Applied Vegetation Science 13: 207–220, 2010
DOI: 10.1111/j.1654-109X.2009.01062.x

Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest

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Abstract

Questions: What influence does mechanical mastication and other fuel treatments have on: (1) canopy and forest floor response variables that influence understory plant development; (2) initial understory vegetation cover, diversity, and composition; and (3) shrub and non-native species density in a second-growth ponderosa pine forest.

Location: Challenge Experimental Forest, northern Sierra Nevada, California, USA.

Methods: We compared the effects of mastication only, mastication with supplemental treatments (tilling and prescribed fire), hand removal, and a control on initial understory vegetation response using a randomized complete block experimental design. Each block ($n = 4$) contained all five treatments and understory vegetation was surveyed within 0.04-ha plots for each treatment.

Results: While mastication alone and hand removal dramatically reduced the midstory vegetation, these treatments had little effect on understory richness compared with control. Prescribed fire after mastication increased native species richness by 150% (+6.0 species m^2) compared with control. However, this also increased non-native species richness (+0.8 species m^2) and shrub seedling density (+24.7 stems m^2). Mastication followed by tilling resulted in increased non-native forb density (+0.7 stems m^2).

Conclusions: Mechanical mastication and hand removal treatments aided in reducing midstory fuels but did not increase understory plant diversity. The subsequent treatment of prescribed burning not only further reduced fire hazard, but also exposed mineral soil, which likely promoted native plant diversity. Some potential drawbacks to this treatment include an increase of non-native species and stimulation of shrub seed germination, which could alter ecosystem functions and compromise fire hazard reduction in the long-term.

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Keywords: California, USA; Forest floor; Incorporation; *Pinus ponderosa*; Plant diversity; Prescribed fire; Sierra Nevada; Tilling.

Nomenclature: Hickman (1993).

Abbreviation: NMDS = non-metric multidimensional scaling.

Introduction

Decades of fire exclusion and past land-use activities have altered the structure, composition, and ecological function in many ponderosa pine (*Pinus ponderosa*) forests in the western United States. As a result, contemporary forests are often characterized by higher tree densities, reduced spatial heterogeneity, greater proportion of shade-tolerant species, increased rates of insect/pathogen-related mortality, and diminished nutrients available to plants compared with pre-settlement forest conditions (Allen et al. 2002; Keane et al. 2002; Moore et al. 2004). Increased tree density and canopy cover related to these forest changes have directly influenced understory vegetation development and persistence, resulting in reduced understory biomass, cover and diversity in many western pine ecosystems (Abella & Covington 2004; Wienk et al. 2004; Wayman & North 2007).

Shifts in the structure and composition of ponderosa pine forests as a result of fire exclusion and/or past land-use practices have also led to greater horizontal and vertical continuity of woody fuels. These fuel conditions have increased the chance of uncharacteristically high-intensity and severe wildfires, prompting recommendations to actively manage fuels to reduce fire hazard and improve resilience within fire-prone ecosystems (Moore et al. 1999; Stephenson 1999; Agee & Skinner 2005). Unfortunately, constraints such as air-quality restrictions (Ottmar et al. 2001) and liability concerns (Yoder et al. 2004) can complicate large-scale use of prescribed fire in many areas. As a result, managers increasingly rely on manual or mechanical methods of fuels treatment (Agee & Skinner 2005). While traditional harvesting equipment is often used to remove commercially viable trees, areas dominated by small, non-commercial trees or shrubs typically rely upon other methods. Where cost can be justified, such as in areas adjacent to homes or within fuel breaks, these smaller fuel types may be cut with a chainsaw and either removed manually off site (hand removal) or piled and burned on site. More recently, land managers in the western United States are increasingly using mechanical mastication to treat these fuel types.

Mechanical mastication involves the use of a boom or front-end mounted rotating blade or drum that shreds live and dead woody material, concentrating these woody fuels in a dense layer on the forest floor (Kane et al. 2009). From a fuels management perspective, mechanical mastication dramatically reduces vertical continuity and mass of the midstory (i.e. shrubs and small trees), thus potentially reducing the incidence of a stand-replacing fire. Mechanical mastication may also further be desirable because of the accumulation of a dense woody debris layer that may inhibit shrub establishment from seed and prolong treatment longevity. However, this physical barrier could also affect germination of other desirable plant species, potentially influencing cover, diversity and composition (Sydes & Grime 1981; Xiong & Nilsson 1999). Subsequent fuel management strategies, such as prescribed fire or incorporation (tilling into the soil), may mitigate this barrier effect by both reducing surface fuel availability and exposing mineral soil. However, these supplemental treatments also cause soil disturbance, which can promote the recruitment of non-native plant species (Keeley 2006) and alter the understory plant community. Experimental use of prescribed fire in masticated fuelbeds has also resulted in fires with long residence times and substantial soil heating (Busse et al. 2005), which may reduce the soil seed bank density relative to other methods of disposal such as incorporation into the soil through tilling.

Recent studies have investigated the effect of several fuel treatment methods (e.g. thinning and/or prescribed fire) on understory vegetation response (Griffis et al. 2001; Metlen et al. 2004; Wienk et al. 2004; Wayman & North 2007). While a few studies have evaluated the effects of mechanical mastication on understory vegetation (Bradley et al. 2006; Sikes 2006; Perchemlides et al. 2008), none have characterized the effects of mastication with supplemental treatments on understory vegetation in forested ecosystems. In addition, there have been no studies that directly compare mechanical mastication treatments with a hand removal treatment. This comparison is useful because it allows us to determine the relative importance of midstory removal alone (hand treatment) in conjunction with adding material to the forest floor (mastication only) or supplementary ground disturbances (incorporation and prescribed fire).

The primary objective of this study was to evaluate the initial understory plant response following mastication of midstory vegetation only, mastication followed by supplemental fuels treatments (prescribed fire or incorporation) and hand removal of shrubs and midstory vegetation compared with untreated control stands. Specifically, this study aimed to evaluate the effects of different fuels treatments on: (1) variables that influence understory plant response (e.g. canopy cover, percentage bare ground); (2) understory plant cover, diversity and composition; and (3) shrub and non-native plant abundance. Lastly, we identified whether particular species were associated with the treatments implemented.

