Soil respiration response to prescribed burning and thinning in mixed conifer and hardwood forests

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Abstract

The effects of management on soil carbon efflux in different ecosystems are still largely unknown, yet crucial to both our understanding and management of global carbon flux. In order to compare the effects of common forest management practices on soil carbon cycling, we measured soil respiration rate (SRR) in a mixed-conifer and hardwood forest that had undergone various treatments from June to August of 2003. The mixed-conifer forest, located in the Sierra Nevada Mountains of CA, was treated with thinning and burning manipulations in 2001 and the hardwood forest, located in the southeastern Missouri Ozarks, was treated with harvesting manipulations in 1996 and 1997. Litter depth, soil temperature, and soil moisture were also measured. We found that selective thinning produced a similar effect on both forests by elevating SRR, soil moisture, and soil temperature, although the magnitude of response was greater in the mixed-conifer forest. Selective harvest increased SRR by 43 % (from 3.38 to 4.82 µmol m\(^{-2}\) s\(^{-1}\)) in the mixed conifer forest and by 14 % (from 4.25 to 4.84 µmol m\(^{-2}\) s\(^{-1}\)) in the hardwood forest. Burning at the conifer site and even-aged harvesting at the mixed-hardwood site did not produce significantly different SRR from controls. Mean SRR were 3.24, 3.42, and 4.52 µmol m\(^{-2}\) s\(^{-1}\), respectively. At both sites manipulations did significantly alter SRR by changing litter depth, soil structure, and forest microclimate. SRR response varied by vegetation patch type- the scale at which treatments altered these biotic factors. Our findings provide forest managers first-hand information on the response of soil carbon efflux to various management strategies in different forests.

Key Words: management, harvest, prescribed burn, litter depth, patch, temperature, moisture, TEF, MOFEP
Introduction

In recent years, the scientific community has identified the need for additional study of carbon flux in both naturally-disturbed (Baker 1995, Dale et al. 2001, Lindenmayer et al. 2004) and managed ecosystems (Chen et al. 2004, Schultze et al. 2000) because of their widespread distribution in terrestrial landscapes. As atmospheric CO$_2$ concentrations continue to rise, it is important to identify and encourage management strategies that promote terrestrial carbon sequestration. Soils are one of the largest carbon pools (Post et al. 1982) and, therefore, changes in soil respiration rates (SRR) can have profound effects on carbon cycling. Several studies have examined the effects of forestry disturbances on SRR (e.g., Gordon et al. 1987, Kowalski et al. 2003, Ma et al. 2004), but it is still uncertain how the interaction of time since disturbance, management type, and forest ecosystem type affect SRR.

An ideal approach to examining the influences of different management techniques on SRR would be a field experiment with different treatments in which vegetation, soil, microclimate, and associated ecological processes (e.g., belowground carbon allocation) are recorded simultaneously. However, few field sites can be so strictly controlled or have the necessary infrastructure to facilitate complete data collection. Our study focused on two experimental forests where extensive research has been conducted and, consequently, key microclimatic variables, ecosystem processes, and structural characteristics have been well documented. Although the two sites differ in climate, soil, and vegetation, studies in both were designed to test how different forest management treatments can influence ecological processes; we also used the same sampling protocol at both sites. Thus, we were able to compare SRR response to
management in different ecosystems to determine if treatments affect SRR similarly regardless of forest ecosystem type.

The mechanisms driving soil respiration may be affected by disturbance but the response may differ with ecosystem type (Euskirchen et al. 2003, Zheng et al. 2005). Many studies have shown that microclimate affects SRR (e.g., Raich and Schlesinger 1992, Schlentner and Van Cleve 1985, Singh and Gupta 1977) and that management can have immediate effects on microclimate. For example, altering a forest canopy can affect solar radiation, air and soil temperature, soil moisture, and humidity (Chen et al. 1999, Ma et al. 2004, Zheng et al. 2000). Thus, we were interested in determining key SRR drivers under different management scenarios via controlled experiments within the two forest ecosystems. In particular, temperature is widely used to describe variation in SRR, usually in $Q_{10}$ models, in which SRR rises exponentially by a constant rate with every $10^\circ$C increase in temperature (Lundegardh 1927). Predictive capabilities usually increase by adding soil moisture, especially in water-stressed ecosystems. Models with these two drivers are often sufficient to explain much of the variation in SRR (e.g., Epron et al. 1999, Janssens et al. 2000, Schlentner and Van Cleve 1985). However, SRR can be influenced by many additional variables, such as soil type, nutrient availability, phenology and vegetative cover type (Singh and Gupta 1977). Photosynthesis might also be important in driving respiration by controlling belowground carbon allocation, rhizosphere respiration, microbial activities, and nutrient quality and quantity (Högberg et al. 2001). Many of these variables may be effected by forest management. It is, therefore, important to consider them as potential influences on SRR under different management regimes.
In this study, we measured SRR after prescribed burning and thinning to determine how management influences SRR in a conifer and a hardwood forest ecosystem. Our study objectives were to: (1) examine the changes of SRR caused by burning and thinning at a hardwood and a conifer forest, and (2) explore the potential effects of management on soil respiration by relating SRR to specific biophysical variables, including soil temperature and moisture, litter depth, vegetative patch type, and treatment type.

