RESEARCH ARTICLE

# VEGETATION RESPONSE TO BURN SEVERITY, NATIVE GRASS SEEDING, AND SALVAGE LOGGING

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## ABSTRACT

As the size and extent of wildfires has increased in recent decades, so has the cost and extent of post-fire management, including seeding and salvage logging. However, we know little about how burn severity, salvage logging, and post-fire seeding interact to influence vegetation recovery long-term. We sampled understory plant species richness, diversity, and canopy cover one to six years post fire (2006 to 2009, and 2011) on 72 permanent plots selected in a stratified random sample to define post-fire vegetation response to burn severity, post-fire seeding with native grasses,

## RESUMEN

A medida que el tamaño y la extensión de los incendios han aumentado en las recientes décadas, también lo ha hecho el costo y el alcance del manejo post-fuego, incluyendo la siembra y las cortas de recuperación. Sin embargo, conocemos poco sobre como la severidad del fuego, las cortas de recuperación y las siembras post-fuego interactúan para influir sobre la restauración de la vegetación a largo plazo. En este estudio muestreamos la riqueza de especies del sotobosque, la diversidad, y la cobertura del dosel vegetal entre uno y seis años después del fuego (2006 a 2009, y 2011) en 72 parcelas permanentes seleccionadas en un muestreo estratificado al azar, para definir la respuesta de la vegetación a la severidad del fuego, siembra and salvage logging on the 2005 School Fire in eastern Washington. Understory vegetation responded rapidly post fire due, in part, to ample low intensity rainfall events in the first post-fire growing season. Vegetation was more diverse with greater plant species richness and diversity (Shannon-Wiener index) in low and moderate burn severity plots in 2006 (species richness 18; diversity 2.3) compared to high burn severity plots (species richness 10; diversity 1.8), with species richness on the high severity plots reaching 19 in the sixth post-fire year, similar to the initial values on the low and moderate burn severity plots. Plants that commonly resprout from rhizomes, bulbs, and other surviving belowground sources were abundant post fire, while those establishing from off-site seed sources, including non-native species, were present but not abundant. Plots seeded with native grass post fire and not salvage logged had the highest canopy cover of graminoid species: more than 30% six years after the fire (in 2011), with low forb (15%) and shrub (1%) canopy cover and species richness. For comparison, high severity plots that were not seeded and not salvage logged had 3% graminoid cover, 14% forb cover, and 26% shrub cover. Plots that had been salvage logged from one to three years after the fire produced less canopy cover of shrubs and forbs, but three times more canopy cover of graminoids on the high burn severity plots by 2011. High severity plots that were salvage logged and not seeded with native grasses had the lowest species richness, diversity, and cover. Very few non-native species were found, regardless of salvage logging

post-fuego de especies gramíneas nativas y cortas de recuperación en el incendio de School Fire ocurrido en 2005, al este de Washington. La vegetación del sotobosque respondió rápidamente después del fuego, debido en parte a abundantes lluvias de baja intensidad en las primeras temporadas de crecimiento tras el fuego. La vegetación fue más diversa con mayor riqueza de especies y diversidad (índice de Shannon-Wiener) en parcelas con severidad de fuego baja y moderada (riqueza de especies 18, diversidad: 2.3) comparado con parcelas con severidad de fuego alta (riqueza de especies 10, diversidad 1.8), con riqueza de especies 19 en parcelas de alta severidad seis años post-fuego, similar a los valores iniciales en las parcelas con baja y moderada severidad del fuego. Plantas que comúnmente rebrotan de rizomas, bulbos y otras que sobreviven por debajo de la superficie del suelo, fueron abundantes después del fuego, mientras que aquéllas que se establecieron de fuentes de semilla ubicadas más allá del perímetro quemado, incluyendo especies exóticas, aparecieron pero no en abundancia. Las parcelas sembradas con especies de gramíneas nativas después del fuego y sin recuperación maderera tuvieron las coberturas más altas de especies graminoides, con más del 30% seis años después del fuego (en 2011), con una cobertura baja de hierbas (15%) y de arbustos (1%) y de riqueza de especies. En contraste, las parcelas con severidad alta que no fueron sembradas y en donde tampoco se recuperó la madera, presentaron un 3% de cobertura de especies graminoides, 14% de cobertura de herbáceas y 26% de cobertura de arbustos. Las parcelas en donde se ha recuperado la madera entre uno a tres años después del fuego, produjeron menor cobertura de dosel de arbustos y herbáceas, pero esta cobertura fue tres veces más alta en el dosel de graminoides en las parcelas con alta severidad del fuego en 2011. Las parcelas con alta severidad del fuego cuya madera se recuperó y que no fueron sembradas con gramíneas nativas, presentaron la más baja riqueza, diversidad y cobertura de especies. Muy pocas especies exóticas fueron en-and seeding. Rapid post-fire growth dominated by native plants of high diversity suggests that this forest's vegetation and soils are highly resilient to disturbance. Overall, burn severity and post-fire seeding with native grasses were more influential than salvage logging on understory plant abundance one to six years after fire.

contradas, independientemente de la recuperación de la madera o de la siembra. El rápido crecimiento post-fuego dominado por plantas nativas de diversidad alta sugiere que la vegetación y los suelos de este bosque son altamente resilientes a las perturbaciones. En general, la severidad del fuego y la siembra post-fuego con especies de gramíneas nativas fue más influyente que la recuperación de madera en la abundancia de plantas del sotobosque, entre uno a seis años después del fuego.

*Keywords*: fire effects, mixed conifer forests, plant succession, post-fire rehabilitation, salvage logging

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## INTRODUCTION

Characterizing post-fire vegetation response is important for predicting how landscapes will respond to large fires, subsequent management activities, and their interactions. The mosaic of burn severities created as fires burn across a landscape of varying vegetation and topography has major implications for post-fire plant species composition, diversity, and abundance (Turner *et al*. 1997, 1999, 2003; Brown and Smith 2000). Post-fire management after large, severe wildfires can often include seeding or mulching to reduce erosion potential and the spread of invasive species, and salvage logging to remove standing dead trees and recover economic value of some of the trees killed by the fire. The number and size of large fires and total area burned has increased in recent decades (Westerling *et al.* 2006, Littell *et al.* 2009), as have the costs of post-fire rehabilitation (Robichaud *et al.* 2000, 2010, 2014), with long-term implications for ecosystem resilience (Abella and Fornwalt 2015). Interactions between the ecological effects of burn severity, seeding with native grasses, and salvage logging on post-fire recovery of native vegetation are little studied and poorly understood.

Within large forest fires, high burn severity alters vegetation (Lentile *et al.* 2007) and prompts post-fire rehabilitation treatments to reduce erosion and invasion by non-native plant species (Robichaud *et al.* 2010), which could alter post-fire vegetation community development. Many experts have predicted that the large fires of recent decades, portions of which burn with high severity (Dillon *et al.* 2011), will become increasingly common in the future (Littell *et al.* 2009, Spracklen *et al.* 2009).

Burn severity is broadly defined by the effects of the fire on soil and vegetation (Lentile *et al.* 2006; Morgan *et al.* 2014). Although burn severity can be measured in a variety of ways (Lentile *et al.* 2006, Keeley 2009; Morgan *et al.* 2014), it is commonly mapped from satellite imagery, validated with field observations, and interpreted as relating to tree mortality (Clark and Bobbe 2006) and soil conditions (Parsons *et al*. 2010). Burn severity can strongly influence post-fire ecosystem recovery (Morgan and Neuenschwander 1988, Lentile *et al.* 2007, Abella and Fornwalt 2015), but the degree to which salvage logging and seeding with native grass alters vegetation response to burn severity is unknown. Hudak *et al.* (2007) found that plots burned with low and moderate burn severity were more spatially variable (with respect to post-fire vegetation and soil conditions) than plots burned with high severity, and also that effects of burn severity on the ground varied at a finer spatial scale than within the overstory. Similarly, Lentile *et al.* (2007) found that in plots burned at high severity, vegetation cover and species diversity was lower and less variable, while species richness immediately post fire was high as some plants survived in unburned microsites but not all thrived thereafter in the changed post-fire environment. Halpern (1988) found that understory vegetation recovery following logging and burning was characterized by initial rapid change varying with disturbance intensity followed by gradual recovery to pre-disturbance composition. Abella and Fornwalt (2015) found that species richness increased in the first decade after the Hayman Fire, which burned in mixed conifer forests: plant species present before the fire flourished along with new colonizers. Further, the prevalence of native plants indicated that the forest vegetation was highly resilient, but less so where fires burned severely.

Ecologists commonly group plant species to aid analysis. Plant growth forms, including shrubs, forbs, and graminoids, are commonly used for evaluating response to disturbance. However, ecologists have also used plant functional types (Chapin *et al.* 1993, 1996) and traits (Cornelissen *et al.* 2003) to understand ecosystem dynamics through species persistence after major disturbances. Short-term vegetation response to disturbance is largely dependent on how plants with differing regeneration strategies (e.g., off-site seeds, seeds that survived the fire in the seedbank, and sprouts from surviving belowground materials) respond to soil heating and thrive in the post-fire environment (McLean 1969, Flinn and Wein 1977, Denslow 1980, Flinn and Pringle 1983, Morgan and Neuenschwander 1988).

Post-fire seeding is commonly used, but has mixed success for reducing erosion and invasive species establishment (Robichaud *et al.* 2000; Hunter and Omi 2006; Peppin *et al.* 2010, 2011; Stella *et al.* 2010). Seeding may inadvertently transport alien plant species and suppress natural regeneration of native woody and herbaceous species (Beyers 2004, Peppin *et al.* 2010, Stella *et al.* 2010). Because seeding with native, locally adapted grasses may be both more successful in establishing grass cover and less disruptive to native vegetation recovery, seeding with native species is increasing (Peppin *et al.* 2011). Both native and non-native perennial graminoids are able to form dense below- and aboveground cover, and often out-compete other early seral regenerating species (Taskey *et al.* 1989) such as native shrubs, forbs, and trees. In their systematic review of studies, Peppin *et al.* (2010) found that 62% of 26 studies reported reduced rates of native vegetation recovery following seeding, but concluded that long-term studies are needed to evaluate lasting effects.

The consequences of salvage logging for vegetation recovery after fire are not well understood (Peterson *et al.* 2009). Post-fire salvage logging is often challenged due to the perception of compounding detrimental ecological effects following fire (McIver and Starr 2001, Beschta *et al.* 2004). Few have studied salvage logging effects on vegetation recovery, but see Klock (1975), Lindenmayer (2006), and Peterson *et al.* (2009). Post-fire salvage logging is done to extract marketable timber (Franklin and Agee 2003, Sessions *et al.* 2004), decrease fuel accumulations (Brown *et al.* 2003, McIver and Ottmar 2007) that could fuel future fires (Donato *et al.* 2006, Keyser *et al.* 2009), and lessen the potential for insect infestation (Brown *et al.* 2003). Opponents of salvage logging cite altered vegetation recovery and nutrient cycling (Lindenmayer and Noss 2006), lost habitat for cavity nesting birds (Hutto 2006), and damage to established tree seedlings (Donato *et al.* 2006). Fire-impacted soils may also be susceptible to mineral soil exposure, displacement, and compaction by logging equipment, resulting in increased potential for sedimentation and erosion (McIver and Starr 2001, Karr *et al.* 2004, Wagenbrenner *et al.* 2015) and potentially compounding the effects of fire on vegetation recovery trajectories.

