

Response of understory vegetation to salvage logging following a high-severity wildfire

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Abstract. Timber is frequently salvage-logged following high-severity stand-replacing wildfire, but the practice is controversial. One concern is that compound disturbances could result in more deleterious impacts than either disturbance individually, with mechanical operations having the potential to set back recovering native species and increase invasion by non-native species. Following the 2002 Cone Fire on the Lassen National Forest, three replicates of five salvage treatments were applied to 15 units formerly dominated by ponderosa pine, covering a range of disturbance intensities from unsalvaged to 100% salvaged. Understory species richness and cover data were collected every two years between 2006 and 2012. Richness of both native and non-native species did not differ among salvage treatments, but both showed strong changes over time. While cover of forbs and graminoids did not differ with salvage treatment, cover of shrubs was significantly reduced at the higher salvage intensities. The three main shrub species are all stimulated to germinate by fire, potentially leaving seedlings vulnerable to any mechanical disturbance occurring immediately postgermination. Many other native perennial species emerge from rhizomes or other deeply buried underground structures and appear to be less affected by salvage harvest. Over time, the plant community in all salvage treatments shifted from dominance by shrubs and forbs to shrubs and grasses. Most of the grasses were native, except *Bromus tectorum* (cheatgrass), which was found in 4% of measurement quadrats in 2006 and 52% in 2012. Our results indicated that understory vegetation change 4–10 years post-high-severity wildfire appeared to be influenced more strongly by factors other than salvage logging.

Key words: high-severity wildfire; non-native species; *Pinus ponderosa*; postfire management; salvage logging; species diversity; species richness; variable retention salvage.

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INTRODUCTION

Prior to active fire suppression, a regime of relatively frequent fire prevailed in most ponderosa pine-dominated forests of the western United States (Agee 1993). Frequent fire did not allow surface fuels to accumulate to any great extent, resulting in wildfires of mostly low-to-moderate intensity and severity (Show and Kotok 1924, Mallek et al. 2013). These fires also reduced the numbers of seedlings maturing into trees and limited the extent of ladder fuels, producing a

forest where extensive stand-replacing fires were rare (Show and Kotok 1924). After many decades to more than a century of fire exclusion, many such forests are now more susceptible to burning at high severity and large fires with relatively high proportion of area burning with stand-replacing severity have become increasingly common (Mallek et al. 2013).

After forested areas experience a stand-replacing wildfire, varied postwildfire management options exist. Logging the fire-killed trees (salvage) to extract economic value before the

wood decays is a common practice, but also controversial (Beschta et al. 2004). Standing snags are important habitat for wildlife species (Blake 1982, Hutto and Gallo 2006, Saab et al. 2007). This snag habitat is ephemeral, however, with most snags falling to the ground within 5–15 years (Keen 1955, Ritchie et al. 2013). Once on the ground, dead wood can provide cover and continue to be important for wildlife (Harmon et al. 1986, Butts and McComb 2000, Ucitel et al. 2003). However, downed wood is also fuel, which can cause subsequent fires to burn at higher intensities, particularly when the large downed logs are rotten (Passovoy and Fule 2006, Knapp 2015). Salvaging the dead timber is one means of reducing the fuels available for subsequent wildfires (Peterson et al. 2015). Unfortunately, the actual effects of salvage are little studied (McIver and Starr 2001), and much of the available literature has until recently been either observational, relatively short term or from experiments with unreplicated treatments.

Many plant species in frequent fire environments have evolved strategies to deal with or benefit from disturbance such as fire. One concern with any type of disturbance, whether fire or mechanical harvest, is the potential for invasion by non-native species which specialize in colonizing early-successional environments (Crawford et al. 2001, Griffis et al. 2001, Freeman et al. 2007). With salvage logging, mechanical harvest is also a secondary disturbance on top of the earlier fire-caused disturbance and concerns have been raised about cumulative or additive effects (Beschta et al. 2004, Lindenmayer 2006). Among those are soil compaction from heavy machinery and the influence of skid trails on bare mineral soil exposure and erosion, with the degree of impact varying with many factors including soil texture, slope, logging system, and timing of logging relative to soil moisture and snowfall (McIver and McNeil 2006, Wagenbrenner et al. 2015). While at least some of the weedy invaders are wind dispersed, mechanical equipment can potentially facilitate the movement of propagules, and a greater abundance of weedy species has been reported along haul roads than in surrounding undisturbed forest (Buckley et al. 2003). Skid trails and other harvest-related impacts could also impede regrowth of understory vegetation (Wagenbrenner et al. 2015) or kill plant seedlings

directly, especially if the harvest takes place after vegetation has already started to recover (Roy 1956, Donato et al. 2006, Lindenmayer and Ough 2006).

Partial salvage may be a means of balancing habitat versus fuel concerns and could potentially mitigate some of the negative impacts of treatment (Lindenmayer and Ough 2006, Macdonald 2007). In this study, we evaluated the intermediate-term (4–10 years) postwildfire (3–9 years postmechanical harvest) of different salvage logging intensities from complete to unsalvaged, including three levels of partial salvage, on the recovery and composition of the understory plant community.

METHODS

The study area is located within the Blacks Mountain Experimental Forest on the Lassen National Forest in the southern Cascade Range of northeastern California. Elevation ranged from 1785 to 1860 m, and the forest is dominated by ponderosa pine (*Pinus ponderosa* [Lawson and C. Lawson]) with lesser amounts white fir (*Abies concolor* [Gord. and Glend.]), incense cedar (*Calocedrus decurrens* [Torr.] Florin), and Jeffrey pine (*P. jeffreyi* [Balf.]). Site productivity is relatively low, with an average of 648-mm precipitation falling yearly, mostly as snow during the fall, winter, and spring. Soils are Typic Argixerolls in the Inville-Patio-Trojan family association, over fractured basaltic bedrock.

