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. 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 2003. The mixed-conifer forest, located in the Sierra Nevada Mountains of California, had been treated with thinning and burning manipulations in 2001, and the hardwood forest, located in the southeastern Missouri Ozarks, had been 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in the mixed-conifer forest and by 14% (from 4.25 to 4.84 $\mu mol \cdot m^{-2} \cdot s^{-1}$) 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$, 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.

Résumé : Bien que cruciaux pour comprendre et gérer le flux global de carbone, les effets de l'aménagement sur les émissions de carbone du sol dans différents écosystèmes sont encore largement inconnus. Afin de comparer les effets des pratiques courantes d'aménagement forestier sur le recyclage du carbone du sol, les auteurs ont mesuré le taux de respiration du sol (TRS) dans une forêt mélangée de conifères et une forêt feuillue qui avaient subi différents traitements de juin à août 2003. La forêt mélangée de conifères, située dans la Sierra Nevada en Californie, avait subi des traitements d'éclaircie et de brûlage en 2001. La forêt feuillue, située dans les monts Ozarks au sud-est du Missouri, avait subi différents traitements de récolte en 1996 et 1997. L'épaisseur de la litière, la température du sol et la teneur en eau du sol ont aussi été mesurées. Ils ont observé que l'éclaircie jardinatoire a produit un effet semblable dans les deux forêts en élevant le TRS, la teneur en eau du sol et la température du sol quoique l'ampleur de la réaction ait été plus forte dans la forêt mélangée de conifères. La coupe de jardinage a augmenté le TRS de 43 % (de 3,38 à 4,82 $\mu mol \cdot m^{-2} \cdot s^{-1}$) dans la forêt mélangée de conifères et de 14 % (de 4,25 à 4,84 $\mu mol \cdot m^{-2} \cdot s^{-1}$) dans la forêt feuillue. Le brûlage dans le cas des conifères et la récolte selon un système équienne dans le cas de la forêt feuillue mélangée n'a pas modifié le TRS comparativement au traitement témoin. Le TRS moyen atteignait respectivement 3,24, 3,42 et 4,52 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Dans les deux stations, les interventions ont significativement affecté le TRS en modifiant l'épaisseur de la litière, la structure du sol et le microclimat de la forêt. La réaction du TRS variait selon le type de peuplement, l'échelle à laquelle les traitements ont modifié ces facteurs biotiques. Leurs résultats constituent une information de première main pour les aménagistes forestiers concernant la façon dont l'émission de carbone du sol réagit à différentes stratégies d'aménagement dans différentes forêts.

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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 whether 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 °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 affected by forest management. It is, therefore, important to consider them to be 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.

Materials and 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°02′W; Fig. 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 (Fig. 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 50 m, ages are up to 420 years old, and mean DBH ranges from 35 cm (red fir) to 53 cm (Jeffrey pine; North et al. 2004). Mean soil temperature (T_s), soil moisture (M_s), and litter depth (LD) vary by patch type and treatment (Table 1).

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 one-third of the total shrub cover (North et al. 2002). Three dominant vegetation patch types have been classified using hierarchical clustering analysis: closed canopy (CC), ceanothus shrub (CECO), and open canopy (OC). 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 Hild.), Jeffrey pine (*Pinus jeffreyii* Grev. & Balf), sugar pine (*Pinus lambertiana* Dougl.), red fir (*Abies magnifica* A. Murr), and incense cedar (*Calocedrus decurrens* (Torr.) Florin). Dominant understory shrub species include mountain whitethorn, bush chinquapin (*Chrysolepis 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 (*Ribes roezlii* Regel), and hazelnut (*Corylus cornuta* Marsh. var. *californica* (A. DC.) Sharp.). Of the 123 herb species identified at TEF, the most common was *Monardella odorratissima* Benth. and *Lupinus adsurgens* E. Drew (North et al. 2002).

Fig. 1. Study sites and experimental treatments. (A) Teakettle Experimental Forest (TEF) is located in California's Sierra Nevada Mountains at 36°58′N, 119°02′W. (B) Missouri Ozark Forest Ecosystem Project (MOFEP) is located in southeastern Missouri at 19°12′W and 37°06′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).

