



Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA

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Abstract

Restoration/fuel reduction treatments are being widely used in fire-prone forests to modify stand structure, reduce risks of severe wildfire, and increase ecosystem resilience to natural disturbances. These treatments are designed to manipulate stand structure and fuels, but may also affect understory vegetation and biodiversity. In this study, we describe prescribed fire and thinning treatment effects on understory vegetation species richness, cover, and species composition in dry coniferous forests of central Washington State, U.S.A. We applied thinning and prescribed fire treatments in factorial design to 12 large (10 ha) management units, and surveyed understory vegetation before treatment and during the second growing season after treatment completion. Many understory vegetation traits changed significantly during the treatment period, regardless of treatment applied, and changes were often proportional to pre-treatment condition. In general, cover declined and species richness increased during the treatment period. Thinning followed by prescribed fire increased species richness, particularly in areas where species richness was low initially. Thinning alone had a similar, but lesser effect. Forb richness was increased by thinning, and shrub richness was increased by the combined thin/burn treatment, but graminoid richness was unaffected. Exotic cover and richness also increased in the combined thin/burn treatment, although they constituted only a very small portion of the total understory. Understory plant cover was not affected by treatments, but did decline from pre- to post-treatment sampling, with cover losses highest in areas where cover was high prior to treatment. Forb cover increased with thinning followed by burning where forb cover was low initially. Burning reduced graminoid cover with or without thinning. Species composition varied within and among treatment units, but was not strongly or consistently affected by treatments. Our study shows that thinning and burning treatments had mostly neutral to beneficial effects on understory vegetation, with only minor increases in exotic species. However, the pre-treatment condition had strong effects on understory dynamics, and also modified some responses to treatments. The maximum benefit of restoration treatments appears to be where understory richness is low prior to treatment, suggesting restoration efforts might be focused on these areas.

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1. Introduction

The prospect of increasingly widespread use of fuel reduction treatments to manage wildfire hazards in fire-prone forests has highlighted the need for a better understanding of the broad range of effects of these treatments on ecosystem structure and function (Allen et al., 2002). Fire exclusion, livestock grazing, and logging practices have combined to alter forest structure and composition and ecosystem functions in many fire-prone forest types of North America over the past century or more (Cooper, 1960; Covington and Moore, 1994;

Harrod et al., 1999; Keane et al., 2002; Hessburg et al., 2005). Changes in forest structure and composition have also altered fire regimes, increasing risks of insect and disease outbreaks (Hessburg et al., 2005) and high severity wildfires (Fulé et al., 2002; Fiedler et al., 2003; Hessburg et al., 2005). As concern over large, stand-replacing fires has grown, forest managers have increasingly turned to prescribed fire and fire surrogate treatments such as mechanical thinning to modify forest structure, reduce surface fuels, and thereby reduce risks of severe wildfire (Arno et al., 1995; Covington et al., 1997; Fiedler et al., 2001; Allen et al., 2002). Although intended primarily to manage potential fire behavior and forest health, these treatments could also impact other aspects of forest ecosystems, including understory vegetation diversity, species composition, and cover. The purpose of this study was to

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evaluate the individual and combined effects of mechanical thinning and prescribed fire on understory vegetation in dry coniferous forests of the eastern Cascade Mountains of Washington State.

Understory vegetation contributes to a wide variety of ecosystem functions (Allen et al., 2002; Kerns et al., 2006) and comprises the vast majority of plant biodiversity (Gildar et al., 2004; Wayman and North, 2007). Thinning and prescribed fire can serve as disturbance processes, modifying understory vegetation by damaging or killing plants, releasing resources, creating establishment sites for colonizing species and expanding populations, and promoting germination of seeds stored in soil and canopy seed banks (Whelan, 1995; Kaye and Hart, 1998; Huffman and Moore, 2004; Gundale et al., 2005). Thinning and prescribed burning may also alter understory vegetation indirectly by altering overstory tree cover and density and their effects on understory microclimate, light, soil water, and nutrient availability. Such overstory–understory interactions have been shown to be important in many fire-prone forest and savanna ecosystems (Moir, 1966; Ffolliott and Clary, 1982; Uresk and Severson, 1989; Riegel et al., 1992; McPherson, 1997; Scholes and Archer, 1997; Naumburg and DeWald, 1999).

Empirical studies of thinning and prescribed fire effects on understory vegetation have produced mixed results. For example, thinning has increased species richness (Wienk et al., 2004; Metlen and Fiedler, 2006) and reduced species richness (Metlen et al., 2004) in dry coniferous forests. Similarly, prescribed fire has increased species richness (Huisinga et al., 2005), reduced species richness (Fulé et al., 2005; Collins et al., 2007), or had no significant effect (Metlen et al., 2004; Metlen and Fiedler, 2006). Treatment effects on understory plant cover can also vary among graminoids, forbs, and shrubs, suggesting differences in tolerances to disturbance (Metlen et al., 2004; Metlen and Fiedler, 2006; Moore et al., 2006; Collins et al., 2007). Treatment effects may be realized over different time scales, as vegetation may be highly resilient to some disturbance impacts (Metlen and Fiedler, 2006), while other treatment effects may cause slower but persistent changes in vegetation structure and composition (McConnell and Smith, 1970). Understory vegetation responses to treatment likely depend on pre-treatment site conditions (Fulé et al., 2005), disturbance season and intensity (Emery and Gross, 2005; Knapp et al., 2007), and the degree to which overstory stand structure is modified (McConnell and Smith, 1970; Abella and Covington, 2004).

Recently, invasion by exotic plants has been increasingly emphasized as a threat to dry forest restoration success (Harrod, 2001; Sieg et al., 2003; Keeley, 2006). Thinning and prescribed fire may facilitate exotic species invasions by disturbing existing vegetation, exposing mineral soil, facilitating the spread of propagules, reducing shading, and increasing soil resource availability (Hobbs and Huenneke, 1992; Davis et al., 2000; Harrod, 2001; Leishman and Thomson, 2005; Keeley, 2006). Indeed, experimental studies have confirmed that thinning and burning treatments in dry forests can lead to increases in exotic species (Griffis et al., 2001; Wienk et al.,

2004; Fulé et al., 2005; Dodson and Fiedler, 2006; Collins et al., 2007), although this is not universally the case (Fulé et al., 2002; Fornwalt et al., 2003; Metlen et al., 2004; Knapp et al., 2007). Further research is needed in dry coniferous forests to distinguish understory responses that are relatively consistent from those that are limited to certain regions, forest types, or sites.

The Fire and Fire Surrogates (FFS) network study was initiated in 1999 with 13 sites established in fire-prone forests throughout the U.S. to address the effects of fuel reduction and forest restoration treatments on ecosystem attributes. Understory vegetation responses have already been documented in eastern Oregon (Metlen et al., 2004; Youngblood et al., 2006), Montana (Metlen and Fiedler, 2006; Dodson and Fiedler, 2006) and California (Collins et al., 2007; Knapp et al., 2007). Here, we examine the effects of thinning and prescribed fire restoration treatments, applied alone and together, on understory vegetation in ponderosa pine/Douglas-fir forests of the eastern Washington Cascades at the Mission Creek FFS site. Specific research questions were:

- (i) Do treatments significantly alter understory plant species richness, total cover, or species composition?
- (ii) Do treatment effects vary for major plant life-forms (graminoids, forbs, and shrubs)?
- (iii) Do treatments increase the abundance (species richness or cover) of exotic plant species?

