AN ABSTRACT OF THE THESIS OF

Gabrielle Snider for the dual degree of Master of Science in Forest Science and Forest Resources presented on March 17, 2010.
Title: Aboveground Vegetation and Viable Seed Bank of a Dry Mixed-Conifer Forest at a Wildland-Urban Interface in Washington State

Abstract approved:

Paul S. Doescher Becky K. Kerns

Dry coniferous forests in the western United States are experiencing severe wildfires, insect outbreaks, forest disease epidemics and a growing presence of invasive species. Policies strongly emphasize reducing hazardous fuels at the Wildland Urban Interface (WUI) where communities and forests intersect. However, these areas present restoration challenges as they tend to have existing populations of exotic and invasive species due to frequent human disturbance and the presence of roads. This research examined the patterns and relationships between aboveground vegetation and seed germinant abundance and richness in relation to seed bank layer, distance to road, and herbicide treatments. The study was located on the eastern slopes of the central Cascade Mountains near Liberty, Washington; a high priority WUI area slated for hazardous fuels reduction. In June 2006 and 2007, herbicide was applied to noxious weeds in treatment plots, and aboveground vegetation, ground cover and site characteristics measured. In September 2007 litter and mineral soil samples were collected, cold-moist stratified and grown in a greenhouse. Six hundred and thirty seeds germinated from litter and mineral soil samples and forty three species identified. Most germinants (77%) and species (36 species) emerged from the litter layer compared to mineral soil (15 species) and the majority were annual forbs, followed by perennial forbs, graminoids and exotic species. Overall germinant density, frequency and richness were low regardless of distance to road, herbicide treatment or seed bank layer. Little similarity was found between the vegetation and seed bank floras. Fourteen percent of germinants were exotic and invasive species, and were found in similar abundances regardless of proximity to road or herbicide treatment. No effect of the herbicide treatment was found in the vegetation or the seed bank. Our findings suggest the contribution of forest seed banks for post-disturbance understories may be relatively low. Persistent vegetation and dispersal from off-site sources will likely play a large role in early succession following disturbance. However, post disturbance studies are needed to fully evaluate the role of the seed bank in early succession.

Aboveground Vegetation and Viable Seed Bank of a Dry Mixed-Conifer Forest at a Wildland-Urban Interface in Washington State

by
Gabrielle Snider

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented March 17, 2010
Commencement June 2010

Master of Science thesis of Gabrielle Snider presented on March 17, 2010.

APPROVED:

Co-Major Professor, representing Forest Science

Co-Major Professor, representing Forest Resources

Head of the Department of Forest Ecosystems and Society

Head of the Department of Forest Engineering, Resources and Management

---

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Gabrielle Snider, Author

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to all those who made this research possible. Thank you to the Joint Fire Science program, Pacific Norwest Research Station, Oregon State University and the United States Forest Service for providing funding and support for this project. Thank you to Dr. Paul Doescher for your academic and scientific counseling; consistent reminders to maintain a balanced life; for urging me to move to Idaho; and for always taking the time to ask how I was doing. Dr. Becky Kerns, I learned an amazing amount watching you successfully maneuver the world of research. You always provided thoughtful critiques, generous support, creative solutions, and an optimism that everything would work out. You have been a remarkable role model and mentor. Michelle Buonopane, thank you for your botanical, statistical and overall extraordinary field and research expertise, and for being my running partner, roommate, social instigator and great friend. Thank you to the rest of my committee, Dr. Patricia Muir, Dr. Steve Radosevich and Dr. Dan Edge for your thoughtful contributions and editing. Thank you to the OSU greenhouse staff for providing technical assistance in the management of my greenhouse and to the many skilled individuals who helped collect my field data; I learned a tremendous amount from each of you. Thank you to my parents, siblings and grandma for always believing in me despite my doubts. And finally, to my husband TJ, I could not possibly put in words the depth of my gratefulness and humility for your unwavering and selfless support of me throughout this process. You continue to teach me the most important lessons in life, thank you.

TABLE OF CONTENTS

Page

Chapter 1. Introduction 1
Background 1
Study Objectives 4
Chapter 2. Seed Bank Ecology in Temperate Forests 6
Chapter 3. Methods 11
Site Description 11
Study Design 17
Plot establishment and experimental design 17
Herbicide application 19
Vegetation and environmental variable sampling 19
Seed bank sampling 20
Greenhouse germination 21
Description of Analysis 23
Vegetation 23
Seed bank 24
Similarity of vegetation and seed bank floras 25
Chapter 4. Results 27
Aboveground vegetation and site characteristics 27
Seed bank density, richness, and composition 30
Seed bank similarity to aboveground vegetation 37
Chapter 5. Discussion and Conclusions 39
Bibliography 45
Appendices 52

LIST OF FIGURES

Figure Page

1. Selected stands (Blocks) and reference location of Liberty, WA................................ 14

2. Aerial photo of the town of Liberty, WA WUI 15

3. Topographic map of Liberty, WA and selected stands.. 16

5. Median germinant density and 95% confidence intervals from combined litter and soil samples at four distance to road categories and across herbicide treatments 32

6. Median germinant density and 95% confidence intervals (CI) between seed bank layers, distance to road categories and across herbicide treatments. 33

7. Species area curves and confidence bands for litter and mineral soil layers. 36

LIST OF TABLES

Table Page

1. Liberty study area environmental, soil, vegetation characteristics and disturbance history. 13

2. Vegetation analysis degrees of freedom table 23

3. Seed bank analysis degrees of freedom table 25

4. Plant functional groups, common species and number of species belonging to each functional group 27

5. Means and 95% confidence intervals (CI) for differences in ground cover and vegetation characteristics between four distances from road categories and across herbicide treatments. 29

6. Seed bank functional groups, common species and number of species in the seed bank 31

7. Means and 95% confidence intervals (CI) for germinant density (m^2) of seed bank functional groups at four distance to road categories, between seed bank layers and across herbicide treatments. 35

8. Mean seed bank richness and 95% confidence intervals (CI) for seed bank layer, road distance and herbicide treatment. 37

LIST OF APPENDICES

Figure Page

1. Aboveground vegetation species list, functional group and family............................. 53

2. Functional group, species, frequency of occurrence (number of subplots), mean density (seedlings/m^2) and cover (%) of vegetation and seed bank taxa. 57

3. Species found exclusively in seed bank... 62

Chapter 1. Introduction

Background

Many dry coniferous forests in the western United States are experiencing large and severe wildfires, insect outbreaks, forest disease epidemics and a growing presence of invasive species (Everett et al. 1994, Vitousek et al. 1996, Harrod and Reichard 2000, Hessburg et al. 2005). In response, federal fire policies have emerged aimed to reduce the threat of "catastrophic" wildfires and improve forest conditions (National Fire Plan 2000, Healthy Forest Restoration Act 2003, and The Ten Year Strategy Implementation Plan 2006). Policies strongly emphasize hazardous fuels reduction at the Wildland Urban Interface (WUI), where communities and forests intersect, and where homogenized forest landscapes, elevated fuel loads, and increased connectivity of fuel loads have led to significant threat of large and severe wildfires (Everett et al. 1994, Hessburg et al. 2005).

However, activities associated with hazardous fuels reduction often lead to an increased presence of exotic plant species as light, water and nutrient availability increase and forest soils are disturbed (Bailey and Tappeiner 1998, Halpern et al. 1999, Keeley 2002, Wienk et al. 2004). Aggressive, exotic species can cause a host of adverse ecological, economic and human health problems, including: loss of biodiversity; displacement of native plants; loss of sensitive species; increased soil erosion; degraded water quality; reduced soil productivity; reduced habitat and wildlife forage; and changes in disturbance characteristics such as fire frequency and intensity (USDA Forest Service 2005, Krueger-Mangold et al. 2006). I use three terms to distinguish between classes of exotic plant species; exotic, invasive and noxious. Exotic species are any successfully reproducing species of foreign origin listed in the USDA plants database as introduced. Noxious weeds and invasive species, terms I use interchangeably, 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 non-native species are of concern to land managers charged with maintaining native biodiversity, invasive species may 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). Federal laws direct agencies to identify actions that may influence the status of invasive plants and instructs them to use relevant programs and authorities to prevent their introduction, to detect and respond rapidly to control their populations, to monitor populations accurately and reliably, and to restore native plant communities where invasion has already occurred (Clinton 1999).

Hazardous fuels reduction at the WUI pose unique problems for land managers responsible for maintaining native understory biodiversity. WUI's often have existing populations of exotic plant species, including invasive species, as a result of repeated human disturbance and the presence of roads (Alston and Richardson 2006). Roads are a dominant feature of a WUI and are known to be a major factor in the spread of exotic species. Several mechanisms have been suggested to explain this relationship. Most widely noted, roads act as corridors for the dispersal of seed and plant material via vehicles and vehicle-caused air turbulence (Tyser and Worley 1992, Forman and

Alexander 1998); they supply reservoirs of propagules for future invasions as weed seeds are transported to the area in road fill and on vehicles (Forman and Alexander 1998, Parendes and Jones 2000); and they provide safe sites for seed germination and establishment as a result of road construction and maintenance activities that create bare areas with deep soil, higher light and resource availability and lower native plant cover (Gelbard and Belnap 2003). Even in areas where exotic plants currently appear only on roads, roadsides and other frequently disturbed areas, their seeds may be dispersing into interior forest areas, creating reservoirs of propagules for future invasion when germination conditions are met. The 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). These species may preempt development of more desirable, later successional species; influencing the course of succession at that site for many years to come (Connell and Slatyer 1977, Pickett et al. 1987).

Current scientific literature and federal land management direction call for an integrated approach to invasive species control in wildland ecosystems. Plans should incorporate: early detection, rapid response and treatment of new invasive plant species populations; a focus on the invaded ecosystem, its management and the ecological mechanisms that facilitate invasion; an expanded and modernized invasive plant treatment toolbox (i.e. mechanical, biological, chemical and/or cultural treatments); and an emphasis on protecting and restoring native plant communities (Hobbs and Humphries

1995, D'Antonio et al. 2004, USDA Forest Service 2005, Krueger-Mangold et al. 2006). The limited use of authorized herbicides in wildland ecosystems, especially along roads, has been employed to slow the development of invasive species populations (USDA Forest Service 2005). However, few studies have tested the effects of herbicide on vegetation and seed bank characteristics in these systems.

The diversity and dynamics of the post-fuels reduction community are influenced by many factors including: existing, past and nearby vegetation, management history, disturbance characteristics, and the viable seeds buried in the forest seed bank (Moore and Wein 1977, Ingersoll and Wilson 1990, 1993, Whittle et al. 1997, Qi and Scarratt 1998, Parks et al. 2005). Which species emerge, both native and exotic, and the importance of the seed bank to understory reinitiation in dry mixed-conifer forests at the WUI is largely unknown. Given the current emphasis on hazardous fuels reduction at the WUI, characterizing the native, exotic and noxious species seed banks is important in planning for desirable post-disturbance community conditions; developing integrated weed management programs; and for complying with State and Federal laws and policies.

Study Objectives

The objectives of this study were to characterize the aboveground vegetation and pre-fuels reduction seed bank in mixed age, mid-elevation, dry-mixed conifer forest stands in a WUI, and to explore implications related to forest restoration and exotic and noxious plant species control. We examined the patterns and relationships between aboveground vegetation and seed germinant abundance and richness in relation to seed bank layer source, distance to road, and herbicide treatments.

Chapter 2. Seed Bank Ecology in Temperate Forests

Seeds found in litter and mineral soil layers are collectively referred to as the seed bank. The "viable" seed bank consists of those seeds that will germinate when light, water, nutrient, temperature, dormancy length or scarification requirements are met (Thompson 2000). The viable seed bank has spatial and temporal dimensions influenced by horizontal and vertical distribution of seeds in the soil profile; and longevity, dormancy and persistence characteristics of seeds in the seed bank (Simpson 1989). The spatial and temporal characteristics of the seed bank influence the development of plant communities and may provide insight into how a community will respond following a disturbance.