Methods

Study site

The study was conducted on the Challenge Experimental Forest located within the Plumas National Forest in the northern Sierra Nevada of California, US (39°29′N, 121°13′W; Fig. 1). Research sites were moderately sloped (0–20%), predominantly west-facing, and ranged between 800 m and 900 m elevation. The climate is broadly characterized as Mediterranean because of its hot dry summers and cool wet winters. The mean annual temperature of the Challenge Experimental Forest is 12.3°C. Mean annual precipitation is 1730 mm with 98% falling as rain between Oct and May (Berg 1990). Soils within the study area are composed of deep, well-drained loam to gravelly loam, xeric Haplohumult soils in the Sites series (USDA-NRCS 2007).

The study site is located within the lower elevational range of the Sierra Nevada mixed-conifer forest type. The dominant overstory species are

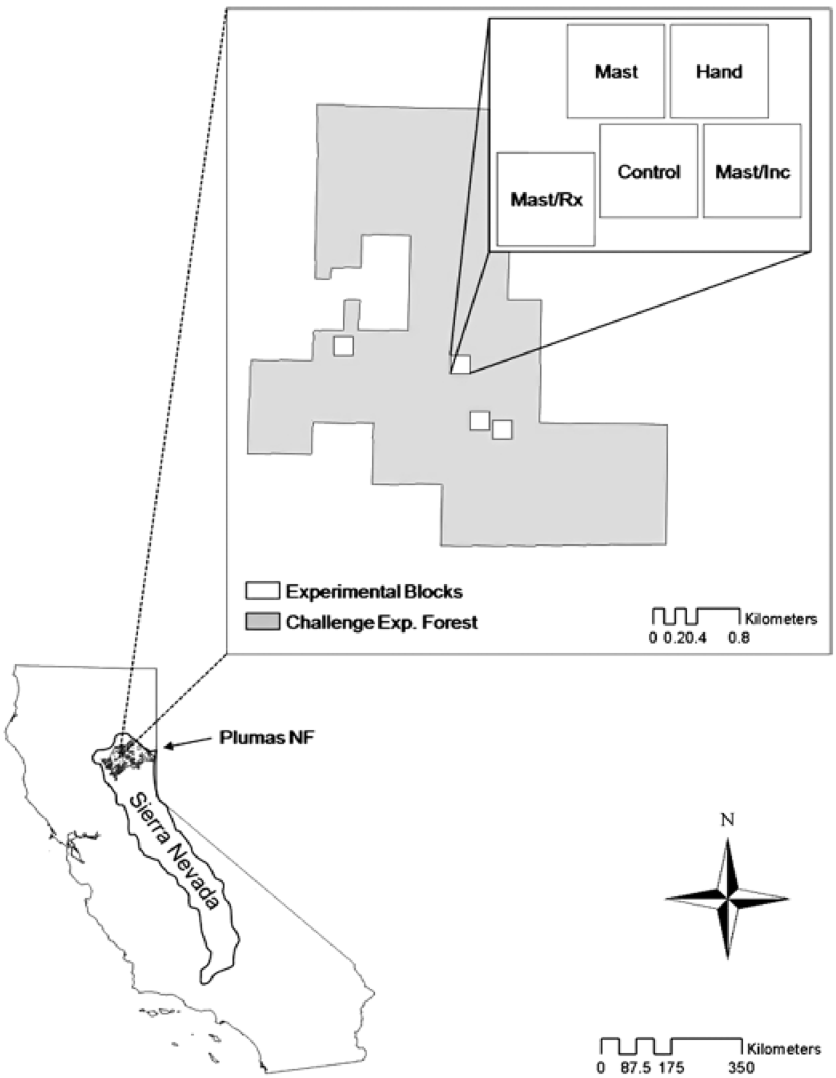

Fig. 1. Location of study area within the Challenge Experimental Forest in the Plumas National Forest, California, US. Inset shows the Experimental Forest boundary with the location of each experimental block. The second inset depicts one of four blocks used within the experimental design (Control = no treatment; Hand = hand removal; Mast = mastication only; Mast/Inc = mastication and incorporation; Mast/Rx = mastication and prescribed fire).

composed of *P. ponderosa* Dougl. ex Law. with occasional *Pinus lambertiana* (Dougl.), *Pseudotsuga menziesii* (Mirbel) Franco, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. and *Calocedrus decurrens* (Torr.) Florin, each representing $<1\%$ of the total conifer density. Before treatment, the dense midstory was composed of hardwood species including *Lithocarpus densiflorus* (Hook. & Arn.) Rehd., *Arbutus menziesii* Pursh and *Quercus kelloggii* Newberry. *Ceanothus integerrimus* Hook. & Arn. and *Arctostaphylos viscida* Parry were the most common shrub species in the understory.

Vegetation throughout much of the study area established after timber harvesting and other land management practices typical in the northern Sierra Nevada during the early 1900s (Berg 1990). Three of the four research blocks were clear-cut in 1963 and were part of a previous study examining regeneration in various-sized openings (McDonald 1983). The other block experienced a wildfire in 1961 and subsequently became a shrub-dominated (*A. viscida* and *C. integerrimus*) community type. In the blocks that were clear-cut, the slash fuels were broadcast burned in 1963 and vegetation regenerated naturally. The block that experienced a wildfire was reclaimed during the 'Penny Pines' program, where shrubs were piled and burned, with *P. ponderosa* seedlings planted in late 1960s and thinned once in the early 1980s. Despite differing land management histories, all blocks contained relatively even-aged, 40- to 45-year old *P. ponderosa* with similar structural characteristics. Mean basal area ($29.0 \pm 3.2\,m^2\,ha^1$) and mean tree density (509.6 ± 52.9 stems ha^{-1}) for all conifers greater than 10 cm diameter at breast height were not significantly different ($P > 0.111$) among blocks.

Experimental design and treatments

A randomized complete block experimental design for was used for the study. Twenty experimental units (ca. 0.4 ha each) were surveyed and permanently monumented in the summer of 2001. All treatments ($n = 5$) were randomly assigned to a plot within each of the four blocks, giving a total of four replicates for each treatment. An exception to the random assignment was made for two units in separate blocks which were placed adjacent to each other for operational ease in prescribed burning. All treatment units in both of these two blocks were located in close proximity to each other and contained structurally and compositionally similar vegetation. Each individual unit was separated from adjacent units or untreated forests by a narrow buffer wide enough for equipment access.