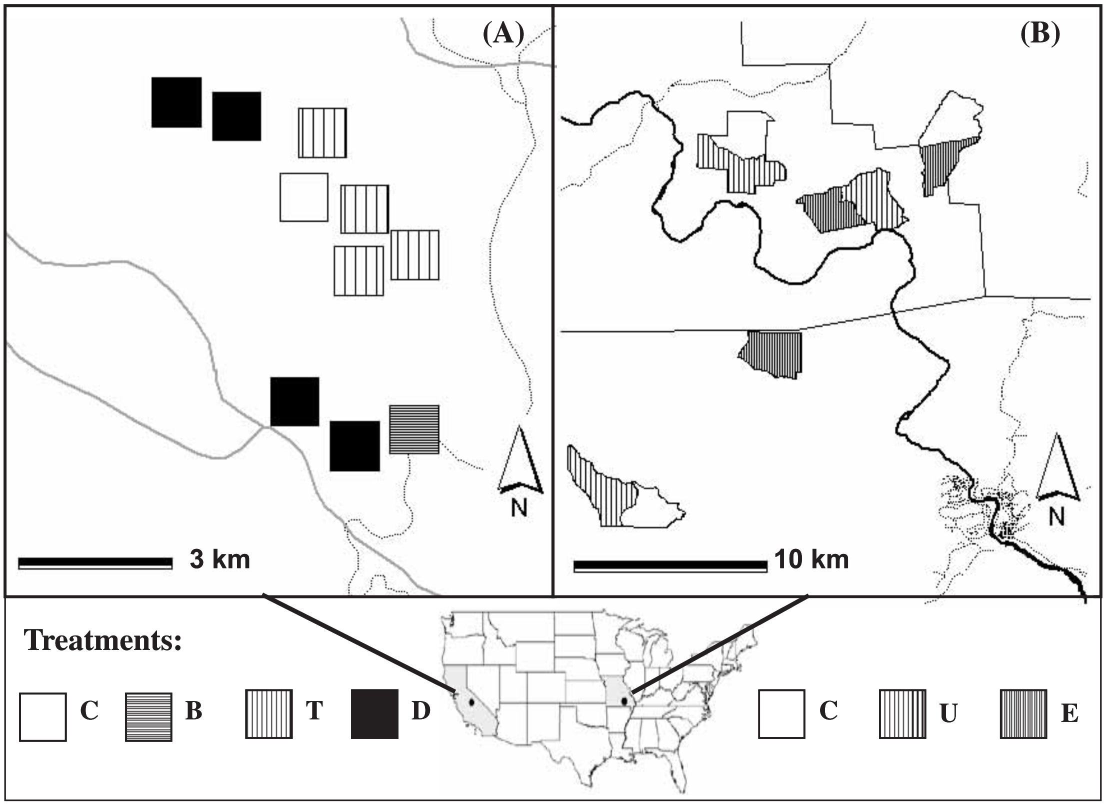
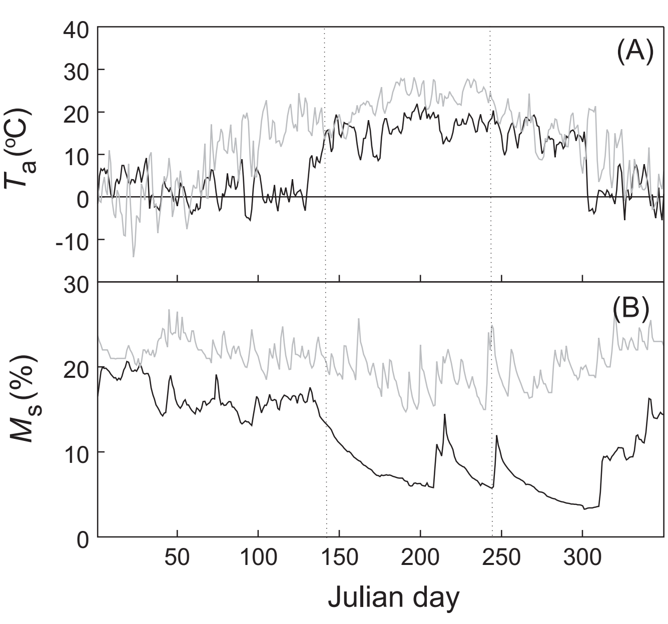