How and where seeds settle in the seed bank are influenced by seed production, species dispersal mechanisms, and physical and biological processes. Seeds may be dispersed as a group or individually, locally, or over a long distance. Seeds of some species (short lived and large seeded) are more likely to be found in litter and upper soil layers, while others species (long lived and small seeds) are more likely to be found buried deeper in the soil profile; others have a uniform distribution throughout (Kellman 1978, Young 1985). Large seeds or seeds dispersed in a cluster are more prone to predation while smaller seeds may undergo significant post-dispersal movement via wind, water, birds, animals and insects (Thompson 2000). Consequently, the distribution of seeds across a horizontal plane is highly variable and clustered in nature (Major and Pyott 1966, Warr et al. 1993). This feature has made estimation of seed bank density and diversity problematic and has led to the development of sampling methods that rely on the collection of many small soil samples to quantify the soil seed bank, as opposed to a few large samples (Gross 1990, Brown 1992, Warr et al. 1993).

Vertical distribution patterns of the seed bank also influence plant community development. Seed burial is a gradual process by which seeds move down the soil profile via soil formation processes and more quickly through biological (i.e. burrowing animals and soil fauna) and physical processes (i.e. freeze-thaw cycles and rainwater percolation) (Warr et al. 1993). The highest proportions of total and viable seeds in forest systems are typically located near or at the surface of the soil profile (Kellman 1970, Moore and Wein 1977, Kramer and Johnson 1987). In the seed bank of a *Pinus ponderosa/Symphoricarpos albus* stand in east-central Washington, nearly three times as many viable seeds were found in the litter layer than in the first 2 cm of mineral soil, and the rate of decline of seed numbers through the mineral soil was approximately 50% for each 2 cm change in depth (Pratt et al. 1984). In two other studies examining seed distribution in conifer forests, 66% (Strickler and Edgerton 1976) and 67% (Kramer and Johnson 1987) of viable seeds were found in litter and the 0-5cm layers.

Temporally, seed bank patterns are influenced by how long a seed can remain viable following dispersal, also called seed longevity, which is determined by both intrinsic (i.e. seed size and shape) and extrinsic (i.e. heat and moisture) mechanisms (Leck et al. 1989). Thompson and Grime (1979) identified two main seed bank strategies of temperate zones based on seed bank persistence; transient and persistent. Species with transient, short-lived, seed banks are those that do not persist for more than one year following dispersal and are adapted to seasonal gaps attributed to normal, predictable mortality in aboveground vegetation. Transient seed banks tend to be made up of large seeded grasses and forbs that require a period of chilling before germination can take place, but following chilling, may germinate at depths and temperatures unfavorable for survival (Thompson and Grime 1979, Warr et al. 1993). Persistent, long lived seed banks are those which remain viable for at least one year following dispersal. These seed banks contain seeds of species characteristic of open habitats, which require high light conditions for germination, and have small, easily buried seeds (Thompson and Grime 1979, Simpson 1989, Warr et al. 1993). Ooi et al. (2007) related persistence and disturbance characteristics to the species that occurred at a particular site. They found that areas with predictable disturbance, such as seasonal drought, tended to support species with short-lived, transient seed banks, while areas prone to unexpected, often temporally and spatially unpredictable disturbance, such as fire, tended to select for species with more persistent seed banks; thus buffering plant populations against environmental variability (Thompson 2000). Seed longevity is also related to depth distribution of seeds in the soil profile in several key ways. Short-lived seeds do not remain viable long enough to become buried in the soil profile (Warr et al. 1993), while long-lived seeds (often small and easily buried) can become incorporated to greater soil depths, further protecting them from seed loss due to germination and predation (Thompson 2000). These patterns have led to the general assumption that deeply buried seeds are older than shallower seeds, providing an indirect measure of seed age at a site and an ecological memory of past communities. Some seed longevity studies suggest seed ages exceeding 100 years, carrying important implications for restoration or maintenance of species populations at a site (Moore and Wein 1977, Kellman 1978, Warr et al. 1993, Thompson 2000).

The relationship of the seed bank and its associated aboveground vegetation is complex. Many studies cite a lack of correlation between species composition of the seed bank and that of the associated vegetation, however, many exceptions exist (Kellman 1970, Strickler and Edgerton 1976, Thompson and Grime 1979, Pratt et al. 1984, Sullivan and Ellison 2006). Understanding when and why the floras are more or less likely to be correlated are essential for evaluating the restoration potential from the seed bank following a disturbance. The "successional hypothesis," which has been used to explain observed differences between the floras, supports the paradigm that as succession proceeds, seed numbers and diversity decline and the aboveground vegetation and the seed bank become increasingly dissimilar (Oosting and Humphreys 1940, Livingston and Allessio 1968, Brown and Oosterhuis 1981). However, sites which undergo frequent disturbance may have seed banks much more similar to existing vegetation. In a frequently logged and fire-affected *Pseudotsuga menziesii* forest in Central British Columbia, 60% of seed bank taxa were represented in the sampled vegetation (Stark et al. 2006). In a frequently burned boreal forest in western Canada as many as half of the species in the seed bank were present in the vegetation (Fyles 1989). While some generalizations can be made about the correlation of the seed bank to aboveground vegetation, they should not be made without consideration of successional stage and disturbance history.

Understanding seed bank dynamics can provide clues to the potential contribution of the seed bank in restoration of mixed-conifer forest understories following disturbance; or alternatively, the need to direct actions to facilitate native understory regeneration. In a seed bank study in young, closed canopy forests in Washington, thinning disturbance resulted in limited germination of forest species and favored recruitment of early seral, exotic species (Halpern et al. 1999). Korb et al. (2005) evaluated the seed banks of *Pinus ponderosa* forests in Arizona following restoration treatments and found the majority of species present in the seed bank and absent from the aboveground vegetation prior to treatments, were either ruderal or exotic plant species. And while seed banks may facilitate the maintenance of species populations (Kemp 1989, Harrod and Halpern 2005), conserve genetic variability or contribute to the restoration of native communities if propagules of desired species are present (Graham and Hutchings 1988, van der Valk and Pederson 1989); they may also inhibit native community restoration and influence the course of succession for many years, if undesirable species are first to emerge (Connell and Slatyer 1977, Pickett et al. 1987, Wilson et al. 1992, Halpern et al. 1999, Korb et al. 2005).

Chapter 3. Methods

Site Description

The study area was located in Washington State on the eastern slopes of the Cascade Mountains, a transitional area between the Cascade Mountain crest to the west and the lower-lying Columbia basalt plateau to the east (USDA-NRCS 2009). The area is characterized by steep, long slopes and narrow valley bottoms carved out by past extensive mountain glaciation and maintained by continued active erosion and down-cutting (Camp et al. 1997). 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). The remaining soils are characterized as coarser sandy loams formed in residuum, colluvium and alluvium derived from sandstone and siltstone with loess and a thin mantle of volcanic ash (USDA Forest Service 2006, USDA-NRCS 2009). Seven major soil series are represented throughout the study area including: Keechelus, Scotties, Jumpe, Kafing, Kiper, Nard and Brisky (Ibid) (Table 1).

Dominant conifer cover species, based on field surveys from this study, are: *Pseudotsuga menziesii* followed by *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: *Symphoricarpos albus*, *Holodiscus discolor*, *Berberis aquilifolium*, *Spiraea betulifolia*, *Ceanothus velutinus*, *Calamagrostis rubescens*, *Carex geyeri* and *Lupinus polyphyllus*. State listed noxious weeds and common exotic plant species include: *Cirsium vulgare*, *Cirsium arvense*, *Centaurea diffusa*, *Centaurea pratensis*, *Artemesia absinthium*, *Potentilla recta* and *Verbascum thapsus*.

The entire study area was within the Swauk Late Successional Reserve (Swauk LSR), an area of forest where the management objective is to protect and enhance conditions of late successional and old-growth forest ecosystems. The Swauk LSR lies at the lower south end of the Swauk watershed at an elevation of ca. 730-1100m in the Okanogan-Wenatchee National Forest (Table 1). Climate is maritime with hot, dry summers and cold, wet winters. Average air temperatures range from -7^{o} C in January to 28^{o} C in July (DEA 2006). Annual precipitation ranges from 114 to 127 cm and occurs primarily as snow during the winter months (Camp 1999). Historically, the area was characterized by a low severity fire regime (frequent, low-intensity) that maintained open stands of *Pseudotsuga menziesii* and *Pinus ponderosa* on dryer sites and denser stands of *Abies grandis* on more mesic sites(USDA Forest Service 2006) . Prior to designation as an LSR, the Liberty Study area underwent periodic commercial logging; mining and grazing continue in some areas to this day (Table 1). Fire, though actively suppressed over the last century, has affected some areas as recently as 1989 (Cle Elum ranger district staff, pers.comm. 2008). Liberty, WA and the surrounding area (designated as a WUI) were identified as an at-risk community through the Swauk Basin Wildfire Protection Plan (2005) and as a high priority area for fuels reduction by the U.S. Forest Service under the authority of the Healthy Forests Restoration Act (2003) (Figures 1, 2 and 3).

Table 1. Liberty study area environmental, soil, vegetation characteristics and disturbance history.

	Liberty Study Area						
Harvest stands (Blocks)	89	129	54	93	29	15	76
Environment							
Elevation (m)	762	792	975	990	1067	1067	1158
Slope (%)	45 - 62	14 - 58	14 - 31	8 - 67	20 - 40	6 - 58	45 - 62
Aspect	S-WNW	ESE-SSE	E-W	SW-NNW	ENE-WSW	NW-NNE	NW-NE
Soils	Kafing Ashy Sandy Loam	Scotties Gravelly Ashy Sandy Loam	Jumpe Stony Ashy Loam	Stony Ashy Sandy Loam	Kiper Stony Ashy Sandy Loam	Brisky Very Cobbly Ashy Loam	Hakker Clay Loam
Mean overstory canopy cover (%)	52.34	44.38	31.20	43.38	44.79	59.17	22.21
Disturbance history							
Grazing	Yes (current)	No	Yes (past)	No	No	No	No
Last commercial harvest	1968	1989	1985	1986	1990 (fire salvage)	1969	1986

