



Prescribed burning and mechanical thinning effects on belowground conditions and soil respiration in a mixed-conifer forest, California

Soung-Ryoul Ryu^{a,*}, Amy Concilio^b, Jiquan Chen^c, Malcolm North^d, Siyan Ma^e

^a Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, United States

^b Department of Environmental Studies, University of California Santa Cruz, Santa Cruz, CA 95064, USA

^c Department of Environmental Sciences, University of Toledo, Toledo, OH 43606, USA

^d U.S. Forest Service, Sierra Nevada Research Center, 1731 Research Park Dr., Davis, CA 95618, USA

^e Department of Environmental Science, Policy & Management, University of California-Berkeley, Berkeley, CA 94720-3114, USA

ARTICLE INFO

Article history:

Received 16 July 2008

Received in revised form 26 November 2008

Accepted 27 November 2008

Keywords:

Soil respiration

Autotrophic soil respiration

Heterotrophic soil respiration

Thinning

Burning

Root

ABSTRACT

Soil respiration (R_s) is a major carbon pathway from terrestrial ecosystems to the atmosphere and is sensitive to environmental changes. Although commonly used mechanical thinning and prescribed burning can significantly alter the soil environment, the effect of these practices on R_s and on the interactions between R_s and belowground characteristics in managed forests is not sufficiently understood. We: (1) examined the effects of burning and thinning treatments on soil conditions, (2) identified any changes in the effects of soil chemical and physical properties on R_s under burning and thinning treatments, and (3) indirectly estimated the changes in the autotrophic soil respiration (R_A) and heterotrophic soil respiration (R_H) contribution to R_s under burning and thinning treatments. We conducted our study in the Teakettle Experimental Forest where a full factorial design was implemented with three levels of thinning, none (N), understory thinning (U), and overstory thinning (O; September to October 2000 for thin burn combination and June and July 2001 for thin only treatments) and two levels of burning, none (U) and prescribed burning (B; fall of 2001). R_s , soil temperature, soil moisture, litter depth, soil total nitrogen and carbon content, soil pH, root biomass, and root nitrogen (N) concentration were measured between June 15 and July 15, 2002 at each plot. During this period, soil respiration was measured three times at each point and averaged by point. When we assumed the uniform and even contribution of R_A and R_H to R_s in the studied ecosystem without disturbances and a linear relationship of root N content and R_A , we calculated the contributions of R_A to R_s as 22, 45, 53, 48, and 45% in UU, UO, BN, BU, and BO, respectively. The results suggested that after thinning, R_s was controlled more by R_H while after burning R_s was more influenced by R_A . The least amount of R_s variation was explained by studied factors under the most severe treatment (BO treatment). Overall, root biomass, root N concentration, and root N content were significantly ($p < 0.01$) correlated with soil respiration with correlation coefficients of 0.37, -0.28, and 0.29, respectively. This study contributes to our understanding of how common forestry management practices might affect soil carbon sequestration, as soil respiration is a major component of ecosystem respiration.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Carbon storage in belowground biomass is twice that of atmospheric carbon (C), and soil respiration (terrestrial R_s : 136 ± 55 pg C yr⁻¹), a major C pathway from the ecosystem to the atmosphere, is more than ten times that of CO₂ release through fossil

fuel combustion (Raich and Schlesinger, 1992; Raich and Potter, 1995; Janssens et al., 2001; Lal, 2008). More specifically, forest soils contain about 45% of all belowground C, an amount equal to atmospheric C (Dixon et al., 1994; Johnston et al., 2004; Litton et al., 2003), and R_s accounts for 67–76% of total forest ecosystem respiration (Janssens et al., 2001; Raich and Potter, 1995). Much of the forested land in the U.S. is, or will be, treated regularly with mechanical thinning and/or prescribed burning (e.g., Ryu et al., 2006; Concilio et al., 2006) for a variety of reasons (e.g., forest fire hazard reduction). These management activities have the potential to significantly influence soil C sequestration because R_s from forest soil is sensitive to environmental conditions that can be altered by

* Corresponding author at: Department of Forestry and Natural Resources, Clemson University, 206 Lehotsky Hall, Clemson, SC 29634, United States. Tel.: +1 864 656 4860; fax: +1 864 656 3304.

E-mail address: nickny@hotmail.com (S.-R. Ryu).

mechanical thinning and/or prescribed burning (Pussinen et al., 2002; Pypker and Fredeen, 2002; Reichstein et al., 2003; Johnston et al., 2004).

Previous studies have focused on identifying the main factors driving R_S under natural conditions, and the effects of management on belowground characteristics and R_S . We have learned that R_S is influenced by complex interactions among physical (e.g., soil temperature and moisture; Lloyd and Taylor, 1994; Rustad et al., 2000), chemical (e.g., soil pH, soil carbon content, and nutrient availability; Ekblad and Nordgren, 2002; Savin et al., 2001), and biological (e.g., type and activity of soil microorganisms, fine root biomass, and vegetation types; Johnston et al., 2004) factors. Among those factors, soil temperature and moisture were traditionally considered to be the most important factors influencing soil respiration, but recent studies suggest that influence of other factors (e.g., litter depth) could overrule their effect in natural (e.g. Campbell et al., 2004; Högberg et al., 2001; Litton et al., 2003; Maier and Kress, 2000; Reichstein et al., 2003) and disturbed (e.g., Euskirchen et al., 2003; Ma et al., 2004) forest ecosystems. Only a few of these studies investigated how management changed the influences (e.g., magnitude and direction) of physical, chemical, and biological factors on R_S . Understanding these processes will be critical to predicting future carbon sequestration in managed forest ecosystems.

This study is a part of a large project (the Teakettle Ecosystem Experiment in Sierra National Forest, California; <http://teakettle.ucdavis.edu/>) and various aspects of soil respiration have been studied at the same location including: spatial patterns of soil respiration across different patch types (Ma et al., 2005), key climatic drivers of soil respiration over seasonal (Ma et al., 2005), diurnal (Ma et al., 2005), and inter-annual scales (Concilio et al., in press), post-disturbance trends in soil respiration after thinning and burning (Ma et al., 2004; Concilio et al., 2006), changes in variables influencing soil respiration after disturbances (Ma et al., 2004; Concilio et al., 2006), and a comparison in soil respiration response to thinning between Teakettle and an eastern deciduous forest (Concilio et al., 2005). These previous studies were focused on quantifying soil respiration rate and understanding biophysical factors, such as temperature and moisture before or after treatments, but little has been learned about mechanisms driving changes in soil respiration or the partitioning of autotrophic and heterotrophic respiration. Therefore, this study was designed to tease apart potential mechanisms to explain how and why we saw the responses to treatments that were documented in earlier work.