Fig. 2. Comparisons of annual microclimatic patterns in 2003: (A) daily mean air temperature (T_a) and (B) soil volumetric moisture (M_s) at Teakettle Experimental Forest (TEF; black line) and Missouri Ozark Forest Ecosystem Project (MOFEP; gray line). The SRR sampling period is identified with the two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



The Missouri Ozark Forest Ecosystem Project (MOFEP) is located in the southeastern Missouri Ozarks (19°12′W and 37°06′N; Fig. 1B). The majority of the landscape lies at less than 300 m in elevation (Xu et al. 1997), slopes range from 2% to 39% with an average of 24%, and aspect ranges from 10° to 340° with an average of 160° (Roovers 2000). The climate is humid and experiences extremes in precipitation, wind, and temperature (Fig. 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 later) and treatment (Table1).

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 to 22.8 cm (Roovers 2000). Dominant overstory species include white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus 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).

Table 1. Mean soil temperature (T_s), soil moisture content (M_s), and litter depth (LD) at Teakettle Experimental Forest (TEF) and Missouri Ozark Forest Ecosystem Project (MOFEP) by treatment and patch type.

Patch type[a]	Treatment	T_s (°C)	M_s (%)	LD (cm)
TEF				
CC	Control	13.74 (3.03)	12.17 (3.84)	4.8 (3.9)
	Burned	16.90 (4.32)	12.60 (3.40)	0.9 (0.9)
	Thinned	17.83 (3.66)	16.33 (5.07)	3.7 (4.4)
	Burn–thin	19.92 (4.97)	12.39 (2.39)	0.7 (0.9)
CECO	Control	16.02 (4.17)	11.71 (2.29)	2.0 (1.4)
	Burned	22.68 (6.32)	11.82 (2.74)	0.7 (0.7)
	Thinned	19.01 (4.03)	14.41 (4.90)	3.4 (4.6)
	Burn–thin	20.34 (4.72)	13.06 (4.50)	1.6 (2.5)
OC	Control	17.66 (5.72)	12.16 (3.68)	2.1 (3.2)
	Burned	22.32 (5.29)	10.17 (3.38)	0.1 (0.0)
	Thinned	20.40 (3.68)	12.72 (3.69)	0.1 (0.0)
	Burn–thin	21.84 (4.50)	12.10 (2.99)	0.5 (0.4)
MOFEP				
HUS	Control	19.29 (3.09)	15.25 (9.10)	3.4 (0.6)
	Even aged	20.87 (3.17)	14.43 (7.99)	2.6 (0.4)
EUB	Control	19.41 (3.24)	14.43 (8.64)	2.9 (1.0)
	Uneven aged	20.24 (2.80)	13.74 (7.08)	2.3 (0.7)
	Even aged	20.03 (2.12)	12.64 (7.04)	2.7 (0.0)
PUB	Control	18.78 (3.14)	13.93 (6.38)	3.7 (0.5)
	Uneven aged	19.66 (2.60)	15.66 (7.56)	2.6 (0.9)
	Even aged	19.12 (2.36)	20.54 (9.30)	2.6 (1.2)
EAB	Control	19.81 (3.28)	17.52 (6.49)	1.4 (0.0)
	Uneven aged	19.48 (2.48)	19.01 (9.28)	4.0 (0.0)
	Even aged	18.60 (2.46)	17.36 (7.82)	2.8 (0.5)
PAB	Control	18.00 (2.90)	21.72 (7.13)	2.2 (0.0)
	Uneven aged	18.94 (3.32)	21.55 (9.53)	3.8 (0.0)
	Even aged	18.51 (2.53)	19.31 (9.98)	2.3 (0.4)
ABS	Control	19.00 (1.83)	17.18 (5.94)	2.0 (0.0)
	Uneven aged	19.90 (3.02)	14.49 (2.10)	2.7 (0.0)
	Even aged	19.16 (2.34)	18.96 (8.33)	2.1 (0.0)

Note: Values are means with standard errors are in parentheses.
[a]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; ABS, alfic bench or shoulder ridge.