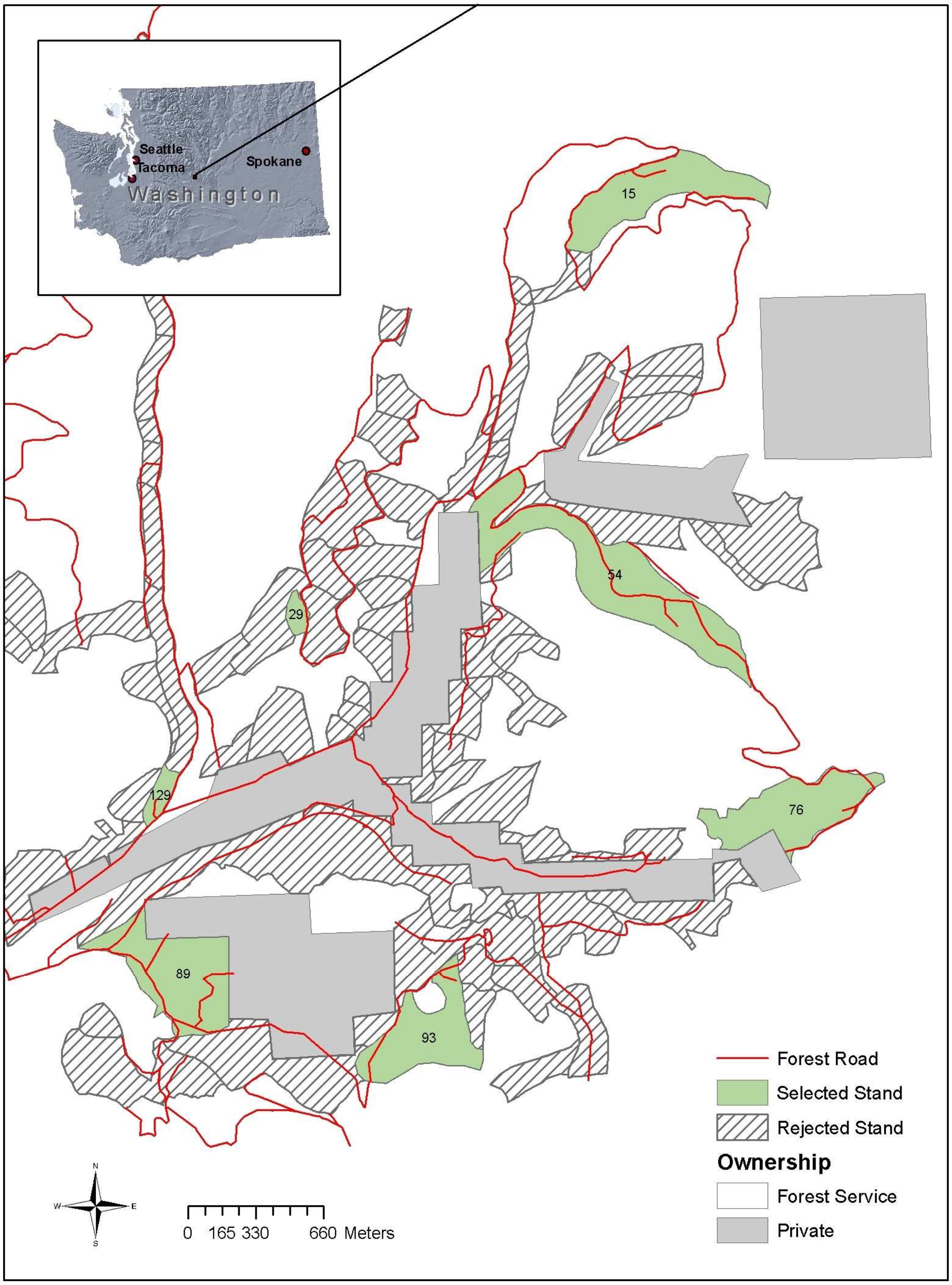


Figure 1. Selected stands (Blocks) and reference location of Liberty, WA

Figure 2. Aerial photo of the town of Liberty, WA WUI

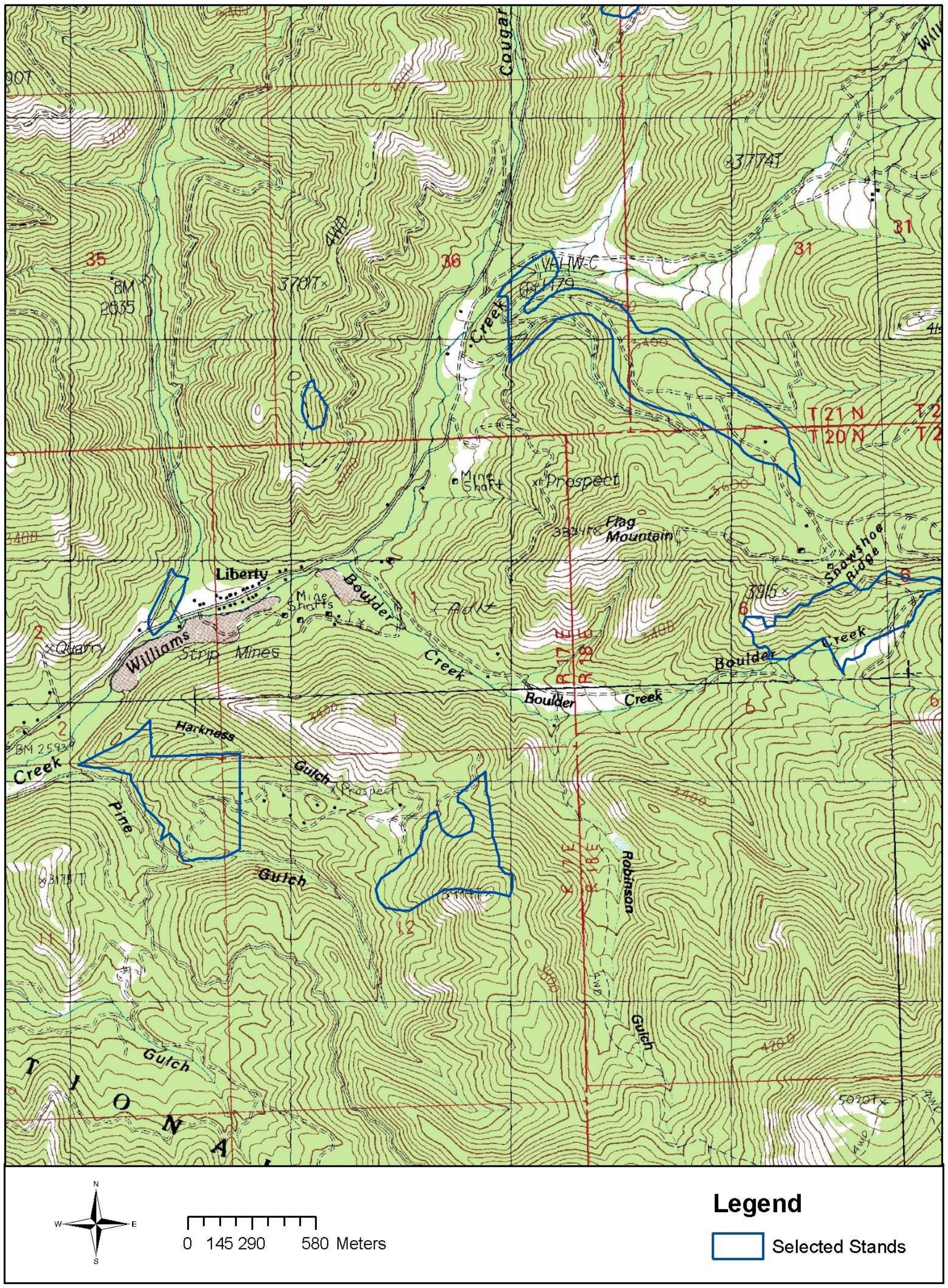


Figure 3. Topographic map of Liberty, WA and selected stands

Study Design

Plot establishment and experimental design

A randomized complete block split plot (distance to road) and split-split plot (distance to road and seed bank layer) design was established in June 2006 to evaluate the effects of herbicide treatment, road distance and seed bank layer on seed bank characteristics; and the effects of herbicide treatment and road distance on aboveground vegetation characteristics. Harvest units for proposed hazardous fuels reduction activities were established in 2006 by Cle Elum Ranger district timber staff based on site and vegetation characteristics and were treated as potential blocks. Boundaries of a harvest unit and a set of predetermined site selection criteria were used to guide block selection. Predetermined selection criteria included: harvest unit positioned along an open access road, adequate area within the harvest unit for the block (200 m X 50 m), average percent slope less than 60%, soil and vegetation types similar to those found in other selected blocks, and noxious weeds present, but not heavily invaded, in the site. Seven blocks within the 648 hectare proposed fuels reduction project met selection criteria and all seven were used in the study (Figures1 and 3).

The block was divided into 2 50 X 50 meter experimental units (EU) with one EU randomly selected as the other for herbicide treatment. Within each EU, three parallel transects running 50 meters perpendicular from the road edge into the forest were established. Along each transect four 3 X 3 meter “distance to road” plots were established at 0 m, 10 m, 20 m and 30 meters from the road edge. Zero to 30 m was determined to be the range of distances needed to capture differences associated with road distance without confounding results by encountering other roads. Nested within each 3 X 3 meter plot was an understory vegetation 1 X 1 m subplot and a 3 m line intercept (Figure 4).

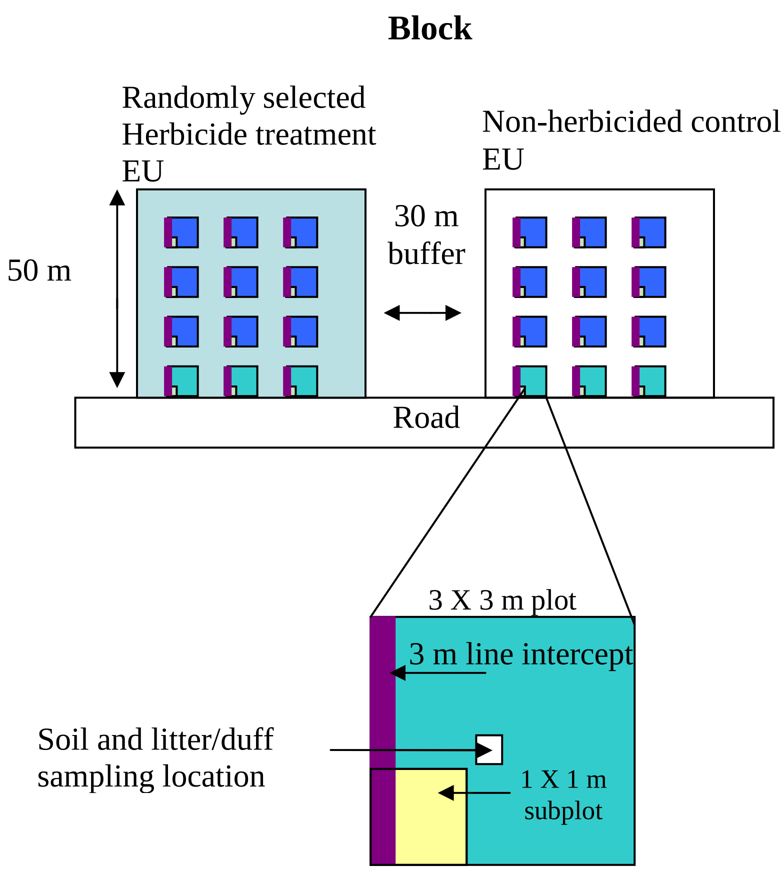


Figure 4. Experimental Block Design. Seven blocks were established throughout the 648 ha project area. Environmental, vegetation and soil data were measured in nested plots and transects in each unit.

Herbicide application

In July, 2006 state-listed noxious weeds in treatment EU's were backpack sprayed with a Tordon®, Blazon® solution and in July 2007 with an Aqua Neat® (6pt/100), LI-700 (3pt/100), Blazon® (3pt/100) herbicide solution. These herbicides target annual and perennial broadleaf plants and are appropriate for the noxious weeds present in the study area. Spot application with a backpack sprayer minimized treatment of non-target species.

Vegetation and environmental variable sampling

Aboveground sampling using a series of nested plots was conducted between June and September of 2006 and 2007. Ground cover and aboveground vascular plant cover (by species) were measured in each 1 X 1 meter subplot by visual estimation using a 1 square meter marked frame (Figure 4). Vouchers of unknown species were collected and taken to the USFS Corvallis Forest Sciences Laboratory for identification or confirmation by Michelle Buonopane, USFS botanist, or to the Oregon State University herbarium for identification or confirmation by Dr. Richard Halse, OSU botanist. Ground cover measurements included: percent bare-ground, litter, live tree bole, dung, rocks, bedrock, coarse woody debris (>10 cm diameter), soil crust, lichen, and stump cover. In the 3 x 3 m plot presence of all rooted vascular plant species was recorded. Tree species, status (live or dead), and diameter at breast height (dbh) were recorded for trees over 1.37 meters in height and tree seedlings were tallied by size class (0-40 cm, 41-80 cm, >80 cm). Overstory canopy cover was measured at each corner of the plot using a moosehorn densitometer (Garrison 1949, Lemmon 1956). Shrub cover was estimated using the line intercept method by recording shrub species and length that intercepted a 3 meter transect (Figure 4). Litter and duff depth were measured at 75, 150 and 225 cm along this transect.