R_S is the sum of autotrophic (R_A) and heterotrophic respiration (R_H) and their contribution to R_S in a forest ecosystem varies a lot. Although the R_A contribution to R_S has a wide range in forest ecosystems (<10 to >90%), it usually falls within a narrower range of 40–60% with a mean of 45.8% (Hanson et al., 2000). The R_A contribution generally increases during the growing season and decreases during the dormant season (Hanson et al., 2000). Uchida et al. (1998) reported that R_A contributed 54% to R_S in a Canadian black spruce forest. There have been no known studies evaluating the R_A contribution to R_S in mixed-conifer forests of the Sierra Nevada. Evaluating the contribution of R_A and R_H is the first step to understanding and predicting soil carbon cycling and sequestration dynamics under changing environmental conditions (Hanson et al., 2000). However, relatively few studies have focused on this topic and, of those, few have studied management effects on the proportion of R_A to R_H . Moreover, it is poorly known how the balance of R_A and R_H might respond to changing climate. The lack of information is mainly due to the complexity of the processes that drive R_A and R_H and to poorly developed methodology in partitioning autotrophic and heterotrophic respiration from soil respiration measurements. Indeed, it is almost impossible to separately measure *in situ* R_H and R_A directly and accurately

without disturbing natural conditions. Recent studies suggested that root production (Campbell et al., 2004; Lee and Jose, 2003) and root nitrogen content or concentration (Burton et al., 1998; Pregitzer et al., 1998) could be proportional to R_A . These indices may offer useful indirect estimates of R_A response to management practices. Furthermore, understanding the effect of disturbances on R_H and R_A will help us model future carbon sequestration in disturbed forest ecosystems (Hanson et al., 2000).

The objectives of the study were to: (1) examine the effect of burning and thinning treatments on soil conditions, (2) identify any changes in the effects of soil chemical and physical properties on R_S under burning and thinning treatments, and (3) indirectly estimate the changes in the contributions of R_A and R_H to R_S under burning and thinning treatments. We hypothesized that burning would decrease R_S by killing fine roots (reduced R_A) and reducing soil microorganisms (reduced R_H), while thinning would maintain or slightly reduce R_S by killing roots (reduced R_A) and increasing organic matter on the forest floor (increased R_H). We also hypothesized that the main factors influencing R_S would change with different combinations of treatments.

2. Materials and methods

2.1. Study site

Teakettle Experimental Forest (TEF) is located in the Sierra National Forest on the west side of the Sierra Nevada range of California. It covers 1300 ha, ranges in elevation from 1980 to 2590 m and receives an average of 1250 mm of annual precipitation, mostly in the form of snow (North et al., 2002). The area experiences a typical Mediterranean climate and the mean air temperature in January and July are 1 and 14.5 °C, respectively (North et al., 2002). TEF has three major vegetation patch types: conifer closed canopy (CC), *Ceanothus cordulatus* Kellogg shrub dominated areas (CECO), and open canopy (OC). CC, OC, and CECO occupy 67.7, 4.7, and 13.4% of the entire study forest, respectively (North et al., 2002). Major conifer species include *Abies concolor* Lindl. ex Hildebr., *A. magnifica* A. Murr., *Pinus lambertiana* Douglas, *P. jeffreyi* Grev. and Balf., and *Calocedrus decurrens* (Torr.) Florin (North et al., 2002). Soils are classified as Xerumbrepts and Xeropsamments (North et al., 2002). Soils at the site vary in physical and chemical properties based on patch type. Closed canopy and *C. cordulatus* patches are characterized by deeper litter layers (Ma et al., 2004) and higher total C and N content (Erickson et al., 2005) than open canopy patches. Plant available N is greatest under the nitrogen fixer, *C. cordulatus* (Erickson et al., 2005).

2.2. Plot design and treatments

Our study was conducted within the larger Teakettle Experiment, which included a full factorial design crossing three levels of thinning, (1) no thin, (2) understory (which followed California spotted owl guidelines), and (3) overstory (shelterwood; leaving 22 evenly spaced large trees ha⁻¹), and two levels of burning, (1) unburned (none) and (2) prescribed burn (Ma et al., 2005). Mechanical thinning took place between September and October of 2000 for burn and thin combination treatments and between June and July of 2001 for the thin-only treatments. The prescribed fire was low-intensity and lit by hand. Burning was applied after the first substantial fall rain in late October 2001 to avoid overstory ignition yet still consume surface fuels and small trees. Fire weather conditions at the time of burning were mild, with clear skies, dry bulb temperatures of 5–13 °C, relative humidity of 39–46%, and variable winds ranging from 0 to 8 km h⁻¹. This resulted in a slow creeping ground fire with mean flame heights under 2 m. Three replicates of each treatment were applied to 4 ha plots (18

plots total). Plots were selected using variogram and cluster analysis to include equal ratios of the three patch types and were not significantly different in tree basal area or density (North et al., 2002). One plot from each treatment was randomly selected for measurement presented in this study. Depending on plot conditions, transects of various length were positioned to evaluate differences in treatment effects on soil respiration and below-ground characteristics. Transects by treatment included three 29 m in length in the control plot (C; unburned–no thin), one 39 m in the unburned–understory thin (UU), one 39 m in the unburned–overstory thin (UO), two 19 m in the burn–no thin (BN), three 19 m in the burn–understory thin (BU), and two 19 m in the burn–overstory thin (BO) plots. Sampling points were located every meter along the transect. For each point, the vegetation patch type was noted. The number of CC, CECO, and OC sampling points in each treatment was 42, 27, and 21 in the C treatment, 25, 12, and 3 in UU, 20, 10, and 10 in UO, 20, 16, and 4 in BN, 20, 5, and 15 in BU, and 35, 21, and 4 in BO, respectively.

2.3. Field measurements

Along each transect, soil respiration (R_S ; $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), volumetric soil moisture (M_S ; %) at 0–10 cm soil depth, and soil temperature (T_S ; °C) at 10 cm depth were measured at least every other week during the 2002 growing season for each sampling point. R_S measurements were taken along all transects from June to August with a portable infrared gas analyzer (EGM-2 Environmental Gas Monitor, PP Systems, UK) with a SRC-1 Soil Respiration Chamber (PP Systems, UK). All PVC collars were placed in the ground in June, 2002. Soil collars were specifically designed and made according to the size of soil chamber of EGM-2 PP Systems. The top of each soil collar had a 1 cm interspace between the inner core and outer collar to ensure that the soil chamber sat stably on the collar and was well sealed during measurements. The bottom of each soil collar was sharpened so that the soil collar could be installed tightly into the forest floor. Collars were 10 cm tall and were placed 1 cm into the ground from the soil surface. After installation, they were allowed to sit for at least 3 days before any measurements were taken to minimize any potential effects of the disturbance. In the closed canopy and ceanothus shrub patches at our site, if the litter layer was deep, the collars did not reach through to the mineral soil layer. In the open canopy patch type, litter was not as deep (and many times barely existent) and collars were inserted directly into mineral soil. The EGM-2 was calibrated weekly with a standard 700 ppm CO_2 gas under ambient air pressure, while barometric pressure readings were taken at the time of sampling for the correction of air pressure difference. To reduce the effect of air temperature on soil respiration, R_S was measured between 9:00 and 16:00 h. R_S , T_S and M_S were measured simultaneously at each sampling point. T_S was measured at a depth of 10 cm using a digital thermometer (Taylor Digital Max/Min, Forestry Suppliers, Inc., USA). M_S was measured using Time Domain Reflectometry (TDR, model 6050XI, Soil Moisture Equipment Corp., Santa Barbara, California, USA). TDR probes were 30 cm long and installed adjacent to each soil respiration collar (about 10 cm away) at a 30° angle to the soil surface to measure M_S within 0–10 cm depth in mineral soil. Litter depth (LD; cm) was defined as the depth of litter from the litter surface to the top of the mineral soil and was also measured at each sampling point (Ma et al., 2004).