2. Methods

2.1. Study sites

The Mission Creek study area is located in the eastern Cascade Range of Washington State at approximately 47°25'N latitude and 120°32'W longitude and is managed by the Okanogan-Wenatchee National Forest. Study sites are within the Mission and Peshastin Creek watersheds west of Cashmere, Washington. Forests are dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) with grand fir (*Abies grandis*) present to abundant in some stands. Common understory species include *Carex geyeri*, *Calamagrostis rubescens*, *Symphoricarpos albus*, *Spiraea betulifolia* and *Rosa* spp. (*Rosa gymnocarpa*, *Rosa nutkana* and *Rosa woodsii*). Soil parent material is primarily non-glaciated sandstone intermixed with some shale and conglomerate (Tabor et al., 1982). Typical soil types found in the area include Haploxerepts, Haploxerolls, Argixerolls, and Haploxeralfs (Soil Survey Staff, 1995).

The climate features warm, dry summers and cool, wet winters. Long, dry summers create extended periods with low fuel moisture and high wildfire potential. Similar nearby forests within the Wenatchee National Forest burned every 6–7 years prior to Euro-American settlement, but mean fire return intervals have increased considerably during the past century (Everett et al., 2000). The nearest weather station with complete records for the duration of the study (Plain, about 32 km north of the study site) has about 68 cm of precipitation annually with

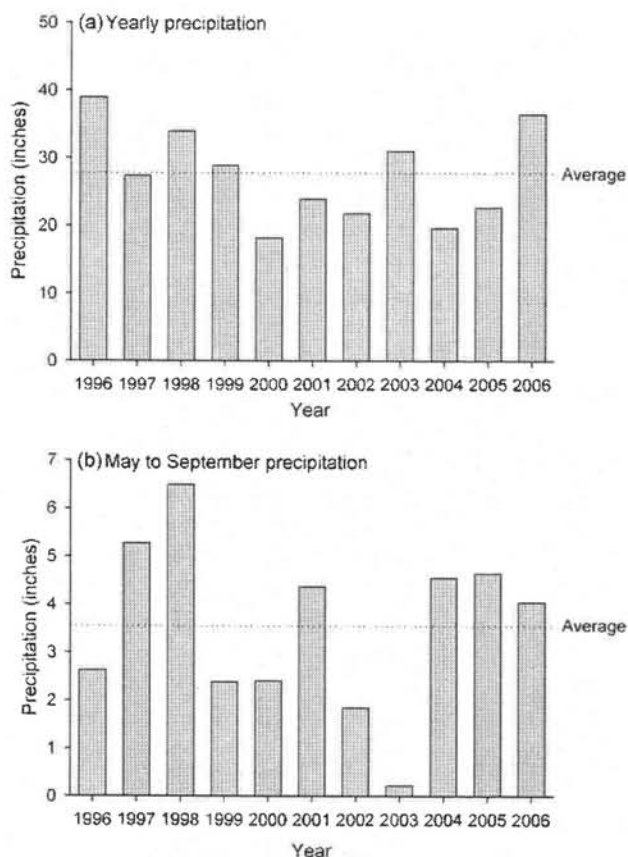


Fig. 1. Precipitation for the last 11 years which included the years of the Fire and Fire Surrogate study (2000–2005) for (a) total annual precipitation and (b) growing season precipitation (May–September) at the nearest weather station with complete data for the entire study period (Plain, WA).

an average annual air temperature of 7.5 °C (Western Regional Climate Center, Plain, <http://www.wrcc.dri.edu>). During the duration of this study precipitation was variable (Fig. 1), especially for the growing season (May–September; Fig. 1b). Between the pre- and post-treatment data collection, there was a marked growing season drought in 2003 (Fig. 1b). Overall for the state of Washington the summer of 2003 (May–August) was the driest on record, and one of the hottest on record (NCDC, 2007).

2.2. Treatments

A total of 30 management units were identified as candidates for inclusion in the study. Units were considered if (1) the majority of the unit was in the *Pseudotsuga menziesii* series (Lillybridge et al., 1995), (2) at least 90% of the unit was forested, (3) the unit contained no plant or animal species that would prevent or constrain treatment, (4) the average slope was less than 50%, and (5) the unit encompassed a relatively square or rectangular area of 10 ha or more. Twelve of the 30 candidate sites were chosen randomly for inclusion in this study (Table 1). Two distinct restoration treatments – mechanical thinning and prescribed burning – were applied in this study, alone and in combination. The study plan called for three replicates of each

treatment combination: (1) thinning alone (thin-only), (2) prescribed burning alone (burn-only), (3) thinning followed by prescribed burning (thin/burn) and (4) no treatment (control). Treatments were randomly assigned to management units initially; however, one burn-only unit was later switched with a control unit due to concerns about prescribed fire management.

The treatment hereafter referred to as thinning was designed to reduce stand basal area to 10–14 m²/ha while promoting a heterogeneous landscape pattern. Units assigned to the thinning treatment were divided into numerous subunits, within which the basal area and density of trees retained was a function of the quadratic mean diameter of the trees present (Harrod et al., 1999). A clumped distribution was emphasized for leave trees, as this was the historical spatial pattern for this area (Harrod et al., 1999). Trees were favored to be left on site if they were large and vigorous with no sign of disease or insect infestation. However, some trees were cut out of all size classes. Merchantable trees were yarded by helicopter, with tops and branches left on-site. Later, hand crews cut smaller non-merchantable trees and they lopped and scattered the slash from both commercial thinning and hand-felling. Thinning treatments were completed in the spring of 2003.

Prescribed fires were ignited by hand and helicopter from late April to early May (spring) of 2004. The vegetation was already actively growing during this period, so live fuel moisture was relatively high, fire severity was low, and coverage was patchy. Within burned units, only 23–51% of the surface area was burned, and the fires were not considered very effective for meeting fuel reduction objectives (Agee and Lolley, 2006). Early green-up and high fuel moisture also caused two of the six scheduled fires to be postponed to a later year (completed in 2006). As a result, the burn-only and thin/burn treatments had only two units each, while the remaining un-burned units were added to the control and thin-only treatments, respectively, giving them four units each (Table 1).

