

RESEARCH ARTICLE

# Vegetation Recovery in Slash-Pile Scars Following Conifer Removal in a Grassland-Restoration Experiment

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## Abstract

A principal challenge to restoring tree-invaded grasslands is the removal of woody biomass. Burning of slash piles to reduce woody residues from forest restoration practices generates intense, prolonged heating, with adverse effects on soils and vegetation. In this study, we examined vegetation responses to pile burning following tree removal from conifer-invaded grasslands of the Oregon Cascades. We quantified the longevity and magnitude of fire effects by comparing ground conditions and the cover and richness of plant species in burn-scar centers (higher-intensity fire) and edges (lower-intensity fire) with adjacent unburned vegetation 7 years after treatment. We interpreted patterns of recovery through the responses of species with differing growth forms, habitat affinities, and clonality. Cover of bare ground remained elevated at the centers, but not at the edges

of scars; however, much of this effect was due to gopher disturbance. Total plant cover, consisting entirely of native species, was comparable in and adjacent to scars. However, richness remained depressed at the scar centers. Cover of grass, meadow, and non-clonal species was comparable in and adjacent to scars, but cover of forb, sedge, residual forest, and clonal species was reduced at the centers. Although scar centers had a simpler community structure (fewer but more abundant species) than the adjacent vegetation, they remained free of exotics and recovered quickly, aided by the soil-disturbing activities of gophers and the regenerative traits of native, disturbance-adapted species. Pile burning can be a viable and efficient approach to fuel reduction in the absence of exotics.

**Key words:** burn pile, fuel reduction, gopher disturbance, meadow restoration, vegetation recovery.

## Introduction

Woody-plant encroachment of grasslands is increasing globally, with profound ecological consequences (Scholes & Archer 1997; Van Auken 2000; Ratajczak et al. 2012). The accumulation of woody biomass in some invaded grasslands presents a fundamental challenge to restoration. Although shrub or tree removal is essential to grassland restoration, it can leave woody residues that impede growth of grassland species and enhance the severity or spread of future wildfires. Burning these residues can also generate substantially higher temperatures or longer-duration heating than occurs during natural grassland fires.

Pile burning is a common method for disposing of woody fuels generated by forest thinning. However, the severity or duration of heating beneath slash piles can have adverse, often

persistent, effects on soil and vegetation. These effects include volatilization or transformation of soil N, changes in soil aggregate stability, increased surface repellency and susceptibility to erosion, loss of microbial/fungal biomass, and mortality of seeds and root systems of plants (Covington et al. 1991; Haskins & Gehring 2004; Korb et al. 2004; Creech et al. 2012). On the other hand, effects of pile burning are highly localized, limited to the scar itself. Severity typically declines from the center to the edge of the scar (Korb et al. 2004; Fornwalt & Rhoades 2011), mirroring the steep gradient in heating (Busse et al. 2013). Despite these localized effects, the potential for burn scars to serve as foci for establishment and spread of exotics is a significant management concern (Haskins & Gehring 2004; Owen et al. 2009).

Vegetation responses to pile burning are shaped by interactions among fire severity, plant traits, soil biota, and the context in which burning occurs. For example, survival of perennial species varies with the type and depth of perennating structures (McLean 1969; Flinn & Wein 1988; Halpern 1989). High-intensity fire is more likely to kill species with stolons or shallow rhizomes than species with deeper perennating structures. Similarly, survival of seeds in the soil varies with seed-coat thickness and depth of burial (Beadle 1940; Santos et al. 2010). Seeds, which are typically concentrated in the

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duff or upper soil horizons, are likely to be lost with high intensity or prolonged heating (Moore & Wein 1977; Clark & Wilson 1994). In the absence of surviving plants, the pace and pattern of burn-scar recovery should reflect the abundance and regenerative traits of species in the surrounding vegetation. Colonization should be quicker for short-lived, ruderal species producing abundant, wind-dispersed seeds (Grime 1977) or for species with vigorous clonal spread (lateral growth via stolons or rhizomes; Bell & Tomlinson 1980; Antos & Halpern 1997). Finally, recovery can be shaped by fire-induced changes in the soil biota, including arbuscular mycorrhizal fungi (Pattinson et al. 1999) or microbial communities (Hebel et al. 2009), that mediate the performance or interactions of plant species (Smith & Read 1997; Hamman & Hawkes 2012; Kardol et al. 2013).

In this study, we examined long-term (7-year) responses of vegetation to pile burning of woody residues following tree removal from conifer-invaded grasslands (or meadows) of the Oregon Cascades—sites that have experienced more than a century of forest development (Halpern et al. 2010; Rice et al. 2012). Two aspects of this system—presence of deep grassland soils and pocket gophers that redistribute large amounts of soil annually—distinguish it from the forests in which pile burning is typically conducted. The current study is part of a larger experiment that tests the potential for grassland restoration using tree removal with and without fire (Halpern et al. 2012). To our knowledge, this is the first study to explore vegetation responses to pile burning in a grassland-restoration context. The larger experiment contrasts two methods of fuel reduction: broadcast versus pile burning (leaving 90% of the ground surface unburned). Understanding the response to fire is critical given uncertainty about its historical role in this system and the trade-offs between fuel reduction and high-severity burning. We reported on the early stages of burn-scar recovery (years 1–3) previously (Halpern et al. 2012). The objectives of the current, longer-term analysis were three-fold: (1) to compare the abundance and diversity of plants in and adjacent to burn scars 7 years after treatment; (2) to determine whether initially large differences in burn severity at the centers and edges of scars persisted after 7 years; and (3) to interpret vegetation recovery through species' functional traits, including growth form, habitat affinity (meadow, residual forest, or ruderal), and clonality (limited/non-clonal vs. highly clonal).