2.4. Soil sampling and process

From June 25 to July 3, 2002, soil samples (0–15 cm depth in soil) were collected from each point along the transect using

a 1.9 cm diameter Oakfield soil sampler after carefully removing forest floor (Ben Meadows company, WI, USA) to quantify total nitrogen (TN; wt/wt.%), total carbon (TC; wt/wt.%), and pH. To insure the samples were representative, four cores at each point were collected and compiled in one plastic bag. Soil samples were air-dried and sieved with 2 mm mesh (Fisher Scientific, PA, USA), and then dried at 65 °C for 48 h. Soil pH was measured in a 1:2 soil and solution ratio using ultra-purified water ($\text{pH}_{\text{H}_2\text{O}}$) and 2 M KCl (pH_{KCl}) for each sample. TC and TN in soil were measured using a Carlo Erba NA 1500 Series 2 CN analyzer (Exeter Analytical, Inc., Chelmsford, MA, USA).

Another set of soil samples was taken to estimate root biomass and root nitrogen concentration using a 7.6 cm diameter soil sampler (custom made) at two depths: 0–10 and 10–20 cm. All soil samples were collected 1 m down-slope from the sampling points to minimize the disturbance effect of soil sampling on soil respiration measurements. We randomly collected soil samples from more than 25% of sampling points for each treatment; 28, 30, 30, 30, 45, and 27% for C, UU, UO, BN, BU, and BS, respectively. The number of CC, CECO, and OC root sampling points in each treatment was 10, 7, and 8 in the C treatment, 6, 4, and 2 in UU, 3, 3, and 6 in UO, 3, 6, and 3 in BN, 6, 3, and 9 in BU, and 9, 7, and 0 in BO, respectively. Each sample was stored in a cooler (<4 °C) and frozen as soon as possible. After thawing in the refrigerator, samples were washed using a root washer (Gillison's Variety Fabrication, Inc., Benzonia, MI, USA) and roots were separated manually by diameter into fine roots (≤ 2 mm) and coarse roots (> 2 mm). The two root fractions per soil sample were placed in separate paper bags, dried at 65 °C for 48 h, and weighed. Total carbon and nitrogen in roots were measured using a 2400 Series II CHNS/O Analyzer (PerkinElmer, Inc., Boston, MA, USA).

2.5. Calculation of R_A and R_H contribution to R_S

It is almost impossible to accurately measure R_A and R_H separately *in situ*. In this study, we aimed to indirectly estimate the changes in contribution of R_A and R_H to R_S by burning and thinning treatments. This approach requires two assumptions: (1) the contribution of R_A and R_H on R_S is uniform in a forest ecosystem without disturbances, and (2) R_A (or R_H) is significantly related to a known factor. We assumed that the contributions of R_A and R_H to R_S were even in this ecosystem without disturbance (the control) and that root N content had a linear relationship with R_A (Burton et al., 1998; Pregitzer et al., 1998; Hanson et al., 2000). However, because we have no proof that the contribution was actually even and we were most interested in responses to treatments in relative rather than absolute terms, we calculated the % change of R_A contribution to R_S by treatment (Eq. (2)). The % change value is constant regardless of any assumed contribution ratio between R_A and R_H in the control. We calculated the estimated value of R_A as follows:

$$R_A = R_{AC} \left(\frac{\text{root } N_{\text{TRT}}}{\text{root } N_C} \right) \quad (1)$$

where R_{AC} is the autotrophic soil respiration in the control, root N_{TRT} is the root N content of the treatment, and root N_C is the root N content of the control. Subsequently, % R_A change due to a treatment can be calculated as follows:

$$\%R_A \text{ change} = \frac{(R_{\text{SBef}} \times R_{\text{AAft}} - R_{\text{ABef}} \times R_{\text{SAft}}) \times 100}{R_{\text{SAft}} \times R_{\text{ABef}}} \quad (2)$$

where R_{SBef} and R_{SAft} are soil respiration before and after treatment, respectively, and R_{ABef} and R_{AAft} are autotrophic soil respiration before and after treatment, respectively.

2.6. Data analysis

We averaged R_s , M_s and T_s measurements (three measurements each) from June 15 to July 15 at each point along the transects to allow comparison to soil chemical and biological data, which were collected only once during the study period. The mean value also allowed us to minimize variation among measurements, including temporal variations. Mean values and standard deviations of pH were calculated after pH was converted to hydrogen ion concentration. Because we sampled from one plot per treatment, linear regression, correlation, and multiple linear regression using Akaike's Information Criterion (AIC) analyses were considered to be the best statistical methods. Linear regression analysis was performed to examine the effects of soil characteristics (T_s , M_s , TC, TN, pH_{H_2O} , pH_{KCl} , LD) on R_s . A multiple regression analysis was conducted for each treatment combination using best Mallows' Cp and AIC to assess the major group of factors influencing R_s for each burning and thinning treatment combination; $R_s = f(T_s, M_s, TC, TN, CN, pH_{H_2O}, LD)$. Spearman correlation was also used to evaluate the relationship between R_s and root characteristics (biomass, N concentration, and N content). All statistical analyses were performed using SAS (SAS version 9, SAS institute, Inc., Cary, NC, USA) and significance was based on an alpha of 0.05 unless otherwise stated. Moreover, mean values were directly compared to evaluate burning and

thinning treatment effects (i.e., burn: C vs. BN, UU vs. BU, and UO vs. BO; thin: C vs. UU and UO, BN vs. BU and BO).

3. Results

3.1. R_s and belowground characteristics

Burning (C vs. BN, UU vs. BU, and UO vs. BO) generally increased T_s , M_s , TN, and TC and decreased R_s , C:N ratio, pH, and LD (Fig. 1). R_s , T_s , M_s , and pH showed a tendency to increase with higher thinning intensity (no thin < understory thin < overstory thin; Fig. 1). Low intensity thinning (understory thin) showed the highest TN and TC levels without burning but the lowest TN and TC with burning (Fig. 1). Low intensity thinning had the lowest LD without burning and the highest LD with burning (Fig. 1).