Wildfire and the fire salvage treatments

The Cone Fire started on 26 September 2002 and burned onto the Blacks Mountain Experimental Forest under extremely dry conditions (Ritchie et al. 2007), resulting in substantial to complete tree mortality in areas that had not recently been mechanically thinned or treated with prescribed burning. The following spring, 15 square units, each two ha in size, were laid out within areas that had burned at uniformly high severity where most or all trees were killed (Figure 1 in Ritchie et al. [2013]). Salvage treatments were then assigned randomly, with the treatments being a range of salvage intensities from fully salvaged (0% tree basal area retained) to unsalvaged (100% of tree basal area retained), and including three intermediate treatments



Fig. 1. One of the 50% basal area retained treatment units of the “variable retention salvage” study, on the Blacks Mountain Experimental Forest, Lassen National Forest, CA, in June 2006, four years after the Cone Fire and three years after salvage harvest. Photograph: Carl Skinner.

(25%, 50%, and 75% of basal area retained, with approximate target basal areas of 4.6, 9.2, and 13.8 m²/ha, respectively, based on an initial survey of standing basal area within the fire perimeter; Fig. 1). Partially salvaged treatments were created with a thinning from below, where snags were marked for removal from smallest to largest until the basal area target was reached.

Mechanical harvest began in the fall of 2003 with tracked feller-buncher cutting and stacking whole trees into small piles, which were then transported to landings using a rubber-tired grapple skidder. While the final basal area for 25% BA retained and 50% BA retained treatments came out close to targeted levels (4.8 and 9.2 m²/ha, respectively), the 75% basal area retained treatment ended up lower than targeted (9.9 m²/ha), possibly due to the difficulty in avoiding all dead trees with heavy equipment or just differences in the prefire stand density (Ritchie and Knapp 2014). Basal area averaged 34.0 m²/ha in the unsalvaged control (Ritchie and Knapp 2014), higher than the average found in the initial survey on which the retention targets were based, probably due to random variation. No mechanical equipment entered the unsalvaged control units. McIver and McNeil (2006) found a significant correlation between number of stems removed during salvage and amount of soil disturbance;

therefore, the salvage treatments likely represent a gradient of disturbance intensity, even if not linear like the basal area removal targets.

Much of the Experimental Forest is grazed by cattle, and no fencing was installed to exclude grazing from the study units. However, grazing was concentrated around meadows and water sources at lower elevations and limited on the upland slopes of the study units. Little evidence of grazing (visual evidence of browsing or presence of “cow pies”) was noted during data collection in all years.

Field sampling

Twenty-five sampling points were systematically placed on a 5 × 5 grid at 25-m intervals within each unit and identified with rebar markers. Using a sampling frame, two 1 m × 1 m quadrats were established at each odd-numbered gridpoint. To avoid the most disturbed area around the gridpoint, the quadrat corners were offset from the gridpoint by 1.41 m in the NE and SW directions. In the early summer of 2006, 2008, 2010, and 2012, all non-tree species occurring within the quadrat frame were recorded and cover was visually estimated according to the following categories: 1 = <1%, 2 = 1–10%, 3 = 11–25%, 4 = 26–50%, 5 = 51–75%, and 6 = 76–100%. Unknown species were

Table 1. Significance values for average species richness in different plant life history and functional group categories within 1 m × 1 m quadrats among salvage harvest treatments and years.

Fixed effects	df	Native	Non-native	Annual	Perennial	Forb	Graminoid	Shrub
		<i>P</i>						
Salvage treatment	4	0.191	0.359	0.562	0.501	0.534	0.078	0.043
Year	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.001
Salvage treatment × Year	12	0.731	0.167	0.532	0.822	0.869	0.402	0.733

collected from outside of the sampling frame (when available) and later identified using the Jepson Manual (1993). Plant names were later updated to the 2012 Jepson Manual, but because species were mostly field identified and not collected, new designations beyond the species level (subspecies and variety) were generally not updated.

The condition of the ground surface for plant growth and seedling establishment within the sampling frame was quantified by visually estimating the cover of bare ground, rock, litter and duff, fine woody debris (<7.6 cm diameter), and large woody debris (>7.6 cm diameter) to the nearest one percent. These latter categories sum to 100%.

Data analysis

Cover categories for individual species were converted to percent cover using the midpoint of the cover range for each category. Data were analyzed with a repeated-measures mixed-model analyses of variance with an autoregressive covariance structure to account for the same units being measured in all four years. Potential issues with inequality of variance among treatments and years were examined by testing residuals for untransformed as well as log-transformed and square-root-transformed data. Square-root-transformation slightly improved the fit of the residuals for cover of annuals, forbs, graminoids, shrubs, litter and duff, rock, fine woody debris, and large woody debris as determined using AIC_c. Native richness and non-native cover were log-transformed. All other analyses were performed on untransformed data. Tukey's test was used to distinguish the significance of differences for all possible combinations of back-transformed (when necessary) means.

To evaluate the relationships between cover of individual species in the final year of data

collection (2012) and physical variables (basal area of trees retained during the salvage harvesting operation, elevation, heat load index [calculated according to McCune and Keon 2002], as well as cover of bare ground, rock, litter, fine woody debris, and coarse woody debris cover), we used non-metric multidimensional scaling (NMDS) ordination (PC-ORD, version 6—McCune and Mefford [2011]). Ordination was based on a Sorensen distance matrix, and five hundred runs were performed with a random starting coordinate (250 with real data, 250 with randomized data). Only species occurring in >3 units were included.

RESULTS

Neither native species richness nor non-native species richness was significantly affected by the degree of salvage harvesting, but both differed significantly among years (Table 1). Average number of native species increased from 2006 to 2010, but then declined below 2006 levels in 2012, while the number of non-native species increased over the course of the study (Table 2). When species were categorized by life-history strategy, both annual and perennial species richness did not differ significantly among salvage harvest treatments, but both demonstrated a significant year effect (Table 1). Number of annual species increased from 2006 to 2010 and then declined dramatically in the final year of the study (2012), while the number of perennial species increased from 2006 levels but plateaued between 2008 and 2012 (Table 2). Different growth forms showed varying outcomes, with forbs and graminoids unaffected by salvage intensity, whereas shrubs were the only plant category significant affected by salvage harvest (Table 1). The unsalvaged treatment contained the greatest shrub species richness

Table 2. Average species richness in different plant life history and functional group categories within 1 m × 1 m quadrats for treatment areas receiving varying levels of salvage harvest (0–100% of basal area [BA] retained) and for all measurement years.

