

Effect of thinning and prescribed fire restoration treatments on woody debris and snag dynamics in a Sierran old-growth, mixed-conifer forest

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Abstract: Forest managers have little information of the effects of common restoration treatments, thinning and burning, on dead woody material (DWM) dynamics in fire-suppressed forests. Fine woody debris (FWD; 0.6–29.9 cm), coarse woody debris (CWD; ≥ 30.0 cm), and snags (≥ 5 cm) were inventoried and mapped in eighteen 4 ha plots before and after applying thinning (overstory, understory, and no thinning) and burning (burn and no burn) treatments. The combination of burning and thinning reduced FWD and CWD quantity and mean piece size, removed highly decayed logs, and increased small (5.0–24.9 cm) snag recruitment. In contrast, thin-only treatments produced similar results but increased FWD and did not remove many small snags. There were no differences in DWM response between the two thinning treatments. Log and snag spatial patterns prior to and following treatment were similar. These results indicate that burning in combination with thinning is more effective at reducing surface FWD and CWD, and removing small trees than are burn-only and thin-only treatments. Although large snags and logs were consumed in the burn, long-term recruitment of these habitat structures relies on managers retaining large-diameter trees. Repeated burns need to be conducted after initial restoration treatments to understand natural patterns of DWM.

Résumé : Les aménagistes forestiers possèdent peu d'information sur les effets des traitements courants de restauration, l'éclaircie et le brûlage, sur la dynamique du matériel ligneux mort (MLM) dans les forêts qui sont protégées contre les incendies. Les débris ligneux fins (0,6 à 29,9 cm) (DLF), les débris ligneux grossiers ($\geq 30,0$ cm) (DLG) et les chicots (≥ 5 cm) ont été inventoriés et cartographiés dans 18 parcelles de 4 ha avant et après avoir pratiqué des traitements d'éclaircie (étage dominant, sous-bois et aucune éclaircie) et de brûlage (brûlage ou non). Le brûlage et l'éclaircie combinés ont réduit la quantité et la dimension moyenne des DLF et des DLG, éliminé les billes fortement décomposées et augmenté le recrutement de petits chicots (5,0 à 24,9 cm). Par contre, l'éclaircie seule a produit des résultats similaires mais a augmenté la quantité de DLF et n'a pas éliminé beaucoup de petits chicots. Il n'y avait pas de différence entre les effets des deux traitements d'éclaircie sur la dynamique du MLM. La distribution spatiale des billes et des chicots était semblable avant et après les traitements. Ces résultats indiquent que le brûlage combiné à l'éclaircie est plus efficace que le brûlage seul ou que l'éclaircie seule pour réduire les DLF et les DLG de surface et pour éliminer les petites tiges. Bien que les gros chicots et les grosses billes aient été consommés par le feu, le recrutement à long terme de ces structures d'habitat dépend de la conservation d'arbres de fort diamètre par les aménagistes. Des brûlages répétés doivent être effectués après des traitements initiaux de restauration pour comprendre la dynamique naturelle du MLM.

[Traduit par la Rédaction]

Introduction

Fire suppression in western forests has dramatically increased the amount and continuity of fine (FWD) and coarse woody debris (CWD) and snags (hereafter, dead woody ma-

terial (DWM)). Studies have demonstrated the important functional role of DWM in forests. For example, DWM is associated with processes such as nutrient cycling, decomposition and respiration, tree regeneration, plant and fungal diversity, and wildlife habitat (Maser and Trappe 1984; Harmon et al. 1986). Managers attempting to restore historic forest conditions are faced with a dilemma of trying to reduce fuel hazards while retaining some DWM for habitat and ecosystem functions (Stephens and Moghaddas 2005). There is little information on historic levels and long-term trends of DWM. Some studies have examined DWM response to spring versus fall burning (Knapp et al. 2005) and different silvicultural prescriptions (Weatherspoon 2000; Stephens and Moghaddas 2005). However, information about retention of old-growth features, such as large standing and downed dead wood, is not well documented for Sierran mixed-conifer forests.

Most models of DWM dynamics were developed with

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data from forests with infrequent, moderate- to high-severity disturbances, such as the Pacific Northwest (Harmon et al. 1986; Spies et al. 1988; Wright et al. 2002) and boreal forests (Lee et al. 1997; Sturtevant et al. 1997), using a chronosequence approach. Models developed assuming infrequent, high-severity disturbances suggest that highly pulsed CWD inputs and removals may produce a U-shaped relationship when abundance is graphed against time (Spies et al. 1988). In contrast, empirical information is lacking to develop an understanding of DWM behavior through time under a frequent (10–25 years), low-severity fire regime, such as that characterized by the Mediterranean-type climate of the Sierra Nevada. In these forests, DWM input and removal is hypothesized to have been more regular in time and space (Skinner 2002) maintaining most of the forest in a crown fire resistant state (Agee 2002). A conceptual model for a frequent low-severity fire by Agee (2002) describes small to moderate DWM inputs and removals over short time periods illustrated as a sawtooth pattern when DWM mass is graphed against time.

In current fire-suppressed forests of the Sierra Nevada, the historic pattern of DWM has been lost (Skinner 2002). This lack of information sometimes has made managers hesitant to apply prescribed fire, because it may reduce large DWM associated with sensitive species such as the Pacific fisher (*Martes pennanti* (Erxleben, 1777)), American marten (*Martes americana* (Turton, 1806)), and their small mammalian prey. Although we know that the flora and fauna of mixed-conifer forests lived with and adapted to fire as an ecological process prior to suppression, forest managers do not fully understand how fire and thinning impact DWM or what general DWM conditions are desired.

Although we cannot quantitatively reconstruct historic DWM conditions, several authors have suggested what patterns were probably more common under frequent, low-intensity fire (Agee 2002; Skinner 2002; Stephens 2004). The amount of DWM consumed by a fire may vary site to site because of several factors, including the season of the burn, wood decay class (Skinner 2002), topography, and aspect (Beatty and Taylor 2001). In general, however, frequent fire regimes should reduce FWD and CWD densities, shift mean piece size toward larger, less decayed pieces, and leave CWD more aggregated. The goal of this study was to examine the effect of widely used Sierra Nevada restoration practices on DWM dynamics in an old-growth, mixed-conifer forest. Our major objectives were to quantify changes in DWM before and after applying a full factorial of prescribed fire and thinning treatments. Specifically, we examined treatment effects on DWM quantity, piece size, decay class, and spatial distribution. Lacking better historical information, we believe that treatments that reduce DWM total abundance and shift conditions toward clusters of fewer, larger, intact pieces may provide general but useful restoration guidelines for managers.

