was higher, and was higher where trees were closer to the soil plots (Table 5). In both 2004 and 2005, deeper litter layers correlated with higher SRR, while greater exposed mineral soil correlated with higher soil temperatures in all 3 years (Table 5). Exposed bare mineral soil was also associated with lower soil moistures in 2003 and 2005; in 2004 plots with deeper litter depths had higher soil moistures. Soil moisture and soil temperature were inversely correlated in all units over all years of sampling, with the strongest relationship in 2005 following burning (Fig. 1). There were no significant relationships between soil Carbon, Nitrogen, and SRR in any unit.

Influence of treatments and plot variables on SRR

Overall, regression analysis indicated that the treatments and the soil plot variables could not explain more than 30% of the variability in SRR. Mastication did not play a significant role in patterns of SRR, as indicated by the lack of significance of the categorical variable in the multiple regression analysis. This result represents no detectable impact of the treatment on SRR in the Granite pine plantations.

Mastication followed by burning ($M + B = 1$) was a significant factor in the multiple regression model along with other predictor variables, but the whole model did not account for more than 30% of the variation in SRR. The negative coefficient associated with the treatment indicator implies that, if all other variables were held constant, soil respiration was 11% lower in masticated and burned plots than in untreated and control units (Table 6). The significance of plot variable-treatment interaction factors suggests that the sensitivity of SRR to litter depth was significantly increased in masticated then burned units (Table 6).

The burn only treatment effect ($Burn = 1$) was also significant when combined with other variables in the multiple regression model:

$$\begin{aligned} \text{Ln}\,(\text{SRR}) &= \beta_0 + \beta_1 T_s + \beta_2 \text{HC} \\ &\quad + \beta_3 \text{RC} + \beta_4 \text{LD} + \beta_5 \text{Burn} \\ &(R^2 = 0.29, F = 10.4, P < 0.0001) \end{aligned} \tag{2}$$

where $\beta_0 = 0.13$, $\beta_1 = 0.07$, $\beta_2 = -0.01$, $\beta_3 = -0.04$, $\beta_4 = 0.08$, and $\beta_5 = -0.16$. Here, interaction factors were not statistically significant, indicating that burning alone did not impact the relationship between soil respiration and the other predictor variables. According to the β_5 coefficient, if all other factors were held constant, burning without pre-burn mastication resulted in the 16% decrease in soil respiration.

The best-fitting model for SRR depicting the treatment effect of prescribed burning in both Mastication + Burn and Burn only units incorporated numerous plot variables, along with interaction effects linking burning with the average distance to the closest trees and the percent of ground occupied by bare mineral soil in the 1-m plot area (Table 7). According to the coefficients estimated in the regression analysis, burning in both treatment types resulted in a reduction of SRR by around 14%. Soil plots distanced further from tree stems and with a greater percentage of the 1-m plot occupied by rocks had lower SRR, while greater bare mineral soil and tree coverage in 1-m plots correlated with higher soil respiration rates (Table 7). The interaction term suggests that SRR sensitivity to tree proximity was lessened by the burning treatment.

Table 5 Pearson's product-moment correlations between plot variables[a] and log-transformed soil respiration in five pine plantation stands in the Stanislaus National Forest, CA

Year	Variable 1	Variable 2	Correlation	Signif. *P*
2003	Ln SRR	RC (%)	−0.29	0.05
	Ln SRR	HC (%)	−0.27	0.08
	Ln SRR	TC (%)	0.25	0.10
	Ln SRR	CT (m)	−0.33	0.03
	M_s (%)	T_s (°C)	−0.48	0.00
	BS (%)	T_s (°C)	0.34	0.02
	TC (%)	T_s (°C)	−0.31	0.04
	LC (%)	M_s (%)	0.28	0.06
	BS (%)	M_s (%)	−0.34	0.02
2004	Ln SRR	CT (m)	−0.33	0.03
	Ln SRR	DD (cm)	0.27	0.07
	Ln SRR	HC (%)	−0.43	<0.01
	Ln SRR	LC (%)	0.33	0.02
	Ln SRR	LD (cm)	0.40	0.01
	Ln SRR	RC (%)	−0.29	0.06
	M_s (%)	T_s (°C)	−0.50	<0.01
	BS (%)	T_s (°C)	0.59	<0.01
	LC (%)	T_s (°C)	−0.57	<0.01
	CT (m)	T_s (°C)	0.56	<0.01
	HC (%)	T_s (°C)	0.35	0.02
	LD (cm)	T_s (°C)	−0.52	<0.01
	DD (cm)	T_s (°C)	−0.45	<0.01
	LD (cm)	M_s (%)	0.27	0.08
	RC (%)	M_s (%)	−0.32	0.03
2005	Ln SRR	LD (cm)	0.31	0.04
	Ln SRR	M_s (%)	−0.32	0.03
	Ln SRR	T_s (°C)	0.39	0.01
	M_s (%)	T_s (°C)	−0.67	<0.01
	BS (%)	T_s (°C)	0.51	<0.01
	LC (%)	T_s (°C)	−0.41	0.01
	RC (%)	T_s (°C)	0.26	0.09
Area burned (%1-m plot)		T_s (°C)	−0.25	0.10
	BS (%)	M_s (%)	−0.27	0.07
	RC (%)	M_s (%)	−0.35	0.02