### *Objectives and Hypotheses*

We quantified the effects of burn severity, salvage logging, and post-fire seeding to help define their individual and combined effects on four different aspects of post-fire vegetation, including understory plant species richness and diversity, and percent canopy cover by plant growth form and regeneration strategy as a functional trait. We measured vegetation on permanent plots for six years after a large wildfire burned in dry mixed conifer forests. We hypothesized that:

1) Species richness and diversity would be:
    a. greater in plots burned with low and moderate burn severity than plots burned with high severity;
    b. reduced by salvage logging, especially on low and moderate severity burns; and
    c. be greatly reduced in areas seeded with grass, and become more similar with time since fire.
2) Abundance of grasses, forbs, and shrubs would all be influenced by burn severity, salvage logging, and seeding, with forbs and shrubs affected less than grasses, and that differences, though persistent, would become less pronounced with time since fire.
3) Abundance of plants grouped by regeneration strategies would all be influenced by burn severity, salvage logging, and seeding, with resprouting plants less affected than those establishing from seed, and that differences, though persistent, would become less pronounced with time since fire.
4) The combined effects of high burn severity, salvage logging, and seeding with grass would result in much lower richness, diversity, and abundance of all growth forms and regeneration strategies.
5) Burn severity would be more influential than salvage logging and native grass seeding on post-fire understory vegetation richness, diversity, and abundance, and that non-native species would be more abundant in areas with high burn severity followed by salvage logging relative to areas without salvage logging and also those with and without grass seeding.

## MATERIALS AND METHODS

### *Study Area*

The August 2005 School Fire burned approximately 21 000 ha of forest and grassland south of Pomeroy, Washington, on the Umatilla National Forest (Figure 1). Much of this mountainous area contains high plateaus deeply cut by canyons, with steep slopes ranging from 10 % to 100 %. The fire burned rapidly due to extremely dry fuels (1000-hour fuel moistures <14 %), high temperatures, and strong winds (Umatilla National Forest, Pomeroy Ranger District, Pomeroy, Washington, USA; unpublished data). The fire burned into drainages on multiple fronts, and long-range spotting was observed up to 1 km from the main fire. Before the fire, invasive plant populations were concentrated along roadsides on about 300 ha throughout the burned area (Umatilla National Forest, Pendleton, Oregon, USA; unpublished GIS data).

The forest vegetation of the study area ranged from mixed-conifer forest of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco),

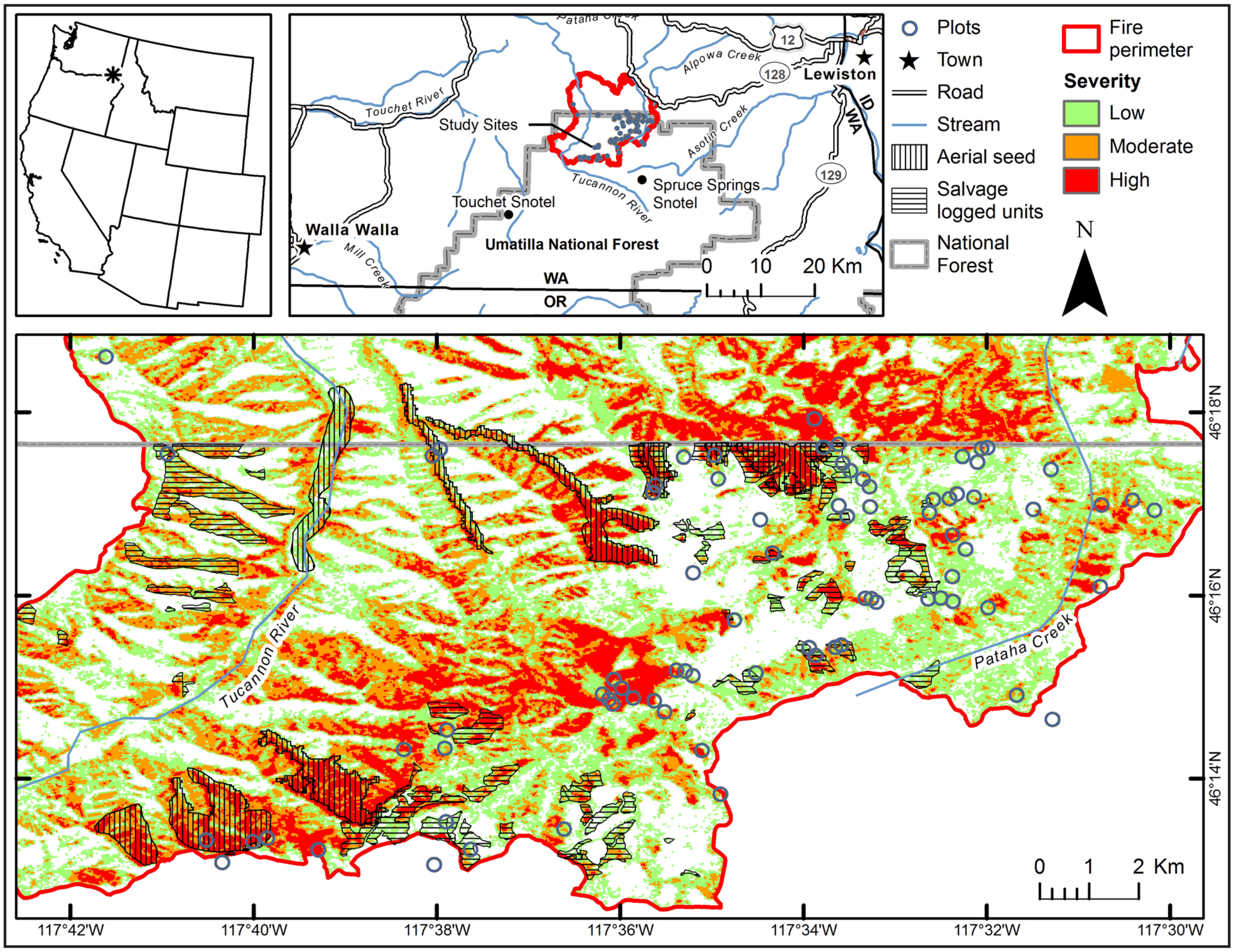


**Figure 1.** Plot locations on the 2005 School Fire in southeastern Washington, USA. Plots were stratified by burn severity, salvage logging (horizontal hatch), and seeding with native grasses (vertical hatch).

grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.) and lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia Engelm. ex S. Watson*) on ridges and plateaus, to ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson)-dominated forests along the Tucannon River. Scouler's willow (*Salix scouleriana* Barratt ex Hook.), white spiraea (*Spiraea betulifolia* Pall.), common snowberry (*Symphoricarpos albus* [L.] S.F. Blake), thinleaf huckleberry (*Vaccinium membranaceum* Douglas ex. Torr), and currant (*Ribes* L.) species are common shrubs. Primary forb species include heartleaf arnica *(Arnica cordifolia* Hook.), fireweed (*Chamerion angustifolium* [L.] Holub), Piper's anemone *(Anemone piperi* Britton ex Rydb.), and common yarrow (*Achillea millefolium* L.). Graminoids are common including bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), California brome (*Bromus carinatus* Hook. & Arn.), pinegrass (*Calamagrostis rubescens* Buckley), Geyer's sedge (*Carex geyeri* Boott), Ross' sedge (*Carex rossii* Boott), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg bluegrass (*Poa secunda* J. Presl.), and others as well as the non-natives cheatgrass (*Bromus tectorum* L.), orchardgrass (*Dactylis glomerata* L.), and bulbous bluegrass (*Poa bulbosa* L.). Introduced, non-native species include prickly lettuce (*Lactuca serriola* L.), common dandelion (*Taraxacum officinale* F.H. Wigg), yellow salsify (*Tragopogon dubius* Scop,), and salsify (*Tragopogon porrifolius* L.).

The dominant soil was an ashy loamy sand: a Loamy-skeletal, isotic, frigid Vitrandic Argixeroll. Soils derived from basalt, loess deposits, and volcanic ash were 0.5 m to 1 m deep on ridges and plateaus but shallower on slopes (Johnson and Clausnitzer 1991; http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx, accessed 17 September 2013).

Average annual precipitation for the years we sampled (2005 to 2011) was 1460 mm, while average annual daily maximum and minimum temperatures were 10.6 °C and 2.1 °C, respectively (data from nearest weather station, Touchet SNOTEL (Figure 1) 1686 station, 46° 6' 36" N, −117° 51' 0" W, elevation 1681 m). Annual precipitation in the year of the fire (2005) was 1135 mm, and in the subsequent six years was 1671 mm, 1285 mm, 1631 mm, 1572 mm, 1455 mm, and 1473 mm. Thus, except for the very dry year of the fire, these years were slightly wetter than long-term average annual precipitation (1434 mm $yr^{-1}$), but similar to average annual daily maximum and minimum temperatures (10.1 °C and 1.5 °C, respectively, from 1989 to 2010).

### *Sampling Design*

We established 72 permanent plots in 2006 at random locations stratified by burn severity, with more plots located in areas burned with moderate and low severity (Table 1) because of greater heterogeneity and variability in the post-fire conditions than in those of high severity (Lentile *et al.* 2007). We based our burn severity strata on a Burned Area Response Classification (BARC) map (US Department of Agriculture, Remote Sensing Applications Center, Salt Lake City, Utah, USA) using differenced Normalized Burn Ratio values from pre-fire and immediately post-fire Landsat 5 TM images (Clarke and Bobbe 2006). We confirmed burn severity classes in the field with a small set of test plots immediately after the fire in 2005 and again in summer 2006 on the full set of plots based on tree mortality with low (<20% tree mortality), moderate (20% to 70% tree mortality) and high (>70% tree mortality) burn severity following Agee (1993). The number of plots per treatment is unequal in Table 1 because we initially select-

**Table 1.** Sampled plots were distributed among treatments that were combinations of burn severity (high, moderate, and low burn severity, or unburned), seeding with native grasses (seeded or unseeded), and whether or not salvage logging had occurred. Plots were located following a stratified random design with respect to burn severity, seeding, and planned salvage logging. Salvage logging was not completed on all planned plots, and seeding was limited to high burn severity plots, which resulted in an unbalanced experimental design.

| Treatment | Number of plots |
|---|---|
| High severity burn, seeded, salvage logged | 2 |
| High severity burn, seeded, not salvage logged | 4 |
| High severity burn, not seeded, salvage logged | 3 |
| High severity burn, not seeded, not salvage logged | 10 |
| Moderate severity burn, salvage logged | 9 |
| Moderate severity burn, not salvage logged | 17 |
| Low severity burn, salvage logged | 6 |
| Low severity burn, not salvage logged | 18 |
| Unburned | 3 |
| **Total number of plots** | **72** |

ed plots based on planned salvage logging and seeding treatments, not all of which were implemented. There were few places where we could find unburned plots with similar site conditions as the plots we sampled in the burned areas. We searched extensively, but only found three unburned locations within the fire perimeter that met our criteria for sampling in that they were neither recently harvested nor heavily used for recreation or other land use (Figure 1).