## Methods

### Study Area

The study site, Bunchgrass Ridge, lies along the western slope of the High Cascades in Oregon (1350-m elevation; 44° 17'N, 121° 57'W). The site supports a 100-ha mosaic of montane meadows and coniferous forests reflecting nearly two centuries of encroachment by *Pinus contorta* (Lodgepole pine) and *Abies grandis* (Grand fir) (Halpern et al. 2010; Rice et al. 2012). Meadows comprise diverse communities of mesic- and dry-site forbs and graminoids (Haugo & Halpern 2007). Forest understories support a mix of shade-tolerant herbs and residual meadow species, whose abundance varies with the duration of tree influence (Haugo & Halpern 2007, 2010).

Soils are deep (>1.7 m), fine to very fine sandy loams originating from andesitic basalt and tephra with varying amounts of glacially derived rock. They grade from Vitric Melanocryands (open meadows) to Aquic Vitricryands (older forests). Profiles suggest dominance by grasslands for centuries (possibly millennia), even in currently forested areas (D. Lammers 2005, USFS Corvallis, OR, personal communication). In open meadows, the Western pocket gopher (*Thomomys mazama*) is active, tunneling and depositing soil at the ground surface (Jones et al. 2008; Case et al. 2013).



Figure 1. Distant view of one of three tree-removal plots before, during, and in the first growing season after pile burning.

The climate is maritime, with cool, wet winters and warm, dry summers. At Santiam Pass (1,488 m), 17 km to the north, temperatures average  $-6.9^{\circ}\text{C}$  (minimum) and  $0.7^{\circ}\text{C}$  (maximum) in January, and  $6.1$  and  $27.8^{\circ}\text{C}$  in July. Precipitation averages  $\sim 220$  cm/year, but is concentrated in winter, resulting in frequent summer drought (data for 1948–1985; Western Regional Climate Center; <http://www.wrcc.dri.edu/summary/climsmor.html>). Snowfall averages  $\sim 11.5$  m/year and snowpack can persist into late May or early June.

Fire, the principal disturbance, occurs infrequently in the montane zone (Morrison & Swanson 1990; Weisberg & Swanson 2003). Evidence of moderate- or high-intensity fire within the last two centuries is lacking at Bunchgrass Ridge (Halpern et al. 2010), although Native Americans may have set low-intensity fires to maintain meadow openings (Burke 1979). Sheep grazing is likely to have occurred in the late 1800s to early 1900s (Johnson 1985), but records of grazing in the study area are lacking.

### Treatment Implementation

The current study is part of a larger meadow-restoration experiment (Halpern et al. 2012). In June 2003, we established nine 1-ha plots within 16 ha of conifer-invaded meadows. Prior to removal, tree density averaged 1,240/ha and basal area,  $40.5\text{ m}^2/\text{ha}$  (Halpern et al. 2010). Plots were randomly assigned to a control or one of two tree-removal treatments in which slash was either broadcast burned or piled and burned ( $n = 3$  per treatment). Trees were cut in winter 2006 on deep, compacted snow. To reduce fuel accumulation, limbs were left attached to the bole. In the pile-burned treatments, slash piles (1.8–2 m tall, 2–4 m in diameter) comprising small boles, limbs, and foliage, were constructed by hand in June 2006 and covered with polyethylene film to shed water (Fig. 1). Piles covered  $\sim 10\%$

of the ground surface in each plot (Halpern et al. 2012). Piles were ignited on 2 November 2006 and burned to completion (95–100% consumption) within 2 days (Fig. 1). On the morning of ignition, temperature was  $5^{\circ}\text{C}$ , relative humidity was 100%, wind was SW at 3.2 km/hour, and cloud cover was complete. Two-day rainfall totaled 3.3 cm.

### Vegetation Sampling

In July 2007, we randomly selected 10 scars from each plot (a total of 30) (Fig. 2). From the center of each scar we ran a transect in a random direction across the edge into unburned vegetation. A permanent quadrat ( $0.2\text{ m} \times 0.5\text{ m}$ ) was established perpendicular to the transect at each of four locations: center (C; higher-intensity burn); edge (E; lower-intensity burn); and unburned vegetation at the edge ( $U_1$ ) and distant from the edge ( $U_2$ ) (Fig. 3). The latter allowed us to assess effects beyond the scar boundary. Although scar diameter varied,  $U_1$  and  $U_2$  were spaced equivalent to C and E (0.5–1.7 m).

Each quadrat was sampled for burn severity (percent cover of white ash and blackened duff/charcoal) in 2007 (year 1); for soil chemistry in 2007 and 2009 (year 3); and for vegetation in 2007, 2009, and 2013 (year 7). Methods for sampling and analyses of soils are described in detail by Halpern et al. (2012). At each sampling date we estimated percent cover of bare ground, recent gopher disturbance (mounds or winter castings, convex in profile), and all plant species. Cover of gopher disturbance could not exceed that of bare ground. Plant nomenclature follows Hitchcock and Cronquist (1973).

### Statistical Analyses

We limited our assessment of vegetation recovery to the most recent (year 7) data, analyzing responses through the functional



Figure 2. Examples of burn scars in 2007 (year 1, left) and 2013 (year 7, right). PVC posts mark the lower left corners of the quadrats used to sample each position; a sampling frame is visible in the 2007 photo.