Methods

Study site

The study was conducted at the Teakettle Experimental Forest (36°58'N, 119°2'W), a 1300 ha old-growth watershed on Patterson Mountain between 1980 and 2590 m elevation,

located 80 km east of Fresno, California, in the Sierra National Forest. Annual precipitation is 135 cm, falling mostly as snow between November and April with a mean 30 year snowfall record of 220 cm and a mean maximum snow depth of 114 cm (range 24–241 cm; North et al. 2002). The most common soil type at Teakettle is a well-drained, mixed, frigid Dystric Xeropsamment formed from decomposed granite (North et al. 2002). The Teakettle Experimental Forest is described in detail by North et al. (2002) (also refer to The Teakettle Experimental Forest website: <http://teakettle.ucdavis.edu>).

The current study was conducted in the mixed-conifer zone at Teakettle, which comprises 65% of the watershed and contains white fir (*Abies concolor* (Gord & Glend.) Lindl., 67.6% of the basal area (BA)), sugar pine (*Pinus lambertiana* Dougl., 7.9% BA), incense cedar (*Calocedrus decurrens* (Torr.) Florin, 13.4% BA), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf., 6.2% BA), and red fir (*Abies magnifica* A. Murr., 3.0% BA). Understory species include California black oak (*Quercus kelloggii* Newberry, 0.5% BA), canyon live oak (*Quercus chrysolepis* Liebm., 0.01% BA), and bitter cherry (*Prunus emarginata* Dougl., 0.03% BA).

The fire history of Teakettle indicates a mean fire-return interval (FRI) of 17 years (North et al. 2005), typical of the mixed-conifer forests of the Sierra Nevada (Skinner and Chang 1996). Median spatial extent of fires at Teakettle has been estimated to be 20 ha with a range of 0.02–83.5 ha (Fiegener 2002).

Experimental design

Within Teakettle's mixed-conifer forest, eighteen 4 ha plots were identified, and an analysis of their tree structure and composition found no significant pretreatment differences among plots (North et al. 2002). Treatments were applied to the 18 plots following a full 2 × 3 factorial design crossing two levels of burning treatments (burn (B) and no burn (U)) and three levels of thinning treatments (C, California spotted owl cut (CASPO); S, shelterwood; and N, no cut) with three replicates per treatment. Two constraints imposed by the Sierra National Forest, grouping of burn units and no thinning along Teakettle's main creek, prevented a fully random assignment of plots to treatments. Two burn blocks and a stream zone were established, and then treatments were randomly assigned within the constraints of each stratum. All plots were measured prior to and following treatment except for the controls (measured once 2001–2003). The understory prescription (CASPO) followed guidelines in the California spotted owl report (Verner et al. 1992), including removal of all trees between 25 and 76 cm diameter at breast height (DBH) while retaining at least 40% canopy cover. The shelterwood cut removed all trees >25 cm DBH while leaving 22 regularly spaced, large-diameter trees per hectare. Trees were hand-felled using a chain saw. Logs were removed with a rubber-tire skidder, and slash was left on site. Thinning treatments were applied in summer 2000 (thin and burn plots) and 2001 (thin only), slash was allowed to dry for 1 year, and the prescribed fire lit in late fall 2001. The prescribed fire was applied by the Sierra National Forest following the first substantial (2 cm) fall rain. Mean daytime temperature during the burn was 13 °C, and relative humid-

ity ranged from 25% to 70%. The percentage of ground cover burned was 35%–70% and 20%–40% in the thinned and unthinned plots, respectively.

Sampling

Prior to treatment, each replicate group per treatment (three plots) had a grid of systematic sample points installed. Each replicate group of three plots had two plots with nine points in the grid with 50 m spacing (3 × 3) and one plot with 49 points at a 25 m spacing (7 × 7).

Fine fuels

Mass of FWD was estimated before and after treatment (the controls were only sampled once) using the planar intercept method (Brown 1974) with modifications. Nine sample points were chosen within each plot based on a mapped systematic grid. We choose to run the fuels' transects off these gridpoints, because they are sample points used by multiple studies in the Teakettle Experiment. For plots with only 9 gridpoints, all gridpoints were used; for plots with 49 gridpoints, 9 gridpoints on a 50 m spacing were chosen. At each point, a random bearing was chosen, and two additional bearings were chosen at 120° from the first. At each bearing, a 15 m line transect was established. DWM that intersected the transect was measured to the nearest millimetre. The number of 0.1–0.6 cm diameter pieces (1 h fuels) and 0.7–2.5 cm diameter pieces (10 h fuels) were recorded along the first 2 m of the transect, and 2.6–7.6 cm diameter pieces (100 h fuels) were recorded along the first 4 m. Pieces 7.7–29.9 cm in diameter (1000 h fuels) were recorded along the entire 15 m transect. For the 1000 h fuels, a cutoff was made in the upper range of the fuel size to avoid overlapping with the CWD inventory, which covers pieces ≥30 cm diameter (see the following). Hereafter, we refer to fuels by size-class rather than burn duration to avoid confusion.

Logs

CWD, defined as downed logs ≥30 cm in diameter (Maser and Trappe 1984) and ≥2 m long, were mapped and inventoried from 1999 to 2004 (pre- and post-treatment). The end-points of each qualifying log were mapped using a surveyor's total station, and the diameters recorded to the nearest millimetre. Log decay was determined using the decay classification of Maser et al. (1979), with modification as follows (1) bark intact, twigs and branches <3 cm present, texture of log intact, shape round, log may be elevated on branch stubs or other objects and is not sagging; (2) bark intact, twigs and branches <3 cm absent, texture of log intact to soft, shape round, log may be elevated on branch stubs or other objects and is not sagging; (3) bark sloughing, twigs and branches <3 cm absent, texture of log soft, shape round, log may be elevated on branch stubs or other objects and if so, branches will be gone or log will be sagging across other objects; and (4) bark gone, twigs and branches <3 cm absent, texture of log soft to blocky, shape round to oval, log is on the ground. Decay class 5 logs were not sampled due to a lack of consistency among observer estimates.

Using the mapped coordinates, log length was calculated. The volume of each log was estimated as a frustrum paraboloid (Husch et al. 1993). Mass (Mg·ha⁻¹) was estimated using the specific gravities of Harmon et al. (1987).

Because we did not record the species of the downed logs in the pretreatment survey and because species were often unidentifiable, we averaged the specific gravities of Harmon et al. (1987) by decay class for the dominate species found at Teakettle, which produced the following densities for the four decay classes: (1) 0.38 g·cm⁻³; (2) 0.32 g·cm⁻³; (3) 0.27 g·cm⁻³; (4) 0.15 g·cm⁻³.

Snags

All snags ≥5.0 cm were mapped using a surveyor's total station. At each snag, diameter and decay class were recorded. Snag height was estimated to the nearest metre by ocular estimation after the technicians had "trained" their eyes using a Criterion laser set to the tree height function. Snags were classified into five decay classes following the methods of Cline et al. (1980) with modification as follows (1) limbs and branches present, top pointed, 100% of bark remaining, sapwood intact and sound; (2) limbs present, but no fine branches, top broken, bark 75%–100% present, sapwood sloughing and firm to soft; (3) remaining branches appear as stubs, top broken, bark 50%–75% present, sapwood sloughing and soft; (4) few or no branch stubs, top broken, bark 25%–50% present, sapwood sloughing and soft to powdery; and (5) no branches remaining, top broken, 0%–5% of bark remaining, sapwood absent.