The five treatments compared in this study were: mastication only (MAST); mastication followed by incorporation (MAST/INC); mastication followed by prescribed burning (MAST/RX); hand removal (HAND); and no treatment/control (CONTROL). All mechanical mastication treatments (MAST, MAST/INC and MAST/RX) were completed in May 2002 using a rotary drum style masticating head with fixed teeth mounted on the front-end of a Rayco crawler model #T275 (Rayco Manufacturing Inc., Wooster, OH, US). Hand removal treatments were completed in May 2002 using chainsaws to cut midstory trees and understory shrubs, with cut debris manually removed from the units. The incorporation (tilling) treatment was completed 1 month after mastication with a 1.8-m wide rototiller that churned the masticated debris into the upper soil layer (to a maximum depth of 15–25 cm). The MAST/INC treatments reduced surface fuel availability by burying some wood into the mineral soil. Herbicides were applied as a split-plot treatment to the MAST and MAST/INC treatments, but are not included in the results reported here. During the application of herbicides, temporary barriers were placed along the split-plot border to avoid overspray into the untreated side.

Prescribed fire was applied to the MAST/RX treatment units 3 yr after the mechanical mastication treatment. Burning was conducted between 31 May and 28 Jun 2005. Each unit was drip torch ignited and burned with strip head and backing fires from the highest point (upper slope) to the lowest point in the unit.

Data collection

Understory vegetation data (all plants below 2 m tall) were collected in the summer of 2006. Vegetation was sampled along an array of five to ten gridpoints systematically placed within each unit. The number of gridpoints sampled varied because sampling was not conducted within the herbicide-treated portions of both the MAST and MAST/INC units. Understory vegetation data were collected in four $1\,m \times 1\,m$ quadrats placed in the four cardinal directions, 1 m away from each gridpoint to minimize the impact of trampling. Within each of the vegetation quadrats, all vascular plant species were identified following Hickman (1993) and assigned a cover class value (1 = <0.25%, 2 = 0.25-0.49%, 3 = 0.5-0.9%, 4 = 1.0-1.9%, 5 = 2.0-4.9%, 6 = 5.0-9.9%, 7 = 10.0-24.9%, 8 = 25.0-49.9%, 9 = 50-74.9%, 10 = 75.0-94.9%, 11 = >95%) by the same observer for all plots. Cover data were averaged at the gridpoint level using the midpoint value of the cover class. In addition, all rooted stems of each non-native herbaceous species and shrubs < 50 cm tall (i.e. seedlings and short shrub species) were counted. The species richness for each treatment was calculated by averaging the number of species found within each $1\,m^2$ quadrat for each of the gridpoints within a treatment unit. Two diversity indices were calculated for each of the treatment types: Simpson's index of diversity (D) and Shannon diversity index (H') (Magurran 1988). At each of the gridpoints surveyed, a spherical densiometer (Lemmon 1956) was used to estimate canopy closure (%).

To evaluate the effect of treatment on the midstory, density and height of tall shrubs (> 50 cm) and small trees (< 10 cm diameter at breast height) were measured using a range pole along $10\,m \times 1\,m$ belt transects placed along a random azimuth radiating from each gridpoint and starting 1 m away from the gridpoint to avoid potentially trampled areas. All individuals were tallied by species and the height of every fifth individual was recorded to the nearest 10 cm. Height measurements ceased after five heights were taken for each species and each transect. In addition to vegetation data, surface fuels were collected within a 50 cm × 50 cm metal frame placed along a random azimuth, positioned 7 m from the gridpoint. Ground cover (woody, bare ground, and litter) for each fuels treatment was estimated by assigning each cover type as the cover class value (previously described) within each frame. In the treatment types where recently fallen litter masked the cover values associated with the immediate post-treatment groundcover (i.e. MAST, MAST/INC, MAST/RX), the post-treatment fallen litter was removed before assigning cover classes.

To evaluate litter (including masticated woody fuels) and duff depth across treatments, four 25-cm long, large-gauge nails were pounded in 10 cm diagonally from each of the frame corners with the nail head flush with the surface of the litter. After progressively removing organic material from the frame and placing it within labeled paper bags, depth of the litter and duff layers was measured as the distance from the top of the nails. Litter consisted of recently fallen needles, leaves and masticated woody debris. The underlying duff was composed of the fermentation horizon and the partially to fully decomposed humus horizon beneath. In the event that a woody fuel particle crossed the frame, the piece was cut along the horizon boundary and segregated into respective horizons/layers. All fuels from each of their respective layers were oven-dried for at least 72 h at 85°C and then weighed.

Data analysis

The vegetation response to each of the fuels treatments was evaluated by calculating the mean cover, frequency and diversity of all species occurring within the quadrats. In addition, mean stem density was calculated for all non-native herbs and shrub species < 50 cm tall. For all shrub species > 50 cm tall, average height and density were calculated.

Data were analysed using an ANOVA in NCSS (Hintze 2007) to test for fuel treatment effects on the following response variables: midstory height, ground cover, fuel depth and load, canopy closure, plant cover, diversity, non-native plant density and shrub density. A mixed-model ANOVA (Sokal & Rohlf 1995) was used with treatment as a fixed variable and block as a random variable. When significant treatment effects were found ($\alpha < 0.05$), tests between individual treatments were conducted using the Tukey–Kramer multiple comparison test (Sokal & Rohlf 1995).

To determine the potential drivers of plant cover and diversity response to the fuel treatments, a correlation matrix using non-parametric Spearman rank correlation was computed. Variables influencing plant response and measures of herb cover, shrub cover, species richness and Simpson index of diversity were included in the correlation matrix.

Assessment of the understory plant community response to the different fuels treatments was conducted using a non-metric multidimensional scaling (NMDS) ordination in PC-ORD version 5.0 (McCune & Mefford 1999). Within the NMDS, Euclidian distance measures were used to generate axes values. An ordination was computed based on frequency data for species occurring in at least 10% of all plots. The frequency dataset represents the proportion of times a species was encountered within all 1 m^2 quadrat subsamples for a given unit. In addition, environmental data associated with the respective treatment sample were overlaid as joint plots to show the variables most responsible ($r^2 \geq 0.2$) for separation of treatment communities in species space. A non-parametric blocked multiple response permutation procedure was used to detect whether understory plant community composition differed significantly among fuels treatments (McCune & Grace 2002). For each analysis, a chance-corrected within-group agreement (A) value was calculated where A is equal to one minus the division between the observed versus the expected weighted mean within-group distance (delta). If $A = 0$, then the heterogeneity within groups is equal to that by chance, while if $A = 1$ (delta = 0), then all items are identical within each respective group. The P-value generated from this procedure represents the probability of getting an equal or smaller value of delta by chance (McCune & Grace 2002). Euclidian distances were used to calculate A values, while groups were assigned based on the fuels treatment.