Linear regression analysis showed that T_s affected R_s positively in the no thin and overstory thin treatments (Fig. 2 Fig. 2a1 and a3) and negatively and significantly in the understory thin treatment (Fig. 2a2). Under heavy thinning (overstory thin), T_s was significantly ($r^2 = 0.15$) related with R_s in the unburned treatment but not in the burned treatment ($r^2 = 0.00$; Fig. 2a3). R_s generally decreased with increasing M_s (Fig. 2b). M_s showed a significantly negative relationship with R_s in the no thin treatment (Fig. 2b1), where M_s explained 7 and 14% of variation in R_s in unburned and burned treatments, respectively (Fig. 2b1). Under the understory

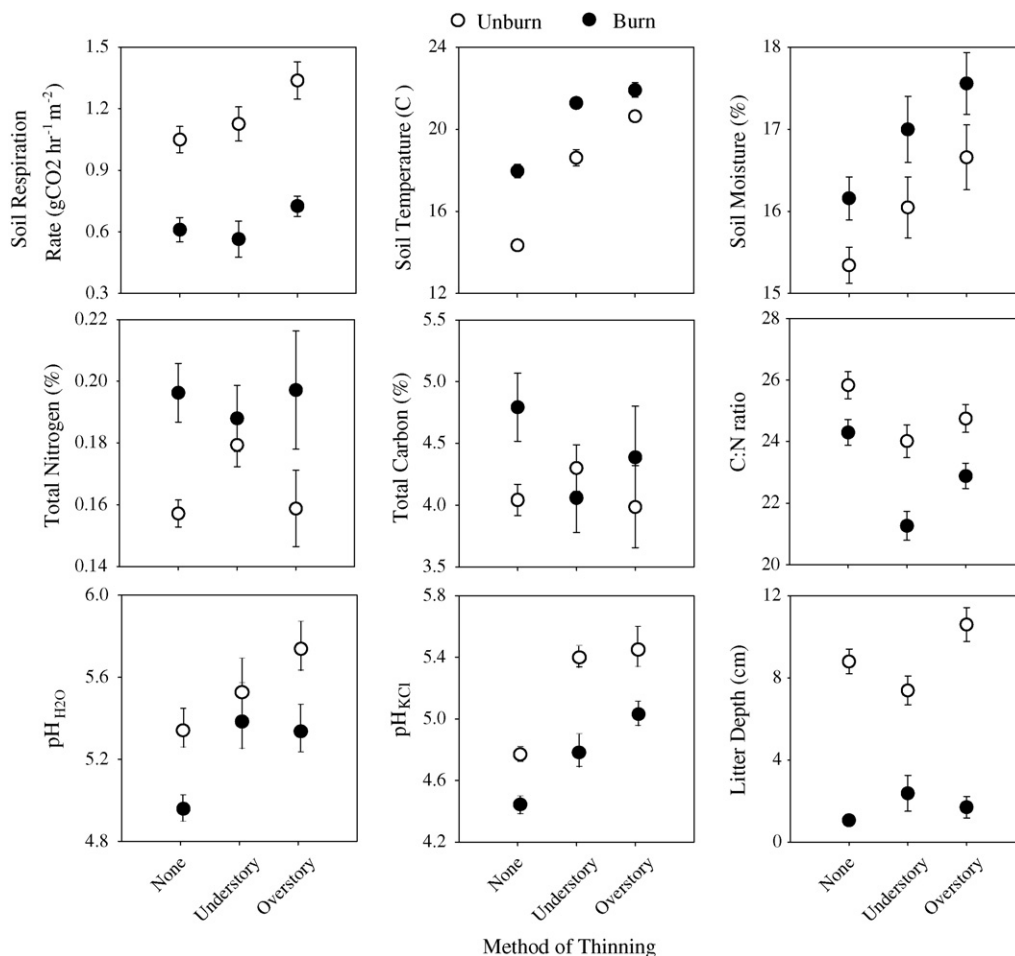


Fig. 1. Summary data showing the effect of experimental burning and thinning (none, understory, and overstory thin) on soil respiration rate, soil temperature, soil moisture, soil total nitrogen content, soil total carbon content, soil C:N ratio, pH_{H_2O} , pH_{KCl} , and litter depth in the study forest. Soil characteristic data are from 0 to 20 cm depth taken between June 25 and July 3, 2002. The sample sizes were 90, 40, 40, 40, 60, and 40 for control, unburned-understory, unburned-overstory, burned-no thin, burned-understory, and burned-overstory, respectively. Soil respiration was measured three times for each sampling point between June 15 and July 15, 2002, and mean values of each point were used for this graph. Solid and empty dots indicate the mean values from burned and unburned treatments, respectively, while error bars represent one standard error.

