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Complex restoration challenges: Weeds, seeds, and roads in a forested Wildland Urban Interface

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ABSTRACT

Federal policies in the US strongly emphasize reducing hazardous fuels at the Wildland Urban Interface (WUI). However, these areas present restoration challenges as they often have exotic weeds, frequent human disturbance, and the presence of roads. Understanding seed banks is important in planning for desirable post-disturbance community conditions, developing integrated weed management programs, and complying with State and Federal regulations. We characterized the aboveground vegetation and seed bank in a WUI composed of mixed age dry-mixed conifer forest stands in central Washington State, and examined patterns and relationships between aboveground vegetation and seed bank germinant abundance in relation to distance to road, seed bank layer, and herbicide treatments. Noxious weed frequency, as well as exotic weed and annual native forb cover, significantly decreased with distance from road, while native graminoid cover increased, declining beyond 20 m. Herbicides did not affect composition of the aboveground community in the short term. Six hundred and thirty seeds germinated from litter and mineral soil samples over a 5 month trial, and 43 species were identified. Most germinants (77%) and species (36 species) emerged from the litter layer compared to mineral soil, and the majority were annual forbs, followed by perennial forbs, native graminoids and exotic species. Little similarity was found between the extant vegetation and seed bank floras. Fourteen percent of germinants were exotic species, and were found in similar abundances regardless of proximity to road or herbicide treatment. Findings from our study suggest that (1) roads strongly influenced aboveground vegetative cover and species composition; (2) seed bank contributions to desirable post-disturbance understory development may be relatively low, especially if activities remove the litter layer; (3) weed populations were largely confined to near road environments, but the weed seed bank, which is a substantial part of the total seed bank, was not; and (4) herbicide treatments were ineffective and did not impact seed banks in the short term.

1. Introduction

Forested landscapes in the western US are experiencing expanding levels of urbanization creating an intermix of housing and wildland vegetation often referred to as the Wildland Urban Interface (WUI) (Radeloff et al., 2005; Theobald and Romme, 2007). These areas are characterized by low and medium housing density, extensive road systems, and a mix of private and public land ownership intermingled. Changes in light, temperature and soil moisture (Saunders et al., 1991) within the WUI are combined with high levels of disturbance and human use that may promote invasive species spread (Trombulak and Frissell, 2000; Alston and Richardson, 2006). These highly fragmented forest systems are also experiencing large and severe wildfires, insect outbreaks, and forest disease epidemics (Everett et al., 1994; Vitousek et al., 1996; Harrod and Reichard, 2000; Hessburg et al., 2005) leading to federal policies that prioritize hazardous fuels reduction where human population and housing values are at risk (Everett et al., 1994; Theobald and Romme, 2007; Schoennagel et al., 2009).

One of the most dominant features of WUI areas is the presence of unpaved roads intersecting forested wildland. It is estimated that 10% of the total US road length is contained within the national forest system alone (Watkins et al., 2003). Roads in particular have important impacts on invasive species spread in that they allow increased use of forest lands by humans (Trombulak and Frissell, 2000; Birdsall et al., 2012), and act as corridors for the dispersal

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of seed and plant materials via road fill and vehicles (Tyser and Worley, 1992; Forman and Alexander, 1998). They also provide safe sites for seed germination and establishment as a result of road construction and maintenance activities that create bare areas with higher light and resource availability and lower native plant cover (Gelbard and Belnap, 2003). Even in areas where exotics are currently restricted to roadsides, seeds may disperse into interior forest areas, creating reservoirs of propagules for future invasion.

Currently, there is only a limited understanding of how roads impact forest soil seed banks in the WUI in particular. Life history strategies of many invasive species support their rapid germination and establishment following a disturbance, contributing to the initial floristic composition of the site (Parks et al., 2005; Radosevich et al., 2007). In an effort to mitigate invasive plant species spread, limited use of authorized herbicides in wildland ecosystems, especially along roads, has been employed (USDA Forest Service and Pacific Northwest Region, 2005). However, the effectiveness of herbicide treatments and their potential impact on soil seed banks are rarely examined. Few studies have been conducted on the effect of herbicide application on seed bank characteristics, and the vast majority of those were conducted in agricultural systems (Roberts and Neilson, 1981; Morash and Freedman, 1989; Buhler et al., 1997).

Given the current emphasis on hazardous fuels reduction at the WUI, understanding how roads and herbicide treatments impact the aboveground native and exotic vegetation and the seed bank is important in planning for desirable post-disturbance community conditions, developing integrated invasive plant management programs, and for complying with state and federal laws and policies. While it has generally been shown that seed banks are poor sources for ecological restoration in many forested environments, most studies have been conducted in less fragmented ecosystems (Korb et al., 2005; Roovrs et al., 2006; Lang and Halpern, 2007; Bossuyt and Honnay, 2008; Valkó et al., 2011). It is unclear how results from these studies translate into the highly fragmented WUI environment and whether disturbance effects are exacerbated in the WUI creating a larger suite of colonizing species within the seed bank. Whether the soil seed bank in a WUI can provide source material for ecological restoration will depend on many factors, including the abundance and richness of native species, their patterns within these fragmented systems in relation to their highly roaded character, and management actions such as herbicide use.

The objectives of this study were to characterize the aboveground vegetation and seed bank in mixed age, mid-elevation, dry mixed conifer forest stands in a WUI prior to scheduled fuel reduction activities, and to explore implications related to forest restoration and exotic and noxious plant species control. We examined patterns and relationships between aboveground vegetation and seed germinant abundance and richness in relation to seed bank layer, distance to road edge, and herbicide treatments. We chose to examine seed bank layer (litter versus mineral soil) because fuel reduction activities often strongly alter the forest litter layer. We address the following broad questions:

- How do roads and herbicide treatments influence plant community and seed bank composition as you move away from the road edge and into the forest interior?
- Can spot herbicide treatments along the road edge mitigate noxious spread in the aboveground vegetation and do these treatments impact the seed bank in the short term?
- Is seed bank composition largely uncoupled or coupled to aboveground vegetation and does this relationship change with distance to road?
- What is the seed bank potential if the forest litter layer is removed with disturbance?