**Methods**

**Study Sites**

Teakettle Experimental Forest (TEF) is located in the Sierra National Forest on the western side of the Sierra Nevada mountain range of California (36°58’N, 119°2’W Figure 1A). It includes 1300 ha, ranges in elevation from 1980 to 2590 m, and is mostly south facing with an average slope of 10% (North et al. 2002). TEF has a Mediterranean climate with hot, dry summers and cold, wet winters and receives an annual average 1250 mm of precipitation, mostly in the form of snow between November and May (North et al. 2002). Mean air temperature ranges from 15.5 °C in the summer to 0.7 °C in the winter (Figure 2). Soil orders are Inceptisols and Entisols and mean litter depths range from 5.4 cm in mixed conifer closed canopy to 0.7 cm in open canopy patches (North et al. 2002). Mean canopy height is 50m, ages range up to 420 years old and mean DBH ranges from 35cm (red fir) to 53cm (Jeffrey pine; North et al. *in press*). Mean soil temperature ($T_s$), soil moisture ($M_s$), and litter depth (LD) vary by patch type and treatment (Table1).
TEF is a patchy ecosystem composed mainly of groups of mixed-conifer trees interspersed with vegetation-free zones and shrub-covered areas dominated by the nitrogen fixing mountain whitethorn (*Ceanothus cordulatus* Kellogg.), which accounts for almost 1/3 of the total shrub cover (North et al. 2002). Three dominant vegetation patch types have been classified using hierarchical clustering analysis: closed canopy (CC), open canopy (OC), and ceanothus shrub (CECO). They occupy 67.7, 13.4, and 4.7% of the entire forest area, respectively (North et al. 2002), with the remainder composed mostly of exposed rock. Dominant conifer species include white fir (*Abies concolor* Lindl. ex Hildebr), Jeffrey pine (*Pinus jeffreyi* Grev. and Balf), sugar pine (*Pinus lambertiana* Douglas), red fir (*Abies magnifica* A. Murr), and incense cedar (*Calocedrus decurrens* (Torr.) Florin). Dominant understory shrub species include mountain whitethorn (*Ceanothus cordulatus* Kellogg.), bush chinquapin (*Chysolepsis sempervirens* (Kellogg) Hjelmqvist), pinemat manzaita (*Arctotaphylos nevadensis* Gray), snowberry (*Symphoricarpos mollis* Nutt.), green leaf manzaita (*Arctostaphylos patula* Greene), bitter cherry (*Prunus emarginata* (Dougl. ex Hook.) D. Dietr.), red flowering currant (*Ribes sanguineum* Pursh), Sierra gooseberry (*R. roezlii* Regel), and hazelnut (*Corylus cornuta* Marsh. var. californica). Of the 123 herb species identified at TEF, the most common was *Monardella odoratissima* Benth. and *Lupinus adsurgens* E. Drew (North et al. 2002).

The Missouri Ozark Forest Ecosystem Project (MOFEP) is located in the southeastern Missouri Ozarks (19° 12’ W and 37° 6’ N, Figure 1B). The majority of the landscape lies at less than 300 m in elevation (Xu et al. 1997), slopes range from 2-39 % with an average of 24 %, and aspect range from 10-340 with an average of 160 (Roovers...
The climate is humid and experiences extremes in precipitation, wind, and temperature (Figure 2) that influence species distribution, through drought and wind-throw (Chen et al. 1997). MOFEP receives an annual average of 1120 mm of precipitation and experiences a mean annual temperature of 13.3 °C (Chen et al. 1997). The soils are mostly Alfisols and Ultisols (Kabrick et al. 2000a). Mean $T_s$, $M_s$, and LD vary by patch type (or ecological land type phase, explained below) and treatment (Table 1).