Treatment and year	Native	Non-native	Annual	Perennial	Forb	Graminoid	Shrub
No. species/m ²							
0% BA retained	8.05	0.36	3.77	4.62	5.34	2.03	1.21 ab
25% BA retained	8.49	0.50	4.10	4.97	5.88	2.25	1.08 a
50% BA retained	8.58	0.49	3.94	5.13	5.78	2.02	1.47 ab
75% BA retained	9.23	0.42	4.32	5.38	6.27	2.04	1.54 ab
100% BA retained (unsalvaged)	8.37	0.33	3.77	4.87	5.44	1.57	1.81 b
Year—2006	8.06 b	0.24 a	4.09 b	4.15 a	5.87 b	1.18 a	1.33 a
Year—2008	9.38 c	0.34 b	4.41 b	5.17 b	6.47 bc	1.94 b	1.40 ab
Year—2010	10.04 d	0.49 c	5.06 c	5.39 b	7.01 c	2.25 c	1.44 bc
Year—2012	6.99 a	0.60 d	2.35 a	5.27 b	3.63 a	2.55 d	1.52 c

Note: Statistically significant differences among back-transformed (when analysis was conducted on transformed data) least-squared means are denoted by different letters, with comparisons lacking letters not significantly different at $P < 0.05$.

(1.81 species/m²); while richness in the fully salvaged and 25% basal area retained treatment (1.21 and 1.08, respectively) were substantially less, only the 25% basal area retained treatment differed significantly from the unsalvaged treatment (Table 2). Number of forb species increased through 2010 and then declined below 2006 levels in 2012, while both graminoid and shrub species increased significantly over time (Table 2).

Salvage treatments had a stronger impact on plant cover than species richness, with native plant cover, perennial plant cover, and shrub cover all highest in the unsalvaged control than in completely or mostly salvage harvested treatments (Tables 3, 4). Non-native, annual, forb, and graminoid cover did not differ among salvage treatments (Table 3). All vegetation categories varied significantly among years (Table 3), with native, non-native, perennial, graminoid, and shrub cover increasing over time and annual and forb cover decreasing over time (Table 4).

One of the biggest concerns with any treatment that causes soil disturbance is the potential for invasion by non-native species. However, overall richness and cover of non-native species were not significantly affected by salvage treatment. In addition, cover and frequency of all individual non-native species common enough to analyze (cheatgrass [*Bromus tectorum* L.], goat's beard [*Tragopogon dubius* Scop.], bull thistle [*Cirsium vulgare* (Savi) Ten.], prickly lettuce [*Lactuca serriola* L.], and tumble mustard [*Sisymbrium altissimum* L.]) did not differ significantly among salvage treatments. While the frequency of non-natives increased over time, the trajectory varied greatly depending on the species. Frequency of cheatgrass and goat's beard increased significantly over time (Fig. 2). Cheatgrass was found in 4% of 1 × 1 m² quadrats in 2006 and 52% of quadrats in 2012, while goat's beard increased from 1% of quadrats to 11% of quadrats over the same period. Frequency of two other species—bull thistle and prickly lettuce—decreased from

Table 3. Significance values for average percent cover in plant life history and functional group categories within 1 m × 1 m quadrats among salvage harvest treatments and years.

Fixed effects	df	Native	Non-native	Annual	Perennial	Forb	Graminoid	Shrub
P								
Salvage treatment	4	0.004	0.892	0.794	0.001	0.704	0.487	0.016
Year	3	<0.001	0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Salvage treatment × Year	12	0.368	0.489	0.407	0.717	0.488	0.579	0.620

Table 4. Average percent cover in different plant life history and functional group categories within 1 m × 1 m quadrats for treatment areas receiving varying levels of salvage harvest (0–100% of basal area [BA] retained) and for all measurement years.

Treatment and year	Native	Non-native	Annual	Perennial	Forb	Graminoid	Shrub
	Cover (%)						
0% BA retained	43.9 a	1.8	7.9	37.1 a	12.3	9.1	23.1 ab
25% BA retained	45.8 ab	2.5	9.9	37.3 a	15.0	10.7	20.7 a
50% BA retained	54.3 ab	2.6	9.0	48.1 ab	12.6	8.4	35.7 ab
75% BA retained	56.9 b	2.2	8.9	50.0 b	13.4	10.1	34.4 ab
100% BA retained (unsalvaged)	57.3 b	1.4	8.0	50.6 b	11.5	5.8	41.2 b
Year—2006	48.2 a	0.6 a	11.3 a	37.3 a	19.2 c	4.3 a	24.6 a
Year—2008	49.7 a	1.3 a	10.6 a	40.1 ab	17.7 c	7.1 b	26.0 a
Year—2010	51.6 ab	3.9 a	8.9 a	45.2 b	11.4 b	11.5 c	31.5 b
Year—2012	56.9 b	5.5 b	5.0 b	55.9 c	6.0 a	13.7 c	41.2 c

Note: Statistically significant differences among back-transformed (when analysis was conducted on transformed data) least-squared means are denoted by different letters, with comparisons lacking letters not significantly different at $P < 0.05$.

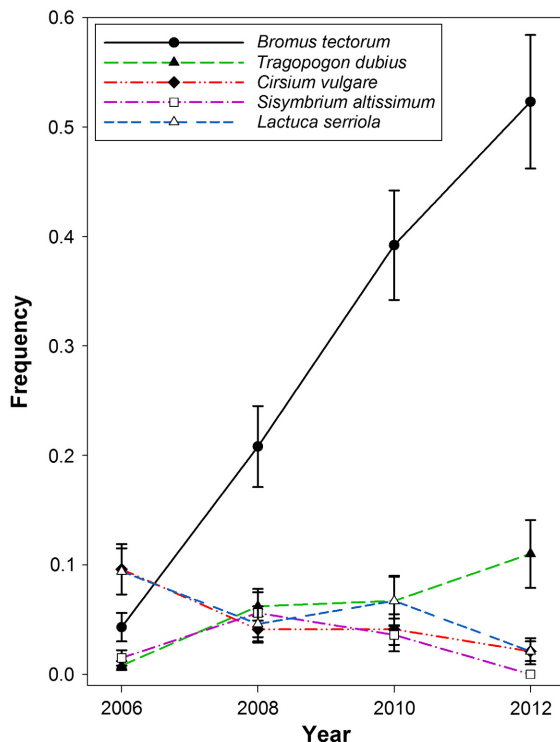


Fig. 2. Frequency (proportion of 1-m² quadrats) of the five most common non-native species found in the study area over time.