Indicator species analyses were performed using PC-ORD version 5.0 (McCune & Mefford 1999) to detect whether individual species were associated with a particular fuels treatment. Both species cover and frequency values were used to calculate indicator values for each species in which each value was averaged at the plot ($n = 4$) and treatment level ($n = 5$). Indicator values can range from 0 to 100, where 100 represents a species that has full fidelity to one particular treatment. The P-values calculated with this procedure represent the probability of obtaining an indicator value equal to or greater than one obtained by chance. Randomly generated data were computed based on a Monte Carlo test with 5000 randomizations (McCune & Grace 2002).

Results

All fuel reduction treatments had a profound effect on midstory fuels, reducing their mass and vertical continuity (Fig. 2). Midstory heights were lower in all fuel treatments compared with the control ($F = 24.71$, $df = 4$, $P < 0.001$) (Table 1). Reductions in the midstory biomass through fuels treatments resulted in a 12% to 26% decrease in canopy closure compared with the control, but because of the high degree of variability, treatment effect was only marginally significant ($F = 3.10$, $df = 4$, $P = 0.057$). Measures of ground cover, with the exception of woody debris cover, were significantly affected by treatment (Table 1). As expected, the control and hand removal treatments had the least bare ground exposed (<7%) and the most litter cover (>75%). The MAST and MAST/INC treatments had the highest woody cover values (>20%). Mastication treatments followed by supplemental ground disturbances (MAST/INC and MAST/RX) had significantly greater proportions of bare ground (34% and 43%, respectively) than both CONTROL and HAND treatments (6% and 4%, respectively; Table 1). Litter depth differed significantly by fuel treatment ($F = 3.69$, $df = 4$, $P < 0.001$), but no significant differences were detected in either litter ($P = 0.072$) or duff ($P = 0.354$) mass among treatments.

Effect of treatments on understory plants

Seventy-one vascular plant species were recorded across all fuel treatments including 10 trees, 16 shrubs, seven graminoids and 38 forbs. Understory plant cover values in all treatments were at least twice those found in the control (Table 2), although this difference only approached statistical significance ($P = 0.062$) because of high within-treatment variability. A treatment effect was detected for densities of native ($P < 0.001$), resprouting ($P < 0.001$), and obligate seeding shrubs ($P < 0.001$), as well as non-native forb species ($P = 0.010$; Table 2). The number of <50-cm tall native, resprouting, and obligate seeding shrub stems was greater in the MAST/RX treatment than in all other treatments, while MAST/INC contained significantly more stems of resprouting species than the control treatment. Both the MAST and MAST/INC treatments contained greater densities of non-native forb individuals (0.7 and 0.8 stems m^2, respectively), when compared to the control, which contained only native forbs (Table 2). For taller shrubs (>50 cm), a significant treatment effect was found for densities

Fig. 2. Photographs showing representative pretreatment conditions within the (a) control (untreated) plots and post-treatment conditions within (b) hand removal, (c) mastication only, (d) mastication and incorporation, and (e) mastication and prescribed fire plots. Photographs (b) to (c) were taken 4 yr post treatment while (e) was taken 1 yr after treatment.

Table 1. Canopy and forest floor response variables (mean ± SE) for fuels treatments in a ponderosa pine forest. The *P*-values represent the results of a mixed model ANOVA ($df = 3$) with significant treatment effects denoted in bold and different superscript letters in rows indicate significant differences between individual treatment types based on results from Tukey–Kramer multiple comparison tests. CONTROL = no treatment; HAND = hand removal; MAST = mastication only; MAST/INC = mastication and incorporation; MAST/RX = mastication and prescribed fire.

Variable	Treatments					*P*-value
	CONTROL	HAND	MAST	MAST/INC	MAST/RX	
Midstory height (cm)	254.8 (29.0)[a]	119.7 (7.9)[b]	120.9 (5.1)[b]	95.7 (10.8)[bc]	64.9 (5.2)[c]	**<0.001**
Canopy closure (%)	96.9 (1.2)	85.1 (4.2)	80.4 (3.4)	81.4 (4.7)	71.2 (4.2)	0.057
Bare ground (%)	6.6 (4.5)[ab]	3.5 (2.0)[b]	7.2 (4.6)[ab]	34.3 (13.9)[ab]	48.5 (15.8)[a]	**0.016**
Woody debris cover (%)	14.1 (7.8)	2.5 (0.4)	26.4 (5.4)	24.9 (7.9)	9.9 (6.5)	0.097
Litter cover (%)	78.9 (6.2)[a]	91.5 (3.6)[a]	61.9 (6.7)[ab]	28.0 (7.7)[c]	31.1 (11.1)[bc]	**<0.001**
Litter depth (cm)	8.1 (1.3)[ab]	5.9 (0.4)[b]	7.8 (0.4)[a]	6.8 (0.5)[ab]	4.0 (0.3)[c]	**<0.001**
Duff depth (cm)	1.6 (0.4)	1.7 (0.3)	2.0 (0.4)	0.5 (0.2)	1.2 (0.3)	0.337
Litter load (Mg ha^{-1})	16.4 (4.9)	10.5 (0.9)	19.5 (2.0)	20.6 (4.1)	9.1 (1.9)	0.072
Duff load (Mg ha^{-1})	10.4 (4.7)	10.3 (2.8)	13.2 (4.2)	5.1 (3.6)	12.5 (3.9)	0.354

Table 2. Understory plant cover and density means (± SE) for fuels treatments in a Sierra Nevada ponderosa pine forest. The *P*-values represent the results of a mixed model ANOVA ($df = 3$) with significant treatment effects denoted in bold and different superscript letters in rows depict significant differences between individual treatment types based on results from Tukey–Kramer multiple comparison test. CONTROL = no treatment; HAND = hand removal; MAST = mastication only; MAST/INC = mastication and incorporation; MAST/RX = mastication and prescribed fire.