MOFEP’s old-growth trees are about 90 years old, mean canopy height is 15.6 m, and mean DBH by species ranges from 4.5 cm to 22.8 cm (Roovers 2000). Dominant overstory species include white oak ($Quercus alba$ L.), black oak ($Q. velutina$ Lam.), scarlet oak ($Q. cocinea$ Muenchh.), shortleaf pine ($Pinus echinata$ P. Mill.), and hickories ($Carya spp$). The most common understory species include flowering dogwood ($Cornus florida$ L.), tick trefoil ($Desmodium nudiflorum$ (L.) DC.), sassafrass ($Sassafras albidum$ (Nutt.) Nees), summer grape ($Vitis aestivalis$ Michx.), black oak, white oak, hog peanut ($Amphoricarpa bracteata$ (L.) Fern.), Virginia creeper ($Parthenocissus quinquefolia$ (L.) Planch.), and blackgum ($Nyssa sylvatica$ Marsh.) (Grabner 2000).

The study sites at MOFEP were classified into Ecological Landtypes (ELT; Kabrick et al. 2000a). Information on geology, soils, and vegetation was included to expand the classification scheme to Ecological Landtype Phases (ELTP; Nigh and Schroeder 2002). We selected six dominant ELTPs for this study, which are referred to as patch types throughout the remainder of the paper: high ultic shoulder/shoulder-ridge or bench (HUS), exposed ultic back-slope (EUB), protected ultic back-slope (PUB),
exposed alfic back-slope (EAB), protected alfic back-slope (PAB), and alfic bench or shoulder-ridge (ABS).

**Experimental Treatments**

At TEF, all experiments were conducted within 18, four-hectare square plots, which were scaled and placed based on variogram and cluster analysis to achieve equal representative percentages of the three main mixed-conifer patch types (North et al. 2002). Three replicates of each of six treatments were assigned to the 18 plots. Treatments were a full factorial design of burning and no burning crossed with no thinning, understory thinning and overstory thinning. Ten plots were randomly selected for sampling in this study to provide replication of each of treatment combination (Figure 1A.). The two types of thinning were combined so that the four management types are: burn only (B), thin only (T), burned and thinned (D), and undisturbed (C). Sampling points at TEF were stratified by three dominant patch types and then randomly selected from a set of established grid points at 25-m intervals located within the four-ha study plots. A minimum of ten replicate patches for each combination of patch type (CC, OC, CECO) and treatment (C, B, T, D) were measured during the 2003 summer.

MOFEP sites were harvested according to even-aged or uneven-aged management in 1996. Missouri Department of Conservation (MDC) Forest Land Management Guidelines were used to define even-aged (E), uneven-aged (U) and no harvest (C) treatments (MDC. 1986). The three management techniques were randomly assigned to nine sites, ranging from 260-527 ha (Xu et al. 1997), using a randomized complete block design (Brookshire et al. 1997). Although even-aged management included a combination of clearcutting and intermediate thinning, our sampling points
were only located within the clearcut areas. Uneven-aged treatments consisted of
harvesting by both single-tree selection and group selection (Kabrick et al. 2000b), but
our plots were all located in areas of single-tree selection. Twelve replicates of each
treatment type (U, E, C) were sampled with at least one (but usually 3) ELTP per
treatment type. The exception was HUS, which did not exist in an even-age managed
plot and was only sampled in the control and uneven-aged plots. Each sampling point
included 8 sub-samples of SRR.

Field Data Collection
A similar protocol was used for collection of field data at both sites. Measurements of
SRR were taken biweekly from June to August at each sampling point with portable
infrared gas analyzers (EGM-2 and EGM-4 Environmental Gas Monitor, PP Systems,
UK) and attached SRC-1 Soil Respiration Chambers (PP Systems, UK). SRR
measurements were taken on PVC collars, which were inserted about 3 cm into the
ground (collars were 5 cm tall) at least one week before measurements were taken to
ensure the soil environment was not disturbed at the time of sampling. SRR
measurements were taken over a 2-minute period between 9:00 and 16:00 hours to
minimize effects of diurnal fluctuation. Simultaneous to SRR measurements, handheld
thermometers (Taylor Pocket Digital Thermometer) measured 10-cm soil temperature
within 30 cm of the PVC collar. Soil moisture between 0-15 cm depth was measured
using a Time Domain Reflectometry unit (Model 6050XI Soil Moisture Equipment
Corp., Santa Barbara, California, USA) within 6 days of soil respiration sampling
provided that no precipitation events occurred in the interim. Past research at TEF has
shown that soil moisture varies little over the period of a week in the summer (Ma et al. 
in press). The EGMs were calibrated weekly with standard, 700-ppm CO\textsubscript{2} gas under
ambient air pressure, and barometric pressure readings were taken at the time of sampling
to correct for differences in pressure.