10% to 7%, respectively, in 2006, to 2% each in 2012 (Fig. 2). Frequency of tumble mustard was highest in the intermediate years 2008 and 2010, 6 and 8 years following the wildfire (Fig. 2).

Despite the increase in non-native species, the most common species over the course of the study were two native shrubs—prostrate ceanothus (*Ceanothus prostratus* Benth.) and snow brush (*Ceanothus velutinus* Douglas), which together comprised about half of the plant cover in all years (Table 5). The most striking changes in the plant community between 2006 and 2012 were the loss of forbs, particularly annuals, and an increase in cover of grasses. By 2012, two native bunchgrasses, squirreltail (*Elymus elymoides* [Raf.] Swezey) and needlegrass (*Stipa occidentalis* S. Watson), were among the five most abundant species (Table 5). This shift from forbs to grasses was even more pronounced when species were listed by frequency of occurrence. Prostrate ceanothus was the second-most commonly encountered species in both 2006 and 2012, but of the top five, the remaining four were all forbs in 2006 (groundsmoke [*Gayophytum diffusum* Torr. and A. Gray], blue-eyed mary [*Collinsia parviflora* Lindl.], cryptantha [*Cryptantha* sp.], and slender phlox [*Microsteris gracilis* (Hook.) Greene]). The most frequent species, groundsmoke, was noted in 92% of the quadrats. By 2012, the most frequent species was squirreltail, which was found in 82% of quadrats. Two other grasses (needlegrass and cheatgrass), along with one forb (annual fireweed *Epilobium brachycarpum* C. Presl), rounded out the top five.

The percentage of the study area covered by bare ground did not differ among the salvage treatments (Table 6), but substantial differences

Table 5. Most common species by percent cover found in the study area in 2006 and in 2012.

2006			2012		
Species	Cover (%)	Growth form	Species	Cover (%)	Growth form
<i>Ceanothus prostratus</i> var. <i>prostratus</i>	18.5	S	<i>Ceanothus prostratus</i> var. <i>prostratus</i>	28.6	S
<i>Ceanothus velutinus</i>	4.0	S	<i>Ceanothus velutinus</i>	6.3	S
<i>Gayophytum diffusum</i> ssp. <i>parviflorum</i>	3.7	F	<i>Arctostaphylos patula</i>	4.5	S
<i>Collinsia parviflora</i>	2.8	F	<i>Elymus elymoides</i>	4.3	G
<i>Wyethia mollis</i>	1.9	F	<i>Bromus tectorum</i>	4.0	G
<i>Stipa occidentalis</i>	1.8	G	<i>Stipa occidentalis</i>	3.1	G
<i>Cryptantha</i> sp.	1.7	F	<i>Carex rossii</i>	1.3	G
<i>Eriophyllum lanatum</i>	1.6	F	<i>Wyethia mollis</i>	1.3	F
<i>Elymus elymoides</i>	1.3	G	<i>Eriophyllum lanatum</i>	1.0	F
<i>Carex rossii</i>	1.1	G	<i>Symphoricarpos mollis</i>	0.8	S
<i>Symphoricarpos mollis</i>	1.0	S	<i>Monardella odoratissima</i>	0.7	F
<i>Microsteris gracilis</i>	1.0	F	<i>Ribes cereum</i> var. <i>cereum</i>	0.4	S
<i>Monardella odoratissima</i>	0.9	F	<i>Lupinus argenteus</i>	0.4	F

Note: S, shrub; G, graminoid; F, forb.

existed among years with bare ground declining from 77% to 28% between 2006 and 2012 (Table 7). Similarly, litter and duff cover did not differ among salvage treatments, but increased from 8% to 64% over the course of the study (Table 7). Percentage of area covered by rock declined slightly over time, while the cover of large woody debris (>7.6 cm diameter) peaked in 2008 (Table 7). Even though differences in large woody debris cover among salvage treatments were statistically significant, with cover numerically highest in the unsalvaged treatment (Table 7), post hoc pairwise comparisons among unsalvaged and salvaged treatments using Tukey's test were not statistically significant at $P < 0.05$. For fine woody debris (<7.6 cm diameter), the salvage treatment $\times$ year interaction was significant (Table 6), with values highest in the

fully salvaged treatment in 2006 and highest in the unsalvaged treatment in 2012 (Fig. 3).

NMDS ordination of the understory plant community in 2012 was optimized by a two-dimensional solution with a final stress of 7.05 ($P = 0.004$). Axis 1 ($R^2 = 0.76$) was most strongly associated with a heat load index (integrating slope and aspect), cover of rock, and slope, while axis 2 ($R^2 = 0.18$) was most strongly associated with cover of litter, cover of bare ground, and basal area of trees retained in the salvage logging operation (Fig. 4).

DISCUSSION

Salvage effects on plants

Of the plant life history and functional group categories examined in this study, only shrubs

Table 6. Significance values for cover of bare ground, litter and duff, rock, fine woody debris (<7.6 cm diameter), and large woody debris (≥ 7.6 cm diameter) within $1 \text{ m} \times 1 \text{ m}$ quadrats among salvage harvest treatments and years.

Fixed effects	df	Bare ground	Litter and duff	Rock	Fine woody debris	Large woody debris
		P				
Salvage treatment	4	0.161	0.400	0.751	0.118	0.048
Year	3	<0.001	<0.001	<0.001	<0.001	<0.001
Salvage treatment $\times$ Year	12	0.170	0.475	0.943	<0.001	0.176

Table 7. Average percent cover of environmental variables within 1 m × 1 m quadrats for treatment areas receiving varying levels of salvage harvest (0–100% of basal area [BA] retained) and for all measurement years.