The study sites at MOFEP were classified into ecological land types (ELT; Kabrick et al. 2000*a*). Information on geology, soils, and vegetation was included to expand the classification scheme to ecological land-type 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 backslope (EUB), protected ultic backslope (PUB), exposed alfic backslope (EAB), protected alfic backslope (PAB), and alfic bench or shoulder ridge (ABS).

Experimental treatments

At TEF, all experiments were conducted within 18 square plots (4 ha each), 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). In 2001, the stands had been treated with thinning and burning manipulations. 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 treatment combination (Fig. 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 4-ha study plots. A minimum of 10 replicate patches for each combination of patch type (CC, OC, CECO) and treatment (C, B, T, D) were measured during summer 2003.

MOFEP sites had been harvested in 1996 and 1997 according to even-aged or uneven-aged management. 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 to 527 ha (Xu et al. 1997), using a randomized complete block design (Brookshire et al. 1997). Although even-aged management included a combination of clear-cutting and intermediate thinning, our sampling points were only located within the clear-cut areas. Uneven-aged treatments consisted of harvesting by both single-tree selection and group selection (Kabrick et al. 2000*b*), 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 three) ELTPs per treatment type. The exception was HUS, which did not exist in an even-aged managed plot and was only sampled in the control and uneven-aged plots. Each sampling point included eight subsamples 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 monitors, PP Systems, Hertfordshire, UK) and attached SRC-1 soil respiration chambers (PP Systems). SRR measurements were taken on PVC collars, which were inserted about 3 cm into the ground (collars were 5 cm tall) at least 1 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-min period between 0900 and 1600 h to minimize effects of diurnal fluctuation. Simultaneous to SRR measurements, handheld thermometers (Taylor pocket digital thermometer) measured soil temperature at 10 cm depth within 30 cm of the PVC collar. Soil moisture between 0 and 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. 2005). The EGMs were calibrated weekly with standard 700-ppm CO_2 gas under ambient air pressure, and barometric pressure readings were taken at the time of sampling to correct for differences in pressure.

Statistical analyses

Data included SRR, T_s at 10 cm depth, M_s between 0 and 15 cm depth, and LD at each sampling point at both sites during the same six sampling periods from 1 June to 31 August 2003. SRR measurements at TEF were corrected for machine error (Ma et al. 2005), since the EGM has been found to overestimate SRR in these conditions (Butnor and Johnsen 2004). Log transformations were made on SRR and M_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 α of 0.05, unless otherwise stated.

Differences among means were tested with repeated measures analysis of variance (ANOVA; SAS version 8.0; SAS Institute Inc. 1999). A two-way nested ANOVA was used to test whether 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 was used to identify significant differences in SRR, $T_{s,}$ and M_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 are based on earlier work in TEF by Ma et al. (2005). 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):

$$[1] \qquad \mathrm{SRR} = \beta_1 \mathrm{e}^{T_s \beta_2}$$

$$[2] \qquad \mathrm{SRR} = b_0 \mathrm{e}^{(b_1 T_s)} \mathrm{e}^{(b_2 M_s)} b_3 T_s M_s$$