Statistical Analyses

Data included SRR, soil temperature at 10 cm depth (T\textsubscript{s}), soil moisture between 0-15 cm
depth (M\textsubscript{s}), and litter depth (LD) at each sampling point at both sites during the same six
sampling periods from June 1\textsuperscript{st} to August 31\textsuperscript{st}, 2003. SRR measurements at TEF were
corrected for machine error (Ma et al. in press) since the EGM has been found to
overestimate SRR in these conditions (Butnor and Johnsen 2004). Log transformations
were made on SRR and M\textsubscript{s}; Shapiro-Wilks tests (Zar 1999) indicated that all data used in
analyses were distributed normally, except for LD. Significance was determined based
on an alpha of 0.05 unless otherwise stated.

Differences among means were tested with repeated measures analysis of
variance (ANOVA; V8.0, SAS Institute Inc., Cary, North Carolina, USA). A two-way
nested ANOVA was used to test if mean SRR was different by site and management
within site. For this analysis, treatments were pooled together as managed (harvested,
thinned, burned) and unmanaged (control). For all other tests, treatments were considered
separately by type (i.e., burned, burned-thinned, thinned, control, even-aged
management, uneven-aged management). Two-way, repeated measures, mixed linear
model ANOVA were used to identify significant differences in SRR, T\textsubscript{s}, and M\textsubscript{s} between
patch (PT) and treatment (TRT) types within each site. Kruskal-Wallis tests (Zar 1999)
were conducted to determine differences in LD by TRT and PT because LD could not be
normalized. We measured the degree of change in SRR, T_s, M_s, and LD with treatment by calculating the percent change as the difference between the mean undisturbed and disturbed value divided by the mean undisturbed value for each sampling date.

To determine the major influences on SRR at each site and within each management regime, we began our analyses with a focus on T_s and M_s, which have often been found to predict soil respiration in most ecosystems and based on earlier work in TEF by Ma et al. (*in press*). We used two nonlinear regression models: (1) the $Q_{10}$ model, which focuses on temperature alone (Lundegardh 1927), and (2) a regression model that incorporated both temperature and moisture (Euskirchen et al. 2003):

$$[1] \quad \text{SRR} = \beta_1 e^{T_s \beta_2}$$

$$[2] \quad \text{SRR} = b_0 \times e^{(b_1 T_s)} \times e^{(b_2 M_s)} \times b_3 \times T_s \times M_s$$

where $\beta_1$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$), $\beta_2$ (°C$^{-1}$), $b_0$, $b_1$, $b_2$, and $b_3$ are coefficients estimated through regression analysis for each site and site-treatment regime. These models are based on the assumption that $T_s \geq 0^\circ$C. Model (2) was adjusted to meet convergence criteria for TEF (2.A) and MOFEP (2.B):

$$[2.A] \quad \text{SRR} = e^{(b_1 T_s)} \times e^{(b_2 M_s)} \times T_s \times M_s$$

$$[2.B] \quad \text{SRR} = e^{(b_1 T_s)} \times e^{(b_2 M_s)} \times T_s \times M_s + b_3$$
where \( b_1, b_2, \) and \( b_3 \) are coefficients estimated through regression analysis and are unique to each site and site-treatment combination. The nonlinear regression procedure (V8.0, SAS Institute Inc., Cary, North Carolina, USA) was used to test the predictive strength of these models for our data.

Previous studies at TEF have found that PT has an important influence on SRR (Ma et al. *in press*) so we used Spearman correlation analysis (Zar 1999) to identify other variables that might drive SRR. Based on these results, we added additional analyses to determine if a model incorporating LD and PT would improve predictive abilities of log transformed SRR:

\[
SRR = f(T_s M_s LD PT TRT)
\]

We also ran the same model without TRT for each site-treatment combination to determine how influences on SRR may change with management:

\[
SRR = f(T_s M_s LD PT)
\]

All nonlinear and general linear models were based on mean data by sampling period, patch, treatment type, and site with a minimum sample size of 48 at the TEF and 56 at MOFEP. Model (3) and (4) were examined with iterative models incorporating different combinations of independent variables to explore the relative contribution of each variable to the overall model. Variables found to consistently make a significant (model
p-value was $\leq 0.10$) contribution to the model $R^2$ value ($\geq 0.20$) were retained in the final model formulation.

**Results**

*SRR Response to Experimental Treatments*

SRR differed significantly by site and by management within site (Figure 3, Table 2). In addition, SRR responded differently by treatment and patch type within the two sites (Table 2). In general, management increased SRR at both sites (Figure 3) but only selective thinning had a significant effect on SRR when treatment types were separated (Figure 4A). Average SRR was 43% higher in thinned than control plots at TEF (4.82 and 3.38 µmol m$^{-2}$ s$^{-1}$, respectively) and 14 % higher at MOFEP (4.84 and 4.25 µmol m$^{-2}$ s$^{-1}$, respectively). Soil temperature ($T_s$), soil moisture ($M_s$), and litter depth (LD) were significantly affected by management at TEF (Figure 4B.1, C.1, and D.1), but not at MOFEP (Figure 4B.2, C.2, and D.2).