2.3. Understory vegetation sampling

Understory vegetation was sampled on six 20 m × 50 m modified Whittaker plots, distributed across the forested areas of each unit. Plots were randomly located within forested areas (i.e., no rocky outcrops or meadows) of the treatment units. Herbaceous plant species (graminoids and forbs) were surveyed on 20 permanent 1-m² quadrats located randomly within each Whittaker plot. Shrub species were surveyed on 10 permanent 50-m² quadrats located systematically on each plot. At each quadrat (regardless of size) a total census of the species of interest (shrubs or herbaceous species) was collected to assess local species richness. For herbaceous quadrats, plant canopy cover was estimated for each herbaceous plant species and for other cover categories (litter, rock, soil, non-vascular plants, and tree boles) based on the probability of intercepting a vertically falling raindrop, with total cover summing to 100%; shrub cover was treated as if it were not present. Where two herbaceous species overlapped, cover was assigned to the taller individual. For shrub quadrats, total cover of each shrub species was also

Table 1

Unit elevation and treatment effects on tree basal area for trees greater than 7.6-cm diameter at breast height (1.37 m)

Unit	Treatment	Mean elevation (m)	Pre-treatment basal area (m ² /ha)	Post-treatment basal area (m ² /ha)
Camas	Thin/burn	1097	34.1	18.4
Crow 1	Thin-only	738	29.0	11.4
Crow 3	Control	747	32.5	33.3
Crow 6	Thin-only	718	29.0	9.1
Pendleton	Control	841	22.7	23.7
Poison	Burn-only	768	30.2	30.9
Ruby	Thin-only	975	38.7	25.5
Sand 19	Control	780	34.0	35.5
Sand 2	Control	683	34.1	34.8
Slawson	Thin-only	838	35.7	20.6
Spromberg	Burn-only	848	42.7	42.9
Tripp	Thin/burn	765	36.1	22.0

estimated using the raindrop interception method with precedence given to taller individuals. Difficulties in species identifications led to some species being surveyed or analyzed at the genus level. Species that could not be identified to the genus level (a total of eight) were assigned a unique identifier.

Understory vegetation surveys were conducted before and after treatment application. Pre-treatment data collection spanned the summers of 2000 and 2001. Pre-treatment sampling year was random with respect to assigned treatments and there was no apparent effect of pre-treatment sample year on any response variable. Post-treatment data were collected for all sites in 2005, the second growing season after burning and third growing season after thinning.

Species cover estimates were averaged from the quadrat level (herbaceous or shrub) to the plot level for each species, thereby producing a dataset with cover for both shrub and herbaceous species. Because the shrubs were ignored when estimating the cover of herbaceous species, total plant cover could exceed 100%. Prior to analysis, plant species were classified as graminoids, forbs, or shrubs, and also classified as exotic or native based on the USDA plants database (USDA, NRCS, 2007). Species cover values were then summed to produce group cover estimates for graminoids, forbs, shrubs, and exotic species. Total plant cover was calculated as the sum of all vascular plant species including graminoid, forb, and shrub cover and seedlings <1 m.

2.4. Statistical methods

Prior to tests, a Type I error rate of 10% ($\alpha = 0.10$) was selected as the threshold for assessing significance of model effects. Treatment effects on cover and species richness of understory vegetation (total plant community, life-form groups, and exotic species) were analyzed with a hierarchical mixed model procedure in SAS (SAS Institute, Version 9.1). Response variables were the change in an attribute (e.g., total cover, species richness, exotic cover) from the pre-treatment survey to the post-treatment survey. The pre-treatment value for each attribute at each plot was included as a predictor variable to account for potential effects of pre-treatment condition on treatment responses. Thinning and burning treatments were

included in the analysis as independent categorical predictor variables (treatment applied or not). For each response variable a full model was fit with thinning, burning, the pre-treatment covariate and all possible interactions. The mixed model allowed the pre-treatment covariate to be tested for significance at the plot level ($n = 72$), while thinning and burning treatments were tested for significance at the unit level ($n = 12$). Non-significant ($P > 0.1$) terms were eliminated from the model using a backward elimination process, starting with the highest-order interaction terms (the three-way interaction of thinning, burning and the pre-treatment condition). Thinning, burning and their interaction were not removed regardless of their significance level to ensure a statistical test of the treatment effects using the complete experimental design. Tests of model assumptions showed small to moderate deviations from parametric assumptions for some variables that were not amenable to transformation. For these variables, results are presented for untransformed data, relying on the robustness of ANOVA to provide accurate results with limited violations of assumptions.

Two variables, forb cover and total species richness, showed significant interactions in the change from pre- to post-treatment between treatment and the pre-treatment condition. Therefore, these variables were allowed to have different slopes depending on treatment. Pair-wise tests were then performed to assess differences in predicted response among treatments at three levels of the pre-treatment variable: the 10th percentile, mean and 90th percentile levels (Littell et al., 2006).

Treatment effects on the understory plant community composition were examined using non-metric multidimensional scaling (NMS, Kruskal, 1964; McCune and Grace, 2002). Plant community data were analyzed at the plot level (Whittaker plots, $n = 72$) using species cover values in each survey period. The ordination analysis was conducted in PC-ORD (McCune and Mefford, 1999) using the "slow and thorough" automated NMS procedure with the Sorenson distance measure and a stability threshold of 0.0001. A randomization procedure with 250 runs was used to determine the probability of finding an equally good solution with randomized data. Mean scores for each treatment unit in each year were calculated from the six plots located within the unit.

3. Results

Understory vegetation was both spatially and temporally dynamic in this study. Study units varied considerably in pre-treatment cover, composition, and species richness of understory vegetation, despite the relatively close proximity of the study units within the watershed. Vegetation cover, composition, and species richness also changed considerably during the treatment period, even on the control plots. Accounting for this spatial and temporal variability in vegetation attributes was critical to accurately assess treatment effects.

3.1. Plant species richness

Total understory species richness generally increased on thinned units, with individual plots gaining up to 16 plant species during the treatment period. Species richness increases were negatively correlated with pre-treatment species richness, however, so that plots with low species richness gained more species on average than plots with high species richness (Fig. 2a). In pair-wise treatment comparisons at pre-treatment richness values of 17 species (10th percentile), 24 species (mean) and 31 species (90th percentile), the thin/burn treatment added significantly more species than all other treatments (all P -values < 0.1). However, this effect was more pronounced where species richness was initially low (Fig. 2a). The thin-only treatment increased species richness significantly more than the burn-only treatment at pre-treatment levels of 17 species

($P = 0.03$) and 24 species ($P = 0.08$). The thin-only also increased species richness significantly more than the control ($P = 0.04$) at the pre-treatment level of 17 species.

Richness response to treatments varied among the different life-forms. As with total species richness, change in shrub species richness was negatively correlated with pre-treatment shrub richness (Table 2; Fig. 2b). There was a significant interaction between thinning and burning for shrub richness (Table 2), with the combined thin/burn treatment increasing shrub species richness more than the additive effects of thinning and burning alone, which were very similar to the control (Fig. 2b). Graminoid species richness increased slightly overall during the treatment period, but was not significantly affected by any treatment or pre-treatment graminoid richness (Table 2; Fig. 2c). Change in forb species richness was negatively correlated with pre-treatment forb richness (Table 2; Fig. 2d). Thinning (thin-only and thin/burn) significantly increased forb richness change (Table 2) adding an estimated 3.2 more species per plot relative to un-thinned (burn-only and control) units (Table 3).