[a] Abbreviations as in Table 3

Given the generally weak relationships depicted by the regression models using categorical identifiers, a second approach was added. In controls, the Burn unit, and the Mastication + Burn units, separate analyses were conducted for each year, so that significant predictor variables correlated with SRR could be identified between both years and treatment types. Overall, model goodness of fit was better when each treatment type was analyzed separately (Table 8). Microclimate, vegetation coverage, forest floor features, and tree proximity were all significant in the best-fitting models for Burn and Mastication + Burn units, while vegetation coverage did not play a role in control units SRR. Statistically significant variables differed between each year within each treatment type, and, except in the Burn

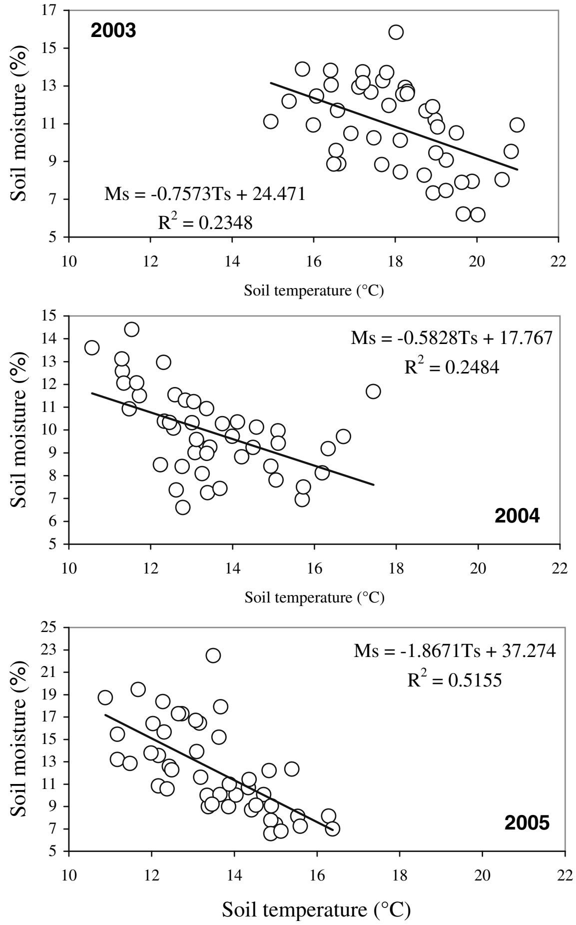

Fig. 1 Linear regression relationships bewteen soil temperature (T_s) and soil moisture (M_s) in all plantation forest units during 2003, 2004, and 2005 sampling seasons

Table 6 Variables with corresponding coefficients and significance of contribution to multiple regression model of log-transformed soil respiration response to mastication followed by prescribed fire (M + B) in two pine plantation stands, Stanislaus National Forest, CA

Parameter[a]	Estimate	Std Error	*t*-ratio	$P > \|t\|$
Intercept	1.675	0.205	8.17	<.0001
M_s (%)	−0.032	0.014	−2.31	0.022
RC (%)	−0.042	0.011	−3.99	0.000
CT (m)	−0.079	0.018	−4.49	<.0001
LD (cm)	0.041	0.018	2.24	0.027
M + B Indicator	−0.108	0.043	−2.51	0.013
M + B Indicator × LD (cm)	0.044	0.018	2.38	0.019

Model $R^2 = 0.30$, $F = 9.15$, $P < 0.0001$

[a] Abbreviations as in Table 3

unit, did not explain more than 62% of the variation in SRR. Model fit was much higher in the Burn unit, with R^2 values ranging from 0.73 for all years combined to over 0.95 for the years separately (Table 8).