Variable	Treatments					*P*-value
	CONTROL	HAND	MAST	MAST/INC	MAST/RX	
Cover (1 m×1 m)						
All species	23.8 (10.5)	81.4 (8.9)	54.5 (9.9)	74.4 (24.0)	71.1 (12.3)	0.062
Native	23.5 (10.6)	77.9 (8.9)	46.9 (9.0)	69.6 (25.3)	65.0 (12.3)	0.062
Non-native	0.3 (0.3)	3.4 (2.5)	7.5 (2.6)	4.3 (1.8)	6.0 (3.8)	0.077
Annual/biennial	0.0 (0.0)	0.1 (0.1)	0.7 (0.6)	0.7 (0.3)	0.6 (0.5)	0.549
Perennial	23.8 (10.5)	81.0 (8.9)	52.9 (8.8)	72.1 (24.0)	69.7 (12.5)	0.062
Forb	14.2 (9.2)	49.7 (5.2)	25.7 (4.2)	42.5 (20.5)	35.3 (15.1)	0.162
Graminoid	0.1 (0.1)	0.1 (0.0)	0.1 (0.0)	0.1 (0.1)	0.0 (0.0)	0.607
Herbaceous	14.3 (9.3)	49.8 (5.2)	25.8 (4.2)	42.6 (20.5)	35.3 (15.1)	0.163
Density (stems m^{-2})						
Non-native Forbs	0.0 (0.0)[b]	0.1 (0.0)[ab]	0.8 (0.3)[a]	0.7 (0.4)[a]	0.4 (0.1)[ab]	**0.010**
Short shrubs/seedlings <50 cm						
All shrubs	3.0 (0.9)[b]	8.8 (1.1)[b]	4.6 (1.9)[b]	11.2 (2.4)[b]	28.1 (3.9)[a]	**<0.001**
Native shrubs	2.9 (0.9)[b]	8.5 (1.2)[b]	4.2 (1.8)[b]	11.0 (2.6)[b]	27.6 (4.0)[a]	**<0.001**
Non-native shrubs	0.1 (0.0)	0.3 (0.2)	0.4 (0.2)	0.2 (0.1)	0.5 (0.4)	0.488
Resprouters	3.0 (0.9)[c]	8.0 (1.4)[bc]	4.7 (1.9)[bc]	9.4 (2.2)[b]	26.7 (3.5)[a]	**<0.001**
Obligate seeders	0.0 (0.0)[b]	0.2 (0.2)[b]	0.2 (0.1)[b]	2.1 (0.7)[b]	17.0 (4.2)[a]	**<0.001**
Tall shrubs >50 cm						
All shrubs	6.1 (3.3)	7.8 (2.1)	7.1 (1.8)	7.2 (1.0)	2.6 (0.6)	0.195
Native shrubs	3.0 (0.9)[ab]	5.8 (0.7)[a]	4.3 (0.6)[ab]	6.3 (1.1)[a]	2.0 (0.6)[b]	**0.015**
Non-native shrubs	3.1 (2.6)	2.0 (1.7)	2.8 (2.2)	0.9 (0.3)	0.6 (0.5)	0.579
Resprouters	5.7 (3.3)	7.7 (2.1)	7.1 (1.8)	7.1 (3.6)	2.4 (0.6)	0.164
Obligate seeders	0.4 (0.1)[a]	0.1 (0.0)[b]	0.0 (0.0)[b]	0.1 (0.0)[b]	0.0 (0.0)[b]	**0.001**

of native ($F = 4.86$, $df = 4$, $P = 0.015$) and obligate seeding shrubs ($F = 9.02$, $df = 4$, $P = 0.001$). The MAST/RX treatment had a lower density of native shrubs than the HAND and MAST/INC treatments and all treatments had significantly fewer tall obligate seeding shrubs compared with the control.

Measures of species diversity differed across fuels treatments for all categories except graminoid richness and the Shannon diversity index (Table 3). In many of the comparisons, MAST/RX was the only treatment that had significantly greater diversity than the control. For annual/biennial, perennial, forb richness and the Simpson index of diversity, the MAST/INC treatment was also significantly greater than the control treatment and did not differ from the MAST/RX treatment (Table 3).

Response variables directly modified by fuels treatments were strongly associated with several vegetation measures (Table 4). For example, midstory

Table 3. Understory species richness and diversity index means (± SE) for fuels treatments in a Sierra Nevada ponderosa pine forest. The *P*-values represent the results of a mixed model ANOVA ($df = 3$) with significant treatment effects denoted in bold and different superscript letters in rows depict significant differences between individual treatment types based on results from Tukey–Kramer multiple comparison test. CONTROL = no treatment; HAND = hand removal; MAST = mastication only; MAST/INC = mastication and incorporation; MAST/RX = mastication and prescribed fire.

Variable	Treatments					*P*-value
	CONTROL	HAND	MAST	MAST/INC	MAST/RX	
Richness (# species m^{-2})						
All species	4.3 (1.5)^{b}	7.2 (1.0)^{ab}	7.4 (0.4)^{ab}	9.9 (1.8)^{ab}	11.3 (0.8)^{a}	**0.002**
Native	4.0 (1.4)^{c}	6.6 (0.9)^{abc}	6.2 (0.1)^{bc}	8.6 (1.8)^{ab}	10.0 (0.9)^{a}	**0.001**
Non-native	0.2 (0.1)^{b}	0.4 (0.1)^{ab}	0.8 (0.3)^{ab}	0.9 (0.1)^{ab}	1.0 (0.5)^{a}	**0.044**
Annual/biennial	0.1 (0.1)^{b}	0.1 (0.1)^{b}	0.4 (0.2)^{ab}	0.9 (0.3)^{a}	0.9 (0.2)^{a}	**0.009**
Perennial	4.2 (1.4)^{b}	6.7 (0.7)^{ab}	6.7 (0.4)^{ab}	8.3 (1.7)^{a}	9.9 (1.0)^{a}	**0.007**
Forb	1.8 (1.0)^{b}	3.7 (0.7)^{ab}	3.9 (0.5)^{ab}	4.5 (1.0)^{a}	5.2 (0.8)^{a}	**0.009**
Graminoid	0.2 (0.2)	0.2 (0.1)	0.2 (0.1)	0.5 (0.2)	0.2 (0.1)	0.194
Herbaceous	1.9 (1.2)^{b}	3.9 (0.7)^{ab}	4.1 (0.6)^{ab}	5.1 (1.2)^{a}	5.4 (0.8)^{a}	**0.010**
Shrubs < 50 cm tall	2.0 (0.4)^{b}	2.9 (0.2)^{b}	2.6 (0.5)^{b}	4.2 (0.6)^{ab}	5.7 (0.4)^{a}	**0.001**
Diversity indices						
Simpson's index of diversity (*D*)	0.3 (0.1)^{b}	0.4 (0.1)^{ab}	0.4 (0.0)^{ab}	0.5 (0.1)^{a}	0.5 (0.0)^{a}	**0.020**
Shannon diversity index (H')	0.1 (0.0)	0.2 (0.0)	0.2 (0.0)	0.2 (0.0)	0.2 (0.1)	0.409