3.2. Cover

Total average understory plant cover declined during the treatment period on most plots, regardless of treatment (Table 3). Change in understory plant cover was negatively correlated with pre-treatment cover (Table 2; Fig. 3a). After accounting for differences in pre-treatment cover among plots,

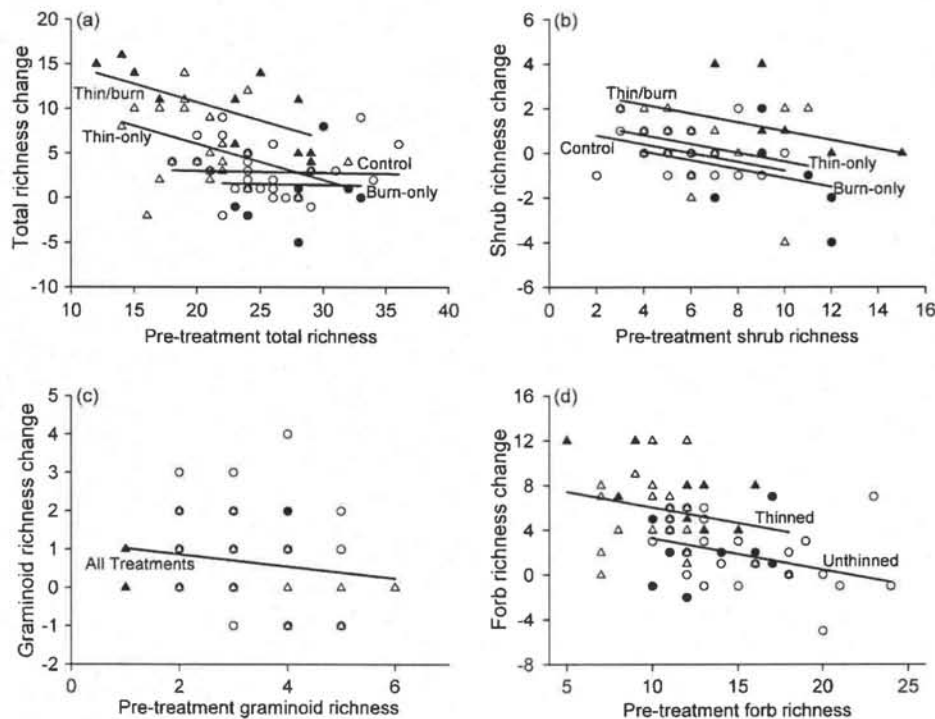


Fig. 2. Scatter plots of plot-level change in richness between pre- and post-treatment for (a) all understory species, (b) shrub species, (c) graminoid species and (d) forb species in relationship to the pre-treatment richness. Lines show modeled treatment and covariate effects across the range of the pre-treatment covariate with separate lines for each significant ($P < 0.1$) treatment effect. Triangles represent thinned plots and circles un-thinned while shaded symbols were burned and unshaded were not burned.

Table 2
Mixed model results for treatment effects on each understory variable in the FFS study

	Thin ^a		Burn ^a		Thin × burn ^a		Pre-treatment ^a	
	F	P	F	P	F	P	F	P
Total cover	0.77	0.4062	2.38	0.1612	0.17	0.6922	75.25	<0.0001
Shrub cover	0.32	0.5870	0.33	0.5792	0.00	0.9633	50.84	<0.0001
Graminoid cover	0.00	0.9488	9.78	0.0141	0.53	0.4867	140.50	<0.0001
Forb cover ^b	0.99	0.3490	3.76	0.0885	0.23	0.6415	42.39	<0.0001
Total richness ^b	8.30	0.0205	3.01	0.1210	9.80	0.0140	4.94	0.0302
Shrub richness	16.84	0.0034	2.13	0.1827	7.54	0.0252	9.66	0.0029
Graminoid richness	1.31	0.2863	0.02	0.8888	0.02	0.8811	1.60	0.2104
Forb richness	9.98	0.0134	1.06	0.3327	2.51	0.1518	6.57	0.0129
Exotic cover	13.10	0.0068	6.09	0.0389	10.04	0.0132	8.74	0.0045
Exotic richness	8.73	0.0183	8.68	0.0185	7.06	0.0289	6.94	0.0108

Significant effects are indicated by bold text.

^a In the mixed model there were eight denominator degrees of freedom for treatments (thin, burn and thin × burn) and 59 for the pre-treatment covariate, all numerator degrees of freedom were one.

^b Forb cover and total richness had significant ($P < 0.1$) treatment × pre-treatment covariate interactions. Therefore, for these variables significance of treatments was evaluated at three levels of the pre-treatment covariate, not the zero value of the pre-treatment covariate as shown in this table (see text).

thinning and burning treatments did not significantly affect total plant cover (Table 2).

The change in cover from pre- to post-treatment varied among life-forms. As with total plant cover, shrub cover change was negatively correlated with pre-treatment shrub cover (Table 2; Fig. 3b), but was not affected by treatments (Table 2). Changes in graminoid cover were also negatively correlated with the pre-treatment graminoid cover (Table 2; Fig. 3c). Controlling for pre-treatment cover, burning significantly reduced graminoid cover (Table 2), with burned units (burn-only and thin/burn) losing about 6.1% more graminoid cover on average than the unburned units (thin-only and control; Table 3). Forb cover change was negatively correlated with pre-treatment forb cover, but the slope of the relationship varied between burned and unburned units ($P = 0.02$, Fig. 3d). At the 10th percentile level of pre-treatment forb cover (2%), the combined thin/burn treatment increased cover significantly more than the control ($P = 0.07$), but not other treatments. At the 90th percentile level of pre-treatment forb cover (21%), the burn-only treatment produced a greater reduction in forb cover than the thin-only ($P = 0.08$), but was not significantly different than the other treatments (Fig. 3d).

3.3. Community response

The final solution of the non-metric multidimensional scaling (NMS) ordination with both pre- and post-treatment data had three axes that explained 81% of the variability in the original data matrix. The final stress of the NMS ordination was 14.2 with an instability of 0.00001 and a low probability of obtaining as good a result by chance ($P = 0.004$). Sites differed considerably in understory community composition, and treatments did not appear to have a strong or consistent affect on the understory community as evidenced by the variability in responses at the twelve study units (Fig. 4). In general, active treatments resulted in no more community change from pre- to post-treatment than was observed in the control treatments, with the thin-only units having the least movement for any of the treatments.

3.4. Exotic species

Nine total exotic species were found in this study. Very few exotic species were documented prior to treatment application, with none found on any of the burn-only and thin/burn

Table 3
Least square means and one standard error for the change in each variable from pre- to post-treatment for each of the four FFS treatment combinations at the mean value of the pre-treatment covariate of the same variable

	Control		Burn-only		Thin-only		Thin/burn	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Total cover	-12.38	2.59	-15.92	3.78	-8.04	2.58	-14.30	3.90
Shrub cover	-5.73	2.27	-7.47	3.26	-4.30	2.24	-5.78	3.17
Graminoid cover	-4.83	1.58	-9.63	2.11	-3.62	1.49	-11.09	2.29
Forb Cover	-0.42	1.05	-0.62	1.52	0.26	1.05	1.35	1.53
Total richness	3.34	0.99	2.42	1.42	4.87	1.01	9.41	1.39
Shrub richness	-0.21	0.26	-0.53	0.38	0.20	0.25	1.57	0.37
Graminoid richness	0.95	0.28	0.85	0.40	0.50	0.28	0.50	0.42
Forb richness	2.69	0.83	2.17	1.08	4.41	0.80	6.88	1.10
Exotic cover	0.02	0.04	-0.01	0.06	0.04	0.04	0.31	0.06
Exotic richness	0.04	0.22	0.14	0.31	0.12	0.22	1.64	0.31