Treatment and year	Bare ground	Litter and duff	Rock	Fine woody debris	Large woody debris
	Cover (%)				
0% BA retained	59.1	23.4	4.9	3.8	2.8
25% BA retained	62.4	25.2	3.4	3.1	2.3
50% BA retained	54.7	27.2	8.0	2.9	2.4
75% BA retained	55.4	29.1	4.0	3.5	2.9
100% BA retained (unsalvaged)	52.4	29.5	4.4	4.3	4.2
Year—2006	77.4 c	7.7 a	6.2 b	6.1 c	2.1 a
Year—2008	77.2 c	10.4 a	4.9 ab	3.4 b	4.5 b
Year—2010	44.3 b	45.7 b	4.6 a	3.0 ab	2.5 a
Year—2012	28.2 a	64.0 c	3.7 a	2.2 a	2.7 a

Note: Statistically significant differences among least-squared means are denoted by different letters, with comparisons lacking letters not significantly different at $P < 0.05$.

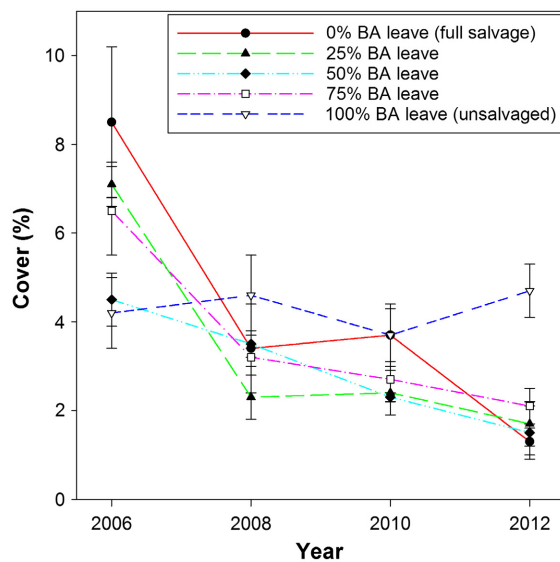


Fig. 3. Percent cover of fine woody fuels (<7.6 cm diameter) in different salvage harvest treatments (as indicated by the percentage of basal area left standing as snags) over time. The first year of the study (2006) was four years after the Cone Fire and three years after the salvage harvest.

showed a significant drop in species richness with increasing salvage intensity. Shrubs made up only a small portion of the total number of species (16%), but comprised 51% of the total understory cover. Shrubs were all native and perennial as well, which explains why cover of these categories also decreased at higher salvage intensities. Our findings were similar to several

previously published studies which reported weak (Macdonald 2007, Morgan et al. 2015) or no differences in understory vegetation between salvaged and unsalvaged forest (Keyser et al. 2009, McGinnis et al. 2010, Peterson and Dodson 2016). As in our study, Stuart et al. (1993) and Morgan et al. (2015) found reduced shrub cover in salvage harvested treatments. In the Morgan et al. (2015) study, reduced forb cover within salvaged treatments was accompanied by increased graminoid cover, compared with unsalvaged areas. Other studies have reported more substantial effects of salvage harvest, such as reduced species diversity and total cover (Leverkus et al. 2014), or a sparser and simplified (less species rich) understory (Purdon et al. 2004).

Variation in the effect of salvage harvest on understory vegetation among published studies is likely due to differences in the postfire plant community including modes of reproduction, intensity of the salvage harvest disturbance, timing of salvage harvest after the high-severity event, as well as the duration of monitoring. Several of the studies reporting an effect of salvage logging on the understory community have noted a reduction in differences between salvaged and unsalvaged treatments with time (Purdon et al. 2004, Kurulok and Macdonald 2007, Keyser et al. 2009, Morgan et al. 2015). While it is possible that vegetation recovery in the years between wildfire/salvage harvest and when data collection began reduced the difference between salvage and no salvage treatments,

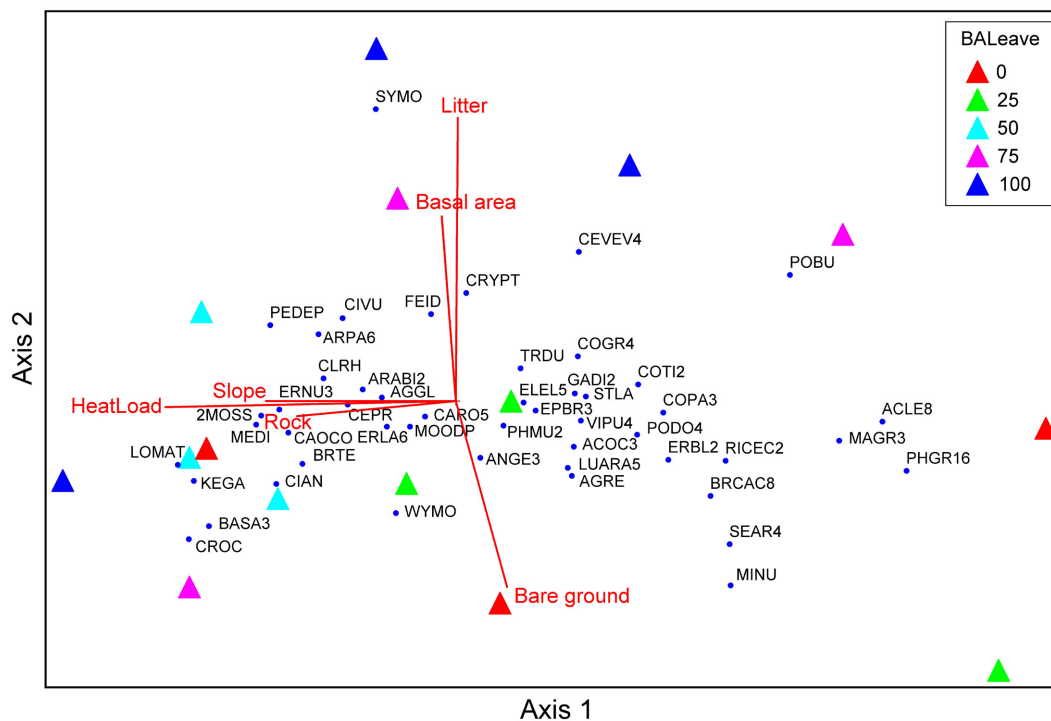


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of plant cover by individual species and by treatment unit (triangles—0% to 100% of basal area retained, three replicates each) in 2012, with joint plot illustrating associations ($R^2 > 0.3$) with environmental variables. Species are listed by their USDA PLANTS database code.

the time $\times$ treatment interaction was not significant for any vegetation variable. Therefore, the relative differences among treatments appeared to be stable during this time period.