Native grass seeding was applied, using a helicopter in October 2005, to some areas burned with high severity (712 ha). The Umatilla National Forest stores native grass seed grown from locally adapted seed sources and sows it to reduce the potential for soil erosion, and to limit the establishment and spread of invasive plants following fire, logging, or other disturbances. Four native grasses were seeded, including Idaho fescue at 1.7 kg ha$^{-1}$ with goals of 34 pure live seed (pls) m$^{-2}$, Sandberg bluegrass at 3.0 kg ha$^{-1}$ for 54 pls m$^{-2}$, California brome at 39.7 kg ha$^{-1}$ for 130 pls m$^{-2}$, and blue wildrye (*Elymus glaucus* Buckley) at 10.3 kg ha$^{-1}$ for 54 pls m$^{-2}$ (Umatilla National Forest, Pendleton, Oregon, USA; unpublished data).

Most (72 %) of the salvage logging on our plots occurred during the fall and winter of 2006 to 2007. To the best of our knowledge, of the remaining salvage logged plots, 14 % were logged during the late fall and winter 2005 to 2006, 9 % in the spring and summer 2007 to 2008, and 5 % in the spring and summer 2008 to 2009 (Lewis *et al*. 2012). Plots salvage logged in 2005 to 2006 prior to field sampling in 2006 were assigned to burn severity class based on both field assessments after the fire in late 2005 and our assessment of stumps and standing trees in the first post-fire year. Although we placed half of all plots in each burn severity class (low, moderate, and high) in locations where post-fire salvage logging was planned (based on existing cruise markings in summer 2006 and information from local managers on the Umatilla National Forest), litigation and weather conditions influenced whether or not the plots were actually salvage logged and affected the timing of the salvage logging that did occur. Salvage logging was more often planned and implemented on plots burned with high severity than on plots burned with low or moderate severity, and the marked salvage units varied in size from 1 ha to almost 90 ha, averaging 12 ha. In 2006, the Umatilla National Forest decision to salvage log on 3818 ha total, including three timber sales on 1486 ha, was appealed. In 2007, the salvage logging prescriptions were changed so that no living, fire-damaged trees with more than 50 % of their basal cambium living were harvested, and all remnant late and old seral trees greater than 53 cm dbh were retained whether they were dead or alive (USDA Forest Service 2007). Salvage operations were primarily ground based; logs were cut and piled with tracked feller bunchers before a rubber-tired forwarder was used to move the logs to a staging area or landing.

### *Data Collection*

Our plots were at least 30 m horizontal distance away from roads to minimize edge effects, and they were located either completely within a planned salvage unit or entirely excluded from salvage. Each 60 m × 60 m (1.1 ha) sample plot fell within a single burn severity class as indicated by the BARC map, and included five 1 m$^2$ subplots where field sampling was performed. One subplot was at the plot center with four more subplots located 30 m slope distance away, with the first directly uphill and the others at 90$^{o}$, 180$^{o}$, and 270$^{o}$ orthogonal azimuths from the central subplot. We logged a minimum of 100 positions at the center of each subplot with a Trimble[1] GeoEx-

[1] Trade names are provided for the benefit of the reader and do not imply endorsement by the US Department of Agriculture.

plorer GPS unit (Trimble Navigation Limited, Sunnyvale, California, USA), then differentially corrected and averaged to a locational certainty of 2 m. We marked the center of all plots with rebar, and we marked and geolocated all subplots so we could sample the same plots and subplots in subsequent years. Plot-level data are aggregated means of the five subplots on each plot.

We identified all plant species present in the 1 m × 1 m subplots and ocularly estimated percent canopy cover for each species and for each plant growth form (graminoid, forb, shrub, tree seedling, and moss or lichen) after standardization among field crew members to reduce sampling error. During sampling, two field technicians concurred on plant identification and ocular estimates, and these were cross-checked at least once each day. Any vegetation hanging into the plot and less than one meter high was considered part of the plot vegetation. We calculated percent tree canopy cover at each subplot using spherical densiometer readings collected facing each of the four cardinal directions surrounding each subplot. When plants could not be identified, we designated and numbered them as unknowns; we later verified all plant species identifications in the Stillinger Herbarium at the University of Idaho. Nomenclature follows the USDA Plants Database (USDA 2014). In the years immediately post fire, plants were generally very small and species identification was often difficult. In order to provide consistent and detailed data, we compared subplot-level species lists between years to identify unknown species when possible.

We measured pre-fire tree density as the total of live and dead trees with dbh greater than 12 cm. These were measured in 2006 on an 8 m diameter circular area around the central subplot on each plot. Of the federally managed areas that burned, 47% (~5935 ha) of the lands had been mechanically treated pre-fire with thinning, prescribed fire, or a combination of prescribed fire and thinning. Unfortunately, despite consultation with local managers, we were unable to confidently assign pre-fire treatment methods to the stands.

### *Species Richness and Diversity*

We calculated species richness and Shannon-Wiener diversity (Magurran 1988) for each plot by year. Species richness was the total number of species found on site. We calculated the Shannon-Wiener diversity index as

$$H' = \Sigma \, [p_i \ln(p_i)], \qquad (1)$$

where $p_i$ = the proportion of cover for an individual species relative to the total coverage of all species found in that plot. The Shannon-Wiener index has been criticized as being overly sensitive to changes in species that occur infrequently and in low coverage (Magurran 1988). We did have species that were uncommon or rare on our plots, but we chose to use this index because of its regular use in plant ecological work and because it can be easily interpreted.

We chose percent canopy cover as the measure of abundance as it is widely used for repeated measurements on permanent plots and is related to the degree to which plants compete for space and resources (Bonham 1989). Unfortunately, cover can vary with soil moisture and environmental conditions. Density and biomass are alternative measures. The plants we sampled varied in size and many of the plants we sampled were rhizomatous, which made counting individuals difficult, and biomass measures require destructive sampling and therefore they are not well suited for repeated measures on the same plots (Bonham 1989). We chose to use ocular estimates of cover on small multiple subplots, recognizing that no single method is optimum for all growth forms and all species.

We used repeated measures mixed-effects models (Pinheiro and Bates 2000) to determine the effects of year (random effect with four degrees of freedom for the five years: 2006, 2007, 2008, 2009, and 2011), treatment (fixed effect with eight degrees of freedom for the nine treatments listed in Table 1), and their interaction (32 degrees of freedom for treatment by year interaction). We analyzed first for species richness, and then separately for species diversity. We conducted statistical analyses in SAS 9.2 (SAS Institute, Cary, North Carolina, USA) using Proc Mixed because this method can be used to model correlations found when analyzing grouped data; it can handle unbalanced, repeated measures; and it can accommodate different covariance structures. If any interaction effects were significant for a particular variable ($P \leq 0.05$), we used the least squares means and simple effects tests (Winer 1971) to better understand the nature of the interaction. Initial analyses of these variables used an optimum covariance structure for each variable chosen with Akaike's information criterion (AIC). For species richness and Shannon-Wiener diversity, an "autoregressive" covariance structure was used. To compare treatment values within year, we used an ANOVA for each variable and the Tukey-Kramer multiple comparison method to control for experiment-wise error.

### *Vegetation Abundance by Plant Growth Form and Regeneration Strategy*

We calculated the average percent cover by plant growth form (graminoid, forb, shrub, tree, and moss or lichen) and post-fire regeneration strategy by summing the averaged observed values on the five 1 m × 1 m subplots for each plot in each year. We identified post-fire regeneration strategies (NS = nonsurvivor; OC = off-site colonizer; SR = survivor rhizomes; RC = residual colonizer; and SRCB = survivor taproot, caudex, or bulb) for each individual species using the categories of Stickney and Campbell (2000), the Fire Effects Information System (FEIS 2010), the USDA Plants Database (USDA 2014), and regional plant identification guides (Taylor and Douglas 1995, Johnson 1998, Kershaw *et al*. 1998). We divided resprouters into two groups based on observations by Morgan and Neuenschwander (1988) that rhizomatous plants respond differently than other resprouters to burn severity, although we did not account for depth of rhizomes, bulbs, and other structures from which plants resprout.

We again used repeated measures mixed-effects models (SAS Proc Mixed, Pinheiro and Bates 2000) to determine the effects of year (random effect with four degrees of freedom for the five years: 2006, 2007, 2008, 2009, and 2011), treatment (fixed effect with eight degrees of freedom for the nine treatments listed in Table 1), and their interaction (32 degrees of freedom for treatment by year interaction). First we analyzed abundance by plant form, and then abundance by regeneration strategy. Because the results of the fixed-effects tests did not change over a variety of candidate covariance structures, we used an "unstructured" covariance structure for all variables to allow for easier comparisons. In order to meet the assumptions of normality and equal variances, we used a square root transformation for cover of all plant forms and most regeneration strategies (Table 2), but we did not need to transform the species richness and diversity measures. With the low amount of cover in each of the survivor rhizome (SR) and residual colonizer (RC) regeneration strategy groups, a square root transformation did not meet the normality and variance assumptions, so a Box-Cox transformation procedure (Box and Cox 1964) led to the use of a one-quarter power transformation, which best stabilized the variance of the residuals.