2. Materials and methods

2.1. Study site

The study was conducted on the eastern slopes of the Cascade Mountains in mixed-conifer dry forest within 1 km of Liberty, Washington (47°15′12″N, 120°40′4″W) at an elevation ca. 730–1100 m in the Okanogan–Wenatchee National Forest (Fig. 1). The Liberty study area is located within a matrix of WUI comprised of medium and low density intermix (> 6 and < 741 housing units km^{-2} and vegetation > 50% of census block), as well as very low density vegetation areas (> 0 and < 6.17 housing units km^{-2} and vegetation > 50% of census block; Radeloff et al., 2005). None of the roads in the study area are paved, and the majority of the soils are loams and clay loams formed in residuum, colluvium and alluvium derived from basalt and andesite with loess and minor amounts of volcanic ash (USDA-NRCS, 2009). Climate is maritime with hot, dry summers and cold, wet winters. Annual precipitation ranges from 114 to 127 cm and occurs primarily as snow during the winter months (Camp, 1999). Dominant conifer species are: *Pseudotsuga menziesii*, *Pinus ponderosa*, *Abies grandis* and *Pinus contorta*. *Larix occidentalis*, *Abies lasiocarpa* and *Juniperus occidentalis* are found as minor overstory components in the study area. Common understory species include: *Ceanothus velutinus*, *Arctostaphylos uva-ursi*, *Spiraea betulifolia*, *Calamagrostis rubescens*, *Carex geyeri* and *Lathyrus pauciflorus* (Table 1). State listed noxious weeds include: *Cirsium vulgare*, *Cirsium arvense*, *Centaurea diffusa*, *Centaurea pratensis*, and *Artemisia absinthium* (Table 1).

2.2. Experimental design

For aboveground vegetation analyses a split-plot randomized complete block (RCB) design was established in June 2006 with two factors: herbicide treatment and distance from road edge (0, 10, 20 and 30 m). Herbicide treatment was the whole-plot treatment, and distance from road edge was the subplot (split) treatment. For seed bank analyses we added a seed bank layer treatment (mineral soil layer and litter layer), creating a split-split plot RCB design. Blocking was based on harvest units ($n = 7$, average size = 16.4 ha) for proposed hazardous fuel reduction activities, established in 2006 by Cle Elum Ranger District timber staff based on site and vegetation characteristics. None of the blocks was adjacent to another (minimum distance between blocks = 1 km). The corner of each block was randomly located within each harvest unit with one edge of the block adjacent to the road. Each block was divided into two 50 × 50-m experimental units (EU) with one EU randomly selected for herbicide treatment and the other as a control. EUs were adjacent in three of the seven blocks with a 30 m buffer separating sampling plots, and were separated by 50 m in the remaining four blocks. In July 2006 state-listed noxious weeds were backpack sprayed with a Tordon® (glyphosate), Blazon® solution and again in July 2007 with an Aqua Neat® (picloram, 6pt/100), LI-700 (3pt/100), Blazon® (3pt/100) herbicide solution in those EUs selected for herbicide treatment and within a 15 m buffer, as well as within 100 m from each block edge and along the adjacent roadside to minimize invasive spread outside of the study blocks. July spraying maximized leaf absorbance but was prior to seed set, and followed district operational standards. These herbicides target annual and perennial broadleaf plants and are appropriate for the noxious weeds present in the study area. This treatment was similar (but more controlled) to treatments that had been ongoing in the area for many years. Herbicide was spot applied to each individual weed with a backpack

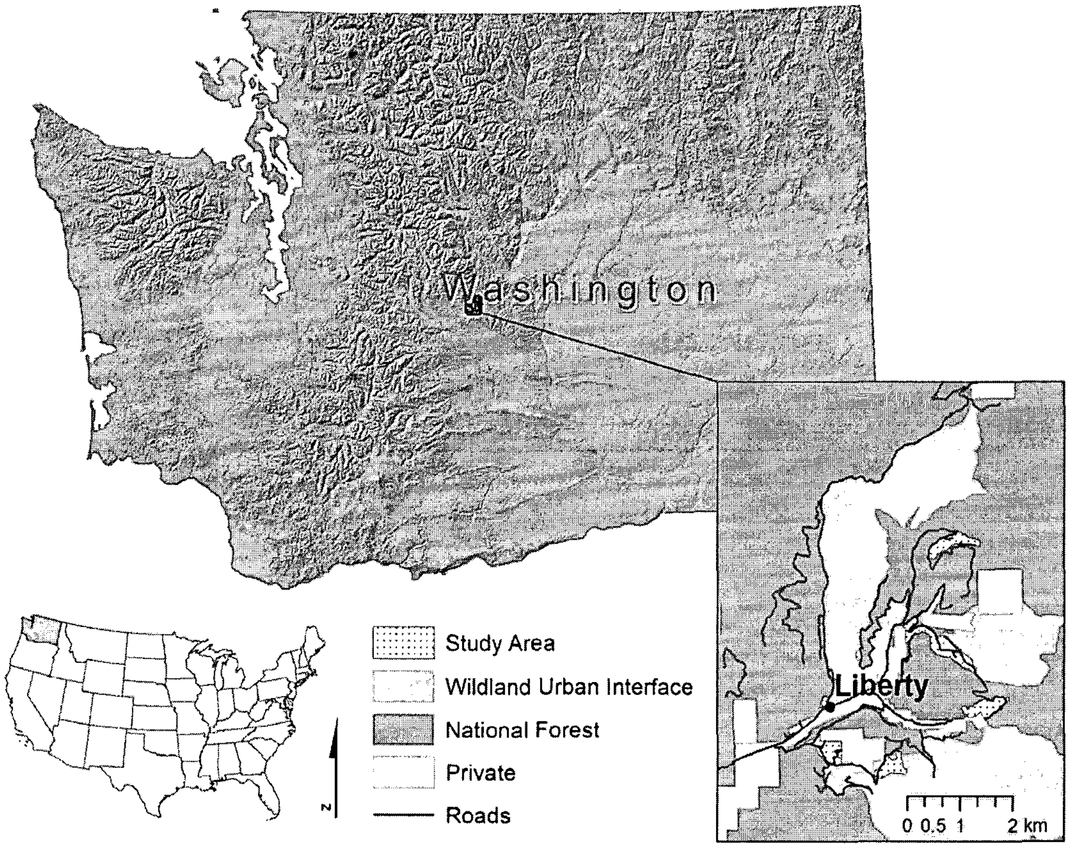

Fig. 1. Liberty study area showing extent of roads, Wildland Urban Interface, land ownership, study area units and the town of Liberty within Washington and the US.

Table 1
Five most dominant species within each functional group in the aboveground understory vegetation with mean cover values across the study area based on 1 × 1-m cover plots.