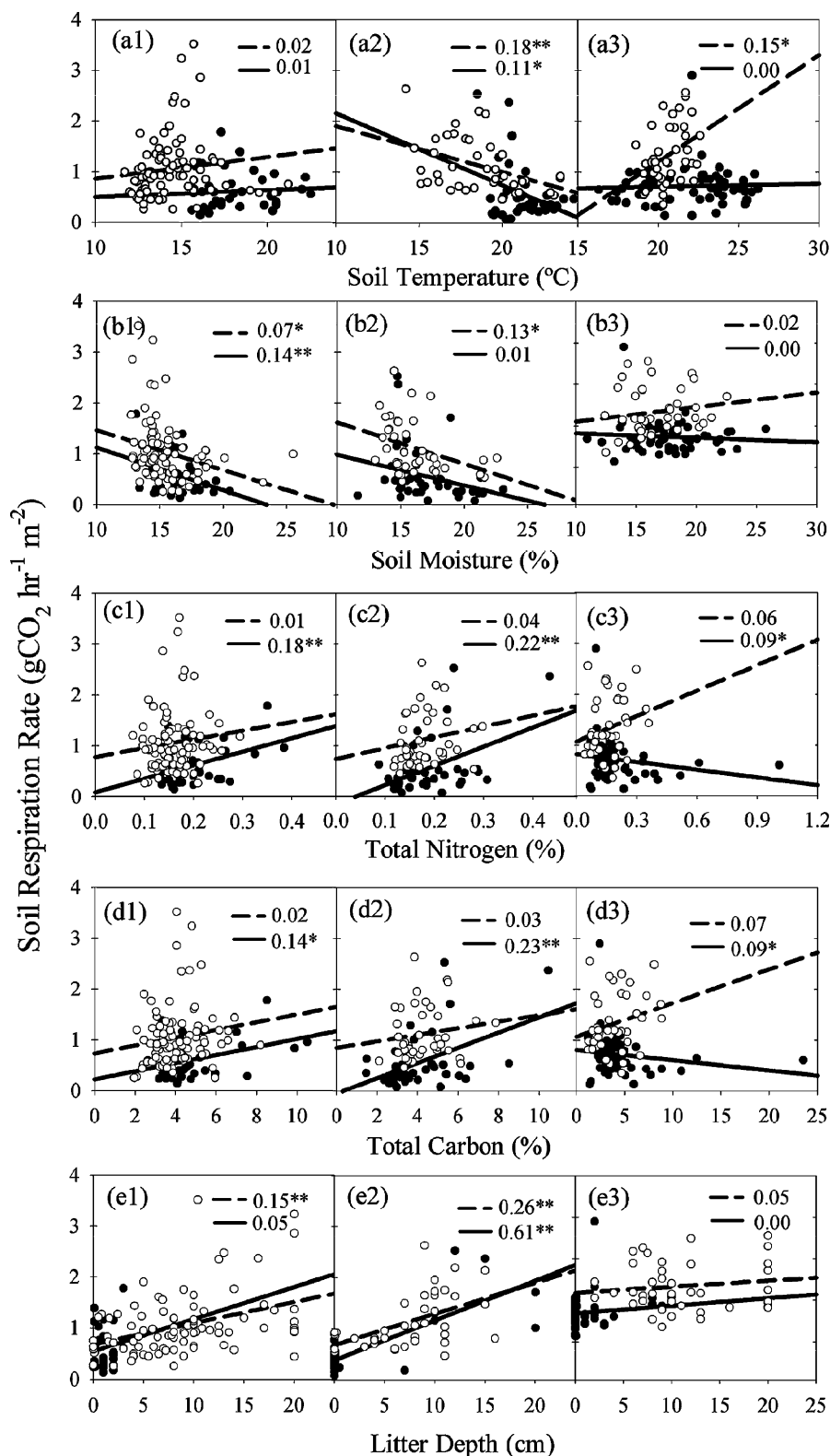


Fig. 2. Linear regression analysis between soil respiration rate ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) with various soil characteristics under none (x1), understory (x2), and overstory (x3) thinning, which show the changes in relationships between soil respiration rate and soil characteristics under different treatment scenarios. Empty and solid dots indicate the mean values from unburned and burned treatments, respectively, while dashed and solid lines represent regression lines followed by regression coefficients (r^2). * and ** indicate significance levels of $p = 0.05$, and 0.01 , respectively.

thin treatment, M_s and R_s were significantly related only without burning ($r^2 = 0.13$).

The relationships between TN and R_s were almost identical to those between TC and R_s (Fig. 2c and d). In both cases, R_s was

significantly related to TN and TC only under the burn treatment, and the relationship between TN:TC and R_s was generally weak ($r^2 < 0.07$) in the unburned treatment. Under the burn treatment, the relationship was positive under no thin and understory thin

Table 1Soil variables that best explain variation in soil respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) for each treatment.

		Unburned		Burned	
		r^2	Variables in model	r^2	Variables in model
Method of thinning	None	0.37	Soil temperature ($^{\circ}\text{C}$), soil moisture (%), total nitrogen (%), and litter depth (cm)	0.41	Soil moisture (%), total carbon (%), and $\text{pH}_{\text{H}_2\text{O}}$
	Understory	0.42	Total carbon (%), C:N ratio, and litter depth (cm)	0.73	Soil temperature ($^{\circ}\text{C}$), total carbon (%), C:N ratio, and litter depth (cm)
	Overstory	0.20	Soil temperature ($^{\circ}\text{C}$) and total carbon (%)	0.06	Total nitrogen (%),

Each set of variables was selected by multiple linear regression analysis using best Cp and Akaike's Information Criterion (AIC).

and negative under overstory thin, and TN and TC explained 18, 22, and 9% and 14, 23, and 9% of R_s variation in the no thin, understory thin, and overstory thin treatments, respectively (Fig. 2c and d).

LD always showed a positive relationship to R_s . In the control plot, LD was significantly related to R_s , explaining 15% of its variation (Fig. 2e1). LD also showed a significant relationship with R_s in the understory thin treatment, where it was the best explanatory factor. LD explained 26 and 61% of the variation in R_s in the unburned and burned treatments, respectively (Fig. 2e2). However, LD values under burned treatments were mainly distributed below 3 cm, which may have skewed the correlation results. The relationships were weak ($r^2 < 0.06$) and insignificant under the overstory thin treatment (Fig. 2e3).

The best environmental variables explaining R_s variation differed among treatments (Table 1). Regression models explained R_s variation better under understory thinning and worse under overstory thinning. R_s variation was explained best by the model in the BU treatment ($r^2 = 0.73$), while the regression model poorly explained R_s variation in the BO treatment ($r^2 = 0.06$). T_s , TC, and LD were the most common variables in the models and were selected three times each (Table 1).

3.2. Treatment effects on root characteristics and R_s

Fine root biomass generally decreased with burning at both depths (0–10 and 10–20 cm) except from C to BN at 10–20 cm (0.48 and 0.49 kg m^{-2} , respectively; Table 2). Fine root biomass was most reduced by burning after the overstory thin (53 and 48% at 0–10 and 10–20 cm, respectively). Surface fine roots (10–20 cm) experienced a greater reduction with burning than deeper fine roots (10–20 cm). Fine root biomass was also generally

decreased with thinning treatments at both depths, with the exception of the comparison between C and UO at 10–20 cm (0.48 and 0.63 kg m^{-2} , respectively). Compared to the C treatment, overall fine root biomass reduction was the largest in BN (52%) followed by BO (49%) and UU (46%). The % biomass reduction of fine roots was generally larger with the burn treatments than thin treatments.

Coarse root biomass decreased at 0–10 cm and increased at 10–20 cm due to burning. At 0–10 cm, it was most reduced under understory thinning (66% reduction) followed by overstory thinning (60% reduction) due to burning, while, at 10–20 cm, it increased over 25, 581, and 79% under no, understory, and overstory thinning, respectively (Table 2). Without burning, both types of thinning treatments increased coarse roots at 0–10 cm by more than 100%. At 10–20 cm, understory thinning decreased coarse root biomass by 41 and 89% with and without burning, respectively, and overstory thinning reduced it by 34 and 54% with and without burning, respectively.

Both burning and thinning tended to increase root N concentration of both fine and coarse roots (Table 2). There were only three occasions when N was reduced by more than 10%: the effect of burning on coarse roots from 0 to 10 cm in the understory thin and from 10–20 cm in the no thin treatment, and the understory thinning effect on coarse roots from 0–10 cm with burning. Compared to the C treatment, root N content changed by –48, +1, –27, –48, and –35% in UU, UO, BN, BU, and BO treatments, respectively, and R_s changed by +18, +12, –31, –46, and –27% in UU, UO, BN, BU, and BO treatments, respectively (Table 2). Mean R_s values from all sampling points and samplings points associated with root samples were almost identical overall (compare Fig. 1 and Table 2).