### *Factors Influencing Vegetation Response*

In order to understand how site-specific variables contributed to vegetation composition, we used regression analysis (Proc GLM, SAS Institute 2001) to analyze the 2009 vege-

**Table 2.** Graminoid, forb, and shrub species listed by scientific names, common names, status (N = native, I = introduced), primary regeneration strategy (NS = nonsurvivor; OC = off-site colonizer; SR = survivor rhizome; RC = residual colonizer; SRCB = survivor taproot, caudex, or bulb), and source for regeneration strategy information. All nomenclature is consistent with the USDA Plants Database (USDA 2014).

| | | Regeneration | | |
|---|---|---|---|---|
| Scientific name | Common name | Status | Strategy | Source[1] |
| **Graminoids** | | | | |
| *Achnatherum thurberianum* (Piper) Barkworth | Thurber's needlegrass | N | SRCB | FEIS |
| *Agrostis scabra* Willd. | rough bentgrass | N | OC | S&C 2000 |
| *Alopecurus* L. spp. | foxtail | N | OC | FEIS |
| *Apera interrupta* (L.) P. Beauv. | dense silkybent | I | OC | Burke Museum |
| *Bromus* L. spp. | brome | N/I | OC | FEIS |
| *Bromus carinatus* Hook. & Arn. | California brome | N | OC | FEIS |
| *Bromus tectorum* L. | cheatgrass | I | OC | S&C 2000 |
| *Calamagrostis canadensis* (Michx.) P. Beauv. | bluejoint | N | SR | FEIS |
| *Calamagrostis rubescens* Buckley | pinegrass | N | SR | S&C 2000 |
| *Carex* L. spp. | sedge | N | RC | S&C 2000 |
| *Carex concinnoides* Mack. | northwestern sedge | N | SR | Burke Museum |
| *Carex geyeri* Boott | Geyer's sedge | N | SR | S&C 2000 |
| *Carex rossii* Boott | Ross' sedge | N | RC | S&C 2000 |
| *Dactylis glomerata* L. | orchardgrass | I | OC | S&C 2000 |
| *Danthonia unispicata* (Thurb.) Munro ex Macoun | onespike danthonia | N | OC | FEIS |
| *Elymus glaucus* Buckley | blue wildrye | N | SRCB | S&C 2000 |
| *Festuca campestris* Rydb. | rough fescue | N | SRCB | FEIS |
| *Festuca idahoensis* Elmer | Idaho fescue | N | SRCB | FEIS |
| *Hordeum jubatum* L. | foxtail barley | N | OC | FEIS |
| *Koeleria macrantha* (Ledeb.) Schult. | prairie Junegrass | N | SRCB | FEIS |
| *Oryzopsis asperifolia* Michx. | roughleaf ricegrass | N | SRCB | Kershaw *et al.* 1998 |
| *Phleum pratense* L. | timothy | I | OC | S&C 2000 |
| *Poa bulbosa* L. | bulbous bluegrass | I | SRCB | FEIS |
| *Poa nervosa* (Hook.) Vasey | Wheeler bluegrass | N | OC | Kershaw *et al.* 1998 |
| *Poa secunda* J. Presl | Sandberg bluegrass | N | SRCB | FEIS |
| *Pseudoroegneria spicata* (Pursh) Á. Löve | bluebunch wheatgrass | N | SRCB | FEIS |
| *Schedonorus pratensis* (Huds.) P. Beauv. | meadow fescue | I | SR | Burke Museum |
| ***Forbs*** | | | | |
| *Achillea millefolium* L. | common yarrow | N/I | OC | S&C 2000 |
| *Actaea rubra* (Aiton) Willd. | red baneberry | N | SRCB | FEIS |
| *Agastache urticifolia* (Benth.) Kuntze | nettleleaf giant hyssop | N | OC | USDA Plants |
| *Agoseris* Raf. spp. | agoseris | N | OC | S&C 2000 |
| *Allium* L. spp. | onion | N/I | SRCB | S&C 2000 |
| *Anaphalis margaritacea* (L.) Benth. | western pearly everlasting | N | OC | S&C 2000 |
| *Anemone piperi* Britton ex Rydb. | Piper's anemone | N | SRCB | S&C 2000 |
| *Antennaria* Gaertn. spp. | pussytoes | N | OC | S&C 2000 |
| *Apocynum androsaemifolium* L. | spreading dogbane | N | SR | S&C 2000 |
| *Arabis hirsuta* (L.) Scop. | hairy rockcress | N | SRCB | Kershaw *et al.* 1998 |
| *Arabis holboellii* Hornem. | Holboell's rockcress | N | OC | S&C 2000 |
| *Arabis sparsiflora* Nutt. | sicklepod rockcress | N | OC | Burke Museum |
| *Arenaria congesta* Nutt. | ballhead sandwort | N | OC | S&C 2000 |
| *Arnica cordifolia* Hook. | heartleaf arnica | N | SR | S&C 2000 |
| *Artemisia ludoviciana* Nutt. | white sagebrush | N | SRCB | Kershaw *et al.* 1998 |
| *Astragalus* L. spp. | milkvetch | N/I | SRCB | S&C 2000 |
| *Besseya rubra* (Douglas ex Hook.) Rydb. | red besseya | N | SR | Kershaw *et al.* 1998 |
| *Brassica* L. spp. | mustard | I | OC | Kershaw *et al.* 1998 |
| *Calochortus apiculatus* Baker | pointedtip mariposa lily | N | SRCB | Kershaw *et al.* 1998 |
| *Capsella bursa-pastoris* (L.) Medik. | shepherd's purse | I | OC | Kershaw *et al.* 1998 |
| *Chamerion angustifolium* (L.) Holub | fireweed | N | OC | S&C 2000 |
| *Circaea alpina* L. | small enchanter's nightshade | N | NS | Kershaw *et al.* 1998 |
| *Cirsium* Mill. spp. | thistle | N/I | OC | S&C 2000 |
| *Cirsium arvense* (L.) Scop. | Canada thistle | I | OC | S&C 2000 |
| *Cirsium vulgare* (Savi) Ten. | bull thistle | I | OC | S&C 2000 |
| *Clarkia pulchella* Pursh | pinkfairies | N | OC | Kershaw *et al.* 1998 |
| *Claytonia perfoliata* Donn ex Willd. | miner's lettuce | N | SRCB | Kershaw *et al.* 1998 |
| *Collinsia grandiflora* Lindl. | giant blue eyed Mary | N | RC | S&C 2000 |

[1]FEIS = Fire Effects Information System (http://www.feis-crs.org/beta/), accessed 7 July 2014; S&C 2000 = Stickney and Campbell 2000; USDA Plants = USDA Plants Database (http://plants.usda.gov), accessed 12 May 2015; Burke Museum = University of Washington Burke Museum (http://www.burkemuseum.org/herbarium), accessed 9 July 2014; Kershaw *et al.* 1998.

**Table 2, continued.** N = native; I = introduced; NS = nonsurvivor; OC = off-site colonizer; SR = survivor rhizome; RC = residual colonizer; SRCB = survivor taproot, caudex, or bulb.

| Scientific name | Common name | Status | Regeneration Strategy | Source[1] |
|---|---|---|---|---|
| *Collomia linearis* Nutt. | tiny trumpet | N | RC | S&C 2000 |
| *Conyza canadensis* (L.) Cronquist | Canadian horseweed | N | OC | Kershaw *et al.* 1998 |
| *Crepis elegans* Hook. | elegant hawksbeard | N | OC | Kershaw *et al.* 1998 |
| *Cryptantha* Lehm. ex G. Don spp. | cryptantha | N | UNK | |
| *Cynoglossum officinale* L. | gypsyflower | I | RC | FEIS |
| *Cypripedium parviflorum* Salisb. | lesser yellow lady's slipper | N | OC | FEIS |
| *Delphinium bicolor* Nutt. | little larkspur | N | OC | Kershaw *et al.* 1998 |
| *Dodecatheon pulchellum* (Raf.) Merr. | darkthroat shootingstar | N | OC | S&C 2000 |
| *Draba verna* L. | spring draba | I | OC | Kershaw *et al.* 1998 |
| *Epilobium* L. spp. | willowherb | N | OC | S&C 2000 |
| *Erigeron* L. spp. | fleabane | N/I | SRCB | Kershaw *et al.* 1998 |
| *Eriogonum* Michx. spp. | buckwheat | N | SRCB | Kershaw *et al.* 1998 |
| *Erysimum capitatum* (Douglas ex Hook.) Greene | sanddune wallflower | N | OC | Kershaw *et al.* 1998 |
| *Erythronium grandiflorum* Pursh | yellow avalanche-lily | N | SRCB | S&C 2000 |
| *Eurybia conspicua* (Lindl.) G.L. Nesom | western showy aster | N | SR | S&C 2000 |
| *Fragaria vesca* L. | woodland strawberry | N | SR | FEIS |
| *Frasera speciosa* Douglas ex Griseb. | elkweed | N | SR | FEIS |
| *Galium boreale* L. | northern bedstraw | N | NS | FEIS |
| *Galium triflorum* Michx. | fragrant bedstraw | N | NS | S&C 2000 |
| *Geum triflorum* Pursh | old man's whiskers | N | SR | FEIS |
| *Goodyera oblongifolia* Raf. | western rattlesnake plantain | N | NS | S&C 2000 |
| *Hackelia* Opiz spp. | stickseed | N | SRCB | Kershaw *et al.* 1998 |
| *Heuchera* L. spp. | alumroot | N | SRCB | Kershaw *et al.* 1998 |
| *Hieracium albiflorum* Hook | white hawkweed | N | RC | FEIS |
| *Hieracium scouleri* Hook. var. *albertinum* (Farr) G.W. Douglas & G.A. Allen | Scouler's woollyweed | N | OC | S&C 2000 |
| *Hydrophyllum capitatum* Douglas ex Benth. | ballhead waterleaf | N | SR | Kershaw *et al.* 1998 |
| *Iliamna rivularis* (Douglas ex Hook.) Greene | streambank wild hollyhock | N | RC | S&C 2000 |
| *Iris missouriensis* Nutt. | Rocky Mountain iris | N | SRCB | Kershaw *et al.* 1998 |
| *Lactuca serriola* L. | prickly lettuce | I | OC | S&C 2000 |
| *Leucanthemum vulgare* Lam. | oxeye daisy | I | SR | Kershaw *et al.* 1998 |
| *Linnaea borealis* L. | twinflower | N | NS | S&C 2000 |
| *Lithophragma parviflorum* (Hook.) Nutt. ex Torr. & A. Gray | smallflower woodland-star | N | SR | Museum |
| *Lomatium dissectum* (Nutt.) Mathias & Constance | fernleaf biscuitroot | N | RC | Kershaw *et al.* 1998 |
| *Lupinus* L. spp. | lupine | N | SRCB | S&C 2000 |
| *Luzula campestris* (L.) DC. | field woodrush | I | RC | S&C 2000 |
| *Madia* Molina spp. | tarweed | N | OC | Kershaw *et al.* 1998 |
| *Maianthemum stellatum* (L.) Link | starry false lily of the valley | N | SR | FEIS |
| *Mitella breweri* A. Gray | Brewer's miterwort | N | SRCB | S&C 2000 |
| *Mitella stauropetala* Piper | smallflower miterwort | N | SR | FEIS |
| *Moehringia lateriflora* (L.) Fenzl | bluntleaf sandwort | N | SR | USDA Plants |
| *Nemophila breviflora* A. Gray | basin nemophila | N | SRCB | Burke Museum |
| *Nothocalais troximoides* (A. Gray) Greene | sagebrush false dandelion | N | SRCB | Burke Museum |
| *Oenothera villosa* Thunb. | hairy evening primrose | N | SRCB | Kershaw *et al.* 1998 |
| *Olsynium douglasii* (A. Dietr.) E.P. Bicknell | Douglas' grasswidow | N | UNK | Burke Museum |
| *Orthilia secunda* (L.) House | sidebells wintergreen | N | NS | S&C 2000 |
| *Osmorhiza berteroi* DC. | sweetcicely | N | SRCB | S&C 2000 |
| *Packera* Á. Löve & D. Löve spp. | ragwort | N | SR | Kershaw *et al.* 1998 |
| *Packera streptanthifolia* (Greene) W.A. Weber & Á. Löve | Rocky Mountain groundsel | N | SRCB | Burke Museum |
| *Pedicularis* L. spp. | lousewort | N | SRCB | Burke Museum |
| *Penstemon* Schmidel spp. | beardtongue | N | SRCB | Kershaw *et al.* 1999 |
| *Penstemon glandulosus* Douglas | stickystem penstemon | N | SRCB | Kershaw *et al.* 1998 |
| *Petasites frigidus* (L.) Fr. | arctic sweet coltsfoot | N | OC | Kershaw *et al.* 2000 |
| *Phacelia* Juss. spp. | phacelia | N | SRCB | S&C 2000 |
| *Plantago lanceolata* L. | narrowleaf plantain | I | SRCB | Burke Museum |
| *Plantago major* L. | common plantain | I | OC | Kershaw *et al.* 1998 |
| *Polemonium pulcherrimum* Hook. | Jacob's-ladder | N | SRCB | Kershaw *et al.* 1998 |
| *Polygonum douglasii* Greene | Douglas' knotweed | N | OC | Kershaw *et al.* 1998 |
| *Potentilla* L. spp. | cinquefoil | N/I | SCRB | Burke Museum |
| *Potentilla argentea* L. | silver cinquefoil | I | SRCB | Kershaw *et al.* 1998 |

[1]FEIS = Fire Effects Information System (http://www.feis-crs.org/beta/), accessed 7 July 2014; S&C 2000 = Stickney and Campbell 2000; USDA Plants = USDA Plants Database (http://plants.usda.gov), accessed 12 May 2015; Burke Museum = University of Washington Burke Museum (http://www.burkemuseum.org/herbarium), accessed 9 July 2014; Kershaw *et al.* 1998.