Functional group	Dominant species[a]
Tree	*Psuedostuga menziesii* (6.5%), *Abies grandis* (5.1%), *Pinus ponderosa* (1.7%), *Pinus contorta* (0.1%), *Larix occidentalis*[b]
Shrub	*Ceonothus velutinus* (10.5%), *Arctostaphylos uva-ursi* (8.4%), *Spiraea betulifolia* (4.9%), *Purshia tridentata* (4.7%), *Symphoricarpos albus* (4.6%)
Native graminoid	*Calamagrostis rubescens* (29.9%), *Carex geyeri* (9.5%), *Elymus glaucus* (1.8%), *Festuca occidentalis* (1.0%), *Agrostis scabra* (1.0%)
Perennial, native forb	*Achillea millefolium* (2.5%), *Arenaria macrophylla* (1.4%), *Lathyrus pauciflorus* (1.1%), *Hieracium* spp. (0.9%), *Arnica cordifolia* (0.6%)
Annual, native forb	*Collinsia parviflora* (0.8%), *Microsteris gracilis* (0.5%), *Collomia grandiflora* (0.2%), *Epilobium minutum* (0.2%), *Cryptantha torreyana* (0.1%)
Exotic	*Agropyron intermedium* (4.4%), *Dactylis glomerata* (1.3%), *Bromus tectorum* (0.8%), *Taraxacum officianalis* (0.3%), *Trifolium repens* (0.2%)
Noxious	*Centaurea pratensis* (0.6%), *Centaurea diffusa* (0.4%), *Cirsium vulgare* (0.01%), *Artemisia absinthifolium*[b]

[a] Nomenclature follows Hitchcock and Cronquist (1973).
[b] Not present in cover plots, but recorded in 3 × 3-m presence/absence plots.

sprayer thus minimizing treatment of non-target species. Noxious weeds were present as sporadic individuals and in very small patches.

Within each EU, three parallel transects running 50 m perpendicular from the road edge into the forest were established. All roads were unpaved, USDA Forest Service roads, used by the public to access housing and recreation and at least ca. 30 years old and all but one road was heavily used (Cle Elum District, pers. comm.). Roads were frequently graded, and infrequently brushed and plowed, and were utilized by logging, grazing and mining operators. Along each transect four 3 × 3-m plots were established at 0, 10, 20 and 30 m from the road edge. Thirty meters was determined to be the necessary distance needed to capture differences associated with road distance without confounding results by encountering other roads. Plots were averaged by distance to road categories for aboveground vegetation results, and by distance to road and seed bank layer for seed bank results.

2.3. Field sampling

Aboveground vegetation was sampled in the summer of 2007 using nested plots. Sampling occurred over 1 year after the 2006 herbicide treatment, but only shortly after the 2007 herbicide treatment. Thus effects from the herbicide treatment for aboveground vegetation should largely be related to the response to the 2006 treatment as mortality effects from the 2007 application may not have been immediate. Ground cover and aboveground vascular plant cover (by species) were measured visually to the nearest percent using a marked 1 × 1-m frame. Ground cover included bare ground, rock and litter. In the 3 × 3-m plot presence of all rooted vascular plant species was recorded. Live tree species and diameter at breast height (dbh) were recorded for trees over 1.37 m in height, and tree seedlings (regenerating conifer density, individuals < dbh) were tallied. While these plots are small for overstory sampling, our focus was on the understory and its immediate environment. Initial sampling in 2006 revealed that the plot size was adequate to detect differences in overstory canopy cover and basal area. Overstory canopy cover was measured at each plot corner using a moosehorn densitometer (Garrison, 1949). Slope and aspect were also measured; aspect was transformed into heat load index using the following equation $\frac{1-\cos(aspect-45)}{2}$, where zero represents the coolest slope (northeast) and one the warmest (southwest) (McCune and Grace, 2002). Shrub cover was estimated using the line intercept method by recording the length of each shrub species that intercepted the 3 m transect. Litter and duff depth was measured at 75, 150 and 225 cm along this transect.

Seed bank sampling was conducted in late September 2007 to ensure inclusion of the current year's seed rain prior to field germination and included both persistent and transient seed banks. Again, sampling occurred over 1 year after the 2006 herbicide treatment, and 2 months after the 2007 herbicide treatment. Samples were collected in the center of the 3 × 3-m plots to allow for comparisons with the aboveground vegetation data and separated into litter/duff and mineral soil samples. Litter was defined as newly fallen organic matter (Oi) combined with the fermentation and humus layers (Oe + Oa) (Soil Survey Division Staff, 1993). Litter was collected from a 10 × 10-cm square, and two mineral soil cores (5 cm wide × 10 cm deep) were extracted with a soil corer from the area cleared of litter/duff and consolidated into a single sample. A conservative 10 cm depth was selected to maximize capture of the seed bank. Litter depth varied, thus sample volume varied widely (50–2133 cm^3). The two mineral soil cores had a total volume of ca. 39.3 cm^3 (not accounting for bulk density). Given differences in litter versus mineral soil depths (and thus volume), we present seed bank density results per cubic centimeter in order to directly compare samples. A total of 336 samples (168 litter and 168 mineral soil samples) were collected from the seven blocks.

2.4. Greenhouse methods

A controlled greenhouse seedling emergence method was used to estimate the germinable fraction of the seed bank. Methods were adapted from Kellman (1970), Strickler and Edgerton (1976) and Kramer and Johnson (1987). Prior to placement in the greenhouse, all samples were weighed and spread over 2–3 cm of vermiculite in a 19 × 28-cm germination tray. Trays were watered to field capacity, allowed to drain for 12–24 h and then transported to a cooler held in darkness at approximately 2 °C for a 60 day moist-cold stratification period. Following stratification, trays associated with a block were randomly assigned to a greenhouse bench. Block was maintained in the cooler and in the greenhouse so random variation associated with blocking and random variation associated with cooler and greenhouse microclimate differences would not be confused. A control tray filled with vermiculite was placed on each of the four benches to test for unintended greenhouse contaminants.

Supplemental lighting consisted of continuous day-length extension lighting to achieve a 16 h photoperiod and 8 h dark period (Landis, 1990). Four 1000 w high-intensity discharge lamps (sodium halide) were used for photoperiodic control and were positioned to provide consistent lighting throughout the greenhouse. Because optimal germination temperature for a wide range of species has been shown to be between 22 and 24 °C (McLemore, 1969; Barnett, 1979; Landis, 1990), and thermoperiodism is preferential to a continuous temperature regime (Landis, 1990), average greenhouse temperatures were maintained at 23 °C during the day and 18 °C at night. Average relative humidity was maintained at approximately 49%.

Samples were watered as needed to maintain moist soil and litter conditions. Seedling emergence was monitored daily. When positive identification of a seedling was not possible, it was transplanted and monitored until it could be identified. If seedling emergence appeared to be the result of vegetative reproduction, the specimen was removed from analysis; however, emergents from *Poa bulbosa*'s bulbils were counted as seedlings in this study. Those seedlings that died before positive identification could be made were identified to their highest taxonomic level, counted and removed from the tray. Germination was tracked for 5 months.