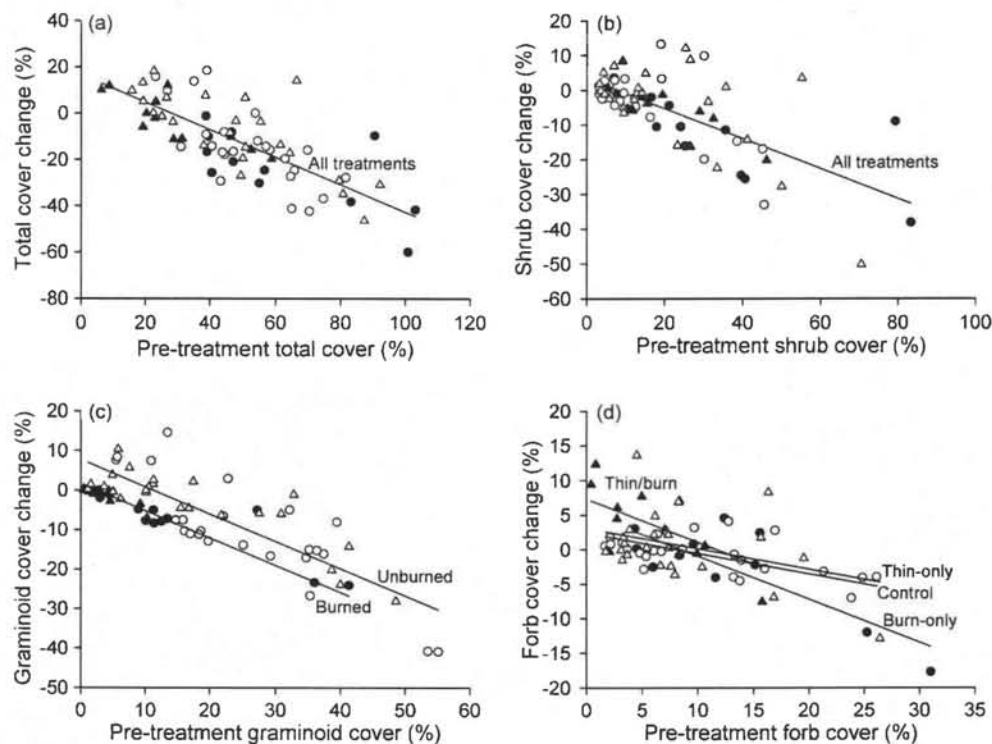


Fig. 3. Scatter plots of change in cover between pre- and post-treatment for (a) all understory species, (b) shrub species, (c) graminoid species and (d) forb species in relationship to the pre-treatment cover. Lines show modeled treatment and covariate effects across the range of the pre-treatment covariate with separate lines for each significant ($P < 0.1$) treatment effect. Triangles represent thinned plots and circles un-thinned while shaded symbols were burned and un-shaded were not burned.

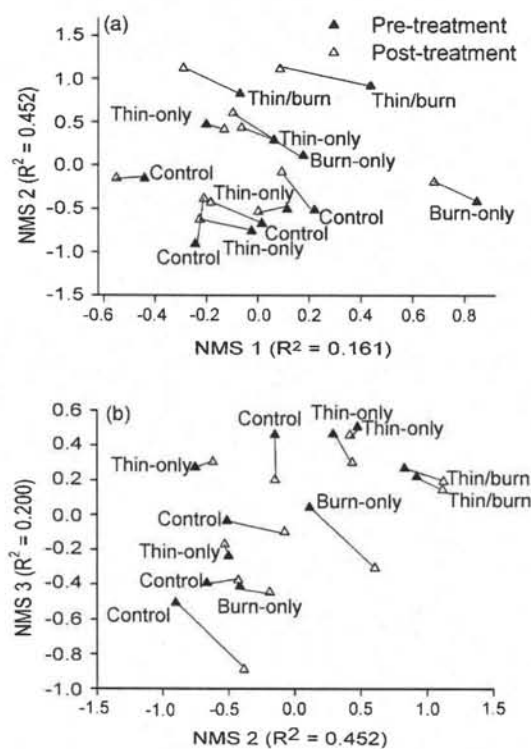


Fig. 4. Non-metric multidimensional scaling ordination scores for each of the 12 sites before and after treatment application on (a) axes 1 and 2 and (b) axes 2 and 3.

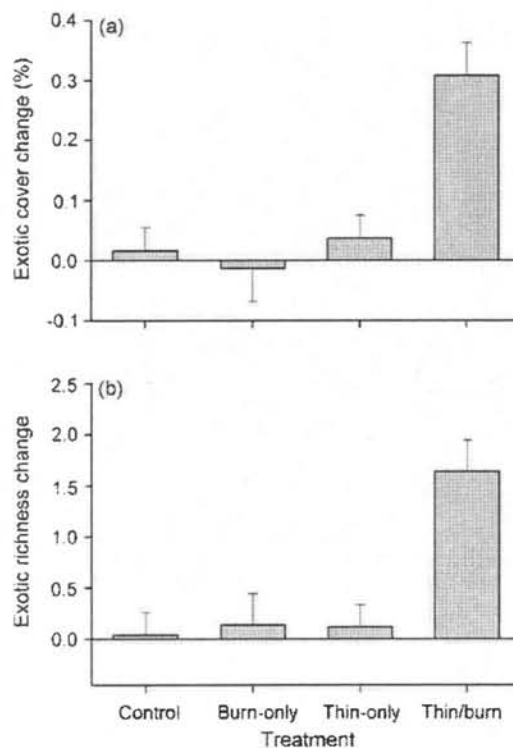


Fig. 5. Least square mean change (with one standard error) in (a) exotic cover and (b) exotic richness from the pre- to post-treatment for each treatment at the mean pre-treatment value for each variable, respectively.

units. The largest increase in the total number of species came in the thin/burn, where there were no exotic species found prior to treatment and seven found after treatment. The increase in exotic cover was largely due to two species, *Cirsium vulgare* and *Lactuca serriola*, both of which were found on at least half of the 12 thin/burn plots after treatment.

The change in exotic cover and richness from pre- to post-treatment was negatively correlated with the pre-treatment value of each, respectively (Table 2). However, treatments also significantly affected exotic cover and richness change, with a significant interaction of thinning and burning (Table 2). At the mean pre-treatment exotic cover, the thin-only, burn-only and control treatment all changed exotic cover by less than 0.05% (Table 3). In contrast, the thin/burn added an estimated 0.3% cover of exotic species (Fig. 5a). At the average pre-treatment exotic richness the thin-only, burn-only and control added less than 0.2 species per plot each, while the combined thin/burn treatment added an average of more than 1.5 exotic species per plot (Fig. 5b).