Why salvage affected cover of shrubs more than other plant groups in this study may lie with the reproductive biology of the three most common shrub species, as well as the timing of harvest relative to germination and growth. Prostrate ceanothus, snowbrush ceanothus, and greenleaf manzanita all contain seed that are stimulated to germinate by heat and/or charate from fire (Quick and Quick 1961, Keeley 1987, Kauffman and Martin 1991), and with the ubiquitous seed bank in most forested environments where such shrubs are present (Knapp et al. 2012), many seedlings are typically found the following spring after a wildfire. While greenleaf manzanita and snowbrush ceanothus are also capable of resprouting from the plant base, prostrate ceanothus, the most abundant shrub by far, recovers from wildfire mainly by germination of

buried seed. If salvage harvest takes place after seedlings have already germinated, seedlings could be crushed by the mechanical logging equipment. Although some seed may remain in the seed bank, without subsequent exposure to heat and/or charate, the postfire shrub frequency and cover are likely determined by this initial postfire pulse of germination. Non-shrub perennials showed the opposite trend, with numerically higher cover in all salvage treatments than in the unsalvaged control. Many of these non-shrub perennial species emerge from deeply buried bulbs, caudexes, or rhizomes following fire (Miller 2000) or other disturbance and are therefore less susceptible than seedlings to losses from tree harvest or skidding of logs (Leverkus et al. 2014). Effect of salvage harvest timing has also been noted for tree seedlings, which are similarly vulnerable to loss in the early postgermination phase (Roy 1956, Donato et al. 2006). Too few tree seedlings were found in our study area to detect a salvage harvest effect, with abundance

attributed mainly to proximity to the few surviving trees (Ritchie and Knapp 2014).

Depending on the management objective, the reduced shrub cover with salvage intensity could be viewed as either a positive or a negative. When especially dense, as is often the case in post-high-severity fire environments (Gratkowski 1974, Nagel and Taylor 2005, Crotteau et al. 2013), shrubs may compete with and slow the initial growth of conifer seedlings (Conard and Radosevich 1982, Zhang et al. 2006). If fast recovery of the forest overstory is a goal, reduced shrub cover may lessen the perceived need for intensive, costly, and sometimes controversial management options used for controlling shrubs, including hand grubbing, mastication, and/or use of herbicides. However, shrubs may also promote tree seedling establishment and growth, especially on hot and dry sites (Dunning 1923, Tappeiner and Helms 1971, Jones 1995). Tappeiner and Helms (1971) noted that on exposed slopes and ridge tops, soil moisture was greater and tree seedling survival rate much higher when growing within mats of prostrate *Ceanothus*, the most common shrub species at our study site. Many of the shrub species with fire-stimulated seeds, such as *Ceanothus* spp., are symbiotic nitrogen fixers, increasing the amounts of available N in the soil and improving conditions for plant growth (Binkley et al. 1982, Conard et al. 1985). In addition, the foliage of prostrate *Ceanothus* is not readily flammable and may have historically provided a barrier that protected small tree seedlings growing within mats of this species from being killed by the frequent low-intensity fires (Dunning 1923, Show and Kotok 1924, Skinner and Taylor 2006).

Among the concerns with salvage harvest is the potential for invasion by non-native weedy species. Many non-native species respond positively to disturbance (Belote et al. 2008, Jauni et al. 2015), so the combined wildfire disturbance and mechanical equipment disturbance might be expected to increase susceptibility to invasion, over wildfire alone. Mechanical equipment can also serve as a vector for dispersal of propagules. However, we saw no evidence of higher non-native species richness or cover in the salvage treatments, similar to findings of others (Purdon et al. 2004, Macdonald 2007, Keyser et al. 2009, McGinnis et al. 2010, Morgan et al. 2015, Peterson

and Dodson 2016). In our study, non-native species, most notably cheatgrass, generally increased over time regardless of salvage intensity. This suggests that non-native species abundance may be driven more strongly by factors external to salvage harvest, such as the initial fire-caused disturbance. In addition, seeds of many of the common non-native species we found are dispersed chiefly by wind. While we did not have any plots in unburned or less severely burned areas, other studies of postfire recovery have shown fire severity to exert a stronger influence on non-native abundance than mechanical disturbance associated with timber harvest (Hunter et al. 2006, Morgan et al. 2015).

Given that plant growth is sensitive to soil damage from skidding and other harvest activities (e.g., Wagenbrenner et al. [2015] reported slower vegetation regrowth on skid and feller-buncher trails), an effect of salvage harvest on native plant categories other than shrubs might have been expected. However, such high-intensity disturbance typically impacts only a portion of harvested areas. Previous studies have reported between 17% (McIver and McNeil 2006) and 34% (Klock 1975) of soil area disturbed by salvage harvest, mainly due to displacement and compaction (McIver and McNeil 2006). Soil compaction, generally considered a negative for plant growth, is most problematic when soils are wet (Johnson et al. 2007, Cambi et al. 2015), and harvest in this case was carried out in dry periods during the fall, following standard U.S. Forest Service practice. The rocky nature of the study area precluded meaningful data collection on soil compaction, but rocky soils may also reduce the magnitude of compaction (Luckow and Guldin 2007).