Snag volume calculation: if a snag had a decay class of 1, it was assumed to have recently died and height was estimated using a local height–diameter equation (J. Innes, unpublished data), and volume was estimated as a paraboloid (Husch et al. 1993). For snags of decay class 2 and greater, the top was assumed to be broken and the ocular height was used; the top diameter was estimated using a taper of 2 cm/m, which was calculated as the mean from the downed logs (Harmon et al. 1987). Using these measures, volume was calculated as a frustrum of a paraboloid (Husch et al. 1993). Mass (Mg·ha⁻¹) of the snags was estimated in the same manner as for logs.

Statistical analysis

Analysis of variance (ANOVA) was used to test for treatment effects on mass for FWD (0.01–29.9 cm) and CWD (≥30 cm); for treatment differences in CWD volume, density, length, percent cover, and mean diameter; and for treatment differences in volume, density, and mass of snags. All data were log_e transformed to meet ANOVA assumptions. CWD was analyzed by decay class with modifications. For CWD, decay classes 1 and 2 were combined and relabeled decay class 1 and decay classes 3 and 4 were combined and relabeled decay class 2. Snags were grouped by decay in a similar way as the logs: decay classes 1 and 2 were grouped into decay class 1, and decay classes 3–5 were grouped into decay class 2. If an ANOVA detected a treatment effect, Tukey's honestly significantly different tests were used to detect which treatments were different.

We used the following linear model in a 2 × 3 factorial:

$$y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk}$$

where

$$i = 1, 2, \dots, a; j = 1, 2, \dots, b; \text{ and } k = 1, 2, \dots, r$$

μ is the the overall mean

Table 1. Results of one-way analysis of variance on pretreatment and post-treatment means of fine (FWD) and coarse woody debris (CWD) mass ($\text{Mg}\cdot\text{ha}^{-1}$) by diameter class at the Teakettle Experimental Forest, California.

Diameter class (cm)	Mass ($\text{Mg}\cdot\text{ha}^{-1}$)						<i>P</i>
	BC	BN	BS	UC	US	UN	
Pretreatment							
FWD							
<0.6	1.6a	1.3a	1.5ab	1.1ab	1.1ab	0.4b	0.0403
0.6–2.5	5.2	2.7	4.0	3.3	3.1	2.7	0.4200
2.6–7.6	5.8	2.9	7.4	7.7	3.7	4.7	0.1400
7.7–29.9	6.7a	4.5a	7.8a	8.1a	5.6a	0.5b	0.0002
CWD							
30.0–59.9	4.9	5.3	2.9	4.5	3.8	2.4	0.3310
60.0–89.9	7.2	9.5	7.7	11.6	6.8	10.4	0.3100
≥ 90	33.9	32.6	26.2	37.4	33.8	42.3	0.1200
Total	65.4	58.7	57.4	73.7	57.9	63.5	0.5000
Post-treatment							
FWD							
<0.6	0.2bc	0.2abc	0.1c	0.5a	0.4ab	0.4ab	0.002
0.6–2.5	2.4ab	2.2b	2.3b	4.7a	3.6ab	2.7ab	0.015
2.6–7.6	6.4	5.3	5.0	8.5	9.9	4.7	0.089
7.7–29.9	1.2ab	0.7b	1.2ab	1.7ab	2.9a	0.5b	0.014
CWD							
30.0–59.9	3.2ab	4.7b	2.5ab	7.1ab	7.4a	2.4b	0.008
60.0–89.9	5.6abc	6.9abc	4.3bc	11.1ab	11.4ab	10.4c	0.004
≥ 90	9.1ab	7.3ab	9.9b	22.3a	16.4a	42.3a	0.004
Total	28.1bc	27.2bc	25.3c	56.1ab	51.9abc	63.5	0.001

Note: Row means followed by the same letter(s) are not significantly different at $\alpha = 0.05$. Column abbreviations: B, burn (conducted in the fall); C, California spotted owl cut (removal of trees 25 and 76 cm diameter retaining 40% canopy cover); S, shelterwood cut (removal of trees >25 cm DBH leaving 22 regularly spaced, large-diameter trees per hectare); N, no cut; U, unburned.

α_i is the effect from the *i*th level of Factor A, $\alpha_i = \mu_i - \mu$ (three levels of cutting: CASPO, shelterwood, and uncut)

β_j is the effect from the *j*th level of Factor B, $\beta_j = \mu_j - \mu$ (two levels of burning: burned and unburned)

$(\alpha\beta)_{ij}$ is the interaction when the *i*th level of factor A and the *j*th level of factor B are combined

ε_{ijk} is the residual components and are assumed to be independent and identically distributed

Linear contrasts were set a priori to test for differences between burning (BC, BN, and BS) and cutting (US and UC) using an α of 0.05.

The spatial pattern of CWD and snags was analyzed using spatial point pattern analysis software (SPPA), version 2.0 with toroidal edge correction (Haase 1995). A univariate Ripley's *K* function analysis was performed (Ripley 1979) at a study distance of 100 m in 5 m increments. To perform the Ripley's *K*, each log was reduced to a point located in the centre of the log calculated from the mapped data coordinates. We used the Laplace transformation and 95% confidence intervals calculated from 100 Monte Carlo simulations.

Results

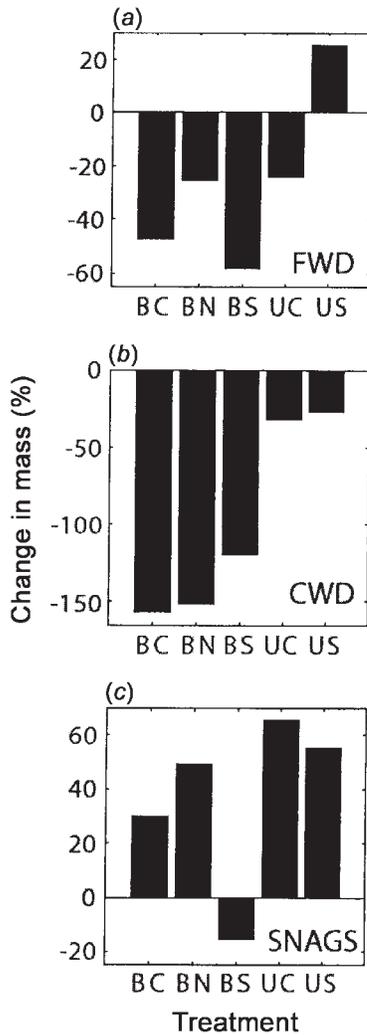
Fine and coarse woody debris

Pretreatment quantities of FWD were consistent across all

treatments except for the controls, which were significantly lower for the <0.6 cm diameter class and the 7.7–30 cm diameter class (Table 1). Fuels in these size categories were within the range of the other plots; however, they tended to be on the lower end of the range for all the control replicates. We believe that the reason for this was that controls 1 and 3 had year-round streams and some wetter areas in them, which resulted in a more humid environment (Thomas Rambo, University of California, Davis, personal communication 2004), higher decay rates, and seasonal flooding. The second control had areas of open granite with little to no vegetation that may have not contained any fuels.