4. Discussion

A central tenant of restoration ecology is that native species are likely to benefit from the re-establishment of natural processes and the conditions that shaped their evolutionary history (Fulé et al., 2002 and citations therein; Kerns et al., 2006). In this study, treatments increased species richness while having little effect on plant community composition and understory cover in the first two to three growing seasons after treatment. These findings correspond with a growing body of evidence that suggests thinning and burning treatments in dry coniferous forests have few detrimental effects on native understory vegetation (Abella and Covington, 2004; Metlen et al., 2004; Metlen and Fiedler, 2006; Moore et al., 2006; Collins et al., 2007; Knapp et al., 2007; Dodson et al., 2007). This is an important outcome from a forest management perspective, as it suggests that restoration treatments designed to modify forest fuels and overstory structure may simultaneously benefit understory species, or at least not have strong adverse impacts.

Previous empirical studies have documented inconsistent restoration/fuel reduction treatment effects on understory species (Keeling et al., 2006). The mixed model approach with the pre-treatment covariate in this study demonstrated the importance of the pre-treatment condition in modifying inter-annual change for most of the understory variables evaluated in this study. This same effect has previously been documented for dry coniferous forests in the southwestern U.S. (Vose and White, 1991; Fulé et al., 2005). Furthermore, for total understory richness and forb cover the pre-treatment condition also modified treatment effects. For each variable other than graminoid richness there was a negative relationship between the pre-treatment value and the change from pre- to post-treatment. The high degree of pre-treatment variability and non-random inter-annual variability in understory cover further emphasize the importance of pre-treatment data and controls

for examining treatment effects on understory vegetation (Wienk et al., 2004).

4.1. Total richness and cover

Previous empirical studies have reported varied effects of thinning and burning treatments on understory richness in dry coniferous forests, with both increases (Wienk et al., 2004; Metlen and Fiedler, 2006), and decreases (Metlen et al., 2004; Fulé et al., 2005; Collins et al., 2007). In this study, thinning, and especially thinning combined with burning, increased species richness relative to the control and burn-only treatments. However, this effect was far more pronounced where species richness was low initially. This suggests that treatment effects on understory vegetation are likely to continue to vary across the landscape, and that the pre-treatment condition will influence the outcome of restoration treatments. However, it is also important to stress that there was no evidence that restoration treatments reduced species richness at any level of pre-treatment richness in this study, and the combined thin/burn treatment increased species richness more than the control at each of the evaluated levels of pre-treatment richness.

While thinning alone resulted in increased richness, the combined thin/burn treatment resulted in significantly greater increases in richness than the thin-only, despite similar changes in overstory basal area for the two treatments (Table 1). This pattern has also been documented in other dry coniferous forests, where the combination of thinning and burning had a more positive effect on understory species than thinning alone (Wayman and North, 2007; Dodson et al., 2007). While thinning can reduce the negative effects of overstory trees on understory vegetation, burning may provide other critical ecological effects that are not accomplished with thinning alone, such as facilitating colonization by creating growing space and receptive seedbeds, promoting germination of seeds stored in soil and canopy seed banks, and increasing nutrient availability (Whelan, 1995; Kaye and Hart, 1998; Huffman and Moore, 2004; Gundale et al., 2005). These results then suggest that the combination of thinning and burning may be the most effective treatment for increasing understory diversity in dry coniferous forest.

Understory cover was not responsive to restoration treatments in this study after accounting for pre-treatment variability. Similarly, other studies have found only minor effects on cover within the first few years following treatments (Abella and Covington, 2004; Metlen et al., 2004; Metlen and Fiedler, 2006). The residual basal area following thinning treatments was almost 18 m²/ha in this study, which may have been too high to facilitate a rapid increase in understory cover. However, with the mixed model we were able to determine that pre-treatment cover had a very strong effect on the cover change from pre- to post-treatment sampling, with the greatest declines on plots that had the highest cover to begin with. The exceptionally dry growing season (May–September) in 2003 (between the pre- and post-treatment samples) may have contributed to this overall decline in cover, perhaps having

greater effects where competition was highest. Studies in the southwestern U.S. have previously documented steep declines in understory abundance due to drought conditions (Fulé et al., 2005; Moore et al., 2006).

Prescribed burning alone produced very little effect on understory plant cover or species richness for any of the understory groups evaluated. Burns in this study were patchy and of low intensity and severity (Agee and Lolley, 2006). Other studies that have evaluated the effects of burning alone in dry coniferous forests have similarly found effects to be small given a couple growing seasons for understory recovery (Metlen et al., 2004; Metlen and Fiedler, 2006; Knapp et al., 2007). However, Huisinga et al. (2005) documented significant increases in understory cover and richness with an intense prescribed fire in dry coniferous forests of Arizona. Knapp et al. (2007) reported seasonal differences in prescribed fire effects on understory vegetation, but noted that differences were likely due to differences in fuel moisture and fire intensity. In this study, thinning augmented surface fuels (Agee and Lolley, 2006) and may have increased fire intensity, thereby increasing the effects of the combined thin/burn treatment. Indeed, the combined effects of thinning and burning on total species richness, shrub richness, and exotic species were greater than the additive effects of the two treatments applied separately. More intense prescribed fires may be necessary in this region to modify overstory structure and understory vegetation with burning alone. If thinning is not an option, managers may want to consider altering spring burning prescriptions to produce more intense fires, or relying more on fall burning when lower fuel moisture in larger fuels can help increase fire severity.

4.2. Life-form responses

Plant life-forms differed in their responses to treatments, a now well-established pattern for dry coniferous forests (Metlen et al., 2004; Metlen and Fiedler, 2006; Moore et al., 2006; Collins et al., 2007; Harrod et al., 2007). Forbs, which contributed greatly to pre-treatment species richness but relatively little to cover, had the most positive response to treatments, increasing richness in response to thinning and increasing cover in response to the combined thin/burn treatment when their cover was initially low. Similar dry coniferous forests in the inland Northwest appear to have many forb species that are able to take advantage of disturbances such as those caused by restoration treatments (Dodson et al., 2007). However, the response of individual forb species may not be consistent within the life-form, as Dodson et al. (2007) found there were individual forb species that were favored by both control and restoration treatments in dry conifer forests of Montana. In this study, forb cover was reduced by burning when forb cover was initially high. Longer term monitoring will be needed to determine if this effect persists over time, as Moore et al. (2006) found that the maximum increase in forbs was not until 5–6 years after thinning and burning treatments in dry conifer forests of the southwestern U.S.

In the literature, variable outcomes have been reported for the response of graminoid species to experimental thinning and

burning treatments with both increases (Griffis et al., 2001; Uresk and Severson, 1989) and decreases (Metlen and Fiedler, 2006; Collins et al., 2007). Despite their relatively large contribution to pre-treatment cover, graminoids had by far the lowest pre-treatment richness of any life-form group in this study, and richness was not responsive to treatment. Graminoid cover was reduced by the treatments that included burning, but was unaffected by thinning. Time since treatment may play a key role, as McConnell and Smith (1970) found a large increase in graminoid cover with thinning treatments 8 years after thinning application in dry conifer forests of Central Washington.