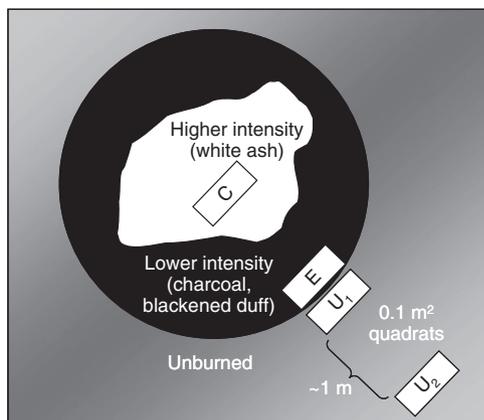


Figure 3. Schematic diagram of the sampling design, showing the spatial arrangement of quadrats ( $0.2 \text{ m} \times 0.5 \text{ m}$ ) used to sample the burn-scar center (C, higher-intensity burn), edge (E, lower-intensity burn), and unburned vegetation at the edge ( $U_1$ ) and distant from the edge ( $U_2$ ).  $U_1$  and  $U_2$  were separated by the same distance as C and E.

traits of species. Each species was classified by growth form (grass, sedge, forb, shrub, or tree); habitat affinity (forest understory, meadow, or ruderal); and clonality (limited/non-clonal or highly clonal). Growth-form and habitat-affinity assignments followed past studies (Haugo & Halpern 2007, 2010; Halpern et al. 2012). Clonality was determined from root system excavations or descriptions in the flora (Hitchcock et al. 1969). For each quadrat we tallied the number and summed the cover of species sharing each trait.

We used randomized block analysis of variance (ANOVA) models to assess the effect of position (C, E,  $U_1$ , or  $U_2$ ), with individual scars treated as blocks (random effect). Previous analyses indicated little variation among experimental plots, thus plot was not included in the models. Separate analyses were conducted for (1) total cover; (2) cover of species by growth form, habitat affinity, and clonality; (3) total richness; and (4) richness by growth form, habitat affinity, and clonality. Standard diagnostics were used to assess normality and homogeneity of variance; log or square-root transformations were applied as necessary. Significant ( $p \leq 0.05$ ) effects of position were followed by Tukey comparisons of means. We also developed rank-abundance, or dominance-diversity curves (Whittaker 1965; Magurran 2004) to compare the distribution of abundance (log mean cover;  $n = 30$ ) and total richness of species among positions. Analyses were conducted with Systat 10.0 (SPSS 2001).

## Results

### Floristics

In year 7, we observed 43 species in the 120 quadrats sampled, including 29 forbs, 7 grasses, 4 sedges, 2 shrubs, and 1 conifer (Table 1). Habitat-affinity groups contained 23 meadow, 15 forest, and 3 ruderal species. We recorded only one exotic, *Tragopogon dubius* (Yellow salsify), present in two quadrats. Eight species (four meadow, three forest, and one unclassified)

were limited to unburned quadrats (seven with just single occurrences; Table 1), whereas only one species was limited to the burn scars (single occurrence).

### Ground-Surface Conditions

In year 7, cover of bare ground was greater at the centers of scars than at the burned edges (E) or in the distant, unburned vegetation ( $U_2$ ); however, it was no greater than in the unburned edge ( $U_1$ ) (Fig. 4). A large percentage (38–46%) of bare ground originated from recent gopher disturbance (mounds and winter castings) (Fig. 4).

### Vegetation

Although burning substantially reduced total plant cover at the centers and edges of scars, by year 7 total cover was not different from that in the unburned vegetation (Fig. 5). However, recovery differed among plant groups. Cover remained depressed at the centers (but not edges) for sedge, forest, and clonal species, but not for meadow species (comprising most plant cover) or for grass, forb, or non-clonal species (Fig. 5).

In contrast to plant cover, scar centers supported fewer species than did the burned edges or unburned vegetation (Fig. 6). Similar responses were observed for forb, forest, and clonal species. Richness of grass, meadow, and non-clonal species was comparable in and adjacent to burn scars (Fig. 6).

The distribution of abundance and total richness of species varied with position (Fig. 7). Scar centers (C) had fewer, more dominant species, resulting in a steep, linear (geometric) rank-abundance curve. In contrast, species in the unburned vegetation ( $U_1$  and  $U_2$ ) had a lognormal (Gaussian) distribution, and those in the burned edge (E), a distribution intermediate to these. Four meadow species accounted for 82% of the total cover at the scar centers: three prolific seed producers, *Bromus carinatus* (California brome), *Elymus glaucus* (Blue wildrye), and *Cirsium callilepis* (Mountain thistle); and the stoloniferous forb, *Fragaria* spp. (Strawberry) (Table 1). The same taxa accounted for 54–58% of total cover at the burned edge and in the unburned vegetation. In contrast, the principal rhizomatous sedge, *Carex pensylvanica* (Long stolon sedge), accounted for only 7% of total cover at the scar centers versus 18–28% at the burned edge or in the unburned vegetation.

## Discussion

Among the principal challenges to restoring tree-invaded grasslands is the removal and efficient disposal of woody biomass—a challenge accentuated by more than a century of forest encroachment in our system (Halpern et al. 2010). Although these grasslands may have been maintained by fire historically, burning after long-term exclusion of fire can have adverse effects because of the accumulation of woody fuels. Creation of slash piles limits the spatial extent of burning, but concentrating fuels invariably leads to higher-severity fire (Busse et al. 2013) and to near or complete mortality of the seed banks and root systems of plants (Haskins & Gehring

**Table 1.** Frequency of occurrence and mean cover of species in the centers and edges of burn scars and in adjacent unburned vegetation ( $n = 30$  quadrats per position).