**Table 2, continued.** N = native; I = introduced; NS = nonsurvivor; OC = off-site colonizer; SR = survivor rhizome; RC = residual colonizer; SRCB = survivor taproot, caudex, or bulb.

| Scientific name | Common name | Status | Regeneration Strategy | Source[1] |
|---|---|---|---|---|
| *Potentilla gracilis* Douglas ex Hook. | slender cinquefoil | N | SRCB | Kershaw *et al.* 1998 |
| *Potentilla recta* L. | sulphur cinquefoil | I | SRCB | FEIS |
| *Prosartes trachycarpa* S. Watson | roughfruit fairybells | N | SR | S&C 2000 |
| *Prunella vulgaris* L. | common selfheal | N | OC | S&C 2000 |
| *Ranunculus* L. spp. | buttercup | N/I | SRCB | FEIS |
| *Ranunculus uncinatus* D. Don ex G. Don | woodland buttercup | N | SRCB | Burke Museum |
| *Rudbeckia alpicola* Piper | showy coneflower | N | SR | Kershaw *et al.* 1998 |
| *Rumex acetosella* L. | common sheep sorrel | I | SR | FEIS |
| *Sedum stenopetalum* Pursh | wormleaf stonecrop | N | OC | Kershaw *et al.* 1998 |
| *Silene* L. spp. | catchfly | N/I | SR | S&C 2000 |
| *Solidago canadensis* L. | Canada goldenrod | N | OC | Kershaw *et al.* 1998 |
| *Stellaria* L. spp. | starwort | N/I | OC | Burke Museum |
| *Stellaria media* (L.) Vill. | common chickweed | I | SR | Kershaw *et al.* 1998 |
| *Tanacetum vulgare* L. | common tansy | I | SR | FEIS |
| *Taraxacum officinale* F.H. Wigg. | common dandelion | I | OC | S&C 2000 |
| *Thalictrum occidentale* A. Gray | western meadow-rue | N | SRCB | S&C 2000 |
| *Thelypodium laciniatum* (Hook.) Endl. ex Walp. | cutleaf thelypody | N | OC | Kershaw *et al.* 1998 |
| *Tragopogon dubius* Scop. | yellow salsify | I | OC | S&C 2000 |
| *Tragopogon porrifolius* L. | salsify | I | OC | Burke Museum |
| *Trautvetteria caroliniensis* (Walter) Vail | Carolina bugbane | N | SR | S&C 2000 |
| *Trifolium repens* L. | white clover | I | OC | S&C 2000 |
| *Triteleia grandiflora* Lindl. | largeflower triteleia | N | SRCB | Kershaw *et al.* 1998 |
| *Urtica dioica* L. | stinging nettle | N/I | SRCB | S&C 2000 |
| *Valeriana occidentalis* A. Heller | western valerian | N | UNK | USDA Plants |
| *Verbascum thapsus* L. | common mullein | I | OC | S&C 2000 |
| *Viola* L. spp. | violet | N/I | SR | Kershaw *et al.* 1998 |
| *Zigadenus* Michx. spp. | deathcamus | N | SRCB | Kershaw *et al.* 1999 |
| *Zizia aptera* (A. Gray) Fernald | meadow zizia | N | SRCB | USDA Plants |
| ***Shrubs*** | | | | |
| *Acer glabrum* Torr. | Rocky Mountain maple | N | SRCB | S&C 2000 |
| *Alnus* Mill. spp. | alder | N | SRCB | FEIS |
| *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem. | Saskatoon serviceberry | N | SRCB | S&C 2000 |
| *Arctostaphylos uva-ursi* (L.) Spreng. | kinnikinnick | N | SRCB | FEIS |
| *Ceanothus velutinus* Douglas ex Hook. | snowbrush ceanothus | N | RC | S&C 2000 |
| *Chimaphila umbellata* (L.) W.P.C. Barton | pipsissewa | N | NS | S&C 2000 |
| *Mahonia repens* (Lindl.) G. Don | creeping barberry | N | SR | FEIS |
| *Menziesia ferruginea* Sm. | rusty menziesia | N | SRCB | S&C 2000 |
| *Philadelphus lewisii* Pursh | Lewis' mock orange | N | SRCB | S&C 2000 |
| *Physocarpus malvaceus* (Greene) Kuntze | mallow ninebark | N | SRCB | S&C 2000 |
| *Prunus* L. spp. | plum | N/I | SRCB | USDA Plants |
| *Prunus emarginata* (Douglas ex Hook.) D. Dietr. | bitter cherry | N | SRCB | USDA Plants |
| *Ribes* L. spp. | currant | N/I | RC | S&C 2000 |
| *Ribes lacustre* (Pers.) Poir. | prickly currant | N | RC | S&C 2000 |
| *Ribes viscosissimum* Pursh | sticky currant | N | RC | S&C 2000 |
| *Rosa* L. spp. | rose | N/I | SRCB | S&C 2000 |
| *Rubus* L. spp. | blackberry | N/I | RC | S&C 2000 |
| *Rubus idaeus* L. | American red raspberry | N/I | RC | S&C 2000 |
| *Rubus parviflorus* Nutt. | thimbleberry | N | SR | S&C 2000 |
| *Salix scouleriana* Barratt ex Hook. | Scouler's willow | N | SRCB | S&C 2000 |
| *Sambucus racemosa* L. | red elderberry | N | RC | S&C 2000 |
| *Spiraea betulifolia* Pall. | white spirea | N | SR | S&C 2000 |
| *Symphoricarpos albus* (L.) S.F. Blake | common snowberry | N | SR | S&C 2000 |
| *Vaccinium membranaceum* Douglas ex Torr. | thinleaf huckleberry | N | SR | S&C 2000 |
| **Trees** | | | | |
| *Abies grandis* (Douglas ex D. Don) Lindl. | grand fir | N | OC | S&C 2000 |
| *Larix occidentalis* Nutt. | western larch | N | RC | S&C 2000 |
| *Picea engelmannii* Parry ex Engelm. | Engelmann spruce | N | OC | S&C 2000 |
| *Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson | lodgepole pine | N | RC | S&C 2000 |
| *Pinus ponderosa* Lawson and C. Lawson | ponderosa pine | N | OC | S&C 2000 |
| *Pseudotsuga menziesii* (Mirb.) Franco | Douglas-fir | N | OC | S&C 2000 |

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tation response (species richness, species diversity, abundance of the three different plant growth forms, and the four different regeneration strategies) by treatment. We used only the 2009 data for this analysis because we anticipated that differences in vegetation response would be evident four years post fire, and that these differences have long-term consequences. We combined slope and aspect to form a continuous variable for ease in statistical analysis {Aspslp = percent slope × [cosine (aspect)]} (Stage 1976). The other site-specific variables were treatment, tree density class, elevation, and average tree canopy cover post fire.

## RESULTS

### *Plant Species Richness and Diversity*

Both richness and Shannon-Wiener diversity of understory plants varied with treatment, year, and the interaction of treatment and year (Figure 2). Plant species richness and diversity were higher on plots burned with low and moderate burn severity than on some unburned plots, and plots burned with high severity had the lowest richness and diversity overall. Salvage logging and seeding both significantly decreased richness and diversity (Figure 2, Table 3). At higher pre-fire tree density, both species richness ($P$ = 0.02) and diversity ($P$ =

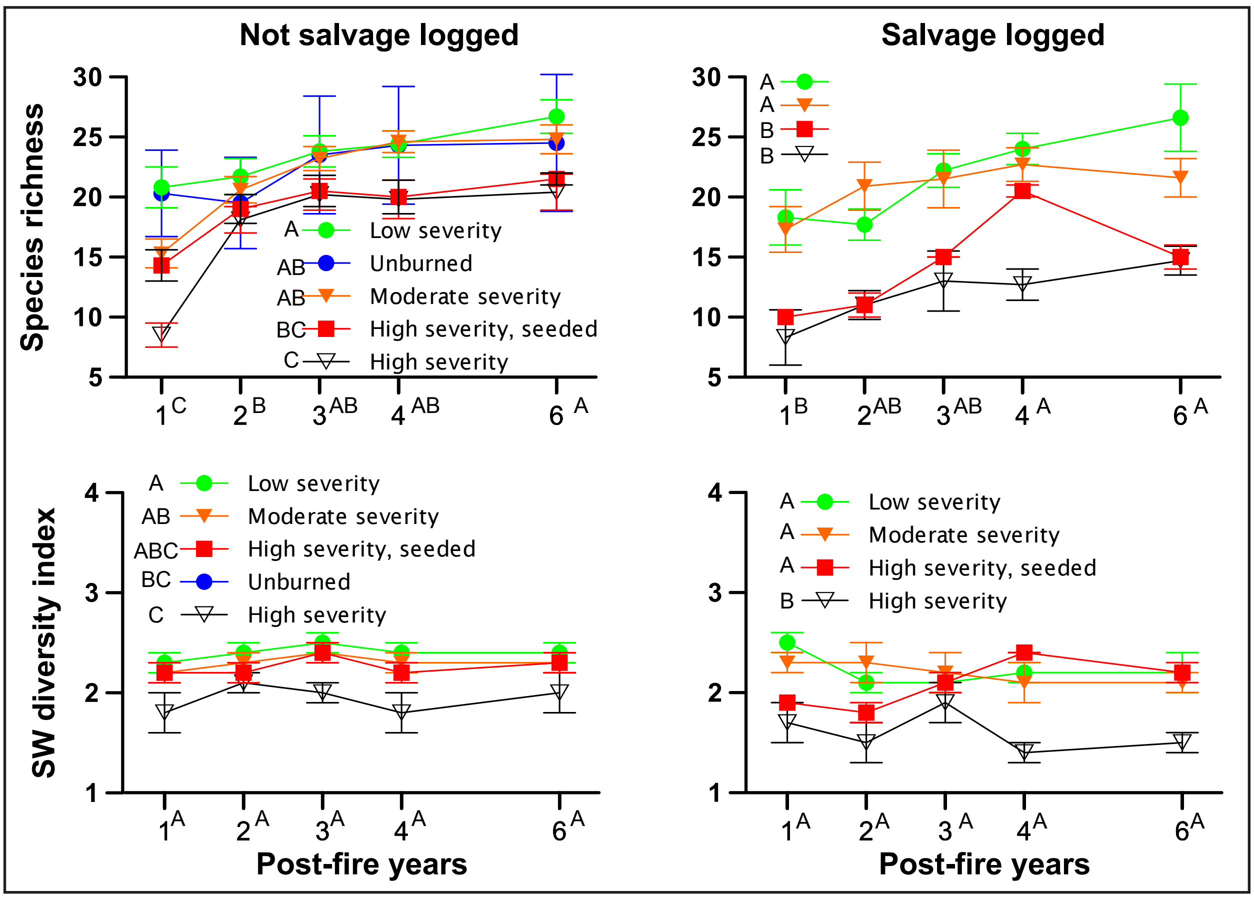


**Figure 2.** Species richness (number of species, top) and Shannon-Wiener (SW) diversity index (bottom) for all severity and seeding treatment combinations. Data are contrasted by not salvage logged (left) and salvage logged (right). Error bars represent standard error. Capital letters next to the years on the *x*-axis and next to the treatments in the legend represent significant differences between means by year or by treatment; legend items are ordered from highest to lowest mean value over all years