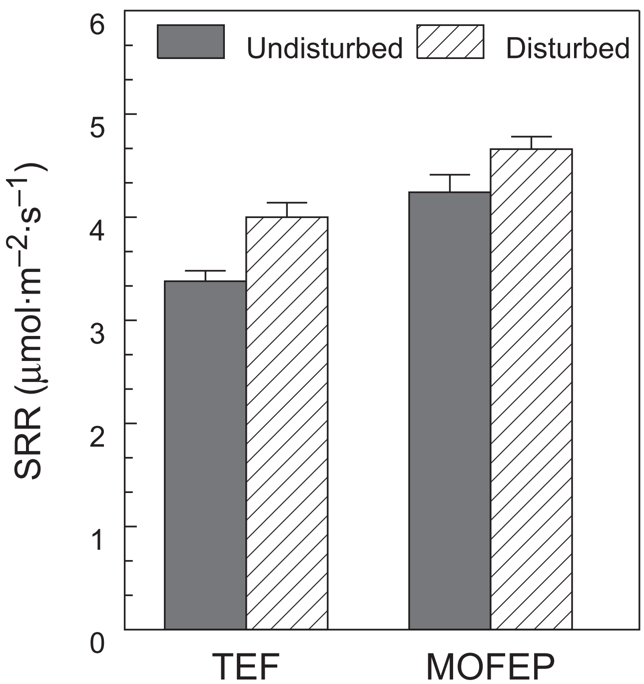
where β_1 (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), β_2 (°C^{-1}), b_0, b_1, b_2, and b_3 are coefficients estimated through regression analysis for each site and site–treatment regime. These models are based on the assumption that $T_s \geq 0$ °C. Model [2] was adjusted to meet convergence criteria for TEF (eq. 2*a*) and MOFEP (eq. 2*b*):

$$[2a] \qquad \mathrm{SRR} = \mathrm{e}^{(b_1 T_s)} \mathrm{e}^{(b_2 M_s)} T_s M_s$$

$$[2b] \qquad \mathrm{SRR} = \mathrm{e}^{(b_1 T_s)} \mathrm{e}^{(b_2 M_s)} T_s M_s + b_3$$

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 (SAS version 8.0; SAS Institute Inc. 1999) was used to test the predictive strength of these models for our data.

Fig. 3. Mean soil respiration rate (SRR) at each study site by disturbance. All treatment types were grouped together and compared to the control plots. Bars represent standard error.



Previous studies at TEF have found that PT has an important influence on SRR (Ma et al. 2005), 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 whether a model incorporating LD and PT would improve predictive abilities of log-transformed SRR:

$$[3] \qquad \mathrm{SRR} = f\,(T_s\ M_s\ \mathrm{LD\ PT\ TRT})$$

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

$$[4] \qquad \mathrm{SRR} = f\,(T_s\ M_s\ \mathrm{LD\ PT})$$

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. Models [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 $\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 (Fig. 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

Table 2. ANOVA results comparing soil respiration rate (SRR) between a hardwood (Missouri Ozark Forest Ecosystem Project; MOFEP) and conifer (Teakettle Experimental Forest; 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.

ANOVA model	Numerator df	Denominator df	F	p
SRR = site management (site)				
Site	1	5	43.23	0.001
Management (site)	2	12	10.21	0.003
SRR = treatment patch				
TEF				
Treatment	3	15	10.83	0.001
Patch	2	10	58.63	0.000
MOFEP				
Treatment	2	14	4.51	0.031
Patch	5	34	7.82	0.000

sites (Fig. 3), but only selective thinning had a significant effect on SRR when treatment types were separated (Fig. 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). T_s, M_s, and LD were significantly affected by management at TEF (Fig. 4B.1, 4C.1, and 4D.1), but not at MOFEP (Fig. 4B.2, 4C.2, and 4D.2).

The management-induced percent change (%Δ) in SRR, T_s, and M_s clearly differed by treatment types at the TEF (Fig. 5A) but not at MOFEP (Fig. 5B). At TEF, treatment effects on M_s were especially evident: thinning treatments producing the greatest change of 20%–40% for most sampling dates; burned and burned–thinned treatments %Δ ranged between –10% and 10%. T_s response also differed by treatment but to a lesser degree than M_s. T_s changed least with thinning-only treatments (2%–20%), while burning-only treatments produced a change of –2% to 28%, and burning and thinning produced a 13%–50% increase. The range of %ΔSRR was highest in thinned plots (30%–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 (Fig. 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 (Fig. 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.