Species	Clonality	Center (C)		Edge (E)		Unburned ( $U_1$ )		Unburned ( $U_2$ )		
		Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Cover (%)	
<b>Grasses: Meadow</b>										
<i>Bromus carinatus</i>	N	70.0	10.4	70.0	9.9	73.3	7.5	66.7	6.8	
<i>Elymus glaucus</i>	N	50.0	7.1	43.3	4.0	40.0	5.4	50.0	8.4	
<i>Festuca viridula</i>	N	3.3	0.1	3.3	0.5	3.3	0.3	3.3	0.2	
<i>Stipa occidentalis</i>	N	3.3	0.1	3.3	0.1	3.3	0.5			
<i>Festuca idahoensis</i>	N					3.3	0.53	3.3	0.3	
<b>Grasses: Forest</b>										
<i>Bromus vulgaris</i>	N	6.7	0.6	6.7	1.7	3.3	0.4	6.7	0.2	
<i>Trisetum canescens</i>	N			3.3	0.1					
<b>Sedges: Meadow</b>										
<i>Carex pensylvanica</i>	CL	40.0	3.1	60.0	17.1	60.0	11.7	56.7	13.9	
<i>Carex hoodii</i>	N					3.3	< 0.1			
<i>Carex pachystachya</i>	N					3.3	1.8			
<b>Sedges: Unclassified</b>										
<i>Carex deweyana</i>	N			6.7	1.4	3.3	0.7			
<b>Forbs: Meadow</b>										
<i>Fragaria species<sup>a</sup></i>	CL	70.0	11.8	66.7	16.5	73.3	18.1	66.7	12.2	
<i>Cirsium callilepis</i>	N	63.3	7.1	66.7	4.7	60.0	3.5	60.0	3.6	
<i>Achillea millefolium</i>	CL	26.7	1.6	13.3	0.2	16.7	0.5	13.3	1.1	
<i>Vicia americana</i>	CL	23.3	1.5	23.3	1.0	16.7	0.5	20.0	0.6	
<i>Lathyrus nevadensis</i>	CL	10.0	0.3	23.3	1.1	23.3	0.7	16.7	0.8	
<i>Microsteris gracilis</i>	N	3.3	< 0.1	3.3	0.1	6.7	0.1	6.7	0.1	
<i>Aster occidentalis</i>	N	3.3	0.1	3.3	0.1	3.3	0.5	6.7	0.2	
<i>Agoseris aurantiaca</i>	N	3.3	< 0.1			3.3	0.3			
<i>Erigeron aliceae</i>	N	3.3	< 0.1			10.0	0.5	3.3	0.4	
<i>Viola nuttallii</i>	N			6.7	0.1	6.7	0.1	3.3	< 0.1	
<i>Hieracium scouleri</i>	N			3.3	0.2	3.3	0.1			
<i>Iris chrysophylla</i>	N			3.3	0.1	3.3	0.2	13.3	0.7	
<i>Aster radulinus</i>	CL							3.3	0.1	
<i>Phlox diffusa</i>	CL							3.3	0.1	
<i>Pteridium aquilinum</i>	CL							3.3	0.1	
<b>Forbs: Forest</b>										
<i>Smilacina stellata</i>	CL	3.3	0.2	26.7	2.4	23.3	0.9	33.3	3.5	
<i>Galium oreganum</i>	CL	3.3	0.3	20.0	1.9	30.0	1.6	33.3	2.2	
<i>Campanula scouleri</i>	CL	3.3	< 0.1	6.7	0.7	13.3	0.7	10.0	0.5	
<i>Viola glabella</i>	CL	3.3	< 0.1	6.7	0.1	6.7	0.1	6.7	0.1	
<i>Arenaria macrophylla</i>	CL			10.0	0.4	20.0	0.5	16.7	0.4	
<i>Hieracium albiflorum</i>	N			6.7	0.1	3.3	0.3	6.7	0.1	
<i>Trientalis latifolia</i>	CL			3.3	< 0.1			3.3	0.1	
<i>Asarum caudatum</i>	CL					10.0	1.3	6.7	3.1	
<i>Rubus lasiococcus</i>	CL					3.3	0.1	3.3	0.2	
<i>Circaea alpina</i>	CL					3.3	< 0.1			
<i>Galium triflorum</i>	CL							3.3	0.1	
<b>Forbs: Ruderal</b>										
<i>Phacelia heterophylla</i>	N	6.7	0.1	6.7	0.1	3.3	< 0.1	3.3	< 0.1	
<i>Polygonum douglasii</i>	N	3.3	0.1			3.3	0.1			
<i>Tragopogon dubius</i>	N			3.3	0.3			3.3	0.5	
<b>Shrubs and trees: Forest</b>										
<i>Abies grandis</i>	N			3.3	< 0.1			3.3	< 0.1	
<i>Symphoricarpos mollis</i>	CL					3.3	0.6	10.0	3.2	
<b>Shrubs and trees: Unclassified</b>										
<i>Sambucus racemosa</i>	N					3.3	0.4			

For each growth-form  $\times$  habitat-affinity group, species are arranged in descending frequency (based on center quadrats). Clonality is coded as N (limited/non-clonal) or CL (highly clonal).

<sup>a</sup>*Fragaria virginiana* and *F. vesca*.

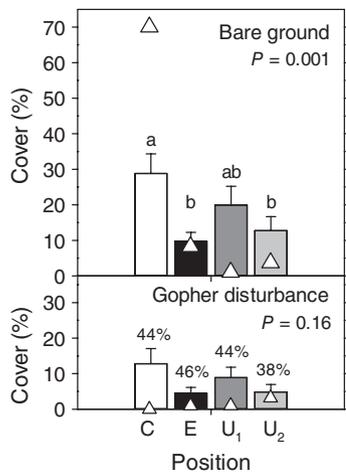


Figure 4. Percent cover of bare ground (mineral soil) and recent gopher disturbance in and adjacent to burn scars after 7 years. Values are means ( $\pm 1$  SE) of  $n = 30$  burn scars. Triangles are mean values in the first growing season (for reference);  $p$  values represent the significance of position in year 7 from a randomized block ANOVA. Different lower case letters denote positions that differ significantly following a significant ANOVA. The percentage of bare ground in year 7 attributable to gopher disturbance is shown in the lower panel.