Additional variables describing fire-induced injuries sustained by the closest trees to each soil plot were also tested for their influence on SRR trends in burned units in 2005. Overall, the prescribed fire was more severe in the Burn only unit, as indicated by higher mean crown damage (scorch + foliage consumption), basal char, and scorch heights (Table 9). Common to both burned Mastication + Burn and Burn only regression models was a positive relationship between soil respiration rates and total crown damage (Tables 10 and 11). The extent of the 1-m plots burned had a significant but small positive effect on SRR in Mastication + Burn units, and a larger and negative effect on SRR in the Burn unit. Scorch height in both burn types was negatively correlated with SRR. These models incorporating only tree injury or tree parameters in Mastication + Burn and Burn units explained 63% and 99% of the variability in SRR, respectively.

Discussion

In order to test whether the treatments had a significant impact on SRR and the relationships between SRR and plot variables, SRR data for all years and treatments were included in the first set of multiple regression models. Mastication had no measurable impact on SRR, and this result was corroborated by the lack of significance of any multiple regression models incorporating a mastication effect. Although resulting models indicated that mastication followed by burning, and burning in general, did play a role in SRR trends, the models incorporating treatment effects accounted for less than 30% of the variation in SRR.

The regression analysis of mastication followed by burning, which coded all other treatments as ‘‘0’’, allowed for a comparison of the combined effect of mastication and burning with both controls and burning alone. This combined treatment reduced total soil respiration. The significant interaction term with litter depth suggests that SRR sensitivity to litter increased as a result of both mastication and burning,

Table 7 Variables with corresponding coefficients and significance of contribution to multiple regression model of log-transformed soil respiration response to burning in masticated and untreated pine plantation sites, Stanislaus National Forest, CA

Parameter[a]	Estimate	Std Error	t-ratio	$P > \|t\|$
Intercept	1.834	0.194	9.48	<.0001
Burn indicator	−0.14	0.047	3.06	0.003
BS (%)	0.011	0.004	3.18	0.002
TC (%)	0.015	0.007	2.13	0.035
CT (m)	−0.225	0.054	−4.16	<.0001
RC (%)	−0.033	0.010	−3.21	0.002
Burn indicator × BS (%)	0.007	0.004	−2.11	0.036
Burn indicator × CT (m)	−0.15	0.054	2.85	0.005

Model $R^2 = 0.23$, $F = 7.60$, $P < 0.0001$

[a] All abbreviation as in Table 3

Table 8 Multiple regression results (Eq. 1) depicting significant biotic and environment factors influencing log-transformed soil respiration rates in pine plantations in the Stanislaus National Forest, CA

Treatment	Year	Significant parameters[a] (estimate)		F value	$P > F$	R^2
Control	2003	M_s (0.12)	Intercept (−0.18)	10.87	0.005	0.41
	2004	LC (0.01), [b]TC (−0.07)	Intercept (0.20)	4.12	0.04	0.35
	2005	ns				
	All Years	CT (−0.06), RC (−0.04)	Intercept (1.34)	12.46	<0.001	0.33
Burn	2003	CT (0.10), LD (−0.01), RC (0.31), HC (−0.03)	Intercept (1.27)	67.06	0.001	0.98
	2004	SC (0.17), BS (0.17), [c]DBH CT (−0.27), LD (0.65)	Intercept (8.42)	19.03	0.007	0.95
	Burned, 2005	DD (0.03), LD (−0.29), BS (0.01)	Intercept (0.52)	38.29	0.001	0.96
	All Years	T_s (0.04), LD (−0.04), RC (−0.02), BS (0.01), TC (0.02), CT (−0.17)	Intercept (1.17)	8.88	<0.001	0.73
Mastication + Burn	2003	BS (−0.18)	Intercept (1.55)	10.67	0.005	0.40
	Masticated, 2004	T_s (0.14), DD (−0.05), LD (0.05), BS (−0.03), HC (−0.007)	Intercept (−1.22)	12.83	<0.001	0.84
	Burned, 2005	LD (0.13)	Intercept (0.21)	10.5	0.005	0.40
	All Years	T_s (0.17), LD (0.11), HC (−0.01)	Intercept (−1.24)	17.84	<0.001	0.52