Table 2

Root biomass, root nitrogen (N) concentration, and root N content by different burn and thin treatments at two soil depths.

	Root type	Depth (cm)	Unburned			Burned		
			Method of thinning			Method of thinning		
			None	Understory	Overstory	None	Understory	Overstory
Soil respiration rate ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$)	N/A	N/A	1.03 (0.46)	1.22 (0.61)	1.15 (0.65)	0.71 (0.42)	0.56 (0.58)	0.75 (0.61)
Biomass (kg m^{-2})	Fine	0–10	0.62 (0.48)	0.28 (0.11)	0.51 (0.26)	0.31 (0.31)	0.24 (0.18)	0.24 (0.11)
		10–20	0.48 (0.24)	0.32 (0.15)	0.63 (0.35)	0.49 (0.22)	0.29 (0.14)	0.33 (0.72)
	Coarse	0–10	0.06 (0.09)	0.12 (0.27)	0.11 (0.18)	0.05 (0.11)	0.04 (0.09)	0.04 (0.08)
		10–20	0.39 (0.56)	0.04 (0.05)	0.18 (0.16)	0.14 (0.15)	0.08 (0.11)	0.22 (0.24)
Nitrogen (%)	Fine	0–10	1.01 (0.21)	0.99 (0.19)	1.07 (0.14)	1.27 (0.24)	1.18 (0.15)	1.28 (0.33)
		10–20	0.84 (0.17)	0.88 (0.17)	0.82 (0.13)	0.82 (0.15)	0.98 (0.18)	1.03 (0.33)
	Coarse	0–10	0.75 (0.55)	0.90 (0.66)	0.78 (0.33)	0.95 (0.78)	0.70 (0.52)	1.03 (0.47)
		10–20	0.52 (0.26)	0.64 (0.29)	0.55 (0.18)	0.42 (0.13)	0.69 (0.28)	0.59 (0.17)
Nitrogen content (g N m^{-2})	Fine	0–10	5.88 (4.28)	2.72 (0.98)	5.27 (2.67)	3.77 (3.62)	2.82 (2.22)	3.01 (1.38)
		10–20	3.98 (2.06)	2.79 (1.46)	5.08 (2.58)	3.91 (1.54)	2.80 (1.42)	3.25 (0.86)
	Coarse	0–10	0.30 (0.47)	0.49 (0.88)	0.92 (1.70)	0.51 (1.48)	0.19 (0.37)	0.47 (0.89)
		10–20	1.92 (2.89)	0.28 (0.37)	0.95 (0.90)	0.58 (0.63)	0.48 (0.66)	1.10 (0.96)
	Total nitrogen content		12.08	6.28	12.22	8.77	6.29	7.83

Reported soil respiration rates are only measured from sampling points associated with the root samples. Data is presented as means (one standard deviation).

Table 3Spearman correlation coefficient (r) between soil respiration rate ($\text{g CO}_2 \text{ h}^{-1} \text{ m}^{-2}$) and root (fine and coarse) characteristics by treatment.

Treatments		Biomass (kg m^{-2})	Nitrogen concentration (%)	Nitrogen content (g N m^{-2})
Burn	Thin			
Unburned	None	0.27 (25)	−0.04 (25)	0.35 (25)
	Understory	−0.16 (12)	0.32 (12)	0.22 (12)
	Overstory	0.54* (12)	0.10 (11)	0.70** (11)
Burned	None	−0.05 (12)	0.17 (11)	0.19 (11)
	Understory	0.41* (18)	−0.43** (17)	0.29 (17)
	Overstory	0.33 (16)	−0.08 (15)	−0.15 (15)
Overall		0.37*** (95)	−0.28*** (91)	0.32*** (91)

Numbers in the parenthesis indicate number of observations.

* Indicates the significance correlation at $p = 0.1$.** Indicates the significance correlation at $p = 0.05$.*** Indicates the significance correlation at $p = 0.01$.

Root biomass, root N concentration, and root N content were overall significantly correlated with R_s (Table 3). However, none of these three root characteristics showed a significant correlation with R_s in more than one treatment (Table 3). Root biomass and fine root N content showed the best correlation coefficient under the UO treatment (0.54 and 0.70, respectively). Generally, fine root characteristics explained variation in R_s better under unburned conditions than burned conditions.

3.3. R_A and R_H estimation

Using Eq. (1), we calculated the mean R_A values as 0.52, 0.27, 0.52, 0.37, 0.27, and 0.33 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in C, UU, UO, BN, BU, and BO, respectively. Consequently, mean R_H values were 0.52, 0.95, 0.63, 0.34, 0.29, and 0.42 $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in C, UU, UO, BN, BU, and BO, respectively. From this, we calculated the contributions of R_A to R_s as 22, 45, 53, 48, and 45% in UU, UO, BN, BU, and BO, respectively. The estimation indicated that the R_A contribution to R_s was reduced by thinning treatments and generally increased by burning treatments: % R_A changes (see Eq. (2)) due to thinning were −56, −9, −9, and −15% (C vs. UU, C vs. UO, BN vs. BU, and BN vs. BO, respectively) and % R_A change due to burning were +5, +118, and −2% (C vs. BN, UU vs. BU, and UO vs. BO, respectively).

4. Discussion

We observed that both burning and thinning treatments increased T_s and M_s , while burning decreased R_s and thinning increased R_s (Fig. 1). Numerous studies (e.g., Rout and Gupta, 1989; Lloyd and Taylor, 1994; Davidson et al., 1998; Epron et al., 1999; Burton and Pregitzer, 2003) have indicated that temperature and moisture are the main factors positively influencing R_s over various climate regions. Therefore, it was somewhat unexpected to see the reduced R_s due to burning with increased T_s and M_s , and the poor correlation of R_s with T_s and M_s (Figs. 1 and 2). We believe that this is because the study focused on the spatial scope of the relationship between R_s and environmental drivers, while T_s and M_s may be more important at explaining temporal variation in R_s . Indeed, at our study site, past research has found that T_s and M_s interact to drive R_s dynamics both seasonally and diurnally (Ma et al., 2005).