**Table 3.** The effect of salvage logging on plant cover type, by regeneration strategy. Plots are compared over all study years with simple effects tests at the same severity level; for example, high burn severity salvage logged plots are compared to high burn severity plots that were not salvage logged. Significant differences between salvage logged and not salvage logged plots are indicated in bold. Unless indicated by a footnote, salvage logging decreased the richness, diversity, or cover of each significant measure.

| | Measure | *F*-value | *P*-value |
|---|---|---|---|
| High burn severity, seeded | **Richness** | **4.53** | **0.03** |
| | Diversity | 1.07 | 0.30 |
| | Grass | 0.20 | 0.66 |
| | Forb | 2.16 | 0.14 |
| | Shrub | 0.13 | 0.72 |
| | Survivor rhizome (SR) | 0.98 | 0.32 |
| | Offsite colonizer (OC) | 0.70 | 0.40 |
| | Survivor taproot, caudex, or bulb (SRCB) | 0.10 | 0.75 |
| | **Residual colonizer (RC)** | **12.56** | **<0.001** |
| High burn severity, unseeded | **Richness** | **12.47** | **<0.001** |
| | **Diversity** | **8.61** | **0.004** |
| | **Grass**[A] | **9.64** | **0.002** |
| | **Forb** | **7.40** | **0.007** |
| | **Shrub** | **9.12** | **0.003** |
| | Survivor rhizome (SR) | 0.49 | 0.48 |
| | Offsite colonizer (OC) | 0.87 | 0.35 |
| | Survivor taproot, caudex, or bulb (SRCB) | 0.06 | 0.80 |
| | **Residual colonizer (RC)** | **7.04** | **0.008** |
| Moderate burn severity | Richness | 0.84 | 0.36 |
| | Diversity | 1.17 | 0.28 |
| | **Grass**[A] | **10.11** | **0.002** |
| | **Forb** | **29.99** | **<0.001** |
| | Shrub | 0.66 | 0.42 |
| | Survivor rhizome (SR) | 0.59 | 0.44 |
| | **Offsite colonizer (OC)** | **8.99** | **0.003** |
| | **Survivor taproot, caudex, or bulb (SRCB)** | **5.16** | **0.02** |
| | Residual colonizer (RC) | 0.58 | 0.45 |
| Low burn severity | Richness | 2.29 | 0.13 |
| | Diversity | 3.42 | 0.07 |
| | Grass | 0.00 | 0.97 |
| | Forb | 1.64 | 0.20 |
| | **Shrub** | **4.14** | **0.04** |
| | Survivor rhizome (SR) | 0.03 | 0.86 |
| | Offsite colonizer (OC) | 0.01 | 0.91 |
| | Survivor taproot, caudex, or bulb (SRCB) | 1.53 | 0.22 |
| | Residual colonizer (RC) | 2.10 | 0.15 |

[A] Grass cover was higher on the salvage logged plots compared to the not salvage logged plots.

0.003) were less four years after the fire, while richness was greater with higher tree canopy cover ($P = 0.005$).

In the first year post fire, species richness was significantly lower on high severity burns than on unburned, low, or moderate severity plots, regardless of whether they were salvage logged or not ($P < 0.001$) (Table 3). In the second, third, fourth, and sixth years post fire, species richness did not differ significantly on plots burned with high, moderate, and low severity that were not salvage logged ($P > 0.05$); species richness increased significantly between the first post-fire year and the sixth post-fire year on both salvage logged and not salvage logged plots (Figure 2). Of plots that were salvage logged, species richness was lower in the fourth post-fire year in high severity burned plots than in either low or moderate burn severity plots ($P = 0.002$). Species richness was higher on the seeded and unseeded high severity plots that were not salvage logged than on the salvage-logged counterparts ($P = 0.03$ and $< 0.001$, respectively) (Table 3).

Species diversity was higher on low severity burned plots compared to high severity burned plots in the second and fourth years post fire ($P = 0.005$ and $P = 0.001$, respectively), and on moderate burn severity plots compared to high severity plots four years post fire ($P = 0.005$). However, species diversity did not differ among treatments in the third and sixth years post fire ($P > 0.05$). Species diversity was also lower on plots that were salvage logged and burned at high severity than in plots burned at low and moderate severity in the second post-fire year ($P = 0.009$). Considering all years together, species diversity was lower on unseeded high severity plots than on low and moderate severity plots (Figure 2), and diversity of the seeded plots was overall higher than the unseeded high-severity counterparts ($P = 0.004$, Figure 2).

### *Plant Growth Form*

Regardless of burn severity and salvage logging, graminoid cover was less than 15% throughout the study period except on plots seeded with native grasses (Figure 3). Within high severity burns, graminoid cover was significantly greater on seeded plots than burned plots that were not seeded for each year measured ($P < 0.05$). In years two and three post fire, graminoid cover was significantly greater on burned seeded plots than on unburned plots

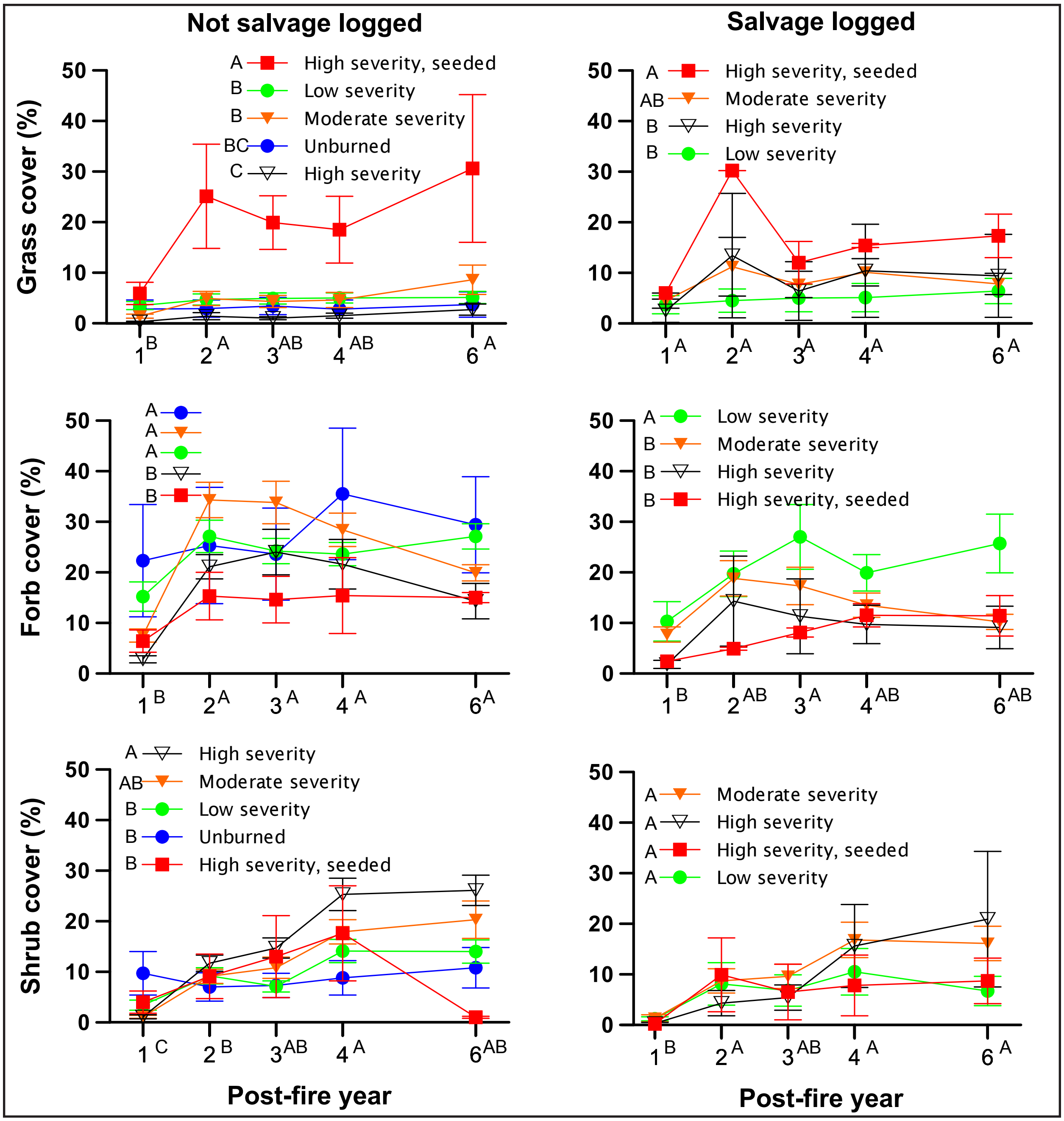


**Figure 3.** Percent canopy cover for grasses, forbs, and shrubs by burn severity. Data are contrasted by not salvage logged (left) and salvage logged (right). Error bars represent standard error. Capital letters next to the years on the *x*-axis and next to the treatments in the legend represent significant differences between means by year or by treatment; legend items are ordered from highest to lowest mean value over all years.

($P < 0.01$ for both). Burn severity ($P = 0.001$), year ($P \leq 0.001$), and the interaction of burn severity and year ($P = 0.009$) all significantly influenced graminoid cover. Interestingly, graminoid cover was higher on the salvage logged moderate and unseeded high severity plots ($P = 0.002$ for both) than on the not salvage logged counterparts (Table 3). However, graminoid cover did not significantly increase during the study period on the salvage logged plots (Figure 3). Elevation was the only site factor to influence graminoid cover ($P = 0.001$) by post-fire year four; graminoid cover was greater at low elevations.