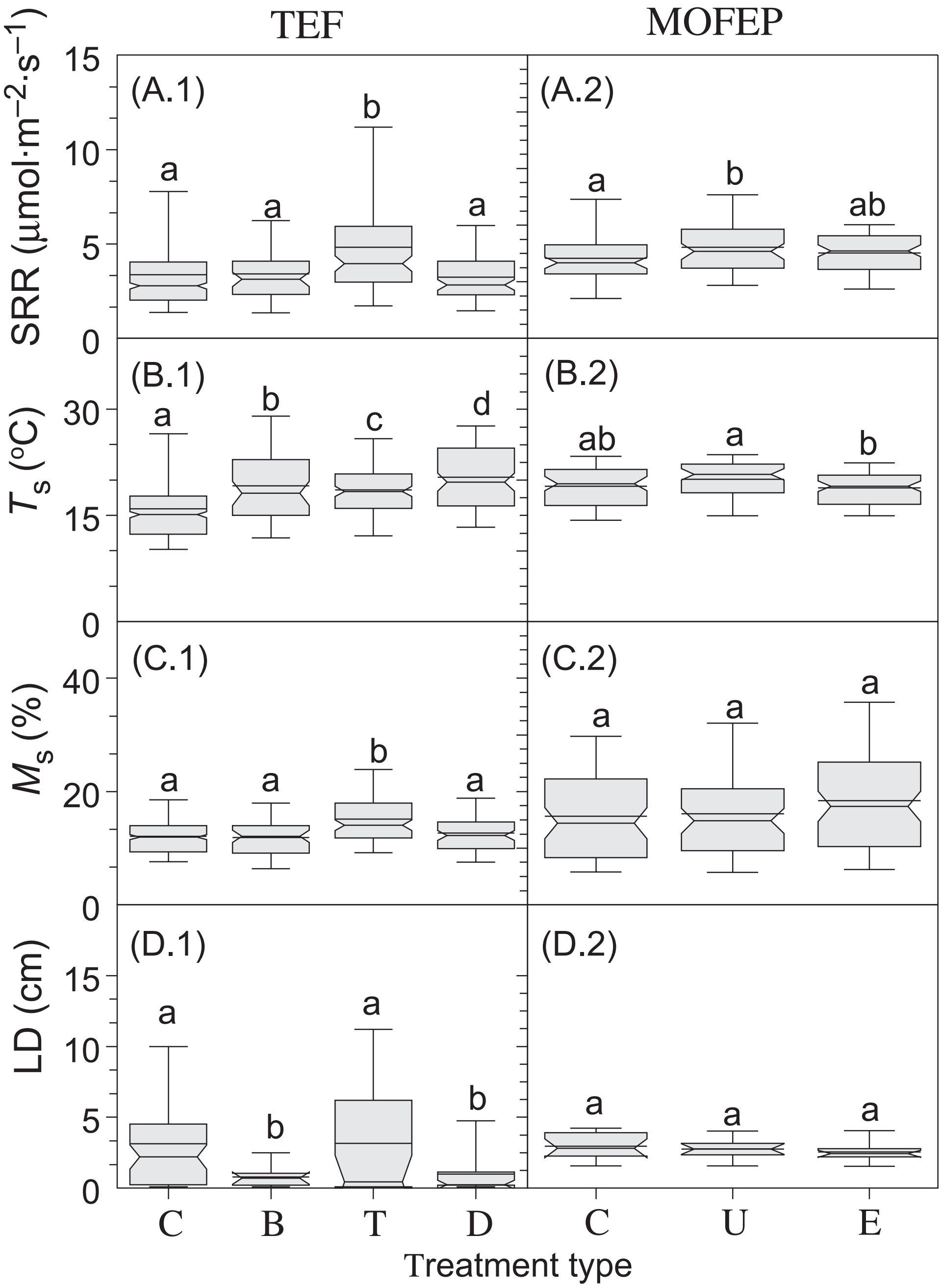
Postmanagement influences on SRR

Regression analyses indicated that T_s and M_s explained little variation in SRR during the summer season in either forest, suggesting that other biophysical factors, such as vegetation types and litter depths, may have regulated postmanaged 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 (~11 °C) at MOFEP compared to that at 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 (α = 0.05). These values were very low in comparison to those from 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 did. 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),