Table 4. Magnitude and direction of Spearman correlation tests between canopy and forest floor response variables, plant cover estimates and diversity measures for fuels treatments in a young ponderosa pine forest of northern California. +/− = $P < 0.05$; ++/− − = $P < 0.01$; and +++/− − − = $P < 0.001$, [1] = Simpson index of diversity.

	n	Herb cover	Shrub cover	Richness	Diversity[1]
Midstory height (cm)	120		− − −	− − −	− − −
Canopy closure (%)	120	−	− −	− − −	− −
Bare ground (%)	120		+	+++	+
Woody debris cover (%)	120	− −			
Litter cover (%)	120		−	− − −	
Forest floor depth (cm)	120			− −	
Litter load (Mg ha^{-1})	120			− −	
Duff load (Mg ha^{-1})	120				
Woody debris load (Mg ha^{-1})	120				

height was negatively correlated with shrub cover, species richness, and Simpson's index of diversity, while canopy closure was negatively correlated with species richness, Simpson's diversity, shrub cover and herb cover. In addition, species richness was negatively correlated with litter cover, forest floor depth and litter load (Table 4). Vegetation measures such as richness, shrub cover and Simpson's diversity were consistently positively correlated with percentage bare ground (Table 4).

The NMDS ordination of frequency-derived plant community data was resolved by three axes, which explained 40.1%, 23.8% and 29.7% of the variation, respectively. Environmental variables that were significantly associated with the ordination gradients were per cent bare ground, canopy closure and litter cover (Fig. 3). For the most part, fuels treatments were situated along a gradient with control and HAND treatments occupying the area with greatest canopy closure and litter cover. The MAST/INC and MAST/RX treatments were located on the other side of the ordination associated with greater canopy openness and greater proportion of bare ground (Fig. 3).

A treatment effect was detected for plant community composition based on the blocked multiple response permutation procedure ($A = 0.139$; $P < 0.0001$). Specifically, plant composition within MAST/RX treatment plots differed from all other treatment types, including the control ($P < 0.05$) and the MAST/INC treatment differed from all treatments ($P < 0.05$), with the exception of the MAST only treatment. Both the HAND and MAST treatments did not differ from one another or the control.

Assessment of individual species response to different fuels treatments was conducted with an indicator species analysis that identified plant species significantly associated with a particular treatment type. Most species that differed in abundance among treatments were significantly associated with either the MAST/INC or MAST/RX treatments (Table 5). For example, cover- and frequency-derived indicator values for two shrub species (*A. viscida* and *C. integerrimus*) were significantly associated ($P < 0.05$) with both MAST/INC and MAST/RX. Two non-native forbs were also associated with particular treatments: *Hypericum perforatum*, a perennial, was associated with the MAST treatment while *Lactuca serriola*, an annual, had a high fidelity to the MAST/RX treatment (Table 5). One native legume (*Vicia* sp.) was only associated with the MAST/RX treatments.

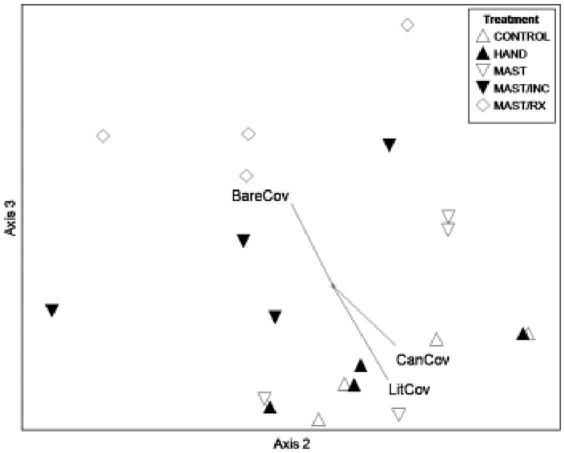

Fig. 3. Plant community analysis results using frequency values for each treatment unit (CONTROL = no treatment; HAND = hand removal; MAST = mastication only; MAST/INC = mastication and incorporation; MAST/RX = mastication and prescribed fire). Positional results were calculated using the non-metric multi-dimensional scaling ordination method. Most of the variation was explained with a three-axes solution; Axis 1 (40.1%), Axis 2 (23.8%) and Axis 3 (29.7%). Significant environmental variables ($r^2 \geq 0.2$) are represented by the joint plots. BareCov = per cent cover of bare ground, CanCov = per cent canopy cover and LitCov = per cent cover of litter.

Discussion

The understory vegetation in this young ponderosa pine forest was strongly influenced by fuel treatments that reduced overstory and midstory cover, as well as, removed debris from the forest floor. The trend towards greater understory plant cover in all fuel treatments compared with untreated areas suggests that understory vegetation is likely responding to the release from shading, increase in growing space, and/or reduction of competition. That the understory was dominated by resprouting perennial species may help explain the relatively rapid plant recovery in all non-control treatments. Had vegetation at our site been composed mostly of species germinating from seed, a markedly slower rate of recovery might have been observed. The experimental units used in our study were relatively small (0.4 ha) and edge effects may therefore be greater than if larger plots were used. For example, edge effects could accelerate the rate of colonization through seed dispersal from adjacent untreated areas (Harper et al. 2005). Thus, larger treatment areas might have had slower recovery rates. Given the species present and patterns observed in the field, however, we believe that the majority of additional species on our site were established through resprouting or germination from the seed bank, so that the influence of seed dispersal into the units was

Table 5. Indicator species analysis of cover and frequency values averaged at the block level ($n = 4$) for individual species associated with a particular fuels treatment type. Indicator values (I.V.) range from 0 to 100, where 100 represents complete fidelity to a particular treatment. The *P*-values represent the probability of obtaining an I.V. as large or larger by chance, an asterisk denotes significance at $\alpha < 0.05$. Computation is based on a Monte Carlo test with 5000 randomizations.