After treatments, there were significant differences in FWD and CWD across all size-classes (Figs. 1a and 1b, Table 1). There was a consistent pattern of reduced FWD and CWD in both burn and cut treatments (Figs. 1a and 1b, Table 1). In the cut-only treatments, FWD decreased overall in the UC treatment but increased in the US treatment (Fig. 1a, Table 1). All treatments decreased in FWD 93%–52% in the <0.6 cm size-class. The UC and US treatments increased 41% and 15% and 9% and 170% in the 0.7–2.5 cm and 2.6–7.6 cm size-classes, respectively. The BC, BN, and BS treatments decreased 53%, 17%, and 41% in the 2.6–7.6 cm size-class, respectively. In the BC and BN treatments, the 2.6–7.6 cm size-class increased 9% and 82%, respectively, but decreased 84% in the BS treatment. All cut-only, burn, and burn-only treatments decreased consistently in the 7.7 cm and greater size classes. The cut-only treat-

Fig. 1. Percent change in mass by treatment of (a) fine woody debris 0.6–29.9 cm, (b) coarse woody debris ≥ 30.0 cm, and (c) snags ≥ 5.0 cm. Controls (UN) were not remeasured and, therefore, were not included.



ments decreased 47%–80% in the 7.6–30 cm size-class but increased 60%–90% in the 30–59.9 cm size-class. The UC treatment decreased 4% and 40% in the 60–89.9 cm and ≥ 90 cm size-classes, respectively, whereas the US treatment increased 66% and decreased 50%, respectively, in these size-classes. Linear contrasts indicated significant differences between burn and cut plots for all size-classes, but differences were not detected between the two thinning intensities.

Coarse woody debris by decay class

There were no significant differences in pretreatment levels of length and density of CWD by decay class (Table 2). After treatments, there were significant CWD differences for length, volume, and density across all decay classes post-treatment, except volume decay class 1 (Table 2). Cut-only treatments greatly increased inputs into length, volume, and density for decay class 1 with moderate decreases in decay class 2 with the exception of density in the US treatment, which increased. In contrast, the BC and BS had small decreases in decay class 1 and large decreases in decay class 2,

except for decay class 1 density in the BS treatment, which increased 53%. The burn-only treatment had small to moderate increases in length, volume, and density into decay class 1 and moderate to large decreases in decay class 2. Linear contrasts indicated significant differences between cut, and cut and burn plots across decay classes and overall, but not among silvicultural prescriptions.

Coarse woody debris by mean diameter and percent cover

Pretreatment CWD percent cover and mean diameter ranged from 2.0 to 3.1%/ha and from 87.2 to 72.2 cm, respectively. Analysis of variance detected a treatment effect on percent cover ($P = 0.0012$) and mean diameter ($P = 0.0001$). Percent log cover decreased across all treatments (range 0.9–2.7%/ha) but more so in the cut and burn and the burn-only treatments (range 0.9–1.3%/ha). Mean diameter decreased by an average of 17 cm across all treatments (range 58.7–62.1 cm). Linear contrasts indicate a treatment effect between the thin-only and the thin and burn plots but no difference within silvicultural treatments.

Snags by decay class

Snag mass increased in the BC, BN, UC, and US treatments but decreased in the BS treatment (Fig. 1c). Analysis of variance detected treatment effects only for density in decay class 1 and for total density (Table 3). Post-treatment patterns for volume and mass across the BC, BS, UC, and US treatments decreased moderately in decay class 1 and increased dramatically (200%–600%) in decay class 2. The BN treatment increased 12% in decay class 1 for volume and mass and decreased 300% in decay class 2. Density increased greatly in the cut and burn and the burn-only treatments for decay class 1 and decreased moderately in the cut-only treatments. Density increased across all treatments in decay class 2 but most noticeably in the burn-only treatment. Linear contrasts detected differences between the cut and the cut and burn treatments for density only.

Snags by diameter class

There were no significant differences in snag characteristics between pretreatment plots except for snag mass and volume in the 45.0–64.9 cm size-class (Table 4). Post-treatment, there were significant differences in mass, volume, and density only in the 5.0–24.9 cm and 25.0–44.9 cm diameter classes (Table 4). Post-treatment in the thin and burn and the burn-only treatments, increases in mass and volume ranged from 300% to 600% in the 5.0–24.9 cm diameter class with the burn-only treatments in the lower range. In general, the BC and BN treatments increased in mass and volume moderately in the other diameter classes, whereas the BS treatment decreased slightly in mass and increased moderately in volume. Density in the BC and BN plots increased 390% and 845%, respectively, in the 5.0–24.9 cm diameter class and 20% in the 25.0–44.9 cm diameter class, with an 11%–13% decrease in 45.0–64.9 and ≥ 65 cm diameter classes, respectively. The BS plot followed a similar pattern but with a less dramatic increase in density in the smaller size-class. In the cut-only plots, mass and volume increased moderately (20%–50%) in the 5.0–24.9 cm diameter class and had low to moderate increases in the

Table 2. Results of one-way analysis of variance on pretreatment and post-treatment means for coarse woody debris length ($\text{m}\cdot\text{ha}^{-1}$), volume ($\text{m}^3\cdot\text{ha}^{-1}$), and density ($\text{no.}/\text{ha}$) by modified decay class at the Teakettle Experimental Forest, California.