Plant community change over time

Both species richness and cover for all plant groups changed significantly over the course of the study. Number of annuals, forbs, and native species increased through 2010 and then declined sharply in 2012. This drop was especially pronounced for annuals, which are expected to be most sensitive to amount and timing of yearly precipitation. During the six-year study period, 2012 was among the driest. Germination of some annuals might also be impeded by litter and duff. The increasing amount of other detritus on the

forest floor (as well as continued growth of perennial grasses, forbs, and shrubs) could additionally help explain the drop in annual species over time. Even some of the weedy forbs that are commonly found following logging induced soil disturbance, such as bull thistle and prickly lettuce became significantly less frequent over the course of the study.

The decline in annual and forb cover was accompanied by an increase in graminoid and shrub cover. While a portion of the threefold increase in grass cover was due to the invasion by cheatgrass, several native perennial bunchgrass species also became an important part of the postfire plant community. Native grasses were believed to have once played a larger role in ponderosa pine-dominated forest ecosystems, but have been squeezed out due to shading at higher tree densities (Jameson 1967, Moore and Deiter 1992). Grasses appear to benefit more than other plant groups from low overstory canopy cover conditions (McConnell and Smith 1970), such as those prevalent following high-severity fire.

Disturbance is thought to hasten non-native invasions by altering resource pools (Elton 1958, Hobbs and Huenneke 1992). If the cover of native plants is reduced by wildfire or salvage logging, more soil water and/or light may be available for non-native species. Either disturbance can enhance the supply of nutrients such as nitrates, formerly tied up in the vegetation (Chambers et al. 2007). Indeed, biomass and seed production of cheatgrass have been shown to increase following wildfire, especially when native vegetation has been removed (Chambers et al. 2007). When native vegetation has not been eliminated or can rapidly re-establish from intact underground structures postfire, these native species also capture available resources, thereby limiting invasibility. The most abundant and most rapidly expanding native perennial grass at our study site (*Elymus elymoides*) has been shown to suppress cheatgrass by exploiting resources more efficiently (Booth et al. 2003). West and Yorks (2002) reported a negative correlation between non-native annual and native perennial grass abundance 20 years after a wildfire, with the least cover of cheatgrass in plots with the highest cover of native perennial grasses. In our study, cover of cheatgrass continued to increase over time, despite corresponding increases in

the cover of native perennials, including grasses. Cheatgrass also increased in frequency and by 2012 was present in over half of quadrats. Still, the average cover of cheatgrass in those quadrats was less than 4%, suggesting that the capacity of this species to both outcompete native species and alter the fire regime is perhaps less pronounced than in other ecosystems it has invaded (e.g., Whisenant 1990). While any increase in non-native species is a concern, with total native plant cover still expanding 10 yr postwildfire and 9 yr postsalvage, it is possible that a longer period of time may be necessary for native species to fully capture resources at the study site, thereby limiting non-native invasion.

Fire and salvage effects on ground cover variables

Many early-successional plant species are adapted to capitalize on the open conditions and bare mineral soil created by disturbance. Nearly complete bare mineral soil exposure is common following high-severity wildfire during dry summer conditions (Benavides-Solorio and MacDonald 2005, Berg and Azuma 2010). Fuel moisture was very low at the time of the Cone Fire, with 10-h fuels at 2% and 1000-h fuels at 5% (Ritchie et al. 2007)—levels at which most if not all potentially combustible material is typically consumed. Harvesting and skidding equipment used during salvage harvest also potentially expose bare soil, but in lesser amounts than high-severity wildfire. While the possibility exists that salvage harvest-caused increases in bare ground cover were no longer evident by the time data collection began, deposition of litter from vegetation regrowth in the year between the Cone Fire and salvage harvest was also likely minimal and any added disturbance would therefore not have appreciably changed the amount of bare soil.

NMDS ordination indicated that in the final year of data collection, the plant community composition was associated with bare ground and litter cover, a gradient which also aligned with basal area of snags retained. While compaction from harvest equipment could lead to more bare soil 10 yr postwildfire, another possibility is that the reduced cover of shrubs in the more heavily salvaged units produced less litter therefore leaving more of the ground bare. Productivity differences among units may also be a factor. Differences between outputs from ordination

and mixed-model ANOVA approaches could be because the ordination was conducted on just the final year's data.

Large woody debris, either left behind by the logging or added as snags fall, can reduce the space available to understory plants. While higher large woody debris cover was found in the unsalvaged treatment, differences between salvaged and unsalvaged treatments were not as pronounced as results reported previously by Ritchie et al. (2013) for the same study units, but using different sampling methods. Ritchie et al. (2013) collected data over a larger area using Brown's transects (Brown 1974) for fuels between 7.7 and 20.3 cm diameter and taper equations for the larger (>20.3 cm) standing snags to estimate cover. They found that in 2010, eight years after the Cone Fire, the percentage of the ground covered by larger (>7.6 cm) fuels approached 10% in the unsalvaged units, compared to 1% in the completely salvaged units. Thus, the difference between studies is likely a sampling issue, with our 1 m × 1 m quadrats insufficient to accurately capture the cover of clumpy and widely dispersed logs (Sikkink and Keane 2008). Small fixed area plots perform better for evaluating the cover of more evenly dispersed fine fuels (Sikkink and Keane 2008).

While fine fuels were in most instances not dense enough to substantially impede the establishment of understory vegetation, our results do provide some new insights relevant to the debate about whether salvage harvest increases or decreases fire risk or hazard. While fuel cover is not the same as the fuel mass reported in other studies, trends in cover with time were consistent with fuel mass results from the same study area, determined using Brown's transects (Ritchie et al. 2013). The most heavily salvaged treatments initially (in 2006) had higher fine-fuel cover than the unsalvaged and partially salvaged treatments, similar to findings for fine-fuel mass in other studies (Donato et al. 2006, McIver and Ottmar 2007, Peterson et al. 2009). However, the relationship between fine-fuel cover and salvage intensity reversed over time. Ten years after the Cone Fire, fine-fuel mass was significantly higher in the unsalvaged treatment than the salvaged treatments. This was likely due to decomposition of fine fuels generated by the salvage harvest, coupled with new fine-fuel additions as standing

snags in the unsalvaged or partially salvaged treatments fell over time. This reversal with time was also reported by Peterson et al. (2015), who studied a chronosequence of sites up to 39 yr postsalvage.