Forbs constituted a majority of total understory plant cover, up to 35%, regardless of whether plots were salvage logged or not. Forb cover was significantly lower on plots that burned at high severity than plots that burned at low severity or those that were unburned ($P \leq 0.001$ for all comparisons). On the plots that were not salvage logged, forb cover was lowest in the first post-fire year and significantly higher in each other year (Figure 3). On the salvage logged plots, forb cover was lower on the moderate and high burn severity plots than on the not salvage logged counterparts ($P < 0.001$ and $P < 0.007$, respectively) (Table 3). Salvage logging might have hindered forb recovery over time; forb cover was not significantly higher in post-fire year six than it was in the first post-fire year (Figure 3). Average tree canopy cover ($P = 0.001$) and combined slope and aspect ($P = 0.01$) affected forb cover four years after the fire; forb cover was greater on more mesic sites.

Shrub cover increased through time regardless of salvage logging or burn severity (Figure 3), which was different than graminoid and forb recovery over the same period. In the first year post fire, shrub cover on plots not salvage logged was significantly lower on high and moderate burn severity plots than on unburned plots ($P = 0.003$), but there were no significant differences in shrub abundance among treatments in subsequent individual years ($P > 0.05$), regardless of whether plots had been seeded or salvage logged. With all years considered, unseeded plots that burned at high severity and were not salvage logged had the highest overall shrub cover (Figure 3), and seeded high severity plots had the lowest shrub cover. In post-fire year six, high severity plots that were seeded had significantly less shrub cover than plots that were not seeded ($P = 0.02$). In year four, shrub cover differed for all treatments ($P \leq 0.05$) with the exception of plots burned with high severity and seeded, but neither salvage logged nor burned. Considering all years, low and high severity plots that were salvage logged had significantly lower shrub cover than the not salvage logged counterparts ($P = 0.004$ and $P = 0.003$, respectively) (Table 3). The only site factor to affect shrub cover in post-fire year four was combined slope and aspect ($P = 0.03$). As combined slope and aspect increased, shrub cover increased.

### *Plant Regeneration Strategies as Functional Traits*

The presence of survivor rhizome (SR) regeneration strategy plants, such as Ross' sedge and bluejoint (*Calamagrostis rubescens* Buckley), varied similarly with time and treatment, whether plots were salvage logged or not (Figure 4). In year one post fire, low, moderate, and high severity plots all had significantly lower cover of survivor rhizomes than unburned plots ($P < 0.001$); year one also had the lowest overall cover compared to the other years (Figure 4). Over all years on the plots that were not salvage logged, unburned and low severity plots had higher SR cover than the moderate and high severity, unseeded plots ($P < 0.001$) (Figure 4). On the salvage logged plots, there was no change in SR cover over time, and only the low severity plots had significantly higher SR cover than the unseeded, high severity plots ($P = 0.02$) (Figure 4). Salvage logging did not appear to have a signifi-

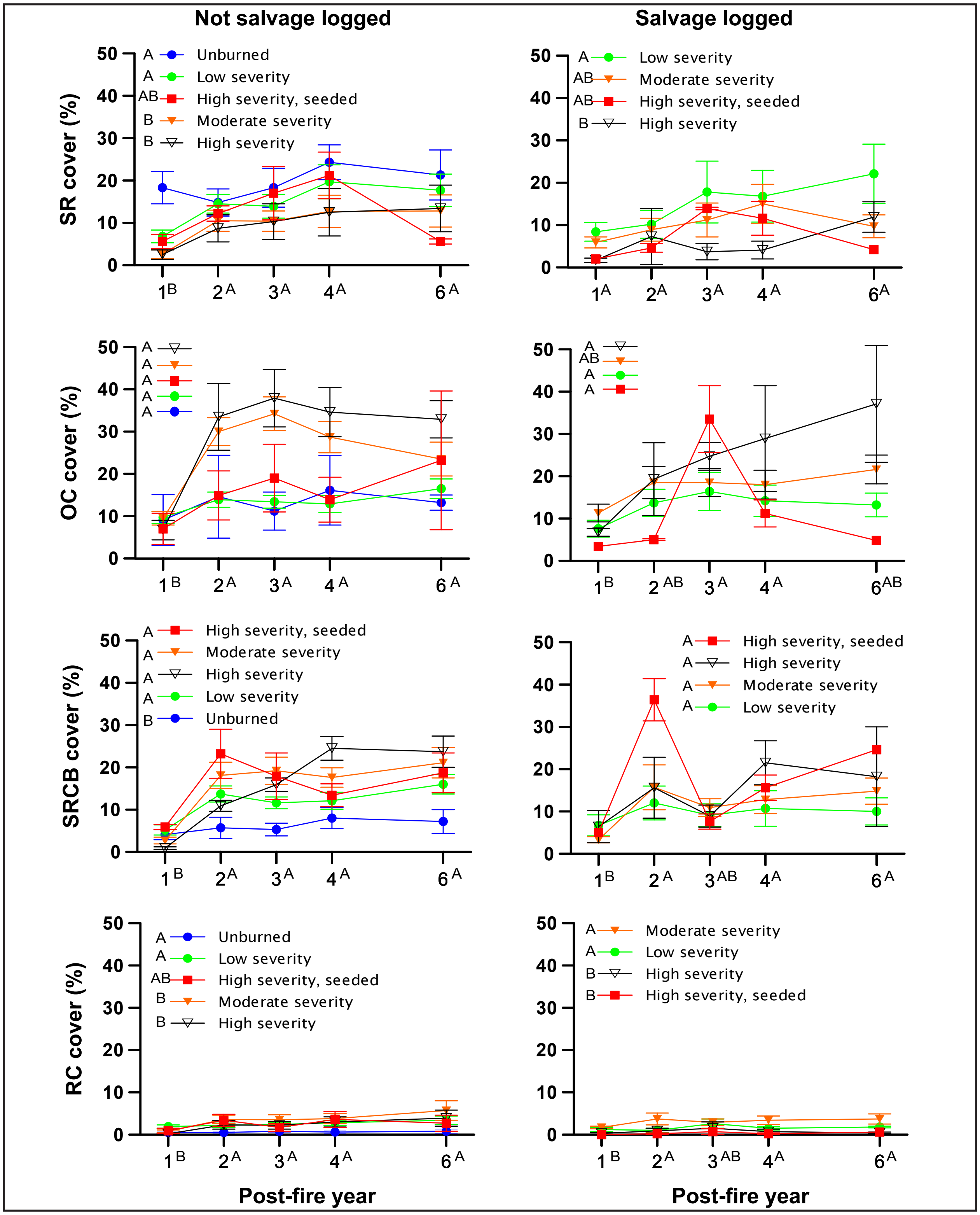


**Figure 4.** Percent canopy cover for four different regeneration strategies (survivor rhizome [SR]; off-site colonizers [OC]; survivor taproot, caudex, or bulb [SRCB]; residual colonizers [RC]) by year, burn severity, salvage logged, and seeded with native grass. Error bars represent standard error. Capital letters next to the years on the *x*-axis and next to the treatments in the legend represent significant differences between means by year or by treatment; legend items are ordered from highest to lowest mean value over all years.

cant effect on SR cover types (Table 3). Average tree canopy cover was the only site factor to influence SR cover ($P = 0.01$) four years after the fire; SR cover was greater where tree cover was greater.

One year post fire, offsite colonizers (OC) canopy cover was low and did not differ by treatment; year one also had the lowest OC cover of any post-fire year (Figure 4). In years two, three, and four post fire, however, moderate and high severity plots had significantly greater canopy cover of OC plants than did low severity plots ($P < 0.005$), and in year three post fire, high severity plots also had significantly greater cover of offsite colonizers than unburned plots ($P < 0.001$). Over all years on the plots that were not salvage logged, moderate and high severity plots had higher OC cover than unburned, low severity, and high severity seeded plots. Offsite colonizers cover on plots that were salvage logged was not statistically different than plots that were not salvage logged, except on the moderate severity plots, where salvage logging decreased OC cover ($P = 0.003$) (Table 3). The OC cover differed with year ($P < 0.001$) and the interaction of year and treatment ($P = 0.003$), but not with treatment ($P = 0.17$). High severity, unseeded plots had higher OC cover than low severity and high severity seeded plots (Figure 4). Prickly lettuce, thistles (*Cirsium* spp. Mill.), and many grasses commonly establish as OC. The OC cover four years after fire increased with greater pre-fire tree density ($P = 0.01$).

Shrubs, forbs, and graminoids that resprout from a survivor taproot, caudex, or bulb (SRCB) increased between the first and sixth post-fire years, regardless of burn severity or salvage logging (Figure 4). In year one post fire, only plots classified as burned with high severity had significantly lower SRCB cover than those classified as low severity ($P < 0.05$). In the second post-fire year, we found abundant cover of Scouler's willow, miner's lettuce (*Claytonia perfoliata* Donn ex Willd.), and Idaho fescue on plots burned with high severity that were seeded but not salvage logged. Also in year two post fire, high severity plots that were both salvage logged and seeded had significantly greater SRCB cover than unburned plots, whereas in year three post fire, moderate severity plots had significantly greater SRCB cover than unburned plots ($P < 0.05$). In year four and six post fire, high severity plots had significantly greater SRCB cover when compared to low severity plots. Over all years, SRCB cover was lower on unburned plots than on all other plots ($P < 0.05$), and salvage logging appeared to affect SRCB cover only on moderate severity plots (compared to the not salvage-logged counterparts) ($P < 0.05$) (Table 3). Four years after the fire, there were no site factors that significantly influenced SRCB cover.

Residual colonizers (RC) plants were in low abundance (<5 %) on all treatments in all years (Figure 4). However low, RC plant cover was greater in the second through sixth post-fire years than in the first year, regardless of salvage logging (Figure 4). On the plots that were not salvage logged, across all years, unburned and low burn severity plots had higher RC cover than moderate and high severity, unseeded plots. Similarly on the salvage logged plots, low and moderate burn severity plots had higher RC cover than high severity plots. Lower RC cover was found on the high severity salvage logged plots, regardless of seeding ($P = 0.008$ unseeded, $P < 0.001$ seeded) (Table 3). Currant, snowbrush ceanothus (*Ceanothus velutinus* Douglas ex Hook.) and Ross' sedge species were plants with this regeneration strategy and were found on many plots. By the fourth post-fire year, RC increased with increasing elevation ($P = 0.04$), and combined slope and aspect ($P = 0.02$).