All evaluations were based on mean yearly values for each plot, where annually $n = 18$ for controls and Mastication + Burn units and $n = 9$ in the Burn unit

[a] All abbreviations as in Table 3. Variables did not include measures of fire-induced tree injuries

[b] Denotes significance of parameters was evaluated at $P < 0.10$; all other values significant at $P < 0.05$

[c] DBH CT represents the diameter of the closet tree to soil plot

and that SRR increased with litter depth. In a review of soil respiration patterns in world forests, greater litter production was clearly related to higher soil respiration rates (Raich and Tufekcioglu 2000). Litter depth has also proved effective in explaining SRR trends in other Sierra Nevada forest types (Concilio et al. 2005; Ma et al. 2005). The increased sensitivity of SRR to litter cover may be indicative of a greater importance of the heterotrophic contribution to total soil respiration after the treatments. The contribution of post-mastication organic matter to the soil increases substrate availability for microbial activity,

Table 9 Mean (standard error) values for fire effects on trees and plot variables after prescribed burning in Burn only and masticated pine plantations

Tree injury variable	Burn (n = 9)	Mastication + Burn (n = 18)	*$P > t$
Basal char (%)	41.76 (6.03)	42.59 (27.08)	0.9
Basal circumference burned (%)	91.94 (5.77)	69.35 (23.55)	0.001
Burn extent in 1-m plot (%)	81.78 (21.38)	64.22 (34.27)	0.12
Char severity rating (CSR) at max. ht.	1.30 (0.30)	1.10 (0.33)	0.04
Crown volume scorched (%)	41.57 (9.34)	17.50 (12.61)	0.001
CSR, below 1′ at max.	2.37 (0.38)	1.82 (0.76)	0.02
DBH (cm)	34.99 (2.67)	33.87 (1.61)	0.27
Dist.to closest burned trees (m)	6.49 (1.65)	8.63 (1.10)	0.27
Foliage consumption (%)	6.85 (1.94)	7.18 (4.63)	0.8
Ht. to live crown base (m)	8.83 (1.12)	5.70 (1.96	0.0001
Max. bark char ht. (m)	2.97 (0.36)	1.46 (1.06)	0.001
Opp. bark char ht. (m)	0.06 (0.06)	0.35 (0.32)	0.002
Sap exudes (0–1)	0.54 (0.41)	0.12 (0.20)	0.02
Scorch ht. at max. (m)	11.07 (1.38)	8.00 (2.23)	0.0002
Scorch ht. at opp. (m)	7.45 (0.78)	5.71 (2.60)	0.02
Total crown damage (TCD) (%)	48.43 (10.58)	24.68 (13.39)	0.001

* Probability result from t-test,α = 0.05

Table 10 Fire-induced tree injury variables with corresponding coefficients and significance of contribution in a multiple regression model of soil representation patterns in a post-fire Burn pine plantation unit, Stanislaus National Forest, CA

Parameter[a]	Estimate	Std Error	t-ratio	$P > \|t\|$
Intercept	1.156	0.041	28.49	<.0001
Burn extent in 1-m plot (%)	−0.008	0.001	−14.19	0.0008
TCD (%)	0.086	0.016	5.47	0.012
Sap exudates (1–0)	−2.219	0.409	−5.42	0.0123
RC (%)	−0.009	0.001	−6.45	0.0076
Bark char ht. Max. (m)	−0.927	0.175	−5.3	0.0131

Model R^2 = 0.99, F = 61.40, P < 0.003

[a] TCD = percent total crown volume scorched and consumed; Bark char ht. at max. = maximum height of bark char; RC as in Table 4

Table 11 Fire-induced tree injury variables with corresponding coefficients and significance of contribution in a multiple regression model of soil respiration patterns in two post-fire masticated pine plantation units, Stanislaus National Forest, CA

Parameter[a]	Estimate	Std Error	t-ratio	$P > \|t\|$
Intercept	0.078	0.094	0.83	0.422
Burn extent in 1-m plot (%)	0.003	0.001	2.27	0.041
TCD (%)	0.133	0.042	3.17	0.007
Basal char (%)	0.026	0.008	3.21	0.007
Scorch ht. at opp. (m)	−0.699	0.215	−3.25	0.006

Model R^2 = 0.63, F = 5.50, P < 0.008

[a] TCD = percent total crown volume scorched and consumed; Basal char = percent of tree bole under 1.37 m height charred; Scorch ht. at opp. = height of crown scorch opposite where maximum occurred

and can accelerate decomposition rates (Sirra-Pietikainen et al. 2001).