2.5. Data analysis

Due to a high number of species present in the aboveground plant community, species were lumped into functional groups rather than analyzed individually. Six functional groups were analyzed: exotic, noxious, annual native forbs, perennial native forbs, native graminoids, and shrubs (Table 1). Exotic species are any successfully reproducing species of foreign origin listed in the USDA plants database as introduced. Noxious weeds are species of foreign origin designated by a state or federal regulatory body as having the potential to cause significant injury to the environment, economy or human health (Clinton, 1999; Plant Protection Act, 2000). While all exotic species are of concern to land managers charged with maintaining native biodiversity, noxious species were the target of our herbicide treatments as they pose a greater threat to the environment than some exotic species, and carry with them more rigorous laws and policies mandating their control (Federal Noxious Weed Act, 1974; Clinton, 1999; Plant Protection Act, 2000).

Aboveground vegetation functional group cover and richness data, as well as ground cover, canopy cover, total plant cover, litter depth, basal area and regenerating conifer density were analyzed as a randomized complete block, split-plot ANOVA design with block as the random effect and main treatment effects (herbicide application and distance to road category), and their interaction, as fixed using Proc Mixed in SAS 9.2 (SAS Institute Inc., 2008). Noxious weed frequency was analyzed rather than cover due to problems with zero-inflated cover data that violated the assumptions of parametric tests. Seed bank density and richness data were analyzed as a randomized complete block split-split plot design with block as the random effect and treatment effects (herbicide, distance to road category and seed bank layer), and their interactions, as fixed effects. Variables were transformed to meet assumptions of normality and equal variance based on assessment of residuals. Means or uncorrected backtransformed means and 95% confidence intervals are presented. Alpha was set at 0.05. Distance to road edge is a quantitative treatment and therefore comparison among distances was done with orthogonal polynomials to determine if there were any significant trends.

Community composition was assessed using non-metric multidimensional scaling (NMS) in PC-ORD 5.1 (McCune and Mefford, 2006). For aboveground vegetation, rare species (present in < 5% of the plots) were removed (McCune and Grace, 2002) and a dummy variable with cover of 0.05% was assigned to all samples to account for plots with no vegetation (Clarke et al., 2006). Vegetation cover data were converted to proportions and arcsine square root transformed (McCune and Grace, 2002). NMS was run in autopilot mode with the Bray-Curtis distance measure, maximum number of iterations of 250 (50 runs with real data) with a random start and an instability criterion of 0.00001. Seed bank data were similarly analyzed with NMS with rare species (present in < 3% of the samples) removed and a dummy variable with emergence density of 0.0001 assigned to all samples to account for samples with no seedling emergence (Clarke et al., 2006). Counts were relativized by species maximum and run in PC-ORD as above. Environmental variables (canopy cover, litter depth, litter cover, tree basal area, bare soil cover, rock cover, heat load index, and slope) were superimposed on NMS ordination results using a joint plot, based on the correlation of each variable with ordination axes, for aboveground vegetation only.

Similarity between the aboveground vegetation and seed bank was assessed using presence/absence data with both NMS (as above) and the blocked multi-response permutation (MRBP) procedure in PC-ORD. A dummy variable of 0.05 was added to samples, as above, to account for samples with no species present to create observations with a species composition of virtually nothing (Clarke et al., 2006). We did not include environmental variable tests for the NMS ordination because the variables would be replicated for each paired sampled. The MRBP was run with the Euclidean distance measure and median alignment with blocks (recommended for randomized block designs; McCune and Grace, 2002) where grouping was the herbicide-road distance-seed bank layer combination. Where the MRBP results were significant we used Indicator Species Analysis in PC-ORD to determine how species were separated into our aboveground vegetation and seed bank groups. We report results for species with $P \leqslant 0.05$ and indicator values greater than 50 (McCune and Grace, 2002) for aboveground vegetation and greater than 20 for the seed bank.

3. Results

3.1. Aboveground vegetation abundance, richness and composition

Two hundred and five vascular plant species were encountered in the study area, and 147 were sampled in the aboveground vegetation with just over a third of the species being perennial native forbs and 22 exotics. Mean total understory plant cover across the study area was 32%, dominated by the native species *C. rubescens*, *C. velutinus* and *C. geyeri*. Shrubs were the most dominant functional group in cover, closely followed by graminoids (Table 2).

Overstory canopy cover and basal area increased with distance from road edge (linear $P < 0.0065$) with overstory cover decreasing slightly beyond 20 m (quadratic $P = 0.0006$) (Table 2). Graminoid cover also increased with distance from road edge, decreasing slightly beyond 20 m (linear $P = 0.0207$, quadratic $P = 0.0016$), while annual native forb and exotic cover, and noxious frequency exhibited the inverse pattern (Table 2). Shrub cover showed an initial increase in cover away from the road, then a sharp decrease. However, this result was not statistically significant. The other functional groups did not differ in cover in response to road distance. There were no effects of short-term (1 year) herbicide treatment on any plant functional group, including noxious weeds.

Overall understory richness, as well as annual native forb richness, decreased with distance from road edge; exotic and noxious weed richness also decreased with distance from road edge, but declined precipitously between 0 and 10 m (Table 2). Eighteen exotic species and five noxious species were encountered. There were no differences in graminoid or perennial native forb richness. For ground cover, both soil and rock cover decreased with distance from road edge, increasing slightly somewhere beyond 20 m, although there were no differences in litter cover (Table 2). Litter depth, however, increased with distance from road edge, decreasing somewhere between 10 and 20 m (linear $P = 0.0176$, quadratic $P = 0.0072$).

Analyses of aboveground community composition showed no trends for herbicide treatment, but separation of the 0 m road edge samples from all other distance to road edge categories is clearly apparent in the ordination result, and was strongest along axis two which captured 25% of the ordination variance (stress = 16.6, instability = 0.00001 after 75 iterations). Canopy cover exhibited the highest correlation ($r^2 = 0.32$) to ordination scores (Fig. 2a). Axes one and three captured 15% and 34% of the remaining ordination variance, respectively. Soil cover was correlated with axis one ($r^2 = 0.25$).

3.2. Seed bank density, richness, and composition

Six hundred and thirty seeds germinated from 90 of the 168 litter samples and 43 of the 168 mineral soil samples. Forty-three vascular plant taxa representing 18 families and 32 genera were identified in the seed bank. A total of sixty germinants (10%) died before they could be positively identified; these were recorded at higher taxonomic levels (36 forbs and 24 grasses). The native annual forbs *Collinsia parviflora* and *Microsteris gracilis* were the most

Table 2
Aboveground vegetation functional group and forest floor results for distance to road edge. Uncorrected backtransformed least squared means and 95% confidence intervals (CI) presented. There were no significant interactions with herbicide treatment. Mean richness values are based on 3 × 3-m plots. See text for detailed descriptions of response variables.