R_A and R_H estimation after treatments showed that burning generally decreased actual R_A (except understory thinning, where it did not change) but increased the contribution of R_A to R_s , which suggests that prescribed burning reduced both R_A and R_H but it decreased R_H more than R_A . Burn treatments can reduce both R_A and R_H by negatively influencing soil microbial biomass and/or activity (Mabuhay et al., 2006) and root biomass (Varner et al., 2005) mainly due to heat radiated during the litter layer

combustion, although the magnitude of R_A and R_H reduction due to fire is still uncertain (Högberg et al., 2001). The uncertainty is mainly due to the complexity of the soil ecosystem and the limitations of sampling methods (Hanson et al., 2000; Raich and Schlesinger, 1992; Wuthrich et al., 2002). It is not clear why burning had more influence on R_H than R_A . We speculate that prescribed burning did not inhibit trees from quick recovery of their root biomass after the fire while it did affect soil microbes longer, which are often suppressed after fire for months (Ahlgren and Ahlgren, 1965; Tiwari and Rai, 1977; Theodorou and Bowen, 1982; Esquilin et al., 2007). In addition to the negative effect of heat radiation, the decrease in organic matter, which is the energy source of soil microbes, would also limit microbial activity. Further studies are needed to better understand the mechanisms driving burning treatment effects on R_A and R_H .

R_A and R_H estimation showed that thinning treatments decreased overall absolute R_A (except C vs. UO) as well as the contribution of R_A to R_s . Thinning treatments reduced both root biomass and root N content in our study, which is in agreement with previous work by Silver and Vogt (1993). They reported a decrease of 40% in fine live root biomass within 2 months after gap creation and an N content loss proportional to root mass loss in a wet forest of Puerto Rico. We believe that the reduced biomass is simply a consequence of root mortality with the harvesting of trees. The decrease in the contribution of R_A to R_s was mainly due to the increase in absolute R_H after thinning. R_H is positively related to temperature and moisture conditions (Yi et al., 2006; Tuomi et al., 2007), and both of these factors can be influenced by thinning. Mechanical thinning increases canopy opening, which increases the amount of sunlight reaching the forest floor and decreases water interception by the canopy. Simultaneously, thinning decreases belowground root biomass. Consequently, we would expect a reduction in competition for water and nutrients. Therefore, thinning treatments would facilitate R_H in this water deficient and nutrient poor environment. Our results indicated that R_s was controlled more by R_H after the thinning treatments, while R_A was a greater influence after the burning treatments.

The group of environmental variables selected during the stepwise process was different among alternative combinations of treatments (Table 1). This suggested that two tested management practices might intervene to change the conventional relationship between soil characteristics and R_s within a few years after treatments. We also observed that tested soil variables changed the direction and magnitude of their relationship with R_s under different combinations of burn and thin treatments, which also suggested that management practice could significantly influence the soil respiration process (Fig. 2). The multiple linear regression models generally explained more than 37% of the variation in R_s in

most treatments, but only 20 and 6% of the variation was explained by tested variables in UO and BO, respectively (Table 1).

The increase in fine root N concentration (Table 2) with burning and thinning treatments suggested higher N availability under these treatments associated with increased TN. Previous studies have revealed that increases in soil N availability resulted in increased fine root N concentration (Jones et al., 1994; Maier and Kress, 2000; Persson et al., 1998; Son and Hwang, 2003) and decreased fine root biomass (Alexander and Fairley, 1983; Gower and Vitousek, 1989; Gower et al., 1992; Maier and Kress, 2000; Son and Hwang, 2003). Reduced root biomass after both treatments might be partially due to higher root N concentration. However, we believe that the main reasons for root biomass reduction were likely to be root mortality from aboveground biomass removal (i.e., thinning) and from heat during the burn.

We found that both treatments generally reduced the fine root biomass at both the 0–10 and 10–20 cm depth in soil (Table 2). The effect of burning on fine root biomass was more apparent in the top layer (Table 2). Our results agreed with previous studies showing fine root reduction for several years after canopy removal (Silver and Vogt, 1993) and burning (Burke and Zepp, 1997).

Multiple regression analysis also indicated that LD might be an important factor influencing R_s (Table 1). Euskirchen et al. (2003) and Maier and Kress (2000) also reported the importance of litter depth on soil respiration in managed forest ecosystems. It was not clear why LD in UU (understory thin only) was lower than that in C and UO (overstory thin only) (Fig. 1). UU showed relatively high soil pH, TN, and TC indicating high organic matter influx, which implies that it likely experienced high rates of litter layer decomposition; UU had the highest TN and TC among unburned treatments. This could contribute to the relatively low LD in UU.

5. Conclusions

Commonly used western forest restoration practices such as mechanical thinning and prescribed burning significantly alter the soil environment. We found that burning decreased R_s and thinning increased R_s in a mixed-conifer Sierran forest, and that environmental factors influencing R_s were altered by both thinning and burning treatments. When we assumed the uniform contribution of R_A and R_H to R_s in a forest ecosystem without disturbances and a linear relationship of root N content and R_A , we found that R_s was controlled more by R_H after thinning, while after burning R_s was more influenced by R_A . Further study is needed to better understand the potential effects of different forest management practices on soil respiration and on changes in the biomass and activity of root and soil microorganisms. Understanding the interaction between soil respiration and management can help us accomplish sustainable carbon management in forest ecosystems, as soil respiration is a major component of ecosystem respiration.

Acknowledgements

This research was funded by the US Forest Service's Sierra Nevada Research Center, the Joint Fire Science Program, and the University of Toledo. We thank Seang-Youn Choi, Mi-han Lee, James Innes, Harold Zald, Josh Reed, and all the summer technicians during the 2002 field season for helping with data collection. We also appreciated constructive suggestions from Dr. Joan L. Walker in US Forest Service and LEES Laboratory members at the University of Toledo.

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.