The management-induced percent change (%Δ) in SRR, $T_s$, and $M_s$ clearly differed by treatment types at the TEF (Figure 5A) but not at MOFEP (Figure 5B). At TEF, treatment effects on $M_s$ were especially evident: thinning treatments producing the greatest change of +20 to 40% for most sampling dates; burned and burned-thinned treatments ranged between −10 and +10 % Δ. $T_s$ response also differed by treatment but to a lesser degree than $M_s$. $T_s$ changed least with thinning-only treatments (+2 to 20%), while burning-only produced a change of −2 to +28%, and burning and thinning produced a 13 to 50% increase. The range of %Δ SRR was highest in thinned plots (+30 to 70% with one outlier at 1%), followed by burned (-28 to +17%), and burned-thinned plots (-
26 to +10%). In contrast, no clear trends existed at MOFEP (Figure 5B), where all
variables exhibited both positive and negative responses without any particular pattern.
A wide range of change in $M_s$ (-35 to +166%) and a much smaller range of change in $T_s$
(-3.9 to +2.4%) existed regardless of treatment.

At both sites, SRR, $T_s$, $M_s$, and LD responded differently to management
depending on patch type (Figure 6, Table 1). SRR was significantly different by
treatment type in CC ($F_{3,15}= 4.40, p=0.021$) and CECO patches ($F_{3,15} = 8.09, p=0.002$),
but not in OC patches ($p=0.269$) at TEF. At MOFEP, SRR was significantly different by
treatment type in PUB ($F_{2,12} = 7.12, p=0.009$) and ABS ($F_{2,8} = 9.77, p=0.007$) patches,
but not in the others. The direction of SRR response to management varied by patch type:
mean SRR at uneven aged thinned sites increased compared to control in PUB, PAB and
ABS and decreased at EUB, and EAB.

Post-Management Influences on SRR

Regression analyses indicated that soil temperature ($T_s$) and moisture ($M_s$) explained little
variation of SRR during the summer season in either forest, suggesting that other
biophysical factors, such as vegetation types and litter depths, may have regulated post-
managed SRR. The $Q_{10}$ model failed to explain more than 5% of SRR variation in either
forest, but model $R^2$ did improve slightly when applying the model by treatment type at
the TEF. The strongest relationship between SRR and $T_s$ was found in the burned
($R^2=0.17, F=141.7$) and burned-thinned ($R^2= 0.12, F=95.1$) plots at TEF; the model did
not improve for the thinned ($R^2= 0.01, F= 71.5$) or control ($R^2= 0.09, F=127.7$) plots. At
MOFEP, even after separating data by treatment type, the model did not explain more
than 5% of SRR variation in any case. These extremely low values were probably due, in
part, to the low range in $T_s$ ($\sim 11^\circ C$) at MOFEP compared to TEF.

The nonlinear $T_s-M_s$ model also failed to provide strong predictive power at either
site ($R^2 < 0.25$), but did improve in some cases when applied to each treatment type
separately. For example, for burned plots at TEF the model explained 36% of variation in
SRR ($F=116.32, p <0.0001$) and at thinned plots, 28% ($F=63.51, p < 0.0001$). At control
plots for MOFEP, the model explained 20% of variation in SRR ($F=2.51, p=0.0778$) but
was not significant ($\alpha=0.05$). These values were very low in comparison to other studies
and we concluded that $T_s$ and $M_s$ were probably not important drivers of SRR during our
sampling period at either forest.

The general linear model using $T_s$, $M_s$, LD, patch, and treatment type as
independent variables explained more variation in SRR at TEF ($R^2 = 0.69$) and at
MOFEP ($R^2 = 0.36$; Table 3) than earlier models. The model yielded an improved fit
when data were analyzed by treatment type at TEF and in the uneven-aged thinned stands
at MOFEP ($R^2 = 0.58$). Although the full model best explained variation in SRR, model
$R^2$ values did not change significantly by excluding $T_s$ or $M_s$ at either site (Table 3). At
TEF, a model including litter depth, patch type and treatment explained 68% of the
variation in SRR; omitting $T_s$ and $M_s$ only reduced $R^2$ by 1%. Likewise, patch type and
litter depth explained most of the variation at the control ($R^2 = 0.76$), burned ($R^2 = 0.56$),
thinned ($R^2 = 0.65$), and burned-thinned ($R^2 = 0.68$) plots at TEF. At MOFEP, patch and
treatment explained 35% of the variation, again only 1% less than the full model. In the
control ($R^2= 0.29$), uneven-aged thinned ($R^2= 0.52$), and even-aged thinned plots ($R^2=
0.23$), patch type alone explained almost as much of the variation as the full model.
However, these values were relatively low so that the variability in our sampling sites may require more intensive sampling for better model fit.