Response variable	0 m		10 m		20 m		30 m		$F_{3,36}$	P
	Mean	CI	Mean	CI	Mean	CI	Mean	CI		
Vegetative abundance										
Total cover	27.2	(14.2–52.3)	41.8	(21.7–80.3)	31.3	(16.3–60.2)	29.3	(15.2–56.3)	1.38	0.2639
Shrub cover	12.6	(1.5–100)	16.8	(1.9–100)	5.4	(0.6–46.5)	4.1	(0.5–35.8)	1.06	0.3797
Graminoid cover	3.5	(1.4–8.6)	13.6	(5.8–28.8)	14.0	(6.0–29.5)	9.1	(3.8–20.5)	6.02	0.0020
Perennial native forb cover	2.6	(1.4–5.1)	2.2	(1.1–4.2)	2.5	(1.3–4.9)	2.5	(1.3–4.8)	0.15	0.9260
Annual native forb cover	1.5	(1.1–2.1)	1.0	(0.7–1.5)	1.0	(0.7–1.5)	0.9	(0.7–1.3)	4.04	0.0142
Exotic cover	3.3	(0.9–11.5)	0.06	(0.02–0.2)	0.03	(0–0.1)	0.01	(0–0.04)	28.23	<0.0001
Noxious frequency	0.23	(0.14–0.39)	0.05	(0.03–0.08)	0.07	(0.04–0.11)	0.06	(0.04–0.10)	10.92	<0.0001
Regenerating conifer density (ha^{-1})	407	(13–13088)	118	(4–3791)	3.6	(0–115)	44.8	(1–1440)	2.68	0.0612
Tree basal area ($m^2\ ha^{-1}$)	7.8	(0.1–34.4)	73.0	(30.0–134.8)	42.0	(11.6–91.1)	96.3	(45.5–165.9)	4.35	0.0102
Overstory canopy cover	14.4	(1.3–27.5)	48.5	(35.4–61.6)	55.8	(42.7–68.9)	51.2	(38.1–64.4)	13.59	<0.0001
Richness										
Total	17.2	(14.5–20.0)	14.1	(11.4–16.8)	13.3	(10.6–16.0)	11.8	(9.1–14.5)	13.91	<0.0001
Graminoid	2.5	(1.8–3.1)	2.6	(2.0–3.2)	2.5	(1.9–3.1)	2.2	(1.6–2.8)	1.24	0.3100
Perennial native forb	4.2	(2.9–5.6)	4.3	(2.9–5.7)	4.1	(2.7–5.4)	3.7	(2.3–5.1)	0.56	0.6437
Annual native forb	3.3	(2.2–4.3)	2.3	(1.3–3.4)	2.0	(0.9–3.0)	1.6	(0.5–2.7)	6.06	0.0019
Exotic	3.4	(2.8–4.1)	1.4	(1.1–1.6)	1.3	(1.0–1.5)	1.2	(1.0–1.4)	59.27	<0.0001
Noxious	0.8	(0.7–1.0)	0.5	(0.4–0.6)	0.5	(0.5–0.6)	0.5	(0.4–0.6)	11.02	<0.0001
Ground cover										
Litter cover	90.8	(80.1–96.0)	91.8	(82.1–96.5)	93.7	(85.9–97.3)	90.4	(79.4–95.9)	0.66	0.5837
Litter depth (cm)	2.2	(1.1–3.2)	4.2	(3.2–5.3)	3.8	(2.8–4.9)	3.7	(2.7–4.7)	5.63	0.0029
Rock cover	3.2	(1.6–6.1)	1.2	(0.6–2.3)	1.2	(0.6–2.2)	1.4	(0.7–2.8)	5.99	0.0020
Soil cover	3.9	(1.6–9.2)	2.0	(0.8–4.8)	1.6	(0.7–4.0)	2.0	(0.8–4.9)	3.43	0.0269

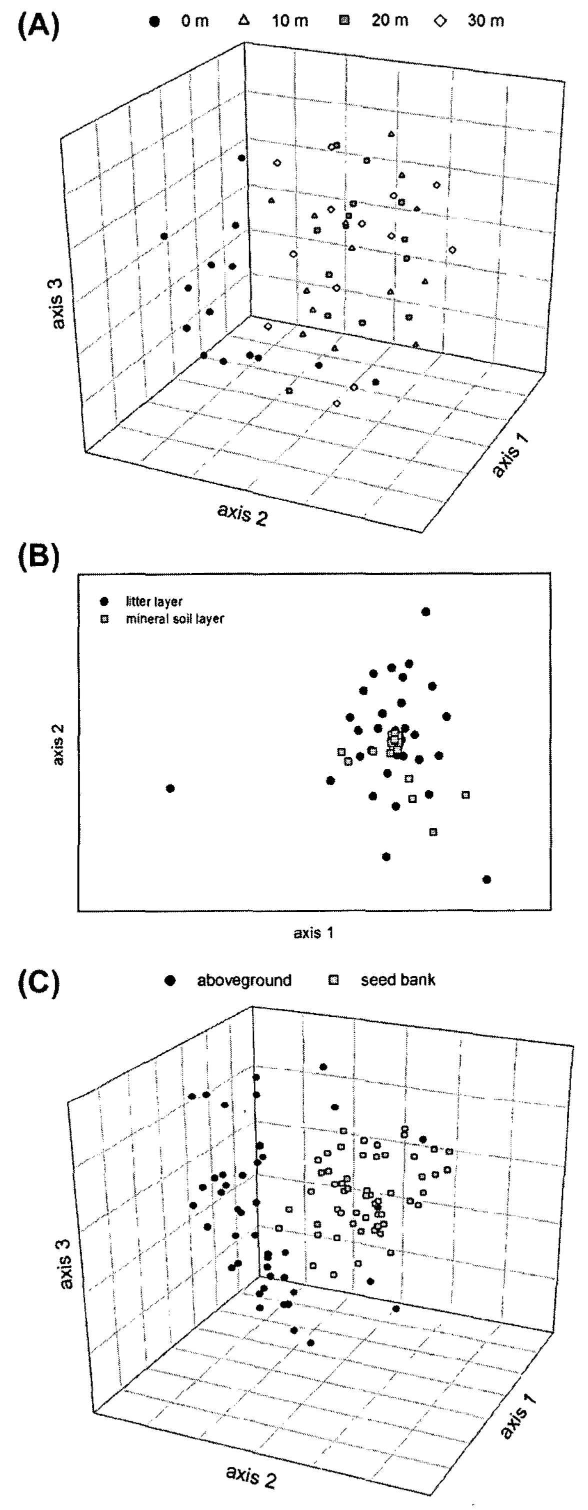

Fig. 2. Non-metric multidimensional scaling ordination results for species composition for (A) aboveground vegetation cover by distance to road edge, (B) seed bank germinant density by layer, and (C) aboveground vegetation and seed bank presence/absence. Symbols are sample units in ordination space.

abundant species in the seed bank. No germinants emerged from the four control trays placed on greenhouse benches. The average germinant density across the study site for mineral soil samples only was 73 m^{-2} (range 0–792).