Decay	BC	BN	BS	UC	US	UN	<i>P</i>
Pretreatment							
Length ($\text{m}\cdot\text{ha}^{-1}$)							
1	116.0	109.6	96.3	117.2	106.5	127.9	0.9259
2	242.3	324.1	187.2	320.6	219.6	219.0	0.1033
Total	358.3	433.7	283.5	437.7	326.1	346.9	0.3612
Volume ($\text{m}^3\cdot\text{ha}^{-1}$)							
1	39.4	37.1	43.1	47.9	34.6	68.2	0.7089
2	143.5ab	169.6a	101.0b	174.2a	155.2ab	155.7ab	0.0375
Total	182.9	206.7	144.1	222.1	189.8	223.9	0.0779
Density ($\text{no.}/\text{ha}$)							
1	14.6	11.7	11.3	12.7	9.5	9.1	0.9619
2	22.8	29.3	20.8	33.4	21.9	19.6	0.1678
Total	37.4	40.9	32.0	46.2	31.4	28.7	0.4352
Post-treatment							
Length ($\text{m}\cdot\text{ha}^{-1}$)							
1	93.6b	137.4ab	93.5b	193.6a	198.7a	127.9ab	0.0100
2	91.7ab	103.2ab	46.8b	201.7a	179.3a	219.0a	0.0010
Total	185.3bc	240.6abc	140.4c	395.3a	378.1a	346.9ab	0.0009
Volume ($\text{m}^3\cdot\text{ha}^{-1}$)							
1	35.5a	39.5a	36.5a	62.2a	54.5a	68.2a	0.1100
2	22.9c	26.4bc	15.9c	82.7a	72.7ab	155.7a	0.0001
Total	58.5cd	66.0bcd	52.4d	144.8ab	127.2abc	223.9a	0.0004
Density ($\text{no.}/\text{ha}$)							
1	14.0a	17.6bc	17.3bc	31.5ab	44.3a	9.1c	0.0001
2	14.0ab	15.3ab	7.9b	29.4a	32.8a	19.6ab	0.0025
Total	28.0c	32.8bc	25.2c	60.9ab	77.1a	28.7c	0.0003

Note: Row means followed by the same letter(s) are not significantly different at $\alpha = 0.05$. See Table 1 for abbreviations. Coarse woody debris is defined here as downed logs with a small-end diameter of ≥ 30 cm. Decay 1, decay classes 1 and 2 summed; decay 2, decay classes 3 and 4 summed.

25.0–44.9 cm, 45.0–64.9 cm, and ≥ 65 cm diameter classes. In the cut-only plots, density increased 20% in the 5.0–24.9 cm diameter class and decreased 20%, 12%, and 3% in the 25.0–44.9 cm, 45.0–64.9 cm and ≥ 65 cm diameter classes, respectively. Linear contrasts detected differences between the thin-only and the thin and burn treatments for all variables except in the 45.0–64.9 cm diameter class. The BN treatment was significantly different for volume and mass in the 5.0–24.9 cm size class than the BS, BC, UC, and US treatments.

Spatial analysis

Pretreatment logs tended to follow three basic spatial patterns: (i) weakly clustered to 30 m becoming random, (ii) strongly clustered to 60 m becoming random, and (iii) strongly clustered past 100 m (Figs. 2a–2c). The snags tended to follow two spatial patterns, similar to the latter two patterns exhibited by logs. For example, the snags followed an almost identical pattern to the logs that were clustered at 60 m and those clustered past 100 m (data not shown). Plots with logs that were weakly clustered to random tended to have snags that were strongly clustered past 100 m. Post-treatment, logs were weakly to strongly clustered to 50 m then became random (actual data not shown, but similar to Fig. 2a) or clustered past 100 m (similar to Fig. 2b). No specific spatial pattern emerged from any treat-

ment. Snag spatial patterns remained relatively unchanged after treatment.

Discussion

The most striking result of this study is the separation between the thin and burn and the thin-only treatments. The effect of burning shifts FWD and CWD into a pattern of reduction in volume, mass, and piece size with a concomitant decrease in density and a shift towards less decayed pieces. Similar responses were seen by Knapp et al. (2005) and Stephens and Moghaddas (2005). This result is contrary to our hypothesis that fire would leave larger pieces behind but supports the hypothesis of a shift towards less decayed pieces. The thin-only treatments resulted in overall decreases in mass of larger pieces, although less so than the burning treatment, with a shift in mass to smaller pieces (logging slash) creating abundant surface fuels (Table 1). Our pretreatment data are similar to the Harmon et al. (1987) and Knapp et al. (2005) studies, which were conducted in mature and old-growth forest, respectively, with similar structures as the Teakettle Experimental Forest. However, volume and mass estimates for snags and CWD were several times higher at Teakettle than in the second-growth, mixed-conifer forest at Blodgett Experimental Forest (Stephens and Moghaddas 2005).

Table 3. Results of one-way analysis of variance on pretreatment and post-treatment means for snag mass ($\text{Mg}\cdot\text{ha}^{-1}$), volume ($\text{m}^3\cdot\text{ha}^{-1}$), and density ($\text{no.}/\text{ha}$) by modified decay class at the Teakettle Experimental Forest, California.

Decay	BC	BN	BS	UC	US	UN	<i>P</i>
Pretreatment							
Mass ($\text{Mg}\cdot\text{ha}^{-1}$)							
1	33.1	29.2	33.3	31.1	29.1	28.6	0.9600
2	7.6	4.7	6.3	10.2	3.9	13.1	0.2400
Total	40.7	33.8	39.6	41.3	33.0	41.6	0.7010
Volume ($\text{m}^3\cdot\text{ha}^{-1}$)							
1	97.0	86.2	96.7	94.3	88.0	84.5	0.9600
2	29.5	18.8	24.0	40.9	17.3	60.7	0.1800
Total	126.5	105.0	120.7	135.2	105.3	145.2	0.5600
Density ($\text{no.}/\text{ha}$)							
1	38.1ab	15.9b	48.5a	28.3ab	24.3ab	25.7ab	0.0490
2	6.8	7.3	9.4	8.0	6.4	14.7	0.2400
Total	44.9	23.3	57.9	36.3	30.7	40.3	0.1120
Post-treatment							
Mass ($\text{Mg}\cdot\text{ha}^{-1}$)							
1	24.5	32.6	11.6	26.6	23.4	28.6	0.1760
2	28.4	17.9	21.8	41.7	27.9	13.1	0.0790
Total	52.8	50.4	33.4	68.3	51.2	41.6	0.2180
Volume ($\text{m}^3\cdot\text{ha}^{-1}$)							
1	71.5	95.8	32.3	82.2	72.1	84.5	0.1360
2	143.5	75.6	115.9	174.0	113.8	60.7	0.1070
Total	215.1	171.4	148.2	256.2	185.9	145.2	0.3140
Density ($\text{no.}/\text{ha}$)							
1	100.2a	81.6a	100.1a	22.8b	21.5b	25.7b	0.0001
2	19.8	9.8	22.9	14.8	10.5	14.7	0.1090
Total	120.0a	91.4a	123.0a	37.6b	32.0b	40.3b	0.0001

Note: Row means followed by the same letter(s) are not significantly different at $\alpha = 0.05$. See Table 1 for abbreviations. Decay 1, decay classes 1 and 2 combined; decay 2, decay classes 3, 4, and 5 combined. Snags are defined as standing dead trees ≥ 5 cm DBH.