The coefficient for the burn indicator shows that fire in pooled Mastication + Burn and Burn only units decreased SRR by about 14%; such reduction of SRR after fire is supported by other reports for forested ecosystems (Weber 1990; O'Neill et al. 2002; Ma et al. 2004). It is also not unexpected that burning increased the sensitivity of SRR to the amount of exposed bare mineral soil in both burned treatment types. As a result of lower albedo (ash cover was black) and lack of insulation provided by woody detritus, bare soil was significantly and positively correlated with soil temperature in 2003–2005.

The fact that soil moisture was lower where more mineral soil was exposed, that T_s and M_s were negatively correlated, and that SRR was negatively correlated with M_s, may have confounded the relationship between SRR and bare soil exposure. Negative or weakened correlation between SRR and soil temperature has been reported elsewhere in the Sierra Nevada under low soil moistures conditions (under ~14%; Concilio et al. 2005; Ma et al. 2005; Tang et al. 2005), and mean soil moistures were less than 15% throughout the period of this study. Soil moisture was generally higher in 2005, especially in Mastication + Burn sites, resulting in a closer and more clearly negative relationship between soil moisture and soil temperature. In a younger ponderosa pine plantation in the Sierra Nevada, Tang et al. (2005) reported negative correlations between SRR and soil moisture only when soil moisture was above 19%. A switch in the ecological dominance from autotrophic to heterotrophic respiration has been used to explain the negative relationship between SRR and T_s in water-stressed ecosystems (Ma et al. 2005).

The importance of tree proximity in all treatment types has multiple explanatory mechanisms. Tree root density, both fine and large, is higher closer to the base of the tree bole, so that autotrophic respiration can be expected to increase with decreasing distance from the tree base (Pangle and Seiler 2002). Litter depth and, in this study, litter cover are higher closer to the bases of trees, owing to the higher canopy proximity responsible for litter production (Hille and Stephens 2005). Thus, tree proximity also suggests greater abundance of substrates for decomposition as well as symbiont sources for ecotomycorrhizae, and a higher resulting heterotrophic respiration contribution. Burning decreased the sensitivity of SRR to tree proximity, again implying that autotrophic respiration importance decreased after the fires in burned units.

Model predictive power and goodness-of-fit were improved when each treatment type was analyzed separately (Concilio et al. 2005). Each of the variables examined could potentially influence soil respiration (Raich and Tufekcioglu 2000). Rather than test pre-determined combinations of variables for each year and treatment, best fitting models were created using significant variables which in combination yielded the highest R^2 values. This resulted in different sets of parameters in each model. Since multiple regression effects account for the effects of the other incorporated variables, the magnitude and signs of the coefficients can change between models. For example, litter depth in the Burn only unit coefficient was positive, then negative in the regression models of SRR between 2004 and 2005. Regression of SRR against litter depth excluding other parameters yielded negative coefficients in both years. It thus appears that burning changed the relationship between litter depth and SRR. Ma et al. (2004) also reported significant positive correlation between litter depth and SRR before thinning and burning, but they found no significant relationship post-treatment.

Overall, the variables measured in this study were more effective in explaining SRR in treated units than in controls. When compared to the best-fit pre-treatment regression model, the post-mastication model explained more than twice the variation in SRR. Forest floor depth was increased by mastication, and reduced by burning; their influence on SRR was only significant after treatments. Again, this may reflect a decreased relative contribution to total soil respiration by autotrophic sources, owing to the reduction in photosynthetic capacity of overstory trees as a result of scorching and consumption of foliage. Hogberg et al. (2001) reported a 54% reduction in soil respiration within 1–2 months after girdling trees in a Scots pine (*Pinus sylvestris* L.) forest. The mean ~70% basal char value in masticated units indicates the possibility of significant cambial injury and potential girdling, which would decrease the supply of photosynthates to roots. A reduction in photosynthate supply would lower root, and therefore total, respiration rates. In addition, any associated root mortality would also impact ecotomycorrhizal fungal biomass and its contribution to total respiration (Hogberg et al. 2001).