2004; Korb et al. 2004; Fornwalt & Rhoades 2011; Creech et al. 2012). We observed these effects in our study: plants were initially absent from the centers of scars and cover was greatly reduced at the edges (Halpern et al. 2012). However, 7 years after burning, we found no difference in total plant cover between scars and adjacent unburned vegetation, in contrast to studies of comparable duration (Covington et al. 1991; Creech et al. 2012).

A widespread concern with pile burning is the simultaneous exposure of mineral soil and increase in available N, to which many exotic (or native ruderal) species respond positively (Haskins & Gehring 2004; Korb et al. 2004). Once established in burn scars, they may serve as foci for wider dispersal (Haskins & Gehring 2004; Owen et al. 2009). In this experiment, exotics (present at low levels in the surrounding landscape) and native ruderals (dominant in the seed bank; Lang & Halpern 2007) rarely established in the burn scars. Elsewhere, limited colonization by exotics has been attributed to low densities in the surrounding forest, thus to low propagule pressure (Creech et al. 2012) or to insufficient time for colonization (Fornwalt & Rhoades 2011). The absence of exotics in this study may reflect the preference of some of the more common species (e.g. *Lactuca muralis* [Wall lettuce]), for shaded environments or the patchy distributions of others (e.g. *Rumex acetosella* [Sheep sorrel]). The paucity of native ruderals—important in other systems (Fornwalt & Rhoades 2011)—may reflect space or resource preemption by meadow forbs and graminoids that strongly dominate the surrounding vegetation (Halpern et al. 2012).

Physical evidence of burn scars can persist for decades in some systems (Selmants & Knight 2003), but is rapidly erased in these grasslands. In year 1, scar centers were characterized by

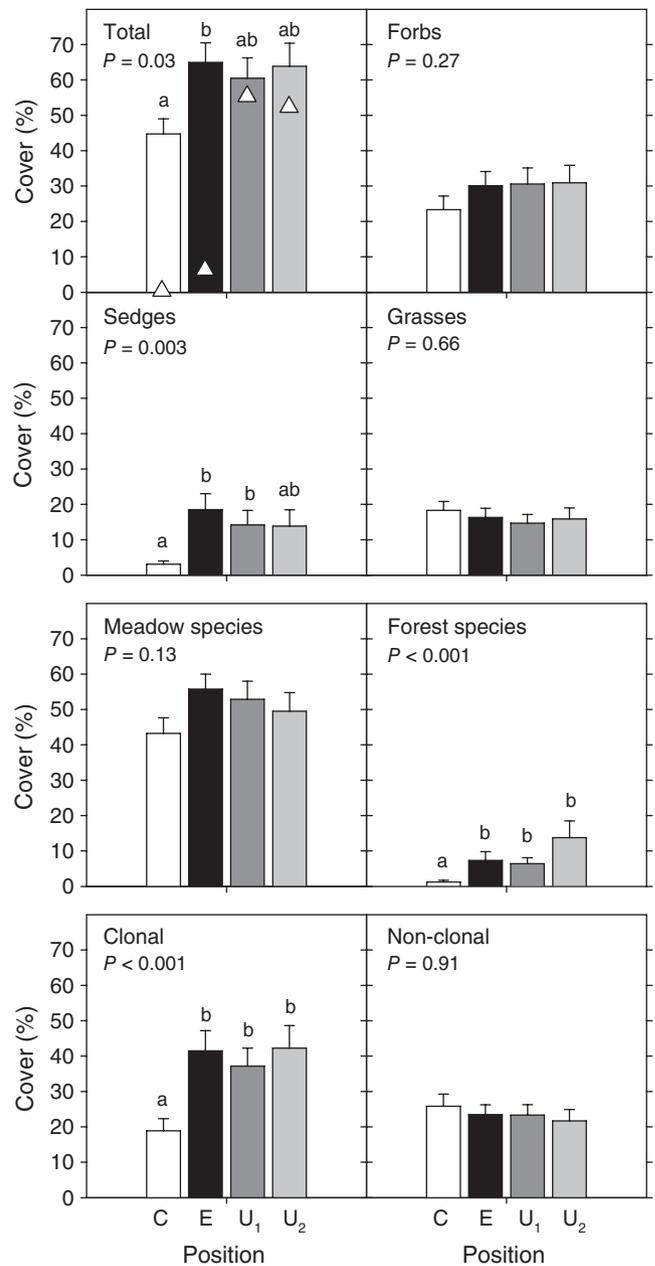


Figure 5. Percent cover of species with differing growth forms (forbs, sedges, and grasses), habitat affinities (meadow and residual forest species), and clonality (highly clonal and limited/non-clonal) in and adjacent to burn scars after 7 years. Triangles in the total cover panel are mean values in the first growing season (for reference). See Figure 4 caption for other details.

white ash (73% cover) and little or no plant cover. Scar edges (comprising most of the scar area) were characterized by blackened duff or charcoal (90% cover) and few plants (~10% of the cover of adjacent unburned vegetation) (Halpern et al. 2012). After 7 years, however, we saw little evidence of physical scarring: bare ground at the centers of scars was greatly reduced and only slightly elevated relative to unburned soils. Much of this comprised recent mounds and winter castings of pocket gophers