The differences between the two silvicultural prescriptions (CASPO vs. shelterwood) did not influence FWD, CWD, or snag retention, suggesting a disconnect between treatment of the overstory and DWM dynamics. Instead, a general pattern emerged separating thin treatments from burn treatments. However, there are long-term differences between thinning and burning when the snags are considered. The thin and burn and the burn-only treatments had a high recruitment of small diameter snags (5.0–24.9 cm). The thin-only treatments had low recruitment of small snags relative to burns but high recruitment of FWD 2.6–7.6 cm. For the burn-only treatments, the absence of disturbance from logging operations minimized the production of FWD and CWD and the removal of small snags. As a result, the burn-only treatment had the largest increase in small snags, which create a potential fire hazard by becoming ladder fuels. These results suggest temporal differences in the fuel loads between thin and burn treatments. Small snags in the burn plots will not be available as fine ground fuel until they fall over; whereas, in the thin plots fine ground fuels are available now. In addition, the ladder-fuel risk of small fire-killed snags in the thin and burn and the burn-only treatments may postpone any future burns until the snags have fallen. Stephens and Moghaddas (2005) found small-diameter snag density increased in their burn-only treatments, similar to our results. However, they found that thinning combined with burning treatments resulted in a reduced number of small snags. These differences are likely due to differences in thinning

treatments between the two studies. For example, Stephens and Moghaddas (2005) used a rotary masticator to remove live and dead trees 2–25 cm, whereas no mechanical treatments were used at Teakettle. These treatment differences may be important for managers in controlling temporal inputs of smaller fuels.

The recruitment of large snags remains a problem for managers (Stephens and Moghaddas 2005). The results of the current study and that of Stephens and Moghaddas (2005) suggest that fire preferentially kills smaller trees and does not impact recruitment of larger snags. The primary pathway for large snag development under a regular fire regime is likely through various pathways such as pathogens, insects, and the senescence of larger trees (Agee 2002; Smith et al. 2005). In the current study, there was an increase, although not statistically significant, in large snag volume with a simultaneous decrease in density for the same size-class, indicating that large snags were recruited; however, the frequency of these structures dropped across the landscape. Therefore, development of large snags likely operates on long time scales, because snags tend to die in place and provide FWD and CWD inputs as they move through the decay process. Pretreatment snag mortality at Teakettle appeared to be higher in localized areas of high density, particularly for smaller trees (Smith et al. 2005). Post-treatment snag mortality at Teakettle, which resulted from the combination of fire treatments coupled with long-term drought, resulted in noticeable mountain pine beetle (*Dendroctonus*

Table 4. Results of one-way analysis of variance on pretreatment means for snag mass (Mg·ha⁻¹), volume (m³·ha⁻¹), and density (no./ha) by 20 cm diameter class at the Teakettle Experimental Forest, California.

Diameter class (cm)	BC	BN	BS	UC	US	UN	P
Pretreatment							
Mass (Mg·ha ⁻¹)							
5.0–24.9	0.3	0.2	0.5	0.3	0.2	0.3	0.3360
25.0–44.9	1.9	0.9	2.3	1.1	0.8	1.3	0.7010
45.0–64.9	2.8a	0.9a	3.3a	1.6ab	1.7ab	2.3ab	0.0184
≥65	35.7	31.8	33.5	38.4	30.2	37.8	0.8060
Total	40.7	33.8	39.6	41.3	33.0	41.6	
Volume (m ³ ·ha ⁻¹)							
5.0–24.9	1.0	0.5	1.6	0.8	0.7	0.8	0.3630
25.0–44.9	5.6	2.8	6.8	3.3	2.6	4.0	0.7710
45.0–64.9	8.3a	3.1b	9.6a	5.2ab	5.4ab	7.5ab	0.0180
≥65	111.7	98.6	102.7	125.9	96.6	132.9	0.6340
Total	126.5	105.0	120.7	135.2	105.3	145.2	
Density (no./ha)							
5.0–24.9	19.7	7.3	27.5	16.1	12.8	15.3	0.2390
25.0–44.9	9.9	4.9	13.3	6.2	5.8	7.5	0.4990
45.0–64.9	5.1	2.3	6.9	3.2	3.7	5.1	0.1250
≥65	10.3	8.8	10.3	10.9	8.4	12.4	0.7360
Total	44.9	23.3	57.9	36.3	30.7	40.3	
Post-treatment							
Mass (Mg·ha ⁻¹)							
5.0–24.9	2.0a	1.1ab	2.4a	0.4bc	0.4bc	0.3c	0.0001
25.0–44.9	2.3	2.5	2.2	1.2	0.8	1.3	0.0900
45.0–64.9	3.1	3.2	2.7	2.1	2.5	2.3	0.4590
≥65	45.4	43.7	26.1	64.6	47.6	37.8	0.1223
Total	52.8	50.4	33.4	68.3	51.2	41.6	
Volume (m ³ ·ha ⁻¹)							
5.0–24.9	5.7a	3.2ab	6.8a	1.4bc	1.3bc	0.8c	0.0001
25.0–44.9	7.9	7.4	8.5	4.4	2.6	4.0	0.1440
45.0–64.9	12.4	10.9	12.5	7.8	9.4	7.5	0.3290
≥65	189.1	149.9	120.5	242.7	172.6	132.9	0.2500
Total	215.1	171.4	148.2	256.2	185.9	145.2	
Density (no./ha)							
5.0–24.9	96.3a	69.2a	97.8a	19.8b	17.8b	15.3b	0.0001
25.0–44.9	11.3ab	10.3ab	14.0a	4.8ab	3.3b	7.5ab	0.0200
45.0–64.9	3.9	3.9	4.2	2.3	3.0	5.1	0.1610
≥65	8.6	8.1	7.1	10.6	7.8	12.4	0.1883
Total	120.0	91.4	123.0	37.6	32.0	40.3	

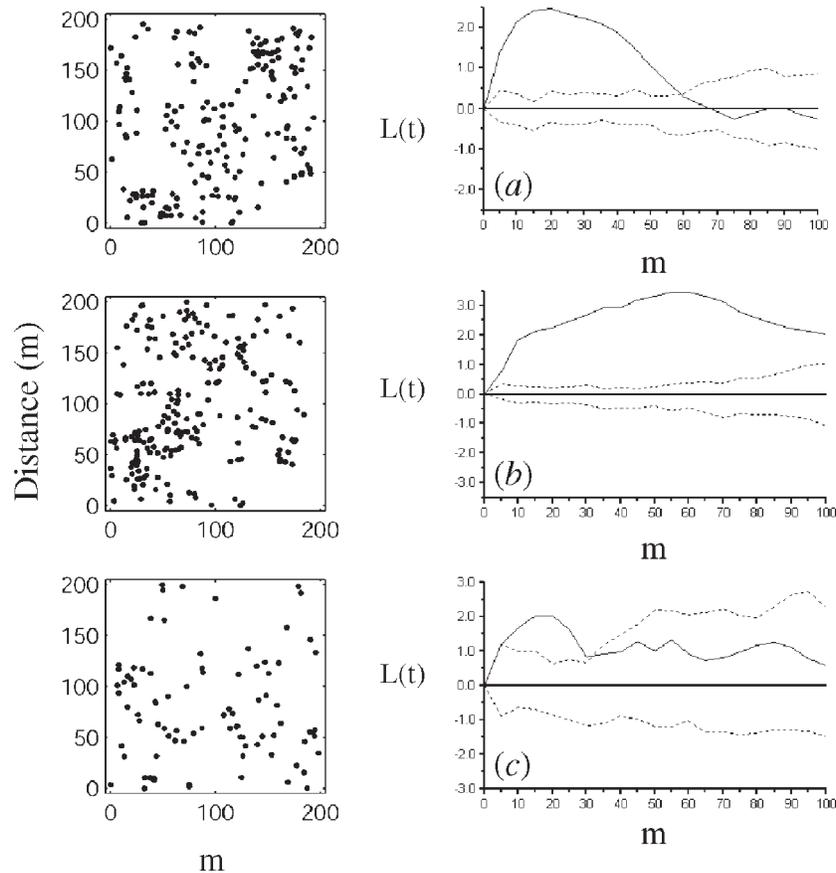
Note: Row means followed by the same letter(s) are not significantly different at $\alpha = 0.05$. See Table 1 for abbreviations. Snags are defined as standing dead trees ≥ 5 cm DBH. See Table 3 for total P values.