Since many of the closest-tree injury variables differed significantly between Burn only plots and those in the Mastication + Burn units, multiple regression analyses were conducted separately. The tree injury measures typically associated with tree mortality, such as total crown damage, and basal char (e.g., Kobziar et al. 2006), were more severe in the Burn unit than in the Mastication + Burn stands, which might explain the stronger predictive ability of the Burn only model. Still, fire-induced injury measures were more closely related to soil respiration rates in masticated stands than were other combined plot variables, and produced a better-fit model (R^2 = 0.63 versus 0.40). That higher measures of tree injury including presence of resin exudates along the tree bole, bark char height, and scorch height were related to lower SRR is not surprising. These injury indicators are associated with tree, and therefore root, mortality (Peterson 1985; Regelbrugge and Conard 1993), and resin exudates are a tree's direct response to injury and/or stress (Trapp and Croteau 2001). The importance of the resin parameter in the model is evidenced by the size of its coefficient; this indicator of tree injury was also most influential to model goodness-of-fit according to partial R^2 values. The translocation of photosynthates from tree roots to supply the flush of resin from the tree's bole may be responsible for decreased SRR in plots located closest to the ''pitching'' trees. Root, ectomycorrhizae, and the microorganisms that feed off sugars leeched from roots would all be affected by a shift in photosynthate out of the roots and rhizosphere (Bhupinderpal-Singh et al. 2003), and certainly by a loss of photosynthetic capacity.

Surprisingly, when all other parameters were held constant, the models for both burned treatment types suggested that increased total crown damage corresponded with higher SRR. Independently, TCD was not significantly related to SRR in the Burn unit, but was positively correlated with SRR (R^2 = 0.30) in Mastication + Burn units. In an old growth ponderosa pine stand, the probability of cambial mortality increased with depth of the O horizons (Ryan and Frandsen 1991). If, as the other models discussed above have suggested, the importance of heterotrophic respiration increases after burning, then the significant relationship between litter depth and TCD (R^2 = 0.27) can help explain this result. Soil plots closer to more severely injured trees also had deeper litter depths, so that the reduction in autotrophic respiration may have been spatially associated with higher substrate availability for soil micro- and macro-organisms. In 2005, litter depth was the sole significant variable in predicting SRR in Mastication + Burn units when tree injury data were excluded.

As is indicated by the year-to-year variation in the driving variables for SRR in the control units, patterns of soil respiration in the treated sites are also likely to change over the next few years. Using published regression equations for ponderosa pine (Kobziar et al. 2006), fire-induced girdling of tree boles or scorching of tree crowns may result in up to 40% tree mortality in the plantations. The associated root mortality would continue to decrease the autotrophic contribution to soil carbon efflux. Yet increases in decomposer activity in response to readily available surface organic matter and decaying roots may raise the heterotrophic contribution to total SRR, even resulting in an eventual recovery of pre-treatment SRR levels (Weber 1990). Long-term studies of burning and mastication impacts on SRR are not available for comparison, but there is a consensus and some limited evidence that human-induced changes in SRR are sensitive to the passage of time (Bupinderpal-Singh et al. 2003; Concilio et al. 2005).

Conclusion

The results of this study are suggestive of three main conclusions: (1) burning results in an increased relative contribution of heterotrophic respiration to total soil respiration, as indicated by the relationships between SRR and plot variables, (2) the variables examined in this study are more closely related to spatial variation in SRR in disturbed than in control sites, and (3) above-ground forest characteristics, especially tree injuries, can be successfully employed to model SRR, and should be considered along with the more-common soil microclimate factors. Predictions for the Sierra Nevada under a climate warming scenario include increased temperatures and droughts in the summer, and warmer and wetter winters (Field et al. 1999). Based on the results of this study, given these climate shifts, microclimate factors would become less effective in modeling soil respiration rates for the growing season in the Sierra Nevada. A similar suggestion was made by authors assessing CO_2 flux under different climate conditions in Taiga forests of Alaska, where global climate warming scenarios were projected to result in an uncoupling between soil CO_2 respiration and temperature (Gulledge and Schimel 2000). This also heightens the relative importance of the impacts of fuels treatments on soil moisture levels, which this study showed were elevated following mastication and burning. Understanding the mechanisms by which soil respiration responds to disturbances is key to predicting how climate warming will influence the global soil pool.

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