- Alexander, I.J., Fairley, R.L., 1983. Effect of N fertilization on populations of fine roots and mycorrhizas in spruce humus. *Plant Soil* 71, 49–53.
- Burke, R.A., Zepp, R.G., 1997. Effect of fire on soil-atmospheric exchange of methane and carbon dioxide in Canadian boreal forest sites. *J. Geophys. Res.* 102, 29289–29300.
- Burton, A.J., Pregitzer, K.S., 2003. Field measurements of root respiration indicate little to no seasonal temperature acclimation for sugar maple and red pine. *Tree Physiol.* 23, 273–280.
- Burton, A.J., Pregitzer, K.S., Zogg, G.P., Zak, D.R., 1998. Drought reduces root respiration in sugar maple forests. *Ecol. Appl.* 8, 771–778.
- Campbell, J.L., Sun, O.J., Law, B.E., 2004. Supply-side controls on soil respiration among Oregon forests. *Global Change Biol.* 10, 1857–1869.
- Concilio, A., Ma, S., Li, Q., LeMoine, J., Chen, J., North, M., Jensen, R., Moorhead, D., 2005. Soil respiration response to burning and thinning in mixed conifer and hardwood forests. *Can. J. For. Res.* 35, 1581–1591.
- Concilio, A., Ma, S., Ryu, S., North, M., Chen, J., 2006. Soil respiration response to experimental disturbances over 3 years. *For. Ecol. Manage.* 228, 82–90.
- Concilio, A., Chen, J., Ma, S., North, M., in press. Precipitation patterns drive inter-annual variation in soil respiration in an old-growth mixed conifer forest. *Climatic Change*. doi:10.1007/s10584-008-9475-0.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4, 217–227.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–190.
- Ekblad, A., Nordgren, A., 2002. Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability? *Plant Soil* 242, 115–122.
- Epron, D., Farque, L., Lucot, E., Badot, P.M., 1999. Soil CO₂ efflux in a beech forest: dependence on soil temperature and soil water content. *Ann. For. Sci.* 56, 221–226.
- Erickson, H.E., Soto, P., Johnson, D.W., Roath, B., Hunsaker, C., 2005. Effects of vegetation patches on soil nutrient pools and fluxes within a mixed-conifer forest. *For. Sci.* 51, 211–220.
- Esquilin, A.E.J., Stromberger, M.E., Massman, W.J., Frank, J.M., Shepperd, W.D., 2007. Microbial community structure and activity in a Colorado Rocky mountain forest soil scarred by slash pile burning. *Soil Biol. Biochem.* 39 (5), 1111–1120.
- Euskirchen, E.S., Chen, J., Gaustafson, E.J., Ma, S., 2003. Soil respiration at dominant patch types within a managed northern Wisconsin landscape. *Ecosystems* 6, 595–607.
- Gower, S.T., Vitousek, P.M., 1989. Effects of nutrient amendments on fine root biomass in a primary successional forest in Hawaii. *Oecologia* 81, 566–568.
- Gower, S.T., Vogt, K.A., Grier, C.C., 1992. Carbon dynamics of Rocky mountain Douglas-fir: influence of water and nutrient availability. *Ecol. Monogr.* 62, 43–65.
- Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115–146.
- Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Höglberg, M.N., Nyberg, G., Ottosson-Lofvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411, 789–792.
- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7, 269–278.
- Johnston, C.A., Groffman, P., Breshears, D.D., Cardon, Z.G., Currie, W., Emanuel, W., Gaudinski, J., Jackson, R.B., Lajtha, K., Nadelhoffer, K., Nelson Jr., D., Post, W.M., Retallack, G., Wielopolski, L., 2004. Carbon cycling in soil. *Front. Ecol. Environ.* 2, 522–528.
- Jones, H.E., Hogberg, P., Ohlsson, H., 1994. Nutritional assessment of a forest fertilization experiment in northern Sweden by root assays. *For. Ecol. Manage.* 64, 59–69.
- Lal, R., 2008. Soil carbon stocks under present and future climate with specific reference to European ecoregions. *Nutr. Cycl. Agroecosyst.* 81, 113–127.
- Lee, K.-H., Jose, S., 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. *For. Ecol. Manage.* 185, 263–273.
- 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.
- Lloyd, J., Taylor, J.A., 1994. On the temperature-dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- 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.
- 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.
- Mabuhay, J.A., Nakagoshi, N., Isagi, Y., 2006. Soil microbial biomass, abundance, and diversity in a Japanese red pine forest: first year after fire. *J. For. Res.* 11, 165–173.
- Maier, C.A., Kress, L.W., 2000. Soil CO₂ evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. *Can. J. For. Res.* 30, 347–359.

- 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. US Forest Service General Technical Report 186.
- Persson, H., Ahlstrom, K., Clemensson-Lindell, A., 1998. Nitrogen addition and removal at Gardsjon-effects on fine-root growth and fine-root chemistry. *For. Ecol. Manage.* 101, 199–205.
- Pregitzer, K.S., Laskowski, M.J., Burton, A.J., Lessard, V.C., Zak, D.R., 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiol.* 18, 665–670.
- Pussinen, A., Karjalainen, T., Makipaa, R., Valsta, L., Kellomaki, S., 2002. Forest carbon sequestration and harvests in Scots pine stand under different climate and nitrogen deposition scenarios. *For. Ecol. Manage.* 158, 103–115.
- Pypker, T.G., Fredeen, A.L., 2002. Ecosystem CO₂ flux over two growing seasons for a sub-Boreal clearcut 5 and 6 years after harvest. *Agric. For. Meteorol.* 114, 15–30.
- Raich, J.W., Potter, C.S., 1995. Global patterns of carbon-dioxide emissions from soils. *Global Biogeochem. Cycle* 9, 23–36.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y.F., Grunzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J.M., Pereira, J.S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., Yakir, D., 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem. Cycles* 17 (article no. 1104).
- Rout, S.K., Gupta, S.R., 1989. Soil respiration in relation to abiotic factors, forest floor litter, root biomass and litter quality in forest ecosystems of Siwaliks in northern India. *Acta Oecol.-Oecol. Plant.* 10, 229–244.
- Rustad, L.E., Huntington, T.G., Boone, R.D., 2000. Controls on soil respiration: implications for climate change. *Biogeochemistry* 48, 1–6.
- Ryu, S., Chen, J., Zheng, D., Bresee, M.K., Crow, T.R., 2006. Simulating the effects of prescribed burning on fuel loading and timber production (EcoFL) in managed northern Wisconsin forests. *Ecol. Model.* 196, 395–406.
- Savin, M.C., Gorres, J.H., Neher, D.A., Amador, J.A., 2001. Biogeophysical factors influencing soil respiration and mineral nitrogen content in an old field soil. *Soil Biol. Biochem.* 33, 429–438.
- Silver, W.L., Vogt, K.A., 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *J. Ecol.* 81, 729–738.
- Son, Y., Hwang, J.H., 2003. Fine root biomass, production and turnover in a fertilized *Larix leptolepis* plantation in central Korea. *Ecol. Res.* 18, 339–346.
- Theodorou, C., Bowen, G.D., 1982. Effects of a bushfire on the microbiology of a South Australian low open (dry sclerophyll) forest soil. *Aust. For. Res.* 12, 317–327.
- Tiwari, V.K., Rai, B., 1977. Effect of soil burning on microfungi. *Plant Soil* 47, 693–697.
- Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., Liski, J., 2007. Heterotrophic soil respiration—comparison of different models describing its temperature dependence. *Ecol. Model.* 211 (1–2), 182–190.
- Uchida, M., Nakatsubo, T., Horikoshi, T., Nakane, K., 1998. Contribution of microorganisms to the carbon dynamics in black spruce (*Picea mariana*) forest soil in Canada. *Ecol. Res.* 13, 17–26.
- Varner, J.M., Gordon, D.R., Putz, F.E., Hiers, J.K., 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel effects and consequences for long-unburned ecosystems. *Restor. Ecol.* 13, 536–544.
- Wuthrich, C., Schaub, D., Weber, M., Marxer, P., Conedera, M., 2002. Soil respiration and soil microbial biomass after fire in a sweet chestnut forest in southern Switzerland. *Catena* 48, 201–215.
- Yi, Y., Xu, M., Zou, X., 2006. Heterotrophic soil respiration in relation to environmental factors and microbial biomass in two wet tropical forests. *Plant Soil* 281 (1–2), 193–201.