ponderosae Hopkins, 1902) kill of larger pines originally retained as seed trees, suggesting that fire may indirectly affect large snag recruitment over the long term (David Rizzo, University of California, Davis, personal communication, 2004). These types of recruitment patterns are stochastic and cannot be controlled by managers, but they do suggest that groups of large snags may be recruited quickly if conditions are favorable. However, for recruitment to occur, there must be large trees available, which may be a problem in second-growth forests.

The spatial distribution of logs and snags can be an important influence on habitat for wildlife species (Spencer et al. 1983; Spencer 1987; Bunnell et al. 2002; McComb 2003). The post-treatment spatial patterns remained within the range of the pretreatment patterns with no specific trends associated with different treatments. This result is contrary

to our hypothesized pattern of a strictly clustered pattern of DWM. However, we have no information as to what distance to expect the DWM to be clustered to, other than to assume it is within the extent of past fires (0.02–83.5 ha; Fiegner 2002). Spatially, DWM is primarily influenced by fire (Agee 2002; Skinner 2002), and fire extent and severity is primarily controlled by factors such as topography and species composition (Beaty and Taylor 2001). Therefore, the results of the spatial analysis may represent what we could expect the natural range of variation to be, given the sample area of our plots (4 ha). A more interesting relationship for managers and ecologists to explore may be the spatial relationship among logs, snags, and live trees and how they respond to fire and thinning. In the current study, the pattern between the logs and snags changed very little. However, it is important to frame these patterns as the result of one burn.

Fig. 2. Three spatial patterns typical of log distribution found in the Teakettle Experimental Forest. On the left are mapped 4 ha plots of the logs, with dots representing the centre of each log's location. On the right are the univariate Ripley's K analyses of the Laplace-transformed values ($L(t)$) of the plots. The broken lines are the 95% confidence intervals. The solid line is the pattern of the stems or logs. The greater the deviation outside the 95% CI, the more significant is the clustering pattern. The stem pattern is considered to be significantly clustered for those distances (x axis) over which the solid line is above the upper broken line, regularly distributed for those distances over which the solid line is below the lower broken line and randomly distributed if it falls between the broken lines. The three patterns are (a) strongly clustered to 60 m then becoming random, (b) strongly clustered to ≥ 100 m, and (c) weakly clustered to 35 m then tending towards random.



To properly restore forests back to a fire-resistant state, most researchers suggest that fire will need to be applied to a stand several times (Kilgore 1972; Arno 2000; Allen et al. 2002; Knapp et al. 2005). Empirical (Swetnam 1993; Stephens 2004) and modeled data (Miller and Urban 2000) have shown that frequent fires increase the heterogeneity of fuels; therefore, we might expect a more consistent pattern of clustering with frequent fire as was also suggested by Knapp et al. (2005).

Mammal habitat has been related to abundance, percent cover, log size, and decay class in western forests (McComb 2003). All of these variables shifted because of treatment effects. Percent cover and mean piece size declined resulting in reduced habitat, and decay shifted toward the lower decay classes resulting in loss of a specific habitat type. Furthermore, habitat was lost through a reduction in larger snags. Unfortunately, snags can also be an operational hazard during harvesting (Stephens and Moghaddas 2005), so some may be cut down. However, framing these changes spatially and temporally across the landscape is important given that regular fire regimes may create a landscape-scale matrix of habitat availability over time.

The shift towards a CWD pool consisting of less decayed

pieces presents a change in what would be considered a functional attribute of CWD. In many forests, maintaining a CWD pool of well-distributed decay classes is important for habitat and species diversity (Harmon et al. 1986; McComb 2003; Marra and Edmonds 2005; Apigian et al. 2006). However, in forests frequently scoured by fire, these highly decayed pieces may not be widely available but may be found only in wetter microhabitats suggesting that DWM may have a narrower range of functions in fire dominated forests than in other systems. For example, in moister systems, CWD serves an important role as nurse logs for many tree species (Harmon et al. 1986). At Teakettle, despite the abundance of large well-decayed logs, there was no relationship between tree seedlings and logs (Gray et al. 2005). Logs do appear to be important habitat for invertebrates in mixed-conifer forests (Marra and Edmonds 2005; Apigian et al. 2006) as noted by Harmon et al. (1987) in Sequoia National Park, California.

Conclusions

Thin and burn treatments were more effective at reducing

fuels than thin-only or burn-only treatments in the old-growth, mixed-conifer forest we studied. The results of this study highlight the effectiveness of burning but also support the practice of repeated burns to properly restore fire-induced patterns back to the forest structure. Further research on DWM dynamics in fire-dominated forests should focus on the response of DWM to repeated fire treatments and the effect of topographic variables. With this type of information we may acquire a better understanding of the baseline quantities and spatial patterns of DWM given frequent disturbance. In addition, managers and ecologists working to restore forests with a frequent fire regime need to think of DWM as a transient structure changing across short time periods as influenced by fire. Instead of focusing primarily on transient FWD and CWD on the ground, more management effort should be placed on managing the source of CWD, mainly large-diameter trees. Retaining large-diameter trees across the landscape will allow for a steady recruitment of snags and logs.