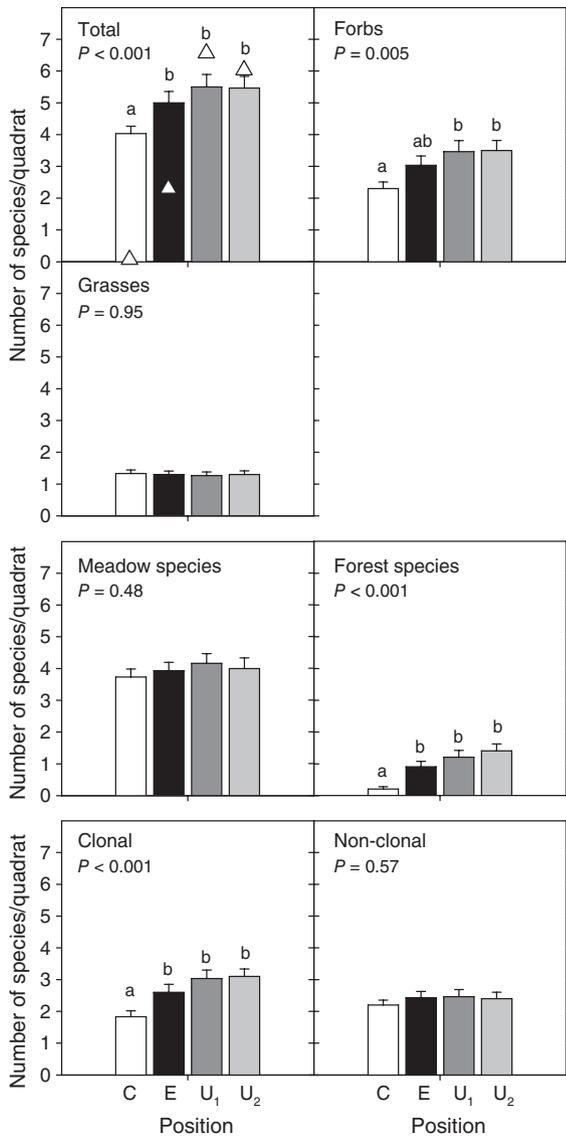


Figure 6. Richness of species with differing growth forms (forbs and grasses), habitat affinities (meadow and residual forest species), and clonality (highly clonal and limited/non-clonal) in and adjacent to burn scars after 7 years. Triangles in the total richness panel are mean values in the first growing season (for reference). See Figure 4 caption for other details.

(Fig. 8), whose activities have increased since tree removal. In fact, the proportion of bare ground attributable to gophers was even greater, as our estimates did not include older mounds and castings previously incorporated into the soil surface. Gophers are prominent in many North American grasslands, disturbing as much as 30% of the ground surface in a given year (Huntly & Reichman 1994). Studies of open-meadow communities at Bunchgrass Ridge suggest that frequent, small-scale disturbances create a shifting mosaic of vegetation states—reducing local dominance of graminoids and enhancing the richness and heterogeneity of species at larger spatial scales (Jones et al. 2008; Case et al. 2013). Rapid immigration of gophers

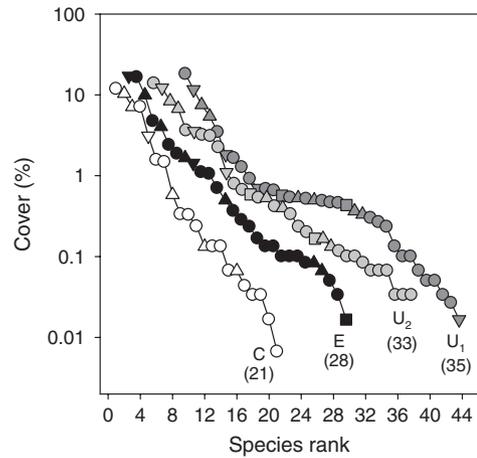


Figure 7. Rank-abundance curves illustrating the distribution of abundance (log mean cover) of species among the 30 quadrats sampled for each position. Curves are separated along the x-axis to avoid overlap; the total number of species recorded is shown in parentheses. Growth forms are coded as follows: forbs = circle, sedges = downward triangle, grasses = upward triangle, trees/shrubs = square.

into the restoration plots has resulted in substantial mixing of fire-affected soils (Halpern et al. 2012). In the absence of controlled experiments, we can only speculate about the benefits of this mixing for recovery of burn scars. Rapid recolonization of gopher-disturbed scars is consistent with the small-scale disturbances to which meadow species are well adapted. However, gophers may also introduce seeds or rhizomes directly into the scars in the process of tunneling and mounding.

In contrast to total cover, local richness and abundance of some functional groups did not show full recovery at the centers of scars. Reduced richness was largely due to the failure to reestablish of many forest herbs that are tolerant of tree removal (increased light; Nelson et al. 2007; Halpern et al. 2012) but not fire (Flinn & Wein 1988; Halpern 1989). Meadow sedges were also under-represented at the centers, but not edges of scars. Although the dominant species, *Carex pensylvanica*, was abundant in the seed bank (unusual among meadow species; Lang & Halpern 2007), seeds were likely destroyed by intense heating beneath the burn piles. Although *C. pensylvanica* is clonal (spreading by rhizomes), its rate of growth was insufficient to establish cover comparable to that in the unburned vegetation. Limited expansion of *C. pensylvanica*, among other clonal species, is consistent with the general observation that vegetative growth plays a small role in burn-scar recovery (Fornwalt & Rhoades 2011; Creech et al. 2012). In contrast, many clonal species showed complete recovery in the edge environments that constituted most of the scar. These included *C. pensylvanica*; meadow forbs (*Fragaria* spp., *Vicia americana* [American vetch], and *Lathyrus nevadensis* [Sierra pea]); and residual forest herbs (*Smilacina stellata* [Starry false Solomon's seal] and *Galium oreganum* [Oregon bedstraw]) (Table 1).