## DISCUSSION

### *Burn Severity Influenced Vegetation Response*

Vegetation cover generally increased steadily after the fire, as we expected, with most differences occurring between plots classified as high severity burns and those plots burned with either low or moderate severity (Figures 2, 3, and 4). Vegetation cover, species richness, and diversity were lower on high severity plots than on plots burned with moderate and low severity both immediately post fire and for the following six years. Lentile *et al*. (2007) and MacDonald (2007) found no significant differences in species richness with burn severity one year after western US wildfires, whereas we found significantly lower species richness and diversity on the high severity plots throughout the study period. Abella and Fornwalt (2015) found that species richness increased immediately after burning, especially on sites burned with high severity, as plants present pre-fire increased in abundance and additional plants established. Further, they found, as we did, that differences persisted, although they became less pronounced between areas burned with different burn severity. Morgan and Neuenschwander (1988) and Lentile *et al*. (2007) found differences in species cover with burn severity. In areas burned with low and moderate severity, plants quickly established in abundance post fire by resprouting, from seeds in the seedbank, or from nearby surviving vegetation (Ryan and Noste 1985). Plots burned with high severity have gaps for plants to establish within, but may have fewer available nutrients, favorable soil properties, and resources for plant colonization. The lack of overstory vegetation combined with a dark ground surface with high albedo can increase plant exposure to high temperatures that cause can cause heat stress. Further, patches of high burn severity often have a greater distance to seed sources from unburned edges, harsher growing conditions, and time lag in regeneration (Lyon and Stickney 1976; Turner *et al.* 1997, 1999, 2003; Hunter *et al.* 2006).

Lentile *et al.* (2007) found, as we did, that understory plant species abundance was highly variable, especially in low severity burns compared to areas burned with high severity within the same fire. Likely this reflects the fine-grained spatial variability of fire effects on the forest floor within low and moderate severity burns (Hudak *et al*. 2007), which creates a variety of microsites for plant survival and post-fire establishment. Differences in site conditions also contributed to multiple regeneration strategies, likely reflecting both differences in site productivity and environmental conditions, and pre-fire vegetation composition—although we do not know the composition of vegetation prior to the fire for our plots.

### *Native Grass Seeding Altered Post-Fire Vegetation Response*

Somewhat surprisingly, plots burned with high severity that were not seeded did not have significantly greater species richness and diversity than high severity burned plots that were seeded. Others have reported decreased native species richness and diversity due to the success of seeded grass species (Taskey *et al.* 1989, Sexton 1998). On our plots seeded with native grass, the graminoid cover was dense in the first growing season (up to 80% canopy cover), likely due to favorable rainfall (Robichaud *et al.* 2013). Nonetheless, other plant species were able to establish and persist, although with lower percent cover than on plots without grass seeding. Hunter and Omi (2006) found that both post-fire canopy cover and species richness of native plants were lower where seeded grass cover was high in Arizona, USA. Our results were similar, with less species richness and lower forb and shrub cover on the high burn severity seeded plots.

Native grass seeding following six large wildfires in Mesa Verde National Park, Colorado, USA, resulted in plant species richness and diversity findings similar to ours (Floyd *et al.* 2006). Seeded plots in that study produced greater diversity and richness than unseeded counterparts, although the plots in Mesa Verde had much lower total vegetation cover than our plots, likely due to drier conditions. We found few non-native species, even in plots that were seeded after fire with grass. Others found non-native species were introduced through seeding (Hunter and Omi 2006, Hunter *et al.* 2006).

Beyers (2004) and Peppin *et al.* (2010) concluded from their reviews of multiple research and monitoring projects that seeding reduced abundance of post-fire native vegetation. For example, Stella *et al.* (2010) documented less abundant forbs for more than a year post fire on plots seeded with a mix of native and non-native grasses. Schoennagel and Waller (1999) found reduced abundance of native plants when frequency and cover of seeded non-native plant species were high. In contrast, Hunter and Omi (2006) found that vegetation cover did not differ for plots burned with high and low severity four years after the Cerro Grande Fire in New Mexico, USA. Peppin *et al.* (2010) suggested that burn severity, the species seeded, and the success of seeding influenced whether seeding altered post-fire vegetation response.

We saw a peak in graminoid cover in the second post-fire year, followed by a slight decline and then a gradual increase through the remainder of the study period (Figures 2, 3, and 4), even though post-fire precipitation was above average. Peppin *et al.* (2010) attributed this common post-fire pattern to the successful establishment of species seeded that then declined in abundance by the fourth year post fire, but on our seeded plots neither total species richness nor graminoid cover declined.

### *Salvage Logging Altered Vegetation Response*

Salvage logging significantly altered species richness, diversity, and understory plant cover one to six years post fire. Plots that were salvage logged generally had less total vegetative cover of shrubs and forbs than plots of similar burn severity that were not salvage logged, but also had a higher percent cover of graminoids in each year. However, vegetation response differences due to burn severity were more pronounced than differences due to salvage logging (Figure 3).

Salvage logging influenced vegetation response perhaps because salvage logging increased bare mineral soil exposure from an average of 43% exposed soil after the fire (but before salvage logging) to an average of 73% exposed soil in year four post fire on plots that were salvage logged (Lewis *et al.* 2012). Further, salvage logged plots burned with low severity had less bare soil (54%) than those that had burned with moderate and high severity (65% and 74%, respectively; Lewis *et al.* 2012). While nearly 75% exposed soil is high, the soil disturbance was largely restricted to the individual salvage units and was not widespread. In general, the salvage logging done on the national forest after the School Fire was low impact by design. Salvage logging that reduces overstory tree canopy cover and standing snags result in altered light penetration, gaps, and microsite conditions on the forest floor (Ricklefs 1977, Gray and Spies 1997) that could increase understory vegetation abundance. Keyser *et al.* (2009) found that understory plant communities on salvage logged plots reached pre-fire percent canopy cover in as little as five years, with no additional invasive species.

Salvage logged high severity burn plots had the lowest species richness and diversity of all plots, especially when they were seeded with native grasses. Salvage logging can shift vegetation structure to favor graminoid species over other understory species (Sexton 1998), likely because graminoids are highly resilient to disturbance and often are not killed by fire due to their growth form and large proportion of live biomass belowground (Bond and van Wilgen 1996). The additional post-fire treatment of seeding with grasses in plots that were salvage logged may likely shift vegetation composition in favor of graminoids.

### *Plant Functional Traits and Pre-Fire Forest Structure and Management*

All resprouters were little affected by salvage logging and seeding, and there were few differences with burn severity. Careful assessment, not just broad classifications such as the ones we used, is needed (Hooper and Vitousek 1998), especially as many plants use multiple regeneration strategies (Lyon and Stickney 1976, Morgan and Neuenschwander 1988). For example, we observed Scouler's willow growing as resprouts and apparently regenerating prolifically from seed.

The pre-fire plant composition is clearly important (Halpern 1988), especially for plants that resprout; however, we do not have pre-fire plant data. Without the pre-fire data, it is difficult to evaluate resilience defined as the degree to which post-fire vegetation resembled pre-fire vegetation, as was done by Abella and Fornwalt (2015). Furthermore, pre-fire forest management would have affected forest structure at the time of the fire, and therefore burn severity as well (Graham *et al.* 1999, 2004; Hudak *et al.* 2011). Analysis by pre-fire forest density classes could prove useful in similar studies in the future, although the confounding effects of forest structure and site make this challenging. While we found site factors to have some effect on vegetation cover, post-fire vegetation composition showed no consistent patterns relative to pre-fire tree density, average tree canopy cover, elevation, or combined slope and aspect. None of these variables had a predominant or predictable effect on vegetation composition on our study plots. This is likely due in part to the unbalanced sampling design making it more difficult to compare factors within and across treatment classes. The numerous forest disturbances (pre-fire treatments, fire at varying severity levels, salvage logging, and seeding) also made it more difficult to test for simple effects, because there were so many treatment classes and combinations to consider. We would recommend future studies carefully limit treatment classes and combinations for more interpretable results.

### *Management Implications and Limitations*

Understory vegetation recovered, but species richness, diversity, and abundance were lower on high severity burns, particularly if those severely burned sites were also salvage logged and seeded with native grasses. Burn severity influenced understory vegetation response more than either salvage logging or post-fire seeding with locally adapted native grasses. Differences were greatest immediately after disturbance, but less pronounced six years post-fire. Nonetheless, the initial differences in understory vegetation could affect future forest development (Abella and Fornwalt 2015). On our plots on this fire, Droske (2012) found much lower density of naturally established Douglas-fir and grand fir tree seedlings on areas burned with high severity (0 trees ha$^{-1}$ to 5166 trees ha$^{-1}$) compared to sites burned with low and moderate burn severities (0 trees ha$^{-1}$ to 31 833 trees ha$^{-1}$), in part because much of the plots that burned with high severity were far from surviving trees that could provide seed. Here on the School Fire, both salvage logging and seeding were limited in extent, and their impacts were carefully managed to minimize detrimental effects. Such practices as using certified weed-free seed with locally adapted native species, and limiting the extent of soil disturbance from salvage logging disturbance should continue. Locally, managers still plan to seed with native grasses after logging and other disturbances, but with lower amounts of seed than was used on the School Fire (D. Groat, Umatilla National Forest, Pomeroy Ranger Station, Pomeroy, Oregon, USA, personal communication). We recommend that managers locally and on other forests carefully consider seed application locations and rate, and highly recommend the use of native seed when available. Minimizing the impact and disturbance from salvage logging is also a fundamental factor when considering short- and long-term vegetation and soil recovery.

Vegetation here was resilient to the combined effects of large fire and post-fire management, as was found by Abella and Fornwalt (2015) on the Hayman Fire. Likely this is related to the relatively forgiving soils that did not experience significant erosion and near to above-average precipitation in the early years post fire (Robichaud *et al*. 2013). Furthermore, this landscape was actively managed through logging, thinning, and burning for decades prior to the fire. Local managers carefully conducted post-fire management to limit potentially detrimental effects.

This study has several limitations. First, salvage logging extended over several years, making it challenging to infer vegetation response as a direct result of salvage logging across the range of burn severities. Second, despite our best efforts, the number of plots was not balanced across burn severity, seeding, or salvage logging treatments. Third, we were unable to fulfill our original intent of attributing the contributions of pre-fire stand conditions (many of which resulted from prior timber harvesting); this is important as prior stand treatments surely influenced burn severity and pre-fire understory vegetation composition. Fourth, without comparison to other studies, it is difficult to generalize without understanding the unique effects of the salvage equipment and intensity applied here, site differences, and post-burn climate. Additional studies that help untangle the complexities associated with interacting disturbances will assist in providing science-based directions for forest managers tasked with managing post-fire landscapes.

## CONCLUSIONS

Burn severity influenced understory vegetation response more than post-fire salvage logging and seeding with locally adapted native grasses. Vegetation cover was lowest on plots burned with high severity fire that were both seeded and salvage logged. Salvage logging did reduce canopy cover in both forbs and shrubs, but cover of graminoids was higher when salvage logged, indicating that salvage logging may not affect all plant forms in the same way. Seeding with locally sourced native grasses allowed native forbs, shrubs, and conifers to establish and grow but in lower abundance when grass cover was high. Initial differences, although pronounced, declined with time so that vegetation richness, diversity, and abundance of shrubs, forbs, and grasses were all similar near the end of the study period, whether they were salvage logged or not. Our findings are consistent with theory and previous findings, suggesting that seeding and salvage logging can hinder the recovery of understory vegetation, especially on sites that burn at high severity. Few studies have similarly monitored the post-fire response of vegetation over half a decade, yet this early successional period shapes forest community development and management implications for interior mixed-conifer forests.

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