Unlike aboveground vegetation, there were no significant differences in germinant density with distance from road edge, except for perennial native forbs. There was a significant interaction between distance to road edge and seed bank layer for perennial native forb germinant density ($F = 4.07$, $P = 0.0118$). While perennial native forb germinant density in the litter layer increased with distance from road edge, declining somewhere beyond 20 m, density in the mineral soil layer showed the exact opposite pattern (layer quadratic $P = 0.0083$). For all other functional groups, including total germinant density, the litter layer had significantly higher germinant density than the mineral soil layer (Table 3). There were no significant differences due to herbicide treatment.

Due to the low number of germinants in a given experimental unit (mean = 2), germinant richness was assessed overall and not by functional group. Germinant richness was significantly higher in the litter layer than the mineral soil layer (Table 3). Seven exotic species and three noxious species were encountered in the litter layer, while only one exotic and one noxious species (both also represented in the litter layer) were encountered in the mineral soil layer. No differences were seen in germinant richness for herbicide treatment or distance to road edge.

Community composition showed similar patterns to germinant density results, with the only compositional differences found between the litter and mineral soil layers (Fig. 2b). Axes 1 and 2 captured 50% and 28% of the ordination variance, respectively, but there was a high level of overlap between both layers (stress = 18.1, instability = 0.00148 after 200 iterations) on both axes. While patterns in composition are evident between the two layers, instability for this ordination was high, possibly due to a high number of samples with few germinants.

3.3. Seed bank similarity to aboveground vegetation

Thirty species were common to both the seed bank and aboveground vegetation floras, almost equally divided between the gramoinoid, forb and exotic groups, with three noxious species. Only 20% of the species detected in the aboveground vegetation were seen in the seed bank. Seven species were present in the seed bank and absent in the vegetation, and those were dominated by native ruderal forbs and exotic species (Table 4), thus 24% of seed bank species were not seen in the vegetation. Species occurring at high frequencies in the vegetation were often absent or nearly absent in the seed bank. *C. rubescens*, the most abundant species in the vegetation, was completely absent from the germinable seed bank. NMS ordination showed no overlap in composition between the seed bank and aboveground vegetation on two of the three ordination axes (stress = 16.04, instability = 0.00001 after 142 iterations) (Fig. 2c). The three axes captured 30%, 31% and 16% of the ordination variance, respectively. Results of the MRBP were consistent with NMS. There was a significant difference between the seed bank and aboveground vegetation ($A = 0.133$, $P < 0.0001$), although compositional differences were fairly small. Examination of similarity at the plot scale showed that only 14 of our seed bank species showed a plot concordance (percentage of plots in which a species occurred within the seed bank and also in the associated aboveground vegetation; Abella et al., 2007) greater than 50; and nearly half of all species showed zero correspondence between the seed bank and the associated aboveground vegetation.

Indicator species analysis showed many species were significant indicators for the aboveground vegetation, but those with the highest scores ($IV > 70$, $P = 0.0002$) were all trees, shrubs or perennial dominant grasses and sedges, with the exception of the perennial forbs *Achillea millefolium* and *Arenaria macrophylla*. Not many species occurred in the seed bank in high enough frequency to be clearly identified as indicators, however two annual native forbs, *Collinsia parviflora* and *Microsteris gracilis*, and two perennial native forbs, *Epilobium watsonii* and *Gnaphalium microcephalum*, were significant indicators ($IV > 20$, $P < 0.003$).

Table 3
Seed bank germinant density by functional group and total germinant richness results for seed bank layer. Uncorrected backtransformed least squared means and 95% confidence intervals (CI) are presented; density values are multiplied by a factor of 1000 to improve clarity. Significant interactions with road edge distance are denoted by an asterisk. See text for detailed descriptions of response variables.

Response variable	Litter layer		Mineral soil layer		$F_{1,48}$	P
	Mean	CI	Mean	CI		
Seed bank germinant						
Total density (cm^{-3})	4.4	(2.3–8.4)	0.74	(0.39–1.4)	43.08	<0.0001
Graminoid density (cm^{-3})	0.36	(0.25–0.52)	0.26	(0.18–0.38)	4.32	0.0431
Perennial native forb density (cm^{-3})	0.53	(0.31–0.91)	0.39	(0.23–0.67)	–*	–*
Annual native forb density (cm^{-3})	1.5	(0.9–2.3)	0.28	(0.18–0.44)	50.58	<0.0001
Exotic density (cm^{-3})	0.34	(0.25–0.47)	0.22	(0.16–0.3)	11.61	0.0072
Noxious presence[a]	0.09	(0.06–0.12)	0.06	(0.04–0.08)	6.39	0.0148
Richness (cm^{-3})	0.002	(0.001–0.004)	0.0005	(0.0003–0.001)	58.89	<0.0001

* Significant distance to road edge by seed bank layer interaction found ($F_{3,48}$ = 4.07, P = 0.0118). Perennial native forb germinant density in the litter layer increases with distance from road edge but starts to decline at some point beyond 20 m (quadratic P < 0.0083); perennial native forb germinant density in the mineral soil layer decreases with distance from road edge, increasing somewhere beyond 20 m.

[a] Number of subplots with noxious germinants.

Table 4
Species encountered in seed bank samples and (1) associated mean seed bank density multiplied by a factor of 1000 to improve clarity (n = 112), (2) frequency (n = 112) in the seed bank, (3) frequency encountered in the 3 × 3-m aboveground vegetation presence/absence plots (n = 56), and (4) assigned functional groups, averaged across the study area.