Rank-abundance curves offer additional insight into the effects of pile burning on community structure. Lognormal



Figure 8. Distant (top) and close (bottom) views of gopher disturbance in and adjacent to burn scars. Residual wood and charcoal are evident in the lower scar (photographed in 2011).

distributions of cover in the unburned vegetation indicated many species of intermediate abundance (Preston 1948; Whittaker 1965). In contrast, the geometric distribution representing scar centers reflected dominance by few species and absence of many of others (mainly forbs; Table 1). Among dominants were those with prolific seed production (*Bromus carinatus*, *Elymus glaucus*, and *Cirsium callilepis*), effective wind dispersal (*Cirsium callilepis*), or vigorous stoloniferous growth (*Fragaria* spp.). These same species dominated the unburned vegetation. Traits leading to successful establishment after tree removal thus appear to benefit recruitment on bare, fire-influenced soils.

Seed addition, scarification, and soil amendments can enhance burn-scar recovery in some forests (Korb et al. 2004; Fornwalt & Rhoades 2011), suggesting that both seed dispersal and environmental factors can influence recovery. For species with short-distance dispersal or low population densities, seeds may be limiting (Stein et al. 2008; Myers & Harms 2009). Alternatively, establishment may be inhibited by persistent changes in soil chemistry (Creech et al. 2012) or in the abundance or composition of fungal symbionts (Korb et al. 2004) or microbial communities (Hebel et al. 2009). In our system, pile burning initially increased available N (primarily  $\text{NH}_4^+\text{-N}$ ) four- to six-fold at the centers of scars and two-fold at the edges (Halpern et al. 2012). By year 3, however, concentrations remained elevated only at the centers (a two-fold increase). After 7 years, plant uptake, microbial immobilization, and leaching are likely to have reduced available N to baseline levels (Covington et al. 1991). In addition, the continuous redistribution of soil by gophers may be as effective as any biotic process, or active intervention, in ameliorating the initial effects of burning.

It is important to place any long-term effects of pile burning in the broader context of these restoration treatments. Although tree removal, with or without burning, effectively shifted dominance from forest to meadow species, many species characteristic of adjacent “reference” meadows were absent or under-represented in the experimental plots (C. B. Halpern, unpublished data; Halpern et al. 2012). The revegetation of burn scars represented an extreme, but localized example of this outcome: scars were colonized by native meadow species, but supported only a subset of those in the adjacent unburned vegetation. It is too early to assess fully the efficacy of tree removal for grassland restoration, thus further monitoring of these experimental plots is clearly warranted. However, results to date suggest that the reassembly process is not hindered by the intense, localized effects of pile burning. That said, there are conditions under which pile burning in grasslands is likely to be detrimental. Larger slash piles (producing larger scars) may limit the recovery of species that reestablish clonally. In addition, at lower elevations (where exotics are more common) or on shallower, lithosolic soils (where fossorial rodents are absent) recolonization by native meadow species may be considerably slower, potentially requiring active reintroduction (e.g. seeding). However, in these montane grasslands of the Cascades, and likely in many other high-elevation systems, pile burning appears to be a safe and efficient method for fuel reduction after tree removal—a viable alternative when fire is not critical to restoration.

#### Implications for Practices

- In conifer-invaded grasslands of the Oregon Cascades, scars from pile burning of woody residues revegetate rapidly (within 7 years). Physical evidence of fire is incorporated into the soil by gophers and revegetation is entirely of native meadow species.

- Pile size can influence the nature and pace of revegetation. Larger scars may show slower recovery of clonal species that are dependent on vegetative spread.
- In the absence of exotics and in the presence of gophers, remediation of meadow soils is not necessary. Where exotics are prevalent (low-elevation grasslands) or gophers are absent (shallow soils), burn scars may be more persistent and susceptible to invasion. In these contexts, managers should consider removing, rather than burning, woody residues.