Seed bank sampling

Seed bank sampling was conducted in late September 2007. Fall sampling was chosen to ensure inclusion of the current year's seed rain prior to field germination as well as ungerminated seeds from previous years. Samples were systematically collected in the center of the 3 X 3 meter plots to allow for comparisons with the aboveground vegetation data (Figure 4). Samples were separated into litter/duff and mineral soil samples to provide information on the differences between these two layers in terms of viable seed density and species composition. Litter was defined as newly fallen organic matter (Oi) combined with the fermentation and humus layers (Oe + Oa) sensu Laughlin (2004). Litter was collected from a 10 X 10 cm square and placed in a zip lock bag marked with site location details. Two mineral soil cores (5 X 10 cm) were extracted with a soil corer from the area cleared of litter/duff and consolidated in a zip lock bag into a single sample. Previous studies (Kellman 1970, Strickler and Edgerton 1976, Moore and Wein 1977, Kramer and Johnson 1987, Archibold O.W. 1989) show the majority of viable seeds to be present in the top 5 cm of the soil profile with decreasing seed densities as depth increases. Thus, we determined a ten centimeter depth would adequately capture the majority of the viable seed bank at our sites. The two mineral soil cores had a total volume of ca. 39.3 cm^3. The volume of litter samples varied with the depth of the forest floor. A total of 336 samples (168 litter and 168 mineral soil samples) were collected from the seven blocks. All litter and mineral soil samples were placed in coolers and transported to Oregon State University where they were prepped for the germination study.

Greenhouse germination

A controlled greenhouse seedling emergence method was used to estimate the germinable fraction of the seed bank. This method has been used in most studies (66%) aimed at quantifying the viable soil seed bank (Gross 1990, Brown 1992). 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 in a thin layer (<3 cm) over 2-3 cm of vermiculite in a 19 X 28 cm germination tray. Trays were watered to field capacity, allowed to drain for 12-24h and then transported to a cooler held in darkness at approximately 2^{o} C for a 60 day moist-cold stratification period. Following stratification, trays associated with a block (24 mineral soil trays and 24 litter trays) 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 windborne seed or other unintended greenhouse contaminants.

Supplemental lighting consisted of continuous day-length extension lighting to achieve a 16 hour photoperiod and 8 hour dark period (Landis et al. 1990). Four 1000 w high-intensity discharge lamps (sodium halide) were used for photoperiodic control. All bulbs were replaced at the beginning of the study and lamps were positioned to provide as consistent lighting as possible throughout the greenhouse. Because optimal germination temperature for a wide range of species has been shown to be between 22^{o} C and 24^{o} C (McLemore 1969, Barnett 1979, Landis et al. 1990), and thermoperiodism is preferential to a continuous temperature regime (Landis et al. 1990), average greenhouse temperatures were maintained at 23° C during the day and 18° C at night. A HOBO U12 Temperature and Relative Humidity Indoor data logger was used to track temperature and relative humidity in the greenhouse. Average relative humidity was maintained at approximately 49 %.

Samples were checked twice daily and watered as needed to maintain moist soil and litter conditions. Watering was done by hand, with a hose fitted with a fogger nozzle sprayer to prevent water pressure damage to emerging seedlings. Seedling emergence was monitored daily and new germinants were marked with color coded toothpicks. As soon as a seedling was identified to the highest taxonomic level possible, it was removed from the tray, recorded in the datasheet, and pressed for future reference. When positive identification of a seedling was not possible, it was transplanted and allowed to grow until it could be identified. If vegetative reproduction was suspected, the specimen was removed from analysis; however, emergents from *Poa bulbosa's* bulbils were counted as seeds 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. This study was terminated on June 13, 2008, five months after initiation.

Description of Analysis

Vegetation

Vegetation data were analyzed as a randomized complete block, split plot design with block as the random effect and treatment (Herbicide application and distance to road category) and interactions between treatments as fixed effects using SAS 9.2 statistical software package. Herbicide was applied at the whole plot level and road distance category was applied at the subplot (split) level (Table 2.)

Table 2. Vegetation analysis degrees of freedom table

Class	DF
Block	6
Herbicide	1
Block*Herbicide	6
Road	3
Road*Herbicide	3
Block*Road*Herbicide + Block*Road	36
Total	55

To characterize the aboveground plant community, species were grouped into six functional groups: exotic, noxious, annual forbs, perennial forbs, graminoids, and shrubs. Differences in mean percent cover of each functional group in herbicided and non-herbicided plots and at four distance to road categories were tested and a significant main effect reported at $p \leq 0.05$. Significance for contrasts of interest were assessed at two levels; $p \leq 0.05$. Using the same procedure, tests were performed for ground cover, canopy cover, total plant cover and litter depth. Due to the absence of noxious weeds in some blocks, tests on noxious weed cover were conducted only using blocks where noxious weeds were present. Variables were transformed, if needed, to meet assumptions of normality and equal variance and back-transformed means reported where applicable. Tukey-Kramer adjustment was used for multiple comparison tests.

Seed bank

To assess how well our sampling regime captured the diversity of species in the seed bank we generated species-accumulation curves and first order jackknife estimates of richness for all species in the litter and mineral soil layers using PCORD 5.19 (McCune et al. 2002, Lang and Halpern 2007). Seed bank data were analyzed as a randomized complete block split-split plot design with block as the random effect and treatments (herbicide, distance to road category and seed bank layer) and interactions between treatments as fixed effects using SAS 9.2 statistical software package. Herbicide was applied at the whole plot level, and seed bank layer and distance to road category were the split-split (Table 3).

Table 3. Seed bank analysis degrees of freedom table

Class	DF
Block	6
Herbicide	1
Block*Herbicide	6
Road	3
Road * Herbicide	3
Block * Road * Herbicide + Block * Road	36
Layer	1
Layer * Road	3
Layer* Herbicide	1
Layer* Road * Herbicide	3
Block*layer + Block*Road* Herbicide *Layer + Block*Layer*Road + Block*Layer* Herbicide	48
Total	111

Differences in mean species richness and overall germinant density were tested and a significant main effect reported at $p \leq 0.05$. Seed bank species were grouped into the same functional groups as the vegetation and differences in mean germinant density between groups was assessed. Germinant density in combined litter and mineral soil layers was also analyzed. Variables were transformed, if needed, to meet assumptions of normality and equal variance and back-transformed means reported where applicable. Tukey-Kramer adjustment was used for multiple comparison tests.

Similarity of vegetation and seed bank floras

To compare the aboveground flora to that of the seed bank, we used three metrics; Sorenson's similarity index (SI), frequency of occurrence (% of subplot), and mean cover or germinant density. SI is a statistic used to compare the species composition similarity of two samples (SI=2C/A+B) where A is the number of species in sample one and B is the number of species in sample two and C are the number of species in common. We calculated SI values at the subplot level and at the whole plot (EU) level. The subplot level calculation represented the site where vegetation was measured and the seed bank sample was taken. The EU level calculation represented a larger, proximate, area where dispersal from adjacent subplots could be expected.

Chapter 4. Results

Aboveground vegetation and site characteristics

One hundred forty-nine vascular plants were sampled in the aboveground vegetation (Appendix 1). The majority of understory species were perennial forbs followed by shrubs, exotics, perennial graminoids and annual forbs (Table 4). Native graminoids had the greatest cover (except for in 0m plots), followed by perennial forbs and exotic species (Table 5). Mean overstory canopy cover was 42% and ranged from 0-100%. Mean total understory plant cover was 44% and ranged from 0-200% (Table 5).

Table 4. Plant functional groups, common species and number of species belonging to each functional group

Plant functional groups	Common understory plants	Functional group richness
Native		
Perennial forbs	*Achillea millefolium, Arenaria macrophylla, Hieracium spp., Lathyrus pauciflorus*	45
Perennial graminoids	*Calamagrostis rubescens, Elymus glaucus, Carex geyeri*	19
Annual forbs	*Collinsia parviflora, Microsteris gracilis*	17
Annual graminoids	*Festuca microstachys*	1
Shrubs	*Spiraea betulifolia, Lupinus polyphyllus, Symphoricarpos albus, Arctostaphylos uva-ursi*	22
Trees	*Pseudotsuga menzisii, Pinus ponderosa, Abies grandis and Pinus contorta*	6
Exotic		
All	*Dactylis glomerata, Agropyron intermedium, Verbascum thapsus Trifolium repens, Taraxacum officina1e, Plantago lanceolata*	22
Noxious	*Cirsium vulgare, Cirsium arvense, Centaurea pratensis, Centaurea diffusa*	5

Mean overstory canopy cover at the road edge was significantly less than canopy cover at all other distances ($F=13.59_{3,36}$, $p<0.0001$) and no differences were observed between any other road distance categories. Mean total understory cover did not differ among road distance categories. Mean litter depth was significantly less in roadside plots than in all other distance categories ($F=5.63_{3,36}$, $P=0.0029$). Shrub cover was highly variable and no differences were detected among any road distance categories (Table 5).

Noxious and exotic plant groups exhibited an inverse pattern to overstory canopy cover. Mean cover was significantly greater at the 0 m distance than all other distance categories ($F=7.84_{3,36}$, $p=0.0004$ and $F=15.63_{3,21}$, $p=0.001$) for noxious and exotic groups respectively; no other differences were detected among road distances for either group (Table 5). Mean native graminoid cover showed the opposite pattern; greater cover in all interior plots than in the road side plots ($F=3.42_{3,36}$, $p=0.027$). No other differences in mean cover were detected within functional groups or ground cover categories between distance to road categories (Table 5). No effect of the herbicide treatment for any plant functional group, including the targeted noxious weed group ($p>0.05$) was found.

Table 5. Means and 95% confidence intervals (CI) for differences in ground cover and vegetation characteristics between four distances from road categories and across herbicide treatments. Letters denote statistical significance (p≤0.05, adjusted Tukey-Kramer). The uppercase letter (e.g. "A") differs from lowercase of the same letter (e.g. "a").

	Distance to Road Categories			
	0 m	10 m	20 m	30 m
Overstory canopy cover (%)	14.4 (1.3-27.5)**a**	48.5 (35.4-61.6)**A**	55.8 (42.7-68.9)**A**	51.2 (38.1-64.4)**A**
Understory vegetation (% cover)				
Total plant cover	36.7 (17.4-55.9)	52.4 (33.2-71.6)	44.8 (25.6-64.1)	42.6 (23.4-61.8)
Exotics (non noxious)	9.2 (5.6-12.8)**A**	1.6 (0-5.2)**a**	0.2 (0-3.7)**a**	0.1 (0-3.7)**a**
Noxious	0.37 (0.12-1.18)**A**	0.005 (0.001-0.02)**a**	0.005 (0.001-0.02)**a**	0.005 (0.001-0.02)**a**
Annual forbs	1.0 (0.6-1.5)	0.7 (0.3-1.1)	0.8 (0.4-1.2)	0.5 (0.1-1.0)
Perennial forbs	3.5 (1.2-5.7)	2.5 (0.3-4.7)	2.9 (0.6-5.1)	3.3 (1.1-5.5)
Graminoids	5.1 (0-15.3)**a**	16.7 (6.5-26.9)	19.5 (9.3-29.7)**A**	18.2 (8.0-28.4)
Shrubs	52.31 (17.09-87.52)	72.5 (37.28-100)	56.38 (21.17-91.60)	33.88 (0.0-69.10)
Ground cover (%)				
Litter	83.9 (72.0-95.9)	90.7 (78.7-102)	92.5 (80.6-104.5)	84.8 (72.8-96.8)
Bare soil	8.4 (0.8-16.1)	2.5 (0-10.2)	2.2 (0-10.0)	6.5 (0-14.2)
Rock	6.1 (2.4-9.8)	1.4 (0-5.2)	1.0 (0-4.7)	1.7 (0-5.4)
Coarse woody debris	0.2 (0-2.0)	2.2 (0.3-3.9)	1.5 (0-3.3)	1.4 (0-3.2)
Litter depth (cm)	2.1 (1.1–3.2)**a**	4.2 (3.2-5.2)**A**	3.8 (2.8-4.8)**A**	3.7 (2.7-4.7)**A**

Seed bank density, richness, and composition

Six hundred and thirty seeds germinated from 90 of 168 litter samples and 43 of 168 mineral soil samples. Forty-three vascular plant taxa representing 18 families and 37 general were identified in the seed bank (Appendix 2). 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). No germinants emerged from the four control trays placed on greenhouse benches. Combined density of seedlings from litter and mineral soil samples from a subplot ranged from 0 to 38 seedlings (0-8,025 seedlings/m^2) with a mean of 3.75 (507/m^2) and a median of 1 (100/m^2) (Appendix 2).