Latin name[a]	Seed bank		Vegetation	
	Density (cm^{-3})	Freq.	Freq.	Functional group
Achillea millefolium	0.048	6	45	Perennial native forb
Agrostis exarata	0.026	1		Native graminoid
Agropyron intermedium	0.081	1	13	Exotic
Apocynum androsaemifolium	0.013	1	10	Perennial native forb
Artemisia absinthium	0.026	1	1	Noxious
Asteraceae sp. 1	0.034	2		Unassigned
Asteraceae sp. 2	0.011	1		Unassigned
Bromus carinatus	0.099	3	20	Native graminoid
Bromus tectorum	0.088	3	9	Exotic
Carex spp.	0.026	2	22	Native graminoid
Caryophyllaceae sp. 1	0.005	1		Unassigned
Cirsium arvense	0.296	7	1	Exotic
Cirsium vulgare	0.057	5	1	Noxious
Collomia grandiflora	0.037	4	27	Annual native forb
Collinsia parviflora	1.082	27	46	Annual native forb
Dactylis glomerata	0.009	1	14	Exotic
Deschampsia elongata	0.215	9	5	Native graminoid
Elymus glaucus	0.474	7	25	Native graminoid
Epilobium angustifolium	0.012	2	6	Perennial native forb
Epilobium minutum	0.016	2	23	Annual native forb
Epilobium watsonii	0.379	13		Perennial native forb
Fabaceae sp.[b]	0.054	2		Unassigned
Festuca spp.	0.386	9	24	Native graminoid
Galium aparine	0.390	3	11	Annual native forb
Galium triflorum	0.036	1	10	Perennial native forb
Gnaphalium microcephalum	0.334	14		Perennial native forb
Hieracium spp.	0.024	1	32	Perennial native forb
Lactuca serriola	0.005	1	1	Exotic
Lithophragma spp.	0.351	6	5	Perennial native forb
Microsteris gracilis	1.331	23	39	Annual native forb
Montia perfoliata	0.248	7	19	Annual native forb
Myosotis discolor	0.083	1	2	Exotic
Osmorhiza chilensis	0.030	2	17	Perennial native forb
Philadelphus lewisii	0.007	1		Shrub
Pinus sp.[b]	0.008	1		Tree
Poaceae spp.[b]	0.417	14		Unassigned
Poa bulbosa	0.323	2	11	Exotic
Purshia tridentata	0.035	2	25	Shrub
Rubus leucodermis	0.128	4		Shrub
Rumex sp.	0.008	1	2	Unassigned
Unknown shrub[b]	0.009	1		Shrub
Spiraea betulifolia	0.026	1	44	Shrub
Unknown dicot[b]	0.425	18		Unassigned
Unknown forb 1[b]	0.016	1		Unassigned
Unknown forb 2[b]	0.022	1		Unassigned
Verbascum thapsus	0.084	5		Exotic

[a] Nomenclature follows Hitchcock and Cronquist (1973).

[b] Not included in seed bank and aboveground vegetation similarity analyses.

4. Discussion

Wildland Urban Interface areas in the western United States present additional challenges for land managers responsible for maintaining native plant biodiversity, particularly following fuel reduction activities. These areas often have altered disturbance patterns from a century of fire suppression, juxtaposed with a long history of frequent human disturbance from road building, logging, grazing, mining and recreation. Our study represents a snapshot of vegetation and seed bank characteristics of a dry mixed-conifer forest in a WUI area in central Washington State.

Our results show road edges strongly influenced aboveground vegetative cover and species composition, and that the roadside edge environment in this study changes in less than 10 m as you move away from the roadside into the forest interior (Harper et al., 2005). Forest roadside edges were characterized by few trees, less forest floor depth, and more rock and soil cover. These areas also have higher cover and richness of exotic species and native annual forbs, and higher noxious species frequency and richness. While more common along the roadside edge, we found exotic individuals up to 30 m into the interior (our furthest interior distance) while noxious species were still limited to 20 m, although maximum invasion distance for individuals was not tested empirically. These results are similar to results from studies examining edge effects and fragmentation in general (Alston and Richardson, 2006; Pauchard and Alaback, 2006; Honu and Gibson, 2008; Lin and Cao, 2009) and indicate that roadside edges in WUI are structured similarly to other forests edges. Exotic, weedy, and pioneer species are located at the edge and the forest interior acts as a barrier for the penetration of these species further into the forest. Pauchard and Alaback (2006) found maximum tree height and overstory canopy cover best predicted alien species richness along highway edges in Gallatin National Forest, although our roads were unpaved, frequently disturbed by grading, and heavily used to access housing and recreation. Because seed availability does not seem to be a limiting factor, the mechanisms for this barrier effect are most likely due to environmental conditions associated with the forest interior (Lin and Cao, 2009); however, defining the forest interior in a WUI is difficult. We found some patterns in environmental variables and aboveground vegetation in relation to distance to road would often change around 20 m from the roadside (i.e., graminoid cover, regenerating conifer density, soil and rock cover, and litter depth). These patterns might be limiting seed germination and may indicate that there is really very limited forest interior or areas of relict forest in such a fragmented landscape. Observationally, we often found old and unused roads and skid trails at the end of our transects, thus we use the term forest "interior" with this qualification in mind.

In stark contrast to aboveground vegetation patterns, our results indicate that road edges did not influence seed bank abundance or composition. We found germinant density, frequency and richness to be low throughout the study area regardless of distance to road, herbicide treatment or seed bank layer. Our germination techniques and small sample size may have limited our ability to capture the full seed bank, however assuming our methods did not indirectly impact one treatment over another, we found interior forested areas had similar exotic and noxious species germinant density and richness as "weedy" roadside areas. And while exotic and noxious species were largely restricted to road sides in the aboveground vegetation, germinants were equally abundant in the forest interior. Thus the forest interior did not necessarily act as a good barrier for the penetration of weedy species' seeds. Lin and Cao (2009) found similar results examining edge effects in tropical and subtropical forests in southwest China. In particular, a problematic invasive species was found along the entire edge-to-forest interior gradient only in the seed bank, but was concentrated within five meters of the edge in the aboveground vegetation (Lin and Cao, 2009). In contrast Honu and Gibson (2008) found diversity of non-natives peaked between the forest edge and the interior, and germinant density of all species declined as you moved away from the edge into the interior forest. Similarly, Devlaeminck et al. (2005) found that ancient forest edges (areas that have been continuously forested for over 200 years) acted as a barrier for seed dispersal, and Cadenasso and Pickett (2008) found the edge acted as a physical barrier when they explicitly tested vegetation structure. However, numerous studies have shown that association with roads greatly increases propagule supply for non-native species, and while the previous studies examined edge effects and often disturbance, they did not include roads (Forman and Alexander, 1998; Pauchard and Alaback, 2006; Birdsall et al., 2012).