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## LITERATURE CITED

- Antos, J. A., and C. B. Halpern. 1997. Root system differences among species: implications for early successional changes in forests of western Oregon. *American Midland Naturalist* **138**:97–108.
- Beadle, N. C. W. 1940. Soil temperatures during forest fires and their effect on the survival of vegetation. *Journal of Ecology* **28**:180–192.
- Bell, A. D., and P. B. Tomlinson. 1980. Adaptive architecture in rhizomatous plants. *Biological Journal of the Linnean Society* **80**:125–160.
- Burke, C. 1979. Historic fire in the central western Cascades, Oregon. Master's thesis. Oregon State University, Corvallis, 130 pages.
- Busse, M. D., C. J. Shestak, and K. R. Hubbert. 2013. Soil heating during burning of forest slash piles and wood piles. *International Journal of Wildland Fire* **22**:786–796.
- Case, M. F., C. B. Halpern, and S. A. Levin. 2013. Contributions of gopher mound and casting disturbances to plant community structure in a Cascade Range meadow complex. *Botany* **91**:555–561.
- Clark, D. L., and M. V. Wilson. 1994. Heat-treatment effects on seed bank species of an old-growth Douglas-fir forest. *Northwest Science* **68**:1–5.
- Covington, W. W., L. F. DeBano, and T. G. Hunstberger. 1991. Soil nitrogen changes associated with slash pile burning in pinyon-juniper woodlands. *Forest Science* **37**:347–355.
- Creech, M. N., L. K. Kirkman, and L. A. Morris. 2012. Alteration and recovery of slash pile burn sites in the restoration of a fire-maintained ecosystem. *Restoration Ecology* **20**:505–516.
- Flinn, M. A., and R. W. Wein. 1988. Regrowth of forest understory species following seasonal burning. *Canadian Journal of Botany* **66**:150–155.
- Fornwalt, P. J., and C. C. Rhoades. 2011. Rehabilitating slash pile burn scars in upper montane forests of the Colorado Front Range. *Natural Areas Journal* **31**:177–182.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**:1169–1194.
- Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* **70**:704–720.
- Halpern, C. B., J. A. Antos, J. M. Rice, R. D. Haugo, and N. L. Lang. 2010. Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. *Journal of Vegetation Science* **21**:717–732.
- Halpern, C. B., R. D. Haugo, J. A. Antos, S. S. Kaas, and A. L. Kilanowski. 2012. Grassland restoration with and without fire: evidence from a tree-removal experiment. *Ecological Applications* **22**:425–441.
- Hamman, S., and C. V. Hawkes. 2012. Biogeochemical and microbial legacies of invasive grasses affect restoration success. *Restoration Ecology* **21**:58–66.
- Haskins, K. E., and C. A. Gehring. 2004. Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland. *Journal of Applied Ecology* **41**:379–388.
- Haugo, R. D., and C. B. Halpern. 2007. Vegetation responses to conifer encroachment in a dry, montane meadow: a chronosequence approach. *Canadian Journal of Botany* **85**:285–298.
- Haugo, R. D., and C. B. Halpern. 2010. Tree age and tree species shape positive and negative interactions in a montane meadow. *Botany* **88**:488–499.
- Hebel, C. L., J. E. Smith, and K. Cromack Jr. 2009. Invasive plant species and soil microbial response to wildfire burn severity in the Cascade Range of Oregon. *Applied Soil Ecology* **42**:150–159.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle.
- Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1969. *Vascular plants of the Pacific Northwest*. Vol 1–5. University of Washington Press, Seattle.
- Huntly, N., and O. J. Reichman. 1994. Effects of subterranean mammalian herbivores on vegetation. *Journal of Mammalogy* **75**:852–859.
- Johnson, R. R. 1985. Historical records inventory for the Willamette National Forest: forest grazing permits. Forest Service Warehouse, USDA Forest Service, Willamette National Forest, Eugene, Oregon.
- Jones, C. C., C. B. Halpern, and J. Niederer. 2008. Plant succession on gopher mounds in western Cascade meadows: consequences for species diversity and heterogeneity. *American Midland Naturalist* **159**:275–286.
- Kardol, P., L. Souza, and A. T. Classen. 2013. Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos* **122**:84–94.
- Korb, J. E., N. C. Johnson, and W. W. Covington. 2004. Slash pile burning effects on soil biotic and chemical properties and plant establishment: recommendations for amelioration. *Restoration Ecology* **12**:52–62.
- Lang, N. L., and C. B. Halpern. 2007. The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. *Canadian Journal of Botany* **85**:557–569.
- Magurran, A. E. 2004. *Measuring biological diversity*. Blackwell Publishing, Oxford, United Kingdom.
- McLean, A. 1969. Fire resistance of forest species as influenced by root systems. *Journal of Range Management* **22**:120–122.
- Moore, J. M., and R. W. Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. *Canadian Journal of Botany* **55**:2408–2412.
- Morrison, P., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. USDA Forest Service General Technical Report PNW-GTR-254, Portland, Oregon.
- Myers, J. A., and K. E. Harms. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. *Ecology Letters* **12**:1250–1260.
- Nelson, C. R., C. B. Halpern, and J. A. Antos. 2007. Variation in responses of late-seral herbs to disturbance and environmental stress. *Ecology* **88**:2880–2890.
- Owen, S. M., C. H. Sieg, C. A. Gehring, and M. A. Bowker. 2009. Above- and belowground responses to tree thinning depend on treatment of tree debris. *Forest Ecology and Management* **259**:71–80.
- Pattinson, G. S., K. A. Hammill, B. G. Sutton, and P. A. McGee. 1999. Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycological Research* **103**:491–496.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* **29**:254–283.
- Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* **93**:697–703.
- Rice, J. M., C. B. Halpern, J. A. Antos, and J. A. Jones. 2012. Spatio-temporal patterns of tree establishment are indicative of biotic interactions during early invasion of a montane meadow. *Plant Ecology* **213**:555–568.

- Santos, L., J. Capelo, and M. Tavares. 2010. Germination patterns of soil seed banks in relation to fire in Portuguese littoral pine forest vegetation. *Fire Ecology* **6**:1–15.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517–544.
- Selmants, P. C., and R. H. Knight. 2003. Understory plant species composition 30–50 years after clearcutting in southeastern Wyoming coniferous forests. *Forest Ecology and Management* **185**:275–289.
- Smith, S. E., and D. J. Read. 1997. *Mycorrhizal symbiosis*. 2<sup>nd</sup> edition. Academic Press, San Diego, California.
- SPSS. 2001. SYSTAT 10.0 for Windows. SPSS Inc., Chicago, Illinois.
- Stein, C., H. Auge, M. Fischer, W. W. Weisser, and D. Parti. 2008. Dispersal and seed limitation affect diversity and productivity of montane grasslands. *Oikos* **117**:1469–1478.
- Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* **31**:197–215.
- Weisberg, P. J., and F. J. Swanson. 2003. Regional synchronicity in fire regimes of western Oregon and Washington, USA. *Forest Ecology and Management* **172**:17–28.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. *Science* **147**:250–260.