Discussion

Treatment effects on SRR

Despite some differences in SRR responses to management in the two forests, we found in both cases that SRR differed by patch type and increased with selective thinning. Treatment effects on SRR varied by patch type possibly because burning and thinning have a highly localized effect on biotic conditions produced by the interaction of the disturbance with the existing patch conditions. For example, a patch of shrubs can significantly increase fire intensity, killing more plants and reducing litter; changes which can reduce post-treatment SRR. In contrast fire burning through an open canopy area may have little effect on soil, vegetation or microclimate conditions, and consequently produce little change in SRR, if pre-treatment fuel is sparse. At a stand level, it may be difficult to identify a mean SRR response to management practices without examining the localized interaction of treatments and patch vegetation.

Previous researchers have also found increases in SRR after thinning (Gordon et al. 1987, Hendrickson et al. 1989) and clear-cutting (Kowalski et al. 2003) in other forests. Therefore, increases in SRR may result from a number of common changes to the soil environment including increased insulation and reduced evapotranspiration (Gordon et al. 1987), higher decomposition of dead roots or aboveground litter layer inputs that could stimulate heterotrophic respiration (Rustad et al. 2000), increased litter quality from fresh leaves and needles of logging slash (Fonte and Schowalter 2004), and
living stump roots consumption of starch reserves (Högberg et al. 2001). Additionally, logging slash has been found to promote productivity of soil micro-flora presumably through an increase in moisture and microbial biomass (Sohlenius 1982) thereby increasing SRR (Mattson et al. 1987).

With the burning treatment, SRR did not significantly differ from control plots despite observations that the ranges of SRR and litter depth were much less at burned and burned-thinned plots than within the control (Figure 4). Fire reduced litter depth variability and may have contributed to increased homogeneity in SRR. Previous research has found decreases in microbial biomass after prescribed burning treatments depending on fire intensity (Pietikainen and Fritze 1993), presumably resulting in decreased heterotrophic respiration. Fire can accelerate mineralization by altering soil pH and other soil properties (Whelan 1995) that may affect both plant and microbial growth and thereby change both autotrophic and heterotrophic respiration rates. We found no significant difference in mean effect of fire on SRR, but this does not necessarily signify a lack of response since fire can have both positive and negative effects on SRR.

The magnitude of SRR response to treatments appears to be time-dependent, because effects were much more pronounced at the mixed–conifer site where treatments were more recent. Recovery time was also different based on treatment type; uneven-aged stands at MOFEP had increased SRR while even-aged stands appeared to have recovered to undisturbed levels. Net primary production, litter-fall, foliage biomass, nutrient accumulation, and fine root biomass can reach a maximum at early canopy closure (Fahey and Hughes 1994, Vogt et al. 1987). This might explain quick recovery at
clear-cut sites in MOFEP, where vigorous growth of stump sprouts (Dey and Jensen 2002) and significant growth of ground cover (Grabner and Zenner 2002) have been reported. At TEF, no change in SRR with thinning was reported one year post-disturbance (Ma et al. 2004), while we found that SRR increased significantly two years after thinning treatment. This difference highlights the need to monitor ecosystem response over consecutive years until full recovery is reached.

Post-treatment influences on SRR

Most ecosystem models have successfully used a nonlinear analysis to evaluate SRR response to changes in climate (i.e. temperature and moisture). We found this approach to be inadequate for explaining SRR variation in our systems, possibly due to spatial heterogeneity in vegetative cover and substrate quality, which could have superseded any differences related to climate. Thus, historic reports that SRR is primarily related to soil moisture and temperature may be overstated. However, our SRR sampling regime emphasized extensive observation of many sites rather than intensive observation of fewer sites. This approach may have produced high within-site variation of observations, making it difficult to distinguish among sites.

Patch type helped explain SRR variation at both sites. Previous research has shown that SRR can vary with vegetative cover due to differences in soil microclimate and structure, detritus quantity and quality, and root respiration (Raich and Tufekcioglu 2000). At TEF, patches have different soil chemical properties (Erickson in press), are structurally heterogeneous resulting from long-term fire suppression (North et al. 2002), and are easily distinguishable based on a strong bimodal (>70% or <40%) canopy cover.
distribution (North et al. 2004). At MOFEP, soil types, aspect, and vegetative cover differ by patch (Grabner 2000), which could all potentially influence SRR through both autotrophic and heterotrophic respiration. At both sites, SRR responded differently to treatments based on patch type and model fit varied by interactions between patch and treatment suggesting that identifying influences on SRR in patchy ecosystems can be more complex with management.