In the short term, several studies have also noted decreased shrub cover following thinning (Collins et al., 2007; Wayman and North, 2007) and burning (Metlen et al., 2004; Metlen and Fiedler, 2006; Wayman and North, 2007) treatments. However, Metlen and Fiedler (2006) and Harrod et al. (2007) found that shrub cover recovered to near pre-treatment levels within two or three growing seasons. Many shrub species in the inland Northwest are adapted to re-sprout or establish from seed following fire (Stickney and Campbell, 2000). Therefore, although burning may kill some individual shrubs, it may also create opportunities for others to establish. In our study, shrub cover was unaffected by treatments two to three growing seasons after treatment. In contrast, the combined thin/burn treatment increased shrub species richness compared to the other treatments suggesting that net establishment of shrubs exceeded any treatment-induced mortality in this treatment.

4.3. Exotic invasion

Although treatment effects on exotic species were generally small in this study, the combination of thinning and burning produced a much greater increase in exotic species cover and richness than would have been expected based on the effects of either treatment alone. This pattern was also observed in Montana ponderosa pine forests (Dodson and Fiedler, 2006), and mixed conifer forests of California (Collins et al., 2007). Griffis et al. (2001) found that exotic species abundance increased as disturbance intensity increased. Similarly, Dodson and Fiedler (2006) found that the cover of some exotic species was correlated with fire scorch heights and basal area reductions, also indicators of treatment intensity/severity. It may be that exotic invasions of forests are limited by both resource availability (e.g., shading, soil nutrients) and seedbed characteristics (e.g., exposed mineral soil), and that in this study it was only the two treatments together that modified overstory structure and forest floor seedbeds sufficiently to promote significant exotic species establishment.

Exotic invasion is dependent on a number of factors including propagules of exotic species, the characteristics of the invading species, and the susceptibility of the system to invasion (Lonsdale, 1999). Increases in exotic invasion with thinning and burning in dry coniferous forests have now been well documented (Griffis et al., 2001; Wienk et al., 2004; Fulé et al., 2005; Dodson and Fiedler, 2006; Collins et al., 2007).

However, treatments do not always result in increased invasion (Fornwalt et al., 2003; Wayman and North, 2007). Monitoring of exotic species prior to, during and following restoration activities may need to become an integral part of restoration in areas where exotic species pose a threat (Harrod, 2001). This could also provide further insight into what factors promote invasion, and allow implementation of strategies to mitigate post-treatment invasion before exotic species become abundant, especially in areas where exotic species are present before treatments, but not yet dominant. Where the expected increase in abundance of exotic species is low, however, treatment effects must be weighed against potential effects of stand replacing wildfire, which paradoxically may result in far greater exotic invasion than restoration treatments (Griffis et al., 2001; Crawford et al., 2001; Hunter et al., 2006; Freeman et al., 2007).

4.4. Management implications

This study showed that restoration treatments designed to modify overstory structure, canopy fuels, and potential wildfire behavior may have few short-term adverse impacts on understory vegetation, and may indeed enhance understory diversity especially where diversity is low prior to treatment. The generality of this finding remains in question, however, as pre-treatment conditions can significantly influence understory responses and different harvesting prescriptions would undoubtedly vary in their impacts on understory vegetation, soils, and overstory structure. Similarly, prescribed burning effects on understory vegetation could vary considerably, depending on whether prescriptions are designed to produce more intense fires that can modify overstory structure (i.e., cause tree mortality) or are simply designed to reduce surface and smaller ladder fuels. For both thinning and prescribed burning, effectiveness monitoring of operational restoration treatments could be of great benefit in establishing the consistency of treatment effects across a wider range of sites and treatments and over time. We recommend the use of before–after measurements on both treatment units and comparable controls, where possible, as this design proved very useful in this study for distinguishing treatment effects from background variability due to climate or other factors.

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References

- Abella, S.R., Covington, W.W., 2004. Monitoring an Arizona ponderosa pine restoration: sampling efficiency and multivariate analysis of understory vegetation. *Restor. Ecol.* 12, 359–367.
- Agee, J.K., Lolley, M.R., 2006. Thinning and prescribed fire effects on fuels and potential fire behavior in an eastern Cascades forest, Washington, USA. *Fire Ecol.* 2, 142–158.
- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12, 1418–1433.
- Arno, S.F., Harrington, M.G., Fiedler, C.E., Carlson, C.E., 1995. Restoring fire-dependent ponderosa pine forests in western Montana. *Restor. Manage. Notes* 13, 32–36.
- Collins, B.M., Moghaddas, J.J., Stephens, S.L., 2007. Initial changes in forest structure and understory plant communities following fuel reduction activities in a Sierra Nevada mixed conifer forest. *Forest Ecol. Manage.* 239, 102–111.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* 30, 129–164.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. Forest.* 92, 39–47.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.W., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in *Pinus ponderosa* forests of the Southwest. *J. Forest.* 95, 23–29.
- Crawford, J.S., Wahren, C.-H.A., Kyle, S., Moir, W.H., 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *J. Veg. Sci.* 12, 261–268.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Dodson, E.K., Fiedler, C.E., 2006. Impacts of restoration treatments on alien plant invasion in *Pinus ponderosa* forests, Montana, USA. *J. Appl. Ecol.* 43, 887–897.
- Dodson, E.K., Metlen, K.L., Fiedler, C.E., 2007. Common and uncommon understory species differentially respond to restoration treatments in ponderosa pine/Douglas-fir forests, Montana. *Restor. Ecol.* 15, 692–704.
- Emery, S.M., Gross, K.L., 2005. Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed *Centaurea maculosa*. *J. Appl. Ecol.* 42, 60–69.
- Everett, R.L., Schellhaas, R., Keenum, D., Sprubeck, D., Ohlson, P., 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *Forest Ecol. Manage.* 129, 207–225.
- Ffolliott, P.F., Clary, W.P., 1982. Understory–Overstory Vegetation Relationships: An Annotated Bibliography. USDA Forest Service General Technical Report INT-136. Intermountain Research Station, Ogden, UT.
- Fiedler, C.E., Arno, S.F., Keegan, C.E., Blatner, K.A., 2001. Overcoming America's wood deficit: an overlooked option. *Bioscience* 51, 53–58.
- Fiedler, C.E., Keegan, C.E., Morgan, T.A., Woodall, C.W., 2003. Fire hazard and potential treatment effectiveness: a statewide assessment in Montana. *J. Forest.* 101, 7.
- Fornwalt, P.J., Kaufmann, M.R., Huckaby, L.S., Stoker, J.M., Stohlgren, T.J., 2003. Non-native plant invasions in managed and protected ponderosa pine/Douglas-fir forests of the Colorado Front Range. *Forest Ecol. Manage.* 177, 515–527.
- Freeman, J.P., Stohlgren, T.J., Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., Brown, C.S., 2007. Rapid assessment of postfire plant invasions in coniferous forests of the western United States. *Ecol. Appl.* 17, 1656–1665.
- Fulé, P.Z., Covington, W.W., Smith, H.B., Springer, J.D., Heinlein, T.A., Huisinga, K.D., Moore, M.M., 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *Forest Ecol. Manage.* 170, 19–41.
- Fulé, P.Z., Laughlin, D.C., Covington, W.W., 2005. Pine-oak forest dynamics five years after ecological restoration treatments, Arizona, USA. *Forest Ecol. Manage.* 218, 129–145.
- Gildard, C.N., Fulé, P.Z., Covington, W.W., 2004. Plant community variability in ponderosa pine forest has implications for reference conditions. *Nat. Areas J.* 24, 101–111.

- Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest Ecol. Manage.* 146, 239–245.
- Gundale, M.J., DeLuca, T.H., Fiedler, C.E., Ramsey, P.W., Harrington, M.G., Gannon, J.E., 2005. Restoration treatments in a Montana ponderosa pine forest: effects on soil physical, chemical, and biological properties. *Forest Ecol. Manage.* 213, 25–38.
- Harrod, R.J., 2001. The effect of invasive and noxious plants on land management in eastern Oregon and Washington. *Northwest Sci.* 75, 85–89.
- Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *Forest Ecol. Manage.* 114, 433–446.
- Harrod, R.J., Fonda, R.W., McGrath, M.K., 2007. The role of fire in the restoration of a ponderosa pine forest, Washington, in: Butler, B.W., Cook, W., (Eds.), *The Fire Environment—Innovations, Management, and Policy; Conference Proceedings. March 26–30, Destin, FL. USDA Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-46*, pp. 315–327.
- Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of pre-settlement and modern eras. *Forest Ecol. Manage.* 211, 117–139.
- Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* 6, 324–337.
- Huffman, D.W., Moore, M.M., 2004. Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *Forest Ecol. Manage.* 198, 105–115.
- Huisinga, K.D., Laughlin, D.C., Fule, P.Z., Springer, J.D., McGlone, C.M., 2005. Effects of an intense prescribed fire on understory vegetation in a mixed conifer forest. *J. Torrey Bot. Soc.* 132, 590–601.
- Hunter, M.E., Omi, P.N., Martinson, E.J., Chong, G.W., 2006. Establishment of non-native plant species after wildfires: effects of fuel treatments, abiotic and biotic factors, and post-fire grass seeding treatments. *Int. J. Wildland Fire* 15, 271–281.
- Kaye, J.P., Hart, S.C., 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. *Ecol. Appl.* 8, 1052–1060.
- Keane, R.E., Ryan, K.C., Veblen, T.T., Allen, C.D., Logan, J., Hawkes, B., 2002. Cascading effects of fire exclusion in rocky mountain ecosystems: a literature review. *USDA Forest Service, Rocky Mountain Research Station. General Technical Report GTR-91*.
- Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. *Conserv. Biol.* 20, 375–384.
- Keeling, E.G., Sala, A., DeLuca, T.H., 2006. Effects of fire exclusion on forest structure and composition in unlogged ponderosa pine/Douglas-fir forests. *Forest Ecol. Manage.* 237, 418–428.
- Kerns, B.K., Thies, W.G., Niwa, C.G., 2006. Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. *Ecoscience* 13, 44–55.
- Knapp, E.E., Schwilk, D.W., Kane, J.M., Keeley, J.E., 2007. Role of burning season on initial understory response to prescribed fire in a mixed conifer forest. *Can. J. Forest Res.* 37, 11–22.
- Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 20, 1–27.
- Leishman, M.R., Thomson, V.P., 2005. Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury soils, Sydney, Australia. *J. Ecol.* 93, 38–49.
- Lillybridge, T.R., Kovalchik, B.L., Williams, C.K., Smith, B.G., 1995. *Field Guide for Forested Plant Associations of the Wenatchee National Forest. USDA Forest Service General Technical Report PNW-GTR-359*. Portland, OR, U.S.A.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schanbenberger, O., 2006. *SAS for Mixed Models*. SAS Institute Inc., Cary, NC, USA.
- Lonsdale, W.M., 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.
- McConnell, B.R., Smith, J.G., 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. *J. Range Manage.* 23, 208–212.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, U.S.A..
- McCune, B., Mefford, M.J., 1999. *PC-ORD: Multivariate Analysis of Ecological Data, Version 5.0*. MjM Software Design, Gleneden Beach, OR, U.S.A..
- McPherson, G., 1997. *Ecology and Management of North American Savannas*. University of Arizona Press, Tucson, AZ, U.S.A..
- Metlen, K.L., Fiedler, C.E., 2006. Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA. *Forest Ecol. Manage.* 222, 355–369.
- Metlen, K.L., Fiedler, C.E., Youngblood, A., 2004. Understory responses to fuel reduction treatments in the Blue Mountains of northeastern Oregon. *Northwest Sci.* 78, 175–185.
- Moir, W.H., 1966. Influence of ponderosa pine on herbaceous vegetation. *Ecology* 47, 1045–1048.
- Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fule, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecol. Manage.* 59, 135–144.
- Naumburg, E., DeWald, L.E., 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. *Forest Ecol. Manage.* 124, 205–215.
- NCDC, 2007. National Climatic Data Center, <http://www.ncdc.noaa.gov/oa/climate/research/2003/aug/st045dv00pcp200308.html>.
- USDA, NRCS, 2007. The Plants Database (<http://plants.usda.gov>, April 18, 2007). National Plant Data Center, Baton Rouge, LA, U.S.A.
- Riegel, G.M., Miller, R.F., Krueger, W.C., 1992. Competition for resources between understory vegetation and overstory ponderosa pine. *Ecol. Appl.* 2, 71–85.
- SAS Institute, 2004. *SAS/STAT 9.1 User's Guide*. SAS Publishing, Cary.
- Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544.
- Sieg, C.H., Phillips, B.G., Moser, L.P., 2003. Exotic plant invasions. In: Friederici, P. (Ed.), *Ecological Restoration of Southwestern Ponderosa Pine Forests*. Island Press, Washington, DC, pp. 251–267.
- Soil Survey Staff, 1995. *Cashmere Mountain Soil Survey: Leavenworth Ranger District Soil Handbook: Non-wilderness. Preliminary report. Okanogan and Wenatchee National Forests, Wenatchee, WA*.
- Stickney, P.F., Campbell, R.B., 2000. *Database for early post-fire succession in Northern Rocky Mountain forests. USDA Forest Service, Rocky Mountain Research Station. General Technical Report GTR-61CD*.
- Tabor, R.W., Waitt, Jr., R.B., Frizell, Jr., V.A., Swanson, D.A., Byerly, G.R., Bentley, R.D., 1982. *Geologic map of the Wenatchee quadrangle, Central Washington. U.S. Geological Survey Investigation Map 1-1311. Scale 1:100,000*. Washington, D.C.
- Uresk, D.W., Severson, K.E., 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. *J. Range Manage.* 42, 203–208.
- Vose, J.M., White, A.S., 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. *Forest Ecol. Manage.* 40, 175–187.
- Wayman, R.B., North, M., 2007. Initial response of mixed-conifer understory plant community to burning and thinning restoration treatments. *Forest Ecol. Manage.* 239, 32–44.
- Whelan, R.J., 1995. *The Ecology of Fire*. Cambridge University Press, Cambridge, UK, p. 346.
- Wienk, C.L., Sieg, C.H., McPherson, G.R., 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. *Forest Ecol. Manage.* 192, 375–393.
- Youngblood, A., Metlen, K.L., Coe, K., 2006. Changes in stand structure and composition after restoration treatments in low elevation dry forests of northeastern Oregon. *Forest Ecol. Manage.* 234, 143–163.