Species	Cover			Frequency		
	Treatment	I.V.	*P*-value	Treatment	I.V.	*P*-value
Arctostaphylos viscida	MAST/INC	66.2	0.008*	MAST/RX	52.0	0.032*
Aster oregoniensis	MAST/RX	43.1	0.187	MAST/INC	45.7	0.074
Ceanothus integerrimus	MAST/INC	53.0	0.048*	MAST/RX	53.5	0.001*
Cirsium vulgare	MAST/INC	32.0	0.426	MAST/INC	46.3	0.053
Gnaphalium canescens	MAST/INC	48.6	0.112	MAST/INC	62.1	0.018*
Hypericum perforatum	MAST	58.6	0.044*	MAST	42.0	0.233
Lactuca serriola	MAST/RX	75.0	0.019*	MAST/RX	75.0	0.020*
Lathrys sulfurous	MAST/INC	70.4	0.027*	MAST/INC	53.6	0.047*
Lotus sp.	MAST/RX	60.0	0.038*	MAST/RX	56.2	0.051
Ribes roezlii	HAND	33.0	0.567	MAST/RX	58.6	0.023*
Toxicodendron diversilobum	MAST/RX	33.6	0.109	MAST/RX	26.7	0.049*
Vicia sp.	MAST/RX	100.0	0.001*	MAST/RX	100.0	0.002*

relatively minor. In addition, trees in the study area (both inside and outside of the plots) were generally <45 yr old and still relatively small; therefore, differences in shading owing to treatment did not extend far from the edge to the interior.

The substantial reduction of the midstory in all fuels treatments compared with the control did not result in marked decreases in canopy closure for treated units (Table 2). The lack of a significant treatment effect on canopy closure is likely explained by the retention of the overstory conifers across all treatments. While the treatment effects on canopy closure and midstory height differed, both serve as surrogate measures of light conditions and were negatively correlated with species diversity measures (Table 4). Other studies have demonstrated a positive relationship between solar radiation and understory plant species richness (Pausas & Austin 2001; North et al. 2005), and increased richness caused by more light penetrating to the forest floor may explain the findings of our study as well.

Across all treatments, the proportion of bare ground was positively correlated with species diversity measures. Two fuels treatments directly increased the amount of bare ground through tilling (MAST/INC) or through burning of forest floor debris (MAST/RX). Conversely, mastication only and hand removal treatments either maintained or decreased the amount of bare ground present compared with the control. Increases in the amount of bare ground may allow for greater recruitment and establishment of individual plant species by reducing competition and increasing the available growing space (Metlen & Fiedler 2006; Collins et al. 2007). While both MAST/INC and MAST/RX provided greater exposed mineral soil, soil disturbance also promoted germination of the shrub seed bank through either physical scarification or chemical cues. The tilling process in the MAST/INC treatment likely scarified the seeds of certain shrub species by churning the surface soil with the machinery (Baskin & Baskin 1999), while the MAST/RX treatment could have promoted germination through heating (Keeley & Bond 1997), presence of charcoal or smoke-triggered germination (Keeley & Fotheringham 1976).

Both litter cover and litter depth were negatively correlated with species richness in all treatments. Control, HAND and MAST treatments generally had greater litter cover and depth values. The presence of litter likely prohibits germination of many species and thus is associated with reduced species richness and diversity (Sydes & Grime 1981; Xiong & Nilsson 1999). Other studies have also found a relationship between forest floor cover and species diversity measures (Sparks et al. 1998; Battles et al. 2001; Knapp et al. 2007).

The addition of organic material to the forest floor through mastication did not contribute to a reduction in species richness compared with either the control or HAND treatments (Table 3). The effect of increasing the cover of woody fuels on the ground in the MAST plots might have been offset by mild ground disturbance caused by mastication equipment that can churn mineral soil or by the increase in available light from midstory removal. Considering that the plant community at our sites consisted of mostly perennial species, resprouting and survival of many previously established plants might be expected if the disturbance is mild enough.

Based on plant community analysis, the compositional shift in the understory plant community was associated with increased bare ground, reduced litter cover and lower canopy closure – variables that were all highest in the MAST/INC and MAST/RX treatments. While the plant community composition was significantly affected by the treatments implemented, the shift in composition seemed to occur along a disturbance gradient of midstory reduction and forest floor removal with the MAST/RX treatment resulting in the greatest change (Fig. 3). Our results are similar to those reported by Wayman & North (2007) in that species groups tended to segregate along the environmental gradients of canopy cover, litter depth (cover in our study), and bare ground. Alteration of the understory plant community as a result of mechanical mastication treatments can be a concern to land managers, especially if a type conversion (e.g. shrubland to grassland) occurs or if non-native species replace native species. Comparison of our data to understory data from nearby intact, fire-maintained ponderosa pine forests would be needed to better answer the question of whether these fuel treatments are shifting the plant community composition closer to historical conditions. In a study conducted in southern Oregon, Sikes (2006) found no significant community alteration as a result of mastication in a northern chaparral shrub community. The inconsistency of the Sikes (2006) findings and our study suggests that mastication may have different effects depending on the plant community type treated. Considering that mastication is becoming increasingly used throughout many forest and shrub lands, more research is warranted on the impact of these treatments on understory plant communities in different vegetation types.

One potential limitation of this study is that treatments were not all completed at the same time, leading to differences in the amount of time available for vegetation recovery prior to sampling. This situation is unavoidable in many fuel and fire treatment effect studies (Streng et al. 1993), and often results from logistical difficulties in implementing all treatments simultaneously. For example, generated fuels often need time to dry after mechanical treatment and to accumulate sufficient needle cast before fire can be applied. In addition, prescribed burning windows are often short owing to weather and air quality restrictions. In our case, prescribed burning in the MAST/RX treatment was intentionally completed 3 yr after all other treatments to allow a needle cast to accumulate and understory vegetation to emerge, so that surface fuels could be further reduced. While differences in time since treatment may have confounded treatment effects on vegetation, we still found a stark treatment effect on species richness that is likely robust to potential time since treatment influences. For example, the MAST/RX treatment had the highest species richness despite having the least time between treatment completion and measurement. This suggests that the difference between treatments involving burning and those not involving burning were potentially greater than shown here. In addition, the majority of species ($>90\%$) were perennials that typically resprout or germinate the first year after treatment, and their presence was therefore likely captured by our sampling procedures, regardless of the time since treatment.