Including litter depth (LD) in our general linear models helped explain SRR variation at TEF, but not at MOFEP. A deeper litter layer can increase SRR at TEF by providing food sources to soil microfauna and microflora. It is unclear why LD had no influence on SRR at MOFEP, but the discrepancy may result from the difference in climate between the two sites. TEF has a prolonged summer drought and photosynthesis is likely restricted by limited water availability. Root respiration is probably low because photosynthesis may fix just enough carbohydrates to maintain basic metabolism (Royce and Barbour 2001). Thus, microbial respiration fueled by the litter layer may be the main contributor to SRR in TEF during the summer. Moreover, under water stress, a deep litter layer plays an important role in protecting soil from moisture loss (Brady and Weil 1999). At MOFEP, the forest is in its active growing season during the summer and distinct seasonal temperature and moisture patterns create favorable conditions for both microbial and root respiration. Consequently, the relative contribution of microbial respiration to total SRR may be less important at MOFEP. In addition, MOFEP receives sufficient precipitation throughout the summer so that a deep litter layer would not be essential to the maintenance of soil moisture levels.
Conclusions

Forest management can have profound effects on soil CO$_2$ efflux. We have begun to identify some of these impacts in a mixed-conifer and hardwood forest two and seven years post-disturbance, respectively. However, evaluating management effects requires long-term monitoring because some changes may occur immediately, as we found with selective thinning, while others may occur only after time or under certain climatic conditions. This study will provide an important baseline from which comparisons over subsequent years can be made to better understand effects of time-since-disturbance, inter-annual variability, and forest ecosystem type on SRR response to prescribed burning and different types of thinning. Response of soil CO$_2$ efflux can be an important gauge in evaluating the impacts of forestry management on carbon cycling in general, because both biotic and abiotic factors influence response and both aboveground and belowground processes have to be considered.

Acknowledgements

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**Table 1**: Mean soil temperature ($T_s$), soil moisture content ($M_s$), and litter depth (LD) at TEF and MOFEP by treatment and patch type (CC= closed canopy, CECO= ceanothus shrub, OC= open canopy, HUS= high ultic shoulder/shoulder ridge, EUB= exposed ultic back-slope, PUB= protected ultic back-slope, EAB= exposed alfic back-slope, PAB= protected alfic back-slope, and ABS= alfic bench or shoulder-ridge). Standard errors are in parentheses.

<table>
<thead>
<tr>
<th>Site</th>
<th>Patch Type</th>
<th>Treatment</th>
<th>$T_s$ (°C)</th>
<th>$M_s$ (%)</th>
<th>LD (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEF</td>
<td>CC</td>
<td>Control</td>
<td>13.74 (3.03)</td>
<td>12.17 (3.84)</td>
<td>4.8 (3.9)</td>
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<tr>
<td></td>
<td></td>
<td>Burned</td>
<td>16.90 (4.32)</td>
<td>12.60 (3.40)</td>
<td>0.9 (0.9)</td>
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<tr>
<td></td>
<td></td>
<td>Thinned</td>
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<td>16.33 (5.07)</td>
<td>3.7 (4.4)</td>
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<tr>
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<td>0.7 (0.9)</td>
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<td>CECO</td>
<td>Control</td>
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<td>11.71 (2.29)</td>
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<td>12.72 (3.69)</td>
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<td>12.10 (2.99)</td>
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<td>MOFEP</td>
<td>HUS</td>
<td>Control</td>
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<td>Even-Aged</td>
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<td>EUB</td>
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<td>19.41 (3.24)</td>
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<td>Uneven-Aged</td>
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<tr>
<td>Even-Aged</td>
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<td>2.6 (1.2)</td>
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<tr>
<td></td>
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<tr>
<td>PAB</td>
<td>Control</td>
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<td>21.72 (7.13)</td>
<td>2.2 (0.0)</td>
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<tr>
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<td>19.16 (2.34)</td>
<td>18.96 (8.33)</td>
<td>2.1 (0.0)</td>
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Table 2: ANOVA results comparing SRR between a hardwood (MOFEP) and conifer (TEF) forest, and by management (disturbance vs. control), treatment type (various levels of burning and thinning including control, prescribed burn, selective thin, selective thin followed by prescribed burn, uneven-aged harvest, and even-aged harvest), and patch type (vegetative patch types at TEF and ecological land type phases at MOFEP) within each site.