Of the identified germinants (570 seedlings), perennial forbs had the greatest number of species, followed by exotics and graminoids (Table 6). Annual forbs, however, were most abundant in the seed bank, followed by perennial forbs, graminoids, exotics and shrubs (Table 7). Only one tree seedling emerged. Ten species were exotic and three of them were state listed noxious weeds (Table 6).

Table 6. Seed bank functional groups, common species and number of species in the seed bank

Seed bank functional groups	Common seed bank species	Functional group richness
Native		
Perennial forbs	*Epilobium ciliatum, Gnephalium microcephalum, Lithophragma spp.*	15
Grasses and sedges	*Deschampsia elongata, Elymus glaucus, Festuca spp.*	9
Annual forbs	*Collinsia parviflora, Microsteris gracilis, Montia perfoliata*	8
Shrubs	*Purshia tridentata, Rubus leucodermis, Spiraea betulifolia*	5
Trees	*Pinaceae*	1
Exotic		
All exotic	*Poa bulbosa, Verbascum thapsus, Bromus tectorum*	9
Noxious	*Cirsium arvense, Cirsium vulgare, Artemisia absinthium*	3

Total germinant density (litter and mineral soil layers combined) did not differ by herbicide treatment ($F=1.82_{1,6}$, $p=0.225$) or distance to road category ($F=2.01_{3,36}$, $p=0.129$) (Figure 5).

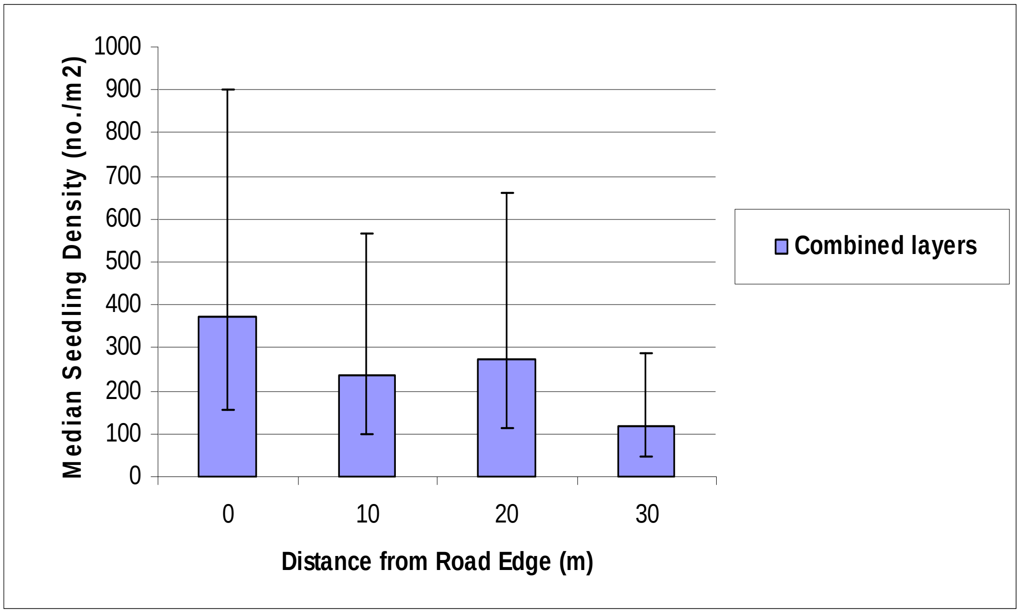


Figure 5. Median germinant density and 95% confidence intervals from combined litter and soil samples at four distance to road categories and across herbicide treatments (p <0.05, Tukey-Kramer).

More germinants (77%) emerged from the litter layer than from the mineral soil layer (23%) across distances from road and herbicide treatments. Density of germinants ranged from 0 to 38 seedlings for litter samples (0-3800 seedlings/m^2) with a mean of 2.88 (288/m^2) and a median of 1 (100/m^2), and from 0 to 28 seedlings for mineral soil samples (0-7,125 seedlings/m^2), with a mean of 0.86 (219/m^2) and a median of 0. However, differences in germinant density between layers depended on distance from road. Density was significantly greater in the litter layer at the 10m and 20m distances, but did not differ from the mineral layer at the 0m and 30m distances (Figure 6).

Within the litter layer, no differences in germinant density were detected between the four distances from road categories (Figure 6). Germinant density did, however, differ between distance categories in the mineral soil layer; the 10 m, 20 m, and 30 m distances all had significantly lower germinant density than the 0 m distance, but did not differ from each other (Figure 6).

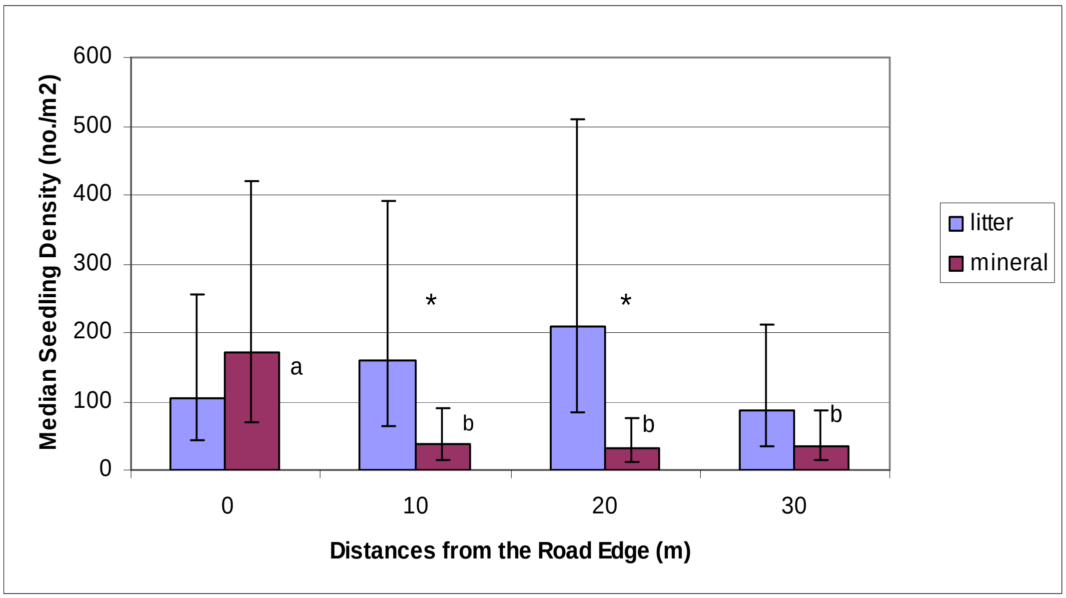


Figure 6. Median germinant density and 95% confidence intervals (CI) between seed bank layers, distance to road categories and across herbicide treatments. An asterisk (*) denotes a statistical difference exists between the mineral and litter layer at a distance from road category. Letter (a) denotes statistical difference between road distances within the mineral layer from letter (b). No differences existed between distances in the litter layer ($p < 0.05$, Tukey-Kramer).

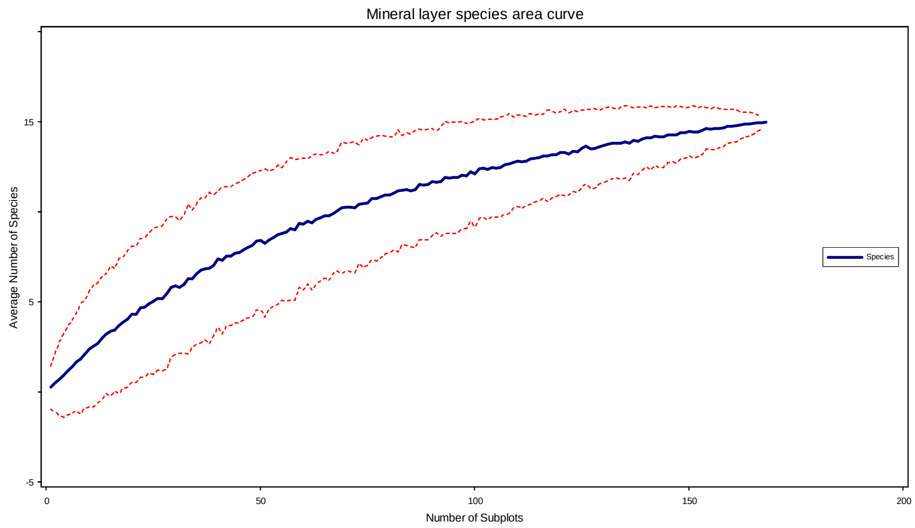
No differences in germinant density between road distance categories were detected within a layer for any functional group except perennial forbs. Perennial forb density in the litter layer was significantly less at the 0m distance than at the 10 m distance. In the mineral layer, perennial forb density was greater at the 0 m distance than at the 20 m distance (Table 7).

Within a road distance category, several differences between layers existed. In general, where differences existed, functional group seed density was greater in the litter layer than that of the mineral layer. Annual forb density was greater in the litter layer than in the mineral soil layer at the 10, 20 and 30 m distances. Perennial forb seed density was greater in the litter layer at the 20 and 30 m distances, but was greater in the mineral soil layer at the 0m distance (Table 7). Noxious weed seed density was greater in the litter layer at the 20 and 30m distances than in the mineral soil layer at those distances. As in the vegetation, we detected no effect of the herbicide treatment on seed density of any plant functional group, including the targeted noxious weed group ($p \leq 0.05$).

Table 7. Means and 95% confidence intervals (CI) for germinant density (m^2) of seed bank functional groups at four distance to road categories, between seed bank layers and across herbicide treatments. Differences between layers are indicated with letters (e.g. "A" differs from "a"), differences between distances within a layer are denoted with numbers (e.g. 1 differs from 2). p≤0.05, adjusted Tukey-Kramer.

	Distance to Road Categories			
	0 m	10 m	20 m	30 m
Total density (layers combined)	372.55 (154.13 - 900.48)	235.10 (97.26-568.23)	273.20 (113.03-660.34)	118.11 (48.86-285.47)
Litter Layer				
Exotics	21.98 (13.41- 36.03)	17.25 (10.52 -28.28)	14.46 (8.52 -24.56)	17.97 (10.96 -29.45)
Noxious	1.66 (0.81-3.40)	1.42 (0.69-2.91)	2.41 (1.18-4.96) **A**	2.97 (1.45-6.06) **B**
Annual Forbs	36.87 (18.68 -72.77)	68.86 (34.89 -135.92)**C**	62.14 (31.48-122.65)**D**	42.86 (21.71-84.59)**E**
Perennial Forbs	15.84 (7.07-35.48)**a, 1**	43.53 (19.43-97.52) **2**	38.70 (17.27-86.71)**b**	27.20 (12.14-60.936)
Sedges and Grasses	37.49 (17.94 - 78.34)	22.82 (10.92 - 47.70)	35.39 (16.93 - 73.95)	21.58 (10.33 - 45.11)
Mineral soil Layer				
Exotics	13.79 (8.41-22.61)	13.79 (8.41-22.61)	12.29 (7.50 -20.15)	10 (6.10 -16.39)
Noxious	1.89 (0.9-3.87)	1.37 (0.67-2.82)	1 (0.49-2.05)**a**	1 (0.49-2.05)**b**
Annual Forbs	25.73 (13.04-50.78)	11.74 (5.94 - 23.17)**c**	15.37 (7.79-30.34)**d**	12.29 (6.23 -24.26)**e**
Perennial Forbs	42.33 (18.90-94.84)**A, 1**	27.05 (12.07-60.59)	13.64 (6.09-30.56)**B, 2**	23.10 (10.31-51.76)
Sedges and Grasses	19.90 (9.52 - 41.60)	16.25 (7.78 - 33.96)	18.66 (8.93– 39.0)	19.02 (9.10 - 39.74)

Species accumulation curves (Figure 7) and first order jackknife estimates of richness (57 litter species, 20 mineral soil species) showed the majority of species were captured with our sampling methods, but that we may have missed some infrequent taxa, particularly in the litter layer.