We also found that germinant density and richness were higher in litter layers compared to mineral soil as seen in similar comparisons elsewhere (Strickler and Edgerton, 1976; Pratt et al., 1984; Korb et al., 2005). However, from a restoration perspective, it is important to note that the majority of germinants were present in the litter layer, which can be removed or disturbed by management activities and wildfire. This germinant density pattern may also partially explain why roadside areas had low germinant density as roadside areas have very little litter cover and depth. But it should be noted that sampling surface area did differ between litter and soil samples, despite accounting for differences in depth, which may underestimate species richness and frequency in the mineral soil samples.

Despite the low abundance of exotic and noxious species in the vegetation (Table 4), several factors may explain why these species were present in soil and litter seed banks in our study even in the most interior locations away from the roads. Common life history strategies of successful invasive species are often characteristics that facilitate successful seed banking including: very high seed output, phenotypic and germination plasticity, adaptations for short- and long-distance dispersal, small seed size and high seed longevity (Baker, 1974, Louda, 1989, Radosevich et al., 2007). *C. vulgare*, a state-listed noxious weed found in our study was introduced from Western Europe, reproduces entirely by seed and can produce up to 120,000 seeds per individual plant (Zouhar, 2002). *A. absinthium*, also a state-listed noxious weed and prolific seed producer found in our study, can germinate in a wide range of environmental conditions, has small seeds and can remain viable in the soil for 3–4 years (Carey, 1994). *Verbascum thapsus* produces an average of 175,000 very small seeds per plant and was found to remain viable in the soil for over 100 years (Fenner and Thompson, 2005; Gucker, 2008). Results from this study suggest that even small populations of exotic species found in the vegetation are contributing to the development of the exotic species component in forest seed banks as far as 30 meters from the road and in both litter and mineral soil layers.

Our analysis showed that there was little similarity in species composition or abundance between the seed bank and vegetation floras, both at the plot scale and by treatment. This result is a typically reported pattern for many ecosystems (Hopfensperger, 2007; Bossuyt and Honnay, 2008), including both young and mature mixed conifer forests elsewhere (Zobel et al., 2007), although higher similarity has been reported in ponderosa pine forests (Abella et al., 2007; Abella and Springer, 2012). Annual and native forbs were associated with the litter and soil seed bank, compared with indicator species such as trees, shrubs or dominant grasses and sedges for the existing aboveground vegetation. But our most dominant grass species in the aboveground vegetation, *C. rubescens*, is a rhizomatous species and its seeds are known not to persist in the soil (Matthews, 2000). This may explain why some of the dominant perennials are absent in our samples, but nevertheless low germinant density and the almost complete lack of native vegetation that currently characterizes the on-site litter and soil seed bank means that it may be unlikely that the native ecosystem could be restored from on-site seed bank sources. Without management intervention (e.g., native seeding), common seed bank species, especially exotic and noxious plants, may exclude or inhibit desirable later successional species until resources are made available by their damage or death, possibly delaying the return of later successional species for considerable lengths of time (Connell and Slatyer, 1977; Pickett et al., 1987).

It is likely that our seed bank sampling technique and/or emergence method did not adequately capture the available propagule source at our sites, and that we have underestimated (1) the restoration potential of the seed bank in this system, and (2) the similarity of the seed bank composition to the aboveground composition. In general, it is expected that the soil and litter seed bank will underrepresent aboveground vegetation because it is difficult to capture all available propagules and provide ideal germination conditions for all species. Some aboveground species do not form large seed banks, yet it is possible that they are present in the seed bank but at levels we are unable to detect using common seed bank sampling procedures and a small sample area (Plue et al., 2012). It has been quantitatively shown in temperate deciduous forests that the number of species detected increases with an increase in total surface area sampled, particularly species with persistent seed banks which tend to be more rare (Plue et al., 2012). Therefore, results regarding the restoration potential of the seed bank in this system and how representative our seed bank results are of aboveground vegetation should be interpreted with these caveats in mind.

In our study we found no differences in vegetation cover, germinant density or species richness between herbicide and non-herbicide plots in any group tested, including the targeted noxious weed group. Small sample size, short-term duration of herbicide application and minimal presence of noxious plants may have influenced the results of tests of abundance in the aboveground vegetation, as well as the lack of differences in the density of noxious weeds in the seed bank. Yet of the studies conducted in agricultural and managed forest systems, few detected differences in seed bank species composition due to herbicide application, although Roberts and Neilson (1981) found decreases in weed seed abundance after 16 years of herbicide application, and Ball and Miller (1990) detected a shift to herbicide resistant species in plots receiving herbicide treatments after 3 years. Morash and Freedman (1989) found no differences in weed seed germination following a single aerial application of herbicide in a silvicultural system, and reductions in the weed seed bank in laboratory studies only after extremely high application rates uncharacteristic of herbicide residue after management application. And 6 years of herbicide application in a crop rotation system increased weed seed abundance in herbicide plots (Menalled et al., 2001). Although noxious weeds were not abundant in our stands, they occur abundantly in patches within the study area. It is possible that overall propagule supply from the surrounding area may be overwhelming the herbicide treatment. It is also possible that the herbicide used is simply not very effective for the targeted species. Further study on the efficacy of herbicide treatments on the abundance of targeted species in the aboveground vegetation, and the possible effects of treatments on the composition and abundance of weed seed banks, is critical to evaluating the use of herbicide as a tool for mitigating exotic species establishment and spread in these systems. The effects of herbicide application duration should also be examined.

Our results have implications for the invasion process of weedy and alien plant species into interior WUI environments. Thinning and other management activities (broadcast or slash pile burning) may exacerbate invasion processes already evident in these forests. Cadenasso and Pickett (2008) explicitly tested whether intact versus thinned deciduous forest edges function as barriers to species invasion into the forest interior, and found more seeds crossed into the thinned forest, and dispersed a longer distance. Post-disturbance floristic recovery may also be hampered by exotic and noxious weed invasion in WUI in particular, even if weed transfer and herbicide protocols are followed because these species are already present in the seed bank, and may be further reduced in areas where road density or other edges (housing boundaries, logging landings, etc.) limit the expanse of interior forest. We have shown that the WUI forest interior may be limited to patches less than 20 meters in length in some areas. Managers may consider following strict weed transfer protocols when conducting operational activities in highly roaded WUI environments, and using effective herbicides or other treatments and native seeding after activities to decrease weed invasion and assist with floristic recovery. While some recommend maintaining interior forest conditions to prevent the spread of undesirable species (Lin and Cao, 2009), this management strategy may be particularly difficult in fragmented WUI areas that necessitate active management to mitigate issues such as fire risk. Yet collaborative approaches that integrate fuel reduction treatments, weed management, post-disturbance vegetative management, and scientific data, may help overcome complex restoration challenges and protect WUI areas from wildfire risk and further invasion of exotic plant species.

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