Studies investigating the relative importance of midstory reductions and removal of the forest floor (typically through burning) have had conflicting results. Some research has indicated that either the removal of the midstory or the reintroduction of fire alone are insufficient to increase understory diversity to a level thought to more closely resemble fire-maintained forests (Griffis et al. 2001; Fulé et al. 2002; Collins et al. 2007). In these studies, increases in understory diversity required both the opening of the canopy (provided by thinning) as well as bare mineral soil exposure (provided by prescribed burning). A recent study investigating the relative importance of ground disturbance and midstory removal in xeric *Pinus palustris* forests suggested that removal of the forest floor and bare mineral soil exposure was proportionally more important than reduction of the midstory in promoting understory plant vigor (Hiers et al. 2007). Results from our study indicate that simple midstory removal treatments (HAND and MAST) do not significantly increase species richness without subsequent consumption of the forest floor through prescribed burning. As our study lacked a prescribed fire only treatment, we cannot directly determine the relative importance of midstory removal and forest floor removal. Considering that understory richness increased more than 50% in the MAST/RX treatment in comparison with midstory removal alone (HAND) we suspect that a fire-alone treatment might increase richness proportionately more than thinning alone.

The response of shrub species varied significantly by fuel treatment, with greater obligate seeder density in the MAST/RX treatment than all other treatments and greater resprouter shrub densities in the MAST/RX and MAST/INC treatment types (Table 2). This shrub response was primarily caused by the presence of two species: *C. integerrimus* and *A. viscida*, both of which are obligate seeders that typically germinate following fire (Keeley et al. 2005). However, seeds can also germinate to a limited extent as a result of mechanical scarification caused by other soil disturbances. Periods of fire exclusion allows long-lived seeds of these species to build up in the soil (Quick 1956) and have resulted in prolific germination and establishment after reintroducing fire. The response of obligate seeding and resprouting shrub species is a fire management concern because proliferation of understory shrubs can reduce the longevity and efficacy of the fuel treatment. New shrub seedlings may require additional treatments to maintain fuel hazard reductions in these forests. However, few of these shrub seedlings will survive if sufficient overstory canopy is retained to shade the forest floor. In many areas of our study, shrub seedling mortality was visually very high. More research is needed throughout fire-prone areas where forests overtop shrub strata to determine the amount of canopy cover of residual vegetation necessary to suppress growth and survivorship of shrub seedlings.

A major concern in administering fuel treatments in fire-prone ecosystems with mechanical treatments and/or with prescribed fire is the development and spread of non-native plant species (Keeley 2006). Mechanical only treatments (MAST and MAST/INC) resulted in significantly greater non-native forb density than the control (Table 2), while MAST/RX treatment increased the richness of non-native species (Table 3). These results are similar to the findings of others that have reported an association between disturbance intensity and increases in non-native plants measures (Griffis et al.

2001; Wienk et al. 2004). Since the prescribed fire treatment was only implemented 1 yr prior to sampling, it is possible that non-native cover in the MAST/RX units may increase and approach or eventually exceed levels found in the mechanical-only treatments (MAST and MAST/INC; Dodson & Fiedler 2006). The most common non-native forb on our study site was the biennial bull thistle (*Cirsium vulgare*). While this species is relatively short-lived, Randall & Rejmánek (1993) found that bull thistle limited growth of *P. ponderosa* saplings in California. Bull thistle and other shade intolerant weedy species may not persist for long in these treated areas as overstory canopy cover increases within the treated areas. Decreases in non-native abundance with time have been noted in other studies (Meiners et al. 2002; Petryna et al. 2002). Whether the proliferation of non-native species is only an ephemeral concern or if their presence and persistence will influence ecosystem function over the long term is not well understood and warrants longer-term studies of vegetation responses to fuel treatments.

Management implications

Mechanical mastication and other fuels treatments must be evaluated from both fuel management and ecological perspectives. Ideally, successful fuel treatments should reduce the potential for atypically severe wildfires while simultaneously maintaining or improving ecosystem integrity (Agee & Skinner 2005). Managing for both objectives often involves substantial trade-offs, especially in areas that have markedly deviated from historical conditions as many fire-prone western US forests have.

From a fuels management perspective, mechanical mastication reduced vertical continuity (i.e. ladder fuels) and mass of midstory fuels (Fig. 2), which can substantially reduce hazard of high-severity wildfire, especially under extreme weather conditions, while also improving firefighter access to better assist efforts in fire suppression (Moghaddas & Craggs 2008). Mastication can also aid in the re-introduction of prescribed fire. In addition, the translocation of live and standing dead fuels to the forest floor as a mulch layer from mastication-alone treatments may indirectly aid fuel management goals by acting as a barrier to the germination of understory plant species (especially obligate seeding shrubs), that may otherwise contribute to the development of surface and/or ladder fuels. Other research has shown that masticated material can still burn with substantial intensity, leading to greater than expected mortality of residual trees (E.E. Knapp, unpublished). Supplemental treatments, such as prescribed fire or incorporation into the soil, can reduce surface fuel availability and thereby decrease surface fire intensity and subsequent overstory mortality. However, as demonstrated by this study, such treatments also expose mineral soil and stimulate the germination of shrub and/or tree species, which may reduce the longevity of the treatment, a particular interest in areas composed of primarily obligate seeding shrub species.

From an ecological perspective, mechanical mastication alone did not reduce the cover and diversity of understory vegetation compared with untreated areas. The depth of the mulch was apparently insufficient to suppress resprouting perennial species, which comprise the bulk of the understory flora in these forests. Results might have differed if the understory consisted of annuals or perennials growing from seed. Removing this mulch with prescribed fire was the only fuel treatment to increase native species richness beyond that found in the untreated control. A drawback to using either the incorporation of the woody debris into the soil or removal through prescribed fire treatments is an increase in non-native species abundance and diversity. All fuel treatments have benefits and limitations: the ideal treatment or combination of treatments to use will depend upon whether the objectives at a site are driven primarily by fire management concerns or restoration of biodiversity.

Acknowledgements. This project was funded by the Joint Fire Science Program, JFSP project #05-2-1-20. J. Stuart, T. Kolb and two anonymous reviewers provided helpful comments on earlier drafts. D. Young set up the study units and provided help on site history and study details. J. Kreye, S. Sandhaus, C. West, R. Glebocki, A. Goldman and Q. Stewart assisted with field data collection and sample processing.

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Received 6 May 2009;
Accepted 4 October 2009.
Co-ordinating Editor: Dr. Juli Pausas