Fig. 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 and A.2), soil temperature (T_s; B1 and B2), soil volumetric moisture (M_s; C.1 and C.2), and litter depth (LD; D.1 and 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), uneven-aged management (U), and even-aged management (E) at MOFEP. Significant differences (α = 0.05) by treatment type within each site are labeled with different letters.



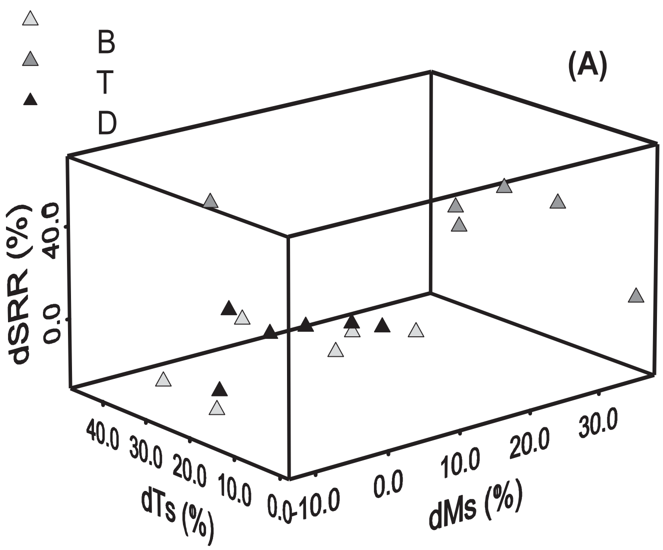
and even-aged thinned plots (R^2 = 0.23), patch type alone explained almost as much of the variation as the full model. However, these values were relatively low so that the variability in our sampling sites may require more intensive sampling for better model fit.

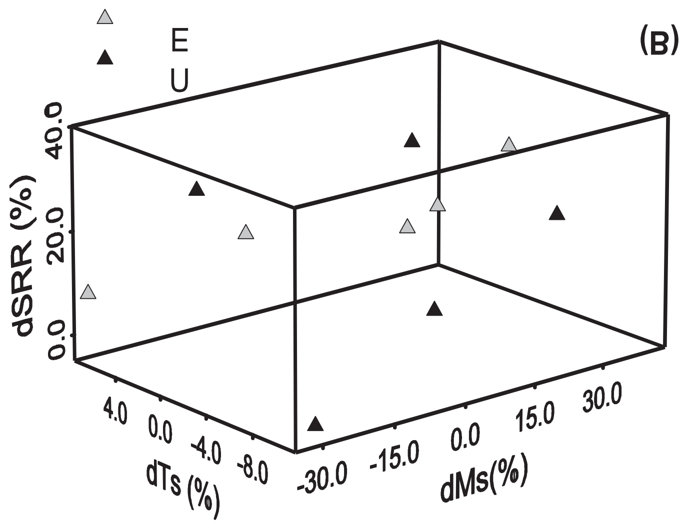
Discussion

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 that can reduce posttreatment 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 pretreatment fuel is sparse. At a stand level, it may

Fig. 5. Percent change of treated to control sites in soil respiration rate (dSRR), soil moisture (dM_s), and soil temperature (dT_s) 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.





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 microflora, 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 (Fig. 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), which 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.