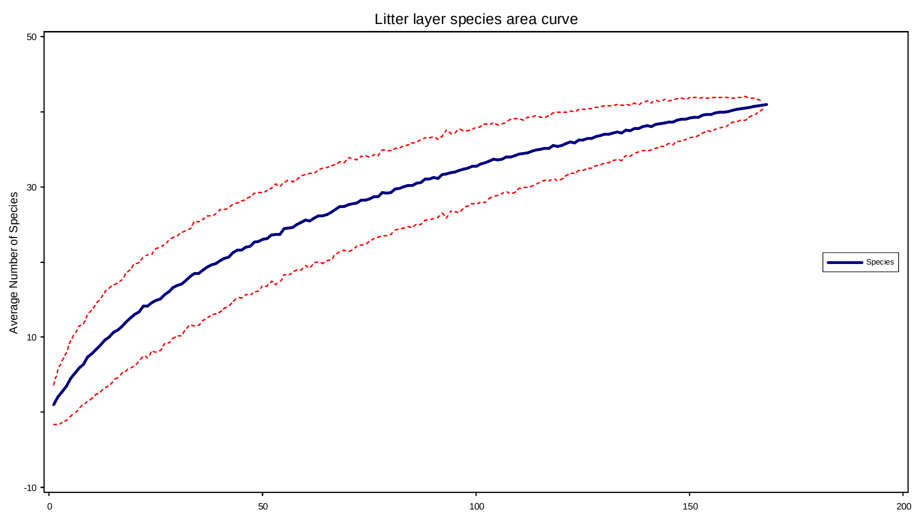


Figure 7. Species area curves and confidence bands for litter and mineral soil layers.

More than twice as many species were present in the litter layer as in the mineral layer (Table 8); however, species composition was fairly similar (Sorenson's Index = 0.5) and all but two species found in the mineral layer were also found in the litter layer (Appendix 1). Mean species richness was greater in the litter layer than in the mineral layer but did not differ between road distance categories or herbicide treatments (Table 8).

Table 8. Mean seed bank richness and 95% confidence intervals (CI) for seed bank layer, road distance and herbicide treatment. p<0.05, adjusted Tukey-Kramer

		Species Richness					
		Mean	Lower CI	Upper CI	F	DF	P-value
Layer					47.8	1,48	**<0.0001**
	Litter	3	2.143	3.857			
	Mineral	1	0.089	1.804			
Road distance					0.52	3,36	0.6729
	0	2.1	1.023	3.12			
	10	2.2	1.13	3.227			
	20	2.1	1.023	3.12			
	30	1.6	0.523	2.620			
Herbicide					0.04	1,6	0.8573
	Herbicide	2.	0.763	3.309			
	No-herbicide	2	0.638	3.184			

Seed bank similarity to aboveground vegetation

The seed bank and vegetation floras present at the time of sampling differed widely. One hundred forty-nine vascular plant species were identified in the aboveground vegetation and 43 vascular plant species were identified in the seed bank (Appendices 1 and 2). Twenty-seven species were common to both floras (Appendices 1 and 2). Seven species were present in the seed bank and absent in the vegetation, and those were dominated by native ruderal and exotic species (Appendix 3). Species occurring at high frequencies in the vegetation were often absent or nearly absent in the seed bank (Appendix 2). *Calamagrostis rubescens*, the most common species in the vegetation, occurred in 50% of vegetation subplots but was completely absent from the germinable seed bank. *Spiraea betulifolia* was present in 30% of vegetation subplots, but only 1% of litter samples and none of the mineral soil samples. *Collinsia parviflora* and *Microsteris gracilis* were the exceptions, with both species ranking highest among species frequency in both floras. Calculation of Sorensen's similarity index (SI) showed similarity of the vegetation and seed bank floras in a subplot was low. Mean SI values ranged from 0.016 to 0.157 on a scale from 0-1 (1 indicates identical species composition). SI values were also low when calculated at the experimental unit level; values ranged from 0.056-0.30.

Species occurring with the highest density in the seed bank (i.e. *Microsteris gracilis, Galium aparine, Epilobium ciliatum and Poa bulbosa,*) had low cover in the vegetation, often much less than 1%; while species with the highest cover in the vegetation (i.e. *Pseudotsuga menziesii* , *Ceanothus velutinus* , *Calamagrostis rubescens* , *Arctostaphylos uva-ursi*) were absent from the germinable seed bank (Appendix 2).

Chapter 5. Discussion and Conclusions

Studies evaluating the post-disturbance restoration potential of the seed bank suggest it is disturbance dependant, species dependant, system dependant, and therefore often difficult to predict (Whittle 1997; Halpern et al. 1999; Korb et al. 2005; Stark et al. 2006; Lang and Halpern 2007). Wildland Urban Interface areas in the western United States present additional challenges for land managers responsible for maintaining native plant biodiversity following fuels 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. Inference from this study should be restricted to areas in the same geographic region with similar management and disturbance histories as ours.

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 source. The viable seed population density found in our study was comparable, but on the low end, to those reported for other temperate coniferous forest communities, which averaged from 0 to 14,463 seeds/m^2 (Oosting and Humphreys 1940, Kellman 1970, Strickler and Edgerton 1976, Moore and Wein 1977, Pratt et al. 1984). There was little similarity in species composition or abundance between the seed bank and vegetation floras. Of the species identified in the seed bank, the majority were annual forbs or early seral forest colonists, including exotic and invasive species, while the vegetation was dominated by perennial graminoids and shrubs. *Collinsia parviflora* and *Microsteris gracilis*, small forest herbs common in dry forests, were found in the greatest numbers and had the highest frequency of occurrence in the seed bank, but constituted less than 1% of the aboveground vegetation cover. The perennial forbs *Epilobium angustifolium, Epilobium ciliatum* and *Gnaphalium microcephalum,* colonists of early seral forests, were also among the most common in the seed bank with exotic and invasive species accounting for nearly 14% of germinants; however, these species had only trace abundance in the vegetation. Similarly, species occurring in high frequencies or abundance in the vegetation were often absent or nearly absent in the seed bank.

These findings suggest the contribution of forest seed banks for restoration of pre-disturbance plant communities, in systems similar to ours, will likely be low. However, some species may still play an important role despite their low abundance in the seed bank. First, species that originate from the seed bank will not likely resemble those found in the existing vegetation, instead favoring annual forest herbs, early seral colonists and exotic and invasive species. The presence of these species, especially exotic and invasive species, 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). Second, exotic and invasive species functional groups had high species richness relative to their abundance in the seed bank and relative to other seed bank functional groups. Consequently, a diverse suite of life history strategies may be available to respond to a variety of germination and establishment conditions following a disturbance, further contributing to a potential inhibitory role in post disturbance native plant community restoration.

Proximity to the road edge had significant and acute effects on the aboveground vegetation, but was less evident in the seed bank. Differences in canopy cover, litter cover and several plant functional groups in the vegetation were observed between the road edge and all other distances from the road, while few differences in the seed bank were observed between distances. Most notably, exotic and invasive species abundance in the vegetation were greater at the road side than in all interior plots, while no difference in abundance of these groups was observed in the seed bank. And even though abundance of exotic and invasive species was low in the vegetation and present only in road side plots, viable seeds of these groups were present in the seed bank with similar abundance in all distance from road categories and between both the litter and mineral soil layers.

Several factors may help to explain the presence of invasive species in the seed bank despite their low abundance in the vegetation. 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). *Cirsium 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). *Artemesia 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.

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). Herbicide application is a tool available to many land managers to mitigate the spread of invasive species; however, its effect on the seed bank, especially in forest wildlands is largely unknown. Of studies conducted in agricultural and managed forest systems, few detected differences in seed bank species composition due to herbicide application (Roberts and Neilson 1981, Morash and Freedman 1989), and those that did, detected a shift to herbicide resistant species in plots receiving herbicide treatments (Ball and Miller 1990) or an overall increase in weed seed abundance in herbicided plots (Menalled et al. 2001). In our study we found no differences in vegetation cover, germinant density or species richness between herbicided and non-herbicided plots in any group tested, including the targeted noxious weed group. Small sample size and minimal presence of noxious plants may have influenced the results of tests of abundance in the aboveground vegetation; however we did not detect an herbicide effect on the density of noxious weeds in the seed bank either. Our results indicated no benefit of herbicide application on the noxious weed cover in the vegetation or noxious weed density in the seed bank. Further study on the efficacy of herbicide treatments on the abundance of targeted species in the above ground vegetation and the possible effects of treatments to the composition and abundance of weed seed banks, is critical to evaluating the use of herbicide as a tool for mitigating invasive species establishment and spread in these systems.

Understanding and utilizing seed bank dynamics in restoration planning may aid in the development of comprehensive and integrated approaches to native plant restoration and invasive species control following fuels reduction. Post disturbance studies and monitoring are needed to evaluate the role of the seed bank in early succession in our study area; however, our study does raise several important considerations which could be tested with additional research regarding understory vegetation management in dry-mixed conifer forests in WUI’s. (1) Low viable seed populations found in this and other studies, may suggest a limited contribution from the seed bank for restoration of forest understories may be expected in systems similar to ours. Persistent vegetation and rapid dispersal of species from off-site sources will likely play primary roles in post-disturbance restoration. Consequently, exotic and invasive species, with their inherently high seed output and rapid colonization characteristics, may be more likely than native understory species to establish on newly disturbed sites. (2) Some species (exotic and invasive species) present in the seed bank may negatively affect post-disturbance plant communities despite low abundance in the vegetation and seed bank, possibly delaying or excluding desirable late successional species from establishing in recently disturbed areas for many years to come. Consequently, selecting fuels reduction techniques that minimize the creation of bare soil areas may minimize germination of exotic and invasive species following disturbance. (4) Further, early and comprehensive monitoring of interior forest areas following fuels reduction activities will be needed for early detection and rapid response to new populations of exotic and invasive species that may emerge from the seed bank or disperse in from off-site sources. (6) Finally, additional research and monitoring of herbicide use in forest wildland ecosystems is necessary to understand the implications of its use on native and invasive species composition in the aboveground vegetation and seed bank floras.

Bibliography

Alston, K. P., and D. M. Richardson. 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biological Conservation **132**:183-198.

Archibold O.W. 1989. Seed bank dynamics in temperate deciduous forest *in* Ecology of Soil Seed banks. *edited by* M.A. Leck, V.T. Parker, R.L. Simpson. Academic Press. New York, New York, USA

Bailey, J. D., and J. C. Tappeiner. 1998. Effects of thinning on structural development in 40-to 100-year-old Douglas-fir stands in western Oregon. Forest Ecology and Management **108**:99-113.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecological Systems **5**:1-24.

Ball, D. A., and S. D. Miller. 1990. Weed seed population response to tillage and herbicide use in three irrigated cropping sequences. Weed Science **38**:511-517.

Barnett, J. P. 1979. Germination temperatures for container culture of southern pines. Southern Journal of Applied Forestry **3**:13-14.

Brown, A. H. F., and L. Oosterhuis. 1981. The role of buried seed in coppicewoods. Biological Conservation **21**:103-127.