<table>
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<tr>
<th>ANOVA Model</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F</th>
<th>p</th>
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<td></td>
<td></td>
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<tr>
<td>Site</td>
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<td>Management (site)</td>
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<td>SRR= Treatment Patch</td>
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<tr>
<td>TEF</td>
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<td>Treatment</td>
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<td></td>
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<tr>
<td>Treatment</td>
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<tr>
<td>Patch</td>
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<td>34</td>
<td>7.82</td>
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Table 3: Predictive ability of general linear models describing SRR variation by site in a mixed conifer (TEF) and hardwood (MOFEP) forest and by treatment type within each site. Variables include soil temperature ($T_s$), soil moisture content ($M_s$), litter depth (LD), vegetative patch type (PT), and treatment type (TRT).

<table>
<thead>
<tr>
<th>Site</th>
<th>$SRR = f(T_s \ M_s \ LD \ PT \ TRT)$</th>
<th>$SRR = f(LD \ PT \ TRT)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F$</td>
<td>$p$</td>
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<td></td>
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<tr>
<td></td>
<td>4.92</td>
<td>0.016</td>
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<td></td>
<td>5.77</td>
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<td>MOFEP</td>
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<td></td>
<td>0.62</td>
<td>0.003</td>
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<td>1.92</td>
<td>0.117</td>
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</table>
Figure Captions

Figure 1. Study sites and experimental treatments. (A) Teakettle Experimental Forest (TEF) is located in California’s Sierra Nevada Mountains at 36° 58’ N, 119° 2’ W and (B) Missouri Ozark Forest Ecosystem Project (MOFEP) is located in southeastern Missouri at 19° 12’ W and 37° 6’ N. Treatment types at TEF included control (C), prescribed burn (B), selective thin (T), and selective thin followed by a prescribed burn (D). At MOFEP, treatment types are control (C), uneven-aged management (U), and even-aged management (E).

Figure 2. Comparisons of annual microclimatic patterns in 2003: (A) daily mean air temperature (T_a), and (B) soil volumetric moisture (M_s) at TEF (black line) and MOFEP (gray line). The SRR sampling period is identified with the two vertical, dashed lines. Hourly data was collected by 18 microclimate stations in TEF and 9 stations in MOFEP and results were averaged by day.

Figure 3: Mean SRR with standard error at each study site by disturbance. All treatment types were grouped together and compared to the control plots.

Figure 4: Box and whisker plots including the median (notch), mean (line), 25 and 75% quartiles and extreme values at the TEF (left) and MOFEP (right). Plots represent soil respiration rate (SRR; A.1 & A.2), soil temperature (T_s; B1 & B2), soil volumetric moisture (M_s; C.1 & C.2), and litter depth (LD; D.1 & D.2) grouped by experimental treatments, including control (C), prescribed burn (B), thin (T), and thin plus burn (D) at the TEF; and control (C), even-age management (E), and uneven-age management (U) at MOFEP. Significant differences (α = 0.05) by treatment type within each site are labeled with different letters.
Figure 5: Percent change of treated to control sites in soil respiration rate (dSRR), soil moisture (dMₚ), and soil temperature (dTₛ) as a measure of degree of response to each of the experimental treatments, including prescribed burn (B), thin (T), and thin plus burn (D) at the TEF; and uneven-age management (U) and even-age management (E) at MOFEP.

Figure 6: Mean and standard error of soil respiration rate (SRR) by patch type and treatment type at the TEF (A) and MOFEP (B). Patch types at the TEF include closed canopy (CC), ceanothus shrub (CECO), and open canopy (OC). At MOFEP, patch types include high ultic shoulder/shoulder-ridge, bench (HUS), exposed ultic back-slope (EUB), protected ultic back-slope (PUB), exposed alfic back-slope (EAB), protected alfic back-slope (PAB), alfic bench or shoulder-ridge (ABS). Treatments are control (C), prescribed burn (B), thin (T), and thin plus burn (D) at TEF and control (C), uneven-aged management (U), and even-aged management (E) at MOFEP. Significantly different SRR (α= 0.05) within each patch type by treatment are labeled with different letters.
Figure 3

The graph shows the SRR (µmol m\(^{-2}\) s\(^{-1}\)) for TEF and MOFEP under undisturbed and disturbed conditions. The undisturbed conditions are represented by solid bars, while the disturbed conditions are represented by hatched bars. The SRR values for TEF under undisturbed conditions are approximately 3.5 µmol m\(^{-2}\) s\(^{-1}\), and for MOFEP under disturbed conditions, the value is slightly higher at around 4.5 µmol m\(^{-2}\) s\(^{-1}\).
Figure 5
Figure 6

(A) SRR (µmol m⁻² s⁻¹) for different patch types and treatments. Bars with different letters (a, b, c) indicate significant differences.

(B) Further analysis showing additional details of the SRR data.

Patch Type: HUS, EUB, PUB, EAB, PAB, ABS.