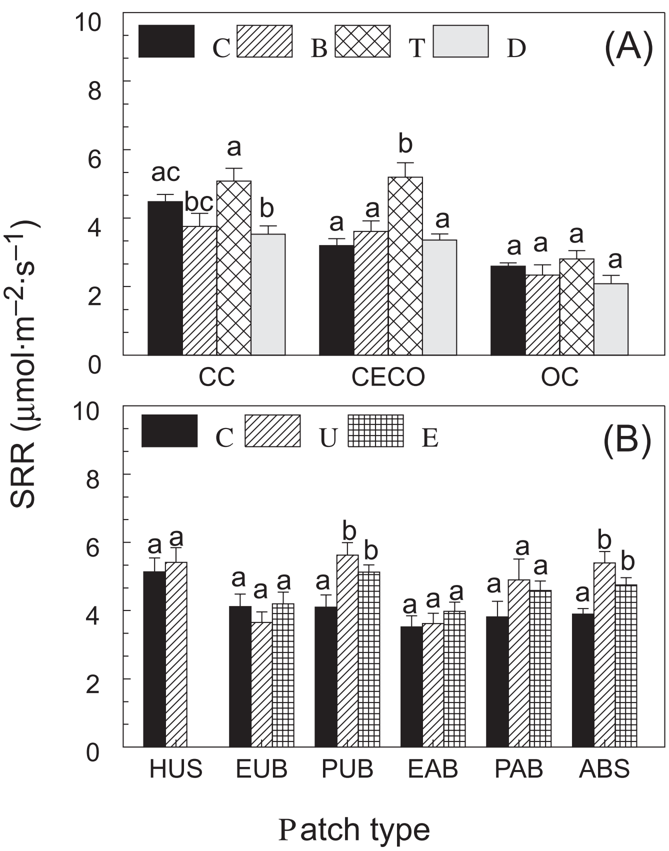
The magnitude of SRR response to treatments appears to be time dependent, because effects were much more pronounced at the mixed-conifer site, where treatments were more recent. Recovery time was also different based on treatment type; uneven-aged stands at MOFEP had increased SRR, while even-aged stands appeared to have recovered to undisturbed levels. Net primary production, litterfall, 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 1 year post-disturbance (Ma et al. 2004), while we found that SRR increased significantly 2 years after the thinning treatment. This difference highlights the need to monitor ecosystem response over consecutive years until full recovery is reached.

Posttreatment 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 because of 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 because of differences in soil microclimate and structure, detritus quantity and quality, and root respiration (Raich and Tufekcioglu 2000). At TEF, patches have different soil

Fig. 6. Mean and standard error of soil respiration rate (SRR) by patch type and treatment type at the Teakettle Experimental Forest (TEF) (A) and Missouri Ozark Forest Ecosystem Project (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 backslope (EUB), protected ultic backslope (PUB), exposed alfic backslope (EAB), protected alfic backslope (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.



chemical properties (Erickson et al. 2005), 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 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.

Table 3. Predictive ability of general linear models describing soil respiration rate (SRR) variation by site in a mixed-conifer (Teakettle Experimental Forest; TEF) and hardwood (Missouri Ozark Forest Ecosystem Project; MOFEP) forest and by treatment type within each site.

	F	p	R^2
SRR = *f* (T_s M_s LD PT TRT)			
TEF	16.4	0.000	0.69
Control	14.55	0.000	0.87
Burn	4.92	0.016	0.71
Thin	8.62	0.001	0.78
Burn–thin	5.77	0.007	0.72
SRR = *f* (LD PT TRT)			
TEF	22.5	0.000	0.68
Control	15.32	0.000	0.76
Burn	4.07	0.033	0.50
Thin	8.31	0.002	0.64
Burn–thin	7.98	0.002	0.63
SRR = *f* (T_s M_s LD PT TRT)			
MOFEP	4.9	0.000	0.36
Control	1.64	0.164	0.34
Uneven aged	0.62	0.003	0.58
Even aged	1.92	0.117	0.32
SRR = *f* (PT TRT)			
MOFEP	7.15	0.000	0.35
Control	2.28	0.074	0.29
Uneven aged	6.29	0.001	0.52
Even aged	2.73	0.062	0.23

Note: Variables are soil temperature (T_s), soil moisture content (M_s), litter depth (LD), vegetative patch type (PT), and treatment type (TRT).

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 2 and 7 years postdisturbance, 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, interannual 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.

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