Brown, D. 1992. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. Canadian Journal of Botany **70**:1603-1612.

Buhler, D. D., R. G. Hartzler, and F. Forcella. 1997. Implications of weed seedbank dynamics to weed management. Weed Science **45**:329-336.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management **95**:63-77.

Camp, A. E. 1999. Age structure and species composition changes resulting from altered disturbance regimes on the eastern slopes of the Cascades Range, Washington. Journal of Sustainable Forestry **9**:39-67.

Carey, J. H. 1994. Artemisia absinthium. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer).

Clinton, W. J. 1999. Executive Order 13112 of February 3, 1999; invasive species. Pages 6183–6186.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist **111**:1119.

D'Antonio, C. M., N. E. Jackson, C. C. Horvitz, and R. Hedberg. 2004. Invasive plants in wildland ecosystems: merging the study of invasion processes with management needs. Frontiers in Ecology **2**:513-521.

Everett, R. L., P. F. Hessburg, M. Jensen, and B. Bormann. 1994. Executive Summary. Vol. 1. Eastside Forest Ecosystem Health Assessment. Page 61 *in* F. S. General Technical Report PNW-GTR-317. U.S. Department of Agriculture, Pacific Northwest Research Station, editor., Portland, OR.

Fenner, M., and K. Thompson. 2005. The ecology of seeds. Cambridge University Press, Cambridge, UK.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecological Systems **29**:207-231.

Fyles, J. W. 1989. Seed bank populations in upland coniferous forests in central Alberta. Canadian Journal of Botany **67**:274-278.

Garrison, G. A. 1949. Uses and modifications for the “moosehorn” crown closure estimator. Journal of Forestry **47**:733-735.

Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology **17**:420-432.

Graham, D. J., and M. J. Hutchings. 1988. Estimation of the seed bank of a chalk grassland ley established on former arable land. Journal of Applied Ecology **25**:241-252.

Gross, K. L. 1990. A Comparison of methods for estimating seed numbers in the soil. Journal of Ecology **78**:1079-1093.

Gucker, C. L. 2008. *Verbascum thapsus*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). .

Halpern, C. B., S. A. Evans, and S. Nielson. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory reinitiation. Canadian Journal of Botany **77**:922-935.

Harrod, R. J., and C. B. Halpern. 2005. The seed ecology of *Iliamna logisepala* (Torr.) Wiggins, an east Cascade endemic. Journal of Natural Areas **25**:246-256.

Harrod, R. J., and S. Reichard. 2000. Fire and invasive species within the temperate and boreal coniferous forests of western North America. Pages 95–101 *in* Proceedings of The First National Congress on Fire Ecology, Prevention, and Management: Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species., Tall Timbers Research Station, Tallahassee, FL.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management **211**:117-139.

Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology **9**:761-770.

Ingersoll, C. A., and M. V. Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbances. Canadian Journal of Botany **68**:1156-1162.

Ingersoll, C. A., and M. V. Wilson. 1993. Buried propagule bank of a high subalpine site: Microsite variation and comparisons with aboveground vegetation. Canadian Journal of Botany **71**:712-717.

Keeley, J. E. 2002. Impact of fire management practices on invasive plants *in* Ecological Society of America 2002 Annual Meeting Abstracts, Tucson, AZ.

Kellman, M. 1978. Microdistribution of viable weed seed in two tropical soils. journal of Biogeography **5**:291-300.

Kellman, M. C. 1970. The viable seed content of some forest soil in coastal British Columbia. Canadian Journal of Botany **48**:1383-1385.

Kemp, P. R. 1989. Seed banks and vegetation processes in deserts. *in* M. A. Leck, V.T. Parker, and R.L. Simpson, editors. Ecology of soil seed banks. Academic Press, New York, New York, USA. pp 258-281.

Korb, J. E., J. D. Springer, S. R. Powers, and M. M. Moore. 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: Clues to site history and restoration potential. Applied Vegetation Science **8**:103-112.

Kramer, N. B., and F. D. Johnson. 1987. Mature forest seed banks of three habitat types in central Idaho. Canadian Journal of Botany **65**:1961-1966.

Krueger-Mangold, J. M., R. L. Sheley, and T. J. Svejcar. 2006. Toward ecologically-based invasive plant management on rangeland. Weed Science **54**:597-605.

Landis, T. D., R. W. Tinus, S. E. McDonald, and J. P. Barnett. 1990. Containers and Growing Media, The Container Tree Nursery Manual. Vol. 2, USDA Forest Service, Washington DC. Pages 41-167.

Lang, N. L., and C. B. Halpern. 2007. The soil seed bank of a montane meadow: Consequences of conifer encroachment and implications for restoration. Canadian Journal of Botany **85**:557-569.

Laughlin, D. C., J. D. Bakker, M. T. Stoddard, M. L. Daniels, J. D. Springer, C. N. Gildar, A. M. Green, and W. W. Covington. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. Forest Ecology and Management **199**:137-152.

Leck, M. A., V. T. Parker, and S. R. L. 1989. Ecology of soil seed banks. Academic Press, Inc, San Diego, CA.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science **2**:314-320.

Livingston, R. B., and M. Allessio. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. Bulletin of the Torrey Botanical Club **95**:58-69.

Louda, S. M. 1989. Seed bank processes *in* Ecology of soil seed banks *edited by* M.A. Leck, V.T. Parker and R.L. simpson. Academic Press, New York, New York.

Major, J., and W. T. Pyott. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Plant Ecology **13**:253-282.

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MJM Software Design Gleneden Beach, Oregon, USA.

McLemore, B. F. 1969. Long stratification hastens germination of loblolly pine seed at low temperatures. Journal of Forestry **67**:419-420.

Menalled, F. D., K. L. Gross, and M. Hammond. 2001. Weed aboveground and seedbank community responses to agricultural management systems. Ecological Applications **11**:1586-1601.

Moore, J. M., and R. W. Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Canadian Journal of Botany **55**:2408-2412.

Morash, R., and B. Freedman. 1989. The effects of several herbicides on the germination of seeds in the forest floor. The Canadian Journal of Forest Research **19**:347-350.

Ooi, M. K. J., T. D. Auld, and R. J. Whelan. 2007. Distinguishing between persistence and dormancy in soil seed banks of three shrub species from fire-prone southeastern Australia. BioOne **18**:405-412.

Oosting, H. J., and M. E. Humphreys. 1940. Buried viable seeds in a successional series of old field and forest soils. Bulletin of the Torrey Botanical Club **67**:253-273.

Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the HJ Andrews Experimental Forest, Oregon. Conservation Biology:64-75.

Parks, C. G., S. R. Radosevich, B. A. Endress, B. J. Naylor, D. Anzinger, L. J. Rew, B. D. Maxwell, and K. A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. Perspectives in Plant Ecology, Evolution and Systematics **7**:137-158.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. Botanical Review **53**:335-371.

Pratt, D. W., R. A. Black, and B. A. Zamora. 1984. Buried viable seed in a ponderosa pine community. Canadian Journal of Botany **62**:44-52.

Public Law 93-629. 1974. Federal Noxious Weed Act. Government Printing Office.

Public Law 106-224. 2000. Plant Protection Act.

Qi, M., and J. B. Scarratt. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Canadian Journal of Botany **76**:872-883.

Radosevich, S. R., J. S. Holt, and C. M. Ghersa. 2007. Ecology of weeds and invasive plants: relationship to agriculture and natural resource management. Wiley-Interscience.

Roberts, H. A., and J. E. Neilson. 1981. Changes in the Soil Seed Bank of Four Long-Term Crop/Herbicide Experiments. Journal of Applied Ecology **18**:661-668.

Simpson, R. L. 1989. Seed banks: General concepts and methodological issues *in* Ecology of soil seed banks. *Edited* by M.A. Leck, V.T. Parker, and R.L. Simpson. Academic Press, Inc., New York, New York, USA. Pages 3-7.

Stark, K. E., A. Arsenault, and G. E. Bradfield. 2006. Soil seed banks and plant community assembly following disturbance by fire and logging in interior Douglas-fir forests of south-central British Columbia. Canadian Journal of Botany **84**:1548-1560.

Strickler, G. S., and P. J. Edgerton. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. Ecology **57**:801-807.

Sullivan, K. A., and A. M. Ellison. 2006. The seed bank of hemlock forests: Implications for forest regeneration following hemlock decline. BioOne **133**:393-402.

Thompson, K. 2000. The functional ecology of soil seed banks *in* Seeds: The Ecology of Regeneration in Plant Communities, 2nd edition. CABI, Oxford, UK.

Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. The Journal of Ecology **67**:893-921.

Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology **6**:253-262.

USDA-NRCS. 2009. Custom soil resource report for Kittitas county area, Washington.

USDA Forest Service. 2005. Pacific Northwest Region Invasive plant program; Preventing and managing invasive plants, Final Environmental Impact Statement. Pacific Northwest Region 6.

USDA Forest Service. 2006. Liberty wildland urban interface fuels reduction project environmental assessment. Okanogan and Wenatchee National Forests, Cle Elum Ranger District.

van der Valk, and R. L. Pederson. 1989. Seed banks and the management and restoration of natural vegetation *in* Ecology of soil seed banks. *edited by* M.A. Leck, V.T. Parker, R.L. Simpson. Academic Press, New York, New York, USA.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. The Journal of American Science **84**:468-478.

Warr, S. J., K. Thompson, and M. Kent. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. Progress in Physical Geography **17**:329.

Whittle, C. A., L. C. Duchesne, and T. Needham. 1997. The importance of buried seeds and vegetative propagation in the development of post-fire plant communities. Environmental Review **5**:79-87.

Wienk, C. L., C. H. Sieg, and G. R. McPherson. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. Forest Ecology and Management **192**:375-393.

Wilson, J. B., H. Gitay, S. H. Roxburgh, W. McG, and R. S. Tangney. 1992. Egler's Concept of Initial Floristic Composition in Succession: Ecologists Citing It Don't Agree What It Means. Oikos **64**:591-593.

Young, K. R. 1985. Deeply buried seeds in a tropical wet forest in Costa Rica. Biotropica **17**:336-338.

Zouhar, K. 2002. Cirsium vulgare. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture. Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer).