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References

- Agee, J.K. 2002. Fire as a coarse filter. *In* Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 2–4 November 1999, Reno, Nev. W.F. Laudenslayer, Jr., P.J. Shea, B.E. Valentine, P.C. Weatherspoon, and T.E. Lisle (*Technical coordinators*). USDA For. Serv. Gen. Tech. Rep. PSW-181. pp. 359–368.
- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., and Klingel, J.T. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* **12**: 1418–1433.
- Apigian, K., Dahlsten, D., and Stephens, S.L. 2006. Fire and fire surrogate treatment effects on leaf litter arthropods in a western Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* **221**: 110–122.
- Arno, S.F. 2000. Fire in western forest ecosystems: effects of fire on flora. *In* Wildland fire in ecosystems. Vol. 2. *Edited by* J.K. Brown and J. Kapler Smith. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-42. pp. 97–120.
- Beaty, M.R., and Taylor, A.H. 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, southern Cascades, Calif., USA. *J. Biogeogr.* **28**: 955–966.
- Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.
- Bunnell, F.L., Boyland, M., and Wind, E. 2002. How should we distribute dead and dying wood? *In* Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 2–4 November 1999, Reno, Nev. W.F. Laudenslayer Jr., P.J. Shea, B.E. Valentine, P.C. Weatherspoon, and T.E. Lisle (*Technical coordinators*). USDA For. Serv. Gen. Tech. Rep. PSW-181. pp. 739–752.
- Cline, S.P., Berg, A.B., and Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wild. Manage.* **44**: 773–786.
- Fiegner, R.P. 2002. The influence of sampling intensity on the fire history of the Teakettle Experimental Forest, Sierra Nevada, California: small fire detection, the composite fire chronology, and fire interval calculation. M.Sc. thesis, Graduate Group in Ecology, University of California, Davis, Calif.
- Gray, A.N., Zald, H.S.J., Kern, R.A., and North, M. 2005. Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. *For. Sci.* **51**(3): 198–210.
- Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's *K* function: introduction and methods of edge correction. *J. Veg. Sci.* **6**: 575–582.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, S.V., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, W., Cromack, K., Jr., and Cummings, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **5**: 133–302.
- Harmon, M.E., Cromack, K., Jr., and Smith, B.G. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. *Can. J. For. Res.* **17**: 1265–1272.
- Husch, B., Miller, C.I., and Beers, T.W. 1993. Forest mensuration. Krieger Publishing, Malabar, Fla.
- Kilgore, B.M. 1972. Impact of prescribed burning on a sequoia mixed-conifer forest. *Proc. Tall Timbers Fire Ecol. Conf.* **12**: 345–375.
- Knapp, E.E., Keeley, J.E., Ballenger, E.A., and Brennan, T.J. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *For. Ecol. Manage.* **208**: 383–397.
- Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H., and Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. *Ecol. Appl.* **7**: 691–701.
- Marra, J.L., and Edmonds, R.L. 2005. Soil arthropods responses to different patch types in a mixed-conifer forest of the Sierra Nevada. *For. Sci.* **51**(3): 255–265.
- Maser, C., and Trappe, J.M. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164. p. 56.
- Maser, C., Anderson, R.G., Cromack, K., Jr., Williams, J.T., and Martin, R.E. 1979. Dead and down material. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. USDA Agric. Handb. No. 553. pp. 78–95.
- McComb, W.C. 2003. Ecology of coarse woody debris and its role as habitat for mammals. *In* Mammal community dynamics. *Edited by* C.J. Zabel and R.G. Anthony. Cambridge University Press, Cambridge, UK. pp. 374–404.
- Miller, C., and Urban, D. 2000. Connectivity of forest fuels and surface fires regimes. *Landsc. Ecol.* **15**: 145–154.
- North, M., Oakley, B., Chen, J., Erickson, H., Gray, A., Izzo, A., Johnson, D., Ma, S., Marra, J., Meyer, M., Purcell, K., Rambo, T., Rizzo, D., Roath, B., and Schowalter, T. 2002. Vegetation and ecological characteristics of mixed-conifer and red fir forests at the Teakettle Experimental Forest. USDA For. Serv. Gen. Tech. Rep. PSW-186.
- North, M., Hurteau, M., Fiegner, R., and Barbour, M. 2005. Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. *For. Sci.* **51**(3): 187–197.

- Ripley, B.D. 1979. Tests of 'randomness' for spatial point patterns. *J. R. Stat. Soc. Bull.* **41**: 368–374.
- Skinner, C.N. 2002. Influence of fire on the dynamics of dead woody material in forests of California and southwestern Oregon. *In Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 2–4 November 1999, Reno, Nev.* W.F. Laudenslayer, Jr., P.J. Shea, B.E. Valentine, P.C. Weatherspoon, and T.E. Lisle (*Technical coordinators*). USDA For. Serv. Gen. Tech. Rep. PSW-181. pp. 445–454.
- Skinner, C.N., and Chang, C. 1996. Fire regimes, past and present. *In Sierra Nevada Ecosystem Project: final report to Congress. Vol. II. Centers for Water and Wildland Resources, University of California, Davis, Calif. Wildland Resour. Cent. Rep. No. 37.* pp. 1041–1069.
- Smith, S.F., Rizzo, D.M., and North, M. 2005. Patterns of mortality in an old-growth mixed-conifer forest of the southern Sierra Nevada, California. *For. Sci.* **51**(3): 266–275.
- Spencer, W.D. 1987. Seasonal rest-site preferences of pine martens in the northern Sierra Nevada. *J. Wildl. Manage.* **51**: 616–621.
- Spencer, W.D., Barrett, R.H., and Zielinski, W.J. 1983. Marten habitat preferences in the northern Sierra Nevada. *J. Wildl. Manage.* **47**: 175–182.
- Spies, T.A., and Franklin, J.F., and Tomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, **69**: 1689–1702.
- Stephens, S.L. 2004. Fuel loads, snag density, and snag recruitment in an unmanaged Jeffrey pine – mixed conifer forest in northwestern Mexico. *For. Ecol. Manage.* **199**: 103–113.
- Stephens, S.L., and Moghaddas, J.J. 2005. Fuel treatment effects on snags and coarse woody debris in a Sierra Nevada mixed conifer forest. *For. Ecol. Manage.* **214**: 53–64.
- Sturtevant, B.R., Bissonette, J.A., Long, J.M., and Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecol. Appl.* **7**: 702–712.
- Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. *Science (Washington, D.C.)*, **262**: 885–889.
- Verner, J., McKelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould, G.I., Jr., and Beck, T.W. 1992. The California spotted owl: a technical assessment of its current status. USDA For. Serv. Gen. Tech. Rep. PSW-133.
- Weatherspoon, P.C. 2000. A proposed long-term national study of the consequences of fire and fire surrogate treatments. *In Proceedings of the Joint Fire Sciences Conference and Workshop, 15–17 June 2000, Moscow, Idaho. Edited by L.F. Neuenschwander and K.C. Ryan.* University of Idaho, Moscow, Idaho. pp. 117–126.
- Wright, P.M., Harmon, M., and Swanson, F. 2002. Assessing the effect of fire regime on coarse woody debris. *In Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 2–4 November 1999, Reno, Nev.* W.F. Laudenslayer, Jr., P.J. Shea, B.E. Valentine, P.C. Weatherspoon, and T.E. Lisle (*Technical Coordinators*). USDA For. Serv. Gen. Tech. Rep., PSW-181. pp. 621–635.