Our results demonstrate that the effect of management actions on fire hazard needs to be evaluated not only temporally, but in terms of development of the entire fuel bed. At our first sampling (2006), the elevated cover of fine fuels resulting from salvage harvest was likely inconsequential to fire hazard, as only 17% of the ground in the 100% salvaged treatment was covered with combustible material—9% fine woody fuels, 2% large woody fuels, and 6% litter—the rest was bare ground. Such low cover would likely result in a very patchy and discontinuous fuel bed where fire would not carry well, if at all. Six years later, accumulated litter from vegetation regrowth covered an average of 64% of the ground. Thatch from the increasing cover of grasses also contributed to the fuel bed. Thus, by the time the fuel bed matured sufficiently to potentially carry fire, fine woody fuel cover was actually less in the fully salvaged treatment than in the unsalvaged or partially salvaged treatments. Our findings may differ from salvage treatments where whole trees are not transported to landings and instead delimbed in the field without subsequent fuel treatment, which would be expected to generate higher fine-fuel loads and greater fuel continuity (Donato et al. 2013).

Fine fuels declined more rapidly with time in fully salvaged units than indicated by the modeled results of Dunn and Bailey (2015), who predicted fine-fuel mass would be higher in salvaged areas for up to 22 yr. The faster decline of fine fuels in our study may be because all snags were removed, with the unmerchantable trees chipped and sold as biomass, whereas Dunn and Bailey's modeled results were based on empirical data from sites where the salvage operation removed only merchantable trees, leaving a source of fine-fuel inputs from the smaller unmerchantable trees over time.

CONCLUSIONS

Salvage logging had only a modest effect on the understory vegetation community in the

intermediate term. Richness and cover of forbs and graminoids were unaffected by salvage logging intensity, but the richness and cover of shrubs were reduced at the highest salvage logging intensities, with differences in response likely related to modes of reproduction. The most common shrub species at the study site contain seed that are stimulated to germinate by heat and/or charate from fire. Seed can survive in the seed bank for centuries (Gratkowski 1962), and seedlings typically emerge in the late spring after snow melts the year following a wildfire. Seedlings are therefore especially vulnerable to loss from mechanical equipment operations occurring after that time. Other perennial species not dependent on fire-stimulated seed for germination were not impacted by salvage harvest. Most emerge from deeply buried rhizomes, bulbs, or caudexes after the aboveground plant parts are killed by wildfire. While these structures could potentially be destroyed by severe logging-caused soil disturbance, the lack of a significant treatment effect suggests that mechanical equipment damage did not exceed this threshold. Graminoids either persisted with wildfire and salvage logging or recolonized the site afterward. Weedy non-native species also showed no difference in richness or cover among treatments. This could be due to the lack of treatment differences in amount of bare mineral soil available for colonization.

While the effect of treatment on shrubs was modest (23% cover in the fully salvaged treatment compared to 41% cover in the unsalvaged treatment), even small differences can have lasting ecological impacts. Less shrub cover may lead to more rapid establishment of non-shrub vegetation, including trees, but also may mean a decline in some of the positive contributions of shrubs to nitrogen fixation or safe sites for species that preferentially establish under the cover of shrubs. Timing of salvage harvest, relative to the wildfire and understory vegetation recovery, and relative to data collection, also likely played a role. Salvage in this case occurred 13–14 months after the wildfire, when understory vegetation was in the initial stages of recovery. Given that all management projects on Federal land are required to go through the NEPA (National Environmental Policy Act) review, delays similar to or longer than in this study are normal. It

remains to be seen whether the impacts to shrubs noted in this study could be mitigated by more rapid salvage harvest, completed prior to shrub seed germination.

One of the concerns with salvage logging is that multiple sequential disturbances might lead to more profound impacts on native ecosystems than either logging or high-severity wildfire alone (Hobbs and Huenneke 1992). Wildfire not only burned all combustible cover on the soil surface, but dramatically altered the light environment by killing all except a few trees in the study area. While the amount of soil disturbance caused by salvage logging was not quantified, mechanical equipment likely disturbed only a portion of the soil surface area affected by the wildfire and removal of dead stems had a lesser impact on light conditions than removal of the canopy by high-severity fire. As pointed out by McIver and Starr (2001), the overwhelming effects of high-severity wildfire on an ecosystem can complicate extracting the added effects of subsequent disturbance. Our data showing increasing non-native richness and cover over time regardless of salvage treatment suggest that disturbance associated with high-severity wildfire may present a bigger threat than the disturbance associated with salvage logging. Although we did not have any plots in adjacent unburned forest as a comparison, evidence from other studies (e.g., Crawford et al. 2001, Griffis et al. 2001, Freeman et al. 2007, Abella and Fornwalt 2015) suggests that the magnitude of invasion is much less in the absence of high-severity wildfire disturbance.

The findings in this study are surely a function of the site and how the treatments were applied; therefore, our results are not universal and more dramatic salvage logging impacts are certainly possible under other circumstances. Conditions at this study site, such as rocky soils and lack of substantial slope, likely reduced the potential for compaction and extensive soil disturbance with mechanical equipment. In addition, care was taken to operate only under conditions that would minimize soil damage. Logging was carried out in the fall, when the soil was dry, which also reduces likelihood of soil compaction. Amount of activity fuel deposited on the forest floor, which may have otherwise interfered with understory plant growth, was minimized by whole tree harvest, with material

brought to a landing and processed there. All of our study units were outside of landings. However, our findings are also in-line with a growing body of evidence from other salvage harvest studies (e.g., Macdonald 2007, Keyser et al. 2009, McGinnis et al. 2010, Morgan et al. 2015, Peterson and Dodson 2016); thus, increasing the level of confidence that longer-term outcomes from postfire logging on understory vegetation might not be substantially different in other frequent fire forest ecosystems in the western United States and elsewhere, as long as care is taken to minimize soil impacts. As Peterson and Dodson (2016) point out, if future studies continue to not find strong longer-term salvage harvest effects on forest understory vegetation, the debates about pros and cons of postfire management could then narrow to variables such as snag habitat and fuel loading that are unequivocally impacted by salvage harvest.

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