APPENDICES

Appendix 1. Aboveground vegetation species list, functional group and family

Species and Functional Group	Family
Exotic Species	
Lactuca serriola	Asteraceae
Matricaria matricarioides	Asteraceae
Taraxacum officinale	Asteraceae
Myosotis micrantha	Boraginaceae
Medicago lupulina	Fabaceae
Melilotus officinalis	Fabaceae
Trifolium pretense	Fabaceae
Trifolium repens	Fabaceae
Plantago lanceolata	Plantaginaceae
Agropyron intermedium	Poaceae
Bromus secalinus	Poaceae
Bromus tectorum	Poaceae
Dactylis glomerata	Poaceae
Phleum pratense	Poaceae
Poa bulbosa	Poaceae
Poa compressa	Poaceae
Poa pratensis	Poaceae
Noxious weeds	
Artemisia absinthium	Asteraceae
Centaurea diffusa	Asteraceae
Centaurea pratensis	Asteraceae
Cirsium arvense	Asteraceae
Cirsium vulgare	Asteraceae
Annual Forbs	
Agoseris heterophylla	Asteraceae
Madia exigua	Asteraceae
Madia gracilis	Asteraceae
Madia minima	Asteraceae
Cryptantha torreyana	Boraginaceae
Athysanus pusillus	Brassicaceae
Stellaria nitens	Caryophyllaceae
Clarkia rhomboidea	Onagraceae
Epilobium minutum	Onagraceae
Gayophytum diffusum	Onagraceae

Collomia grandiflora	Polemoniaceae
Collomia linearis	Polemoniaceae
Microsteris gracilis	Polemoniaceae
Polygonum sawatchense	Polygonaceae
Montia perfoliata	Portulacaceae
Galium aparine	Rubiaceae
Collinsia parviflora	Scrophulariaceae
Perennial Forbs	
Angelica canbyi	Apiaceae
Hieracium sp.	Apiaceae
Osmorhiza chilensis	Apiaceae
Apocynum androsaemifolium	Apocynaceae
Achillea millefolium	Asteraceae
Agoseris grandiflora	Asteraceae
Anaphalis margaritacea	Asteraceae
Antennaria neglecta	Asteraceae
Antennaria racemosa	Asteraceae
Arnica cordifolia	Asteraceae
Aster foliaceus	Asteraceae
Balsamorhiza sagittata	Asteraceae
Cichoreae spp.	Asteraceae
Hieracium albiflorum	Asteraceae
Hieracium scouleri	Asteraceae
Luina nardosmia	Asteraceae
Solidago canadensis	Asteraceae
Tragopogon dubius	Asteraceae
Achlys triphylla	Berberidaceae
Boraginaceae sp.	Boraginaceae
Arenaria macrophylla	Caryophyllaceae
Stellaria jamesiana	Caryophyllaceae
Stellaria longipes	Caryophyllaceae
Pterospora andromedea	Ericaceae
Pyrola picta	Ericaceae
Pyrola secunda	Ericaceae
Pyrola sp.	Ericaceae
Lathyrus pauciflorus	Fabaceae
Vicia Americana	Fabaceae
Geranium viscosissimum	Geraniaceae
Hydrophyllum capitatum	Hydrophyllaceae

Phacelia hastate	Hydrophyllaceae
Epilobium angustifolium	Onagraceae
Goodyera oblongifolia	Orchidaceae
Paeonia brownie	Paeoniaceae
Rumex salicifolius	Polygonaceae
Trientalis latifolia	Primulaceae
Thalictrum occidentale	Ranunculaceae
Fragaria virginiana	Rosaceae
Potentilla glandulosa	Rosaceae
Galium triflorum	Rubiaceae
Lithophragma bulbifera	Saxifragaceae
Lithophragma parviflora	Saxifragaceae
Castilleja miniata	Scrophulariaceae
Pedicularis racemosa var. racemosa	Scrophulariaceae
Lomatium nudicaule	Umbelliferae
Lomatium triternatum	Umbelliferae
Unknown forb 10	Unknown
Unknown forb 2	Unknown
Unknown forb 9	Unknown
Viola adunca	Violaceae
Graminoids	
Carex geyeri	Cyperaceae
Carex pachystachya	Cyperaceae
Carex rossii	Cyperaceae
Carex sp.3	Cyperaceae
Carex sp.4	Cyperaceae
Carex sp.5	Cyperaceae
Luzula campestris	Juncaceae
Agrostis scabra	Poaceae
Bromus carinatus	Poaceae
Calamagrostis rubescens	Poaceae
Deschampsia elongata	Poaceae
Elymus glaucus	Poaceae
Festuca idahoensis	Poaceae
Festuca microstachys	Poaceae
Festuca occidentalis	Poaceae
Melica sp.	Poaceae
Poa nervosa	Poaceae
Poa sandbergii	Poaceae

Sitanion hystrix	Poaceae
Stipa lemmonii	Poaceae
Stipa occidentalis	Poaceae
Trisetum canescens	Poaceae
Shrubs, trees, vines	
Acer glabrum var. douglasii	Aceraceae
Berberis aquifolium	Berberidaceae
Lonicera ciliosa	Caprifoliaceae
Pachistima myrsinites	Celastraceae
Juniperus occidentalis	Cupressaceae
Arctostaphylos uva-ursi	Ericaceae
Chimaphila umbellata var. occidentalis	Ericaceae
Vaccinium sp.	Ericaceae
Lupinus polyphyllus	Fabaceae
Ribes cereum	Grossulariaceae
Ribes sp.	Grossulariaceae
Abies grandis	Pinaceae
Abies lasiocarpa	Pinaceae
Larix occidentalis	Pinaceae
Pinus contorta	Pinaceae
Pinus ponderosa	Pinaceae
Pseudotsuga menziesii	Pinaceae
Ceanothus sanguineus	Rhamnaceae
Ceanothus velutinus	Rhamnaceae
Amelanchier alnifolia	Rosaceae
Crataegus douglasii	Rosaceae
Holodiscus discolor	Rosaceae
Prunus emarginata	Rosaceae
Prunus virginiana	Rosaceae
Purshia tridentata	Rosaceae
Rosa spp.	Rosaceae
Rubus parviflorus	Rosaceae
Spiraea betulifolia var. lucida	Rosaceae
Populus tremuloides	Salicaceae
Salix scouleriana	Salicaceae
Penstemon fruticosus	Scrophulariaceae
Unknown shrub 3	Unknown
Unknown shrub 5	Unknown

Appendix 2. Functional group, species, frequency of occurrence (number of subplots), mean density (seedlings/m^2) and cover (%) of vegetation and seed bank taxa.

	Vegetation		Seed bank					
			Litter			Mineral soil		
	Cover	Freq.	Density	Freq.	Counts	Density	Freq.	Counts
Exotic Species								
Bromus tectorum	0.26	5.36	3.57	2.38	6			
Lactuca serriola			0.6	0.6	1			
Medicago lupulina	0.01	1.79						
Myosotis discolor			4.17	0.6	7			
Agropyron intermedium	1.46	11.31	2.98	0.6	5			
Dactylis glomerata	0.44	12.5	0.6	0.6	1			
Phleum pratense	0.01	1.79						
Plantago lanceolata	0.02	2.38						
Poa bulbosa	0.04	4.76	17.86	1.19	30			
Poa compressa	0.02	3.57						
Taraxacum officinale	0.09	11.31						
Trifolium repens	0.06	2.98						
Verbascum thapsus			4.17	1.79	7	4.54	1.19	3
Noxious Weeds								
Centaurea diffusa	0.12	1.19						
Artemisia absinthium			0.6	0.6	1			
Centaurea pratensis	0.2	3.57						
Cirsium arvense			8.93	4.76	15			
Cirsium vulgare			1.19	1.19	2	4.54	1.79	3

Annual Forbs								
Collinsia parviflora	0.27	44.05	54.17	15.48	91	18.18	2.38	12
Collomia grandiflora	0.07	11.9	2.38	2.38	4			
Cryptantha torreyana	0.04	6.55						
Epilobium minutum	0.07	11.31	0.6	0.6	1	1.51	0.6	1
Galium aparine	0.03	4.76	16.07	2.38	27			
Madia exigua	0.02	2.98						
Madia gracilis	0.02	2.98						
Microsteris gracilis	0.17	32.14	40.48	15.48	68	3.03	1.19	2
Montia perfoliata	0.04	7.14	2.38	2.38	4	9.09	2.38	6
Polygonum sawatchense	0.02	4.76						
Perennial Forbs								
Achillea millefolium	0.82	30.36	4.76	3.57	8			
Agoseris grandiflora	0.03	1.19						
Anaphalis margaritacea	0.02	1.19						
Angelica canbyi	0.03	1.79						
Antennaria neglecta	0.02	2.38						
Apocynum androsaemifolium	0.13	4.17	1.19	0.6	2			
Arenaria macrophylla	0.45	27.38						
Arnica cordifolia	0.21	7.14						
Balsamorhiza sagittata	0.1	2.98						
Epilobium angustifolium			1.19	1.19	2			
Epilobium ciliatum			14.29	7.14	24	27.26	1.79	18
Fabaceae spp.			1.19	1.19	2			
Fragaria virginiana	0.13	2.98						
Galium triflorum	0.03	4.17	0.6	0.6	1			0

Gnaphalium microcephalum			11.9	5.36	20	37.87	5.36	25
Goodyera oblongifolia	0.02	0.6						
Hieracium albiflorum	0.05	1.79						
Hieracium scouleri	0.04	2.38						
Hieracium sp.	0.29	18.45	1.19	0.6	2			
Lathyrus pauciflorus	0.37	14.88						
Lithophragma spp.			13.69	2.38	23	37.87	1.79	25
Lomatium nudicaule	0.01	2.38						
Lomatium triternatum	0.06	7.74						
Osmorhiza chilensis	0.06	4.17				6.06	1.19	4
Phacelia hastata	0.02	1.19						
Potentilla glandulosa	0.02	1.79						
Pyrola spp.	0.01	0.6						
Rumex spp.						1.51	0.6	1
Thalictrum occidentale	0.12	2.98						
Tragopogon dubius	0.01	2.38						
Trientalis latifolia	0.04	1.79						
Vicia americana	0.15	9.52						
Viola sp.	0.01	1.19						
Asteraceae 2 SB			1.79	1.19	3			
Asteraceae 3 SB			0.6	0.6	1			
Caryophyllaceae spp.			0.6	0.6	1			
Saxifragaceae sp.	0.05	2.98						
Unknown forb 1 SB			0.6	0.6	1			
Unknown forb 1 Veg	0.04	5.36						
Unknown forb2 SB			0.6	0.6	1			

Graminoids								
Festuca microstachys	0.03	2.98						
Agrostis exarata			1.79	0.6	3			
Agrostis scabra	0.31	1.79						
Bromus carinatus	0.18	11.9	3.57	1.79	6			
Calamagrostis rubescens	9.95	49.4						
Carex geyeri	3.18	36.9						
Carex pachystachya	0.02	1.19						
Carex rossii	0.02	0.6						
Carex spp 4,5 V	0.09	5.36						
Carex spp.	0.02	0.6	1.79	1.19	3			
Deschampsia elongata	0.02	2.38	2.98	2.38	5	33.32	3.57	22
Elymus glaucus	0.6	19.05	11.31	3.57	19	1.51	0.6	1
Festuca idahoensis	0.16	2.38						
Festuca occidentalis	0.31	4.17						
Festuca sp.	0.15	6.55	24.4	5.95	41	1.51	0.6	1
Luzula campestris	0.03	1.19						
Poa nervosa	0.01	1.79						
Sitanion hystrix	0.05	0.6						
Trisetum canescens	0.04	3.57						
Melica sp.	0.01	1.79						
Poacea spp.	0.01	2.38	10.12	6.55	17	10.6	3.57	7
Shrubs/Trees/Vines								
Abies grandis	1.71	5.95						
Amelanchier alnifolia	0.59	8.33						
Arctostaphylos uva-ursi	2.79	11.31						

Berberis aquifolium	0.71	10.12						
Ceanothus sanguineus	0.06	0.6						
Ceanothus velutinus	3.48	7.74						
Chimaphila umbellata	0.11	2.98						
Holodiscus discolor	0.46	2.38						
Lonicera ciliosa	0.01	0.6						
Lupinus polyphyllus	0.47	14.88						
Pachistima myrsinites	0.27	5.95						
Philadelphus lewisii			0.6	0.6	1			
Pinaceae spp.			0.6	0.6	1			
Pinus contorta	0.02	1.19						
Pinus ponderosa	0.57	8.33						
Prunus emarginata	0.15	1.79						
Pseudotsuga menziesii	2.17	16.67						
Purshia tridentata	1.57	7.74	1.79	1.19	3			
Rosa spp.	0.81	10.12						
Rubus leucodermis			2.38	1.79	4	1.51	0.6	1
Salix scouleriana	1.48	2.98						
Spiraea betulifolia var. lucida	1.65	30.36	1.79	1.19	3			
Symphoricarpos albus	1.54	11.9						
Vaccinium sp.	1.31	5.36						
Unknown shrub SB			0.6	0.6	1			
Unknown dicot			10.12	7.14	17	19.69	5.36	13
Totals	**43.94**		**288.78**		**485**	**219.6**		**145**

Appendix 3. Species found exclusively in seed bank.

Species	Origin	Life Form
Myosotis discolor	E	Forb
Verbascum thapsus	E	Forb
Epilobium ciliatum	N	Forb
Gnaphalium microcephalum	N	Forb
Agrostis exarata	N	Grass
Philadelphus lewisii	N	Shrub
Rubus leucodermis	N	Shrub