

AN ABSTRACT OF THE THESIS OF

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Title: Seed Bank Response to Juniper Expansion in the Semi-arid Lands of Oregon, USA

Abstract approved:

Richard F. Miller

Expansion of *Juniperus occidentalis* into the sagebrush steppe has resulted in significant changes in understory composition. A consequence of increased *J. occidentalis* dominance may be a depletion of the seed bank. The potential for depletion is problematic because a reduction in the amount of species available from the seed bank may compromise site resiliency. During disturbances that disrupt current vegetation, a reduction in recruitment from the seed bank could cause the site to be more vulnerable to colonization by weedy species or could lead to a reduction in the amount of cover protecting the soil surface and thus increase site susceptibility to erosion. This research evaluated the effects of the relative abundance of *J. occidentalis* on the soil seed bank. Questions addressed were: 1) is species richness negatively correlated with *J. occidentalis* cover; 2) does the diversity of weedy species increase along a gradient of *J. occidentalis* cover; and 3) does seed density decrease as *J. occidentalis* cover increases? We also attempted to identify seed bank depletion thresholds based on seed density. Two eastern Oregon sagebrush steppe sites were chosen to represent the juniper woodland-sagebrush steppe region. These sites displayed a range of *J. occidentalis* canopy cover. Soil and litter samples were collected in the fall of 2006 and 2007 and subjected to both cold-wet and warm-dry

stratification. Germination occurred over a period of eight months under greenhouse conditions. Linear and Poisson regression techniques were used to evaluate relationships. A non-parametric deviance reduction approach was used for threshold detection and a threshold strength index was used to evaluate the strength of the identified thresholds. No statistically significant relationships were detected between *J. occidentalis* cover and species richness or weedy species diversity at either site in either year, with the exception of Bridge Creek in 2007 which showed a positive correlation between *J. occidentalis* cover and seed bank species diversity. The results for seed density were more complex. In 2006, *J. occidentalis* cover was strongly related to seed density at Devine Ridge but in 2007 there was no evidence of a correlation. At Bridge Creek in 2006, there was a weak relationship between increasing *J. occidentalis* cover and decreasing seed density but in the second year the pattern differed suggesting a positive correlation between *J. occidentalis* cover and seedling density. This variability in results suggests a complex relationship between *J. occidentalis* cover and seed bank composition. This relationship may partially depend on weather conditions, and a more lengthy study period would be valuable in discerning whether such a correlation exists. Concerning threshold detection, seed bank depletion thresholds were identified across both sites and years but their strength was very weak. These findings indicate that a reliable seed bank depletion threshold, as defined in this study, may not exist for these sites at least over the course of this study. Though these results were negative, the approach was useful and pursuit of its further development is suggested for evaluation of other suspected thresholds.

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Seed Bank Response to Juniper Expansion in the Semi-arid Lands of Oregon, USA

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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.

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CONTRIBUTION OF AUTHORS

Dr. Richard Miller, Dr. Jane Mangold and Dr. Dave Pyke contributed to the design and writing of Chapter 2. Jaime Ratchford assisted in data collection.

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Chapter 1: Introduction

Juniper Expansion

Woody plant expansion is occurring in many places across North America (Archer et al. 1995, Van Auken 2000, Briggs et al. 2005). *Juniperus virginiana* (eastern red cedar) encroachment is an issue in the Midwest (Barth 2002) as is *Prosopis glandulosa* (honey mesquite) in the Southwest (Ansley et al. 2001). Of concern in the northwestern Great Basin is *Juniperus occidentalis* (western juniper) (Miller and Rose 1995). This small arid land tree reaches 7-20 m in height. Its small, distinctive, round cones are covered in bluish bloom (Jensen et al. 2002) and are consumed by several species of birds including *Myadestes townsendi* (Townsend's solitaire), *Sialia currucoides* (mountain bluebird), and *Turdus migratorius* (American robin) (Poddar and Lederer 1982, Miller et al. 2005, Reinkensmeyer et al. 2007). *Odocoileus hemionus* (mule deer) use stands of *J. occidentalis* for shelter during winter months (Leckenby and Adams 1986) and several small mammals, including *Neotoma* (woodrat) species, nest in and around these trees (Verts and Carraway 1998). Old growth *J. occidentalis* are typically found on rocky outcrops (Miller et al. 2005, Johnson and Miller 2008) but the majority of the populations are found on many different soil types (Driscoll 1964) at a variety of topographic positions and elevations (Miller and Rose 1995, Gedney et al. 1999) and the species range appears to be continually expanding.

Extent of Expansion

As discussed by Miller and Wigand (1994), the range of this species, as well as other *Juniperus* species, has varied considerably during the last 12,000 years. The arrival of *J. occidentalis* in Oregon is dated at approximately 4,800 years BP and today the species occupies the northwestern portion of the Great Basin covering 3.6 million hectares in east-central Oregon, northeastern California, northwestern Nevada, and southwestern Idaho (Miller et al. 2005). Though it is possible that the range of *J.*

occidentalis may have been larger in extent during prehistory (Mehring and Wigand 1987), *J. occidentalis* expansion during the past 130 years has occurred at an unprecedented rate (Miller and Wigand 1994, Miller and Rose 1995). The cause of this expansion has been primarily attributed to reduced fire occurrence (Burkhardt and Tisdale 1976, Miller and Rose 1999). Elevated CO₂ levels (Knapp et al. 2001), optimal climatic conditions for reproduction, and heavy grazing (Miller and Rose 1995, Archer et al. 1995) may also be implicated.

Consequences of Expansion

Though experimental verification is difficult to come by (Belsky 1996), *J. occidentalis* invasion is thought to impact hydraulic processes (Eddleman and Miller 1992), and increase the potential for erosion that increases the export of nutrients off site. As *J. occidentalis* begins to dominate a site, effective precipitation can also decrease due to the canopy interception (Larsen 1993, Young et al. 1984) and overall increase in transpiration from *J. occidentalis*. Though not specifically evaluated for *J. occidentalis*, changes in the soil water distribution (Breshears et al. 1997) and increased shading (Johnsen 1962) may also occur during woody plant expansion. Because of the potential for *J. occidentalis* to capture water, nutrients and light at a higher rate than other species, there is the potential for increased competition with understory vegetation. These factors may be the cause of the decrease in understory vegetation sometimes associated with *J. occidentalis* encroachment (Burkhardt and Tisdale 1969, Knapp and Soule 1998, Miller et al. 2000, Allen and Nowak 2008).

Decreases in the abundance and diversity of understory vegetation in the sagebrush steppe are undesirable for several reasons. First, many sites affected by *J. occidentalis* expansion are utilized for livestock grazing; understory grasses and forbs are the primary forage plants for these animals. Second, these sites are valued wildlife habitat (Longland and Bateman 2002) especially for sagebrush obligates including *Centrocercus urophasianus* and *C. minimus* (sage grouse) (Crawford et al. 2004), *Brachylagus idahoensis* (pygmy rabbit), and *Antilocapra americana* (pronghorn).

antelope) (Paige and Ritter 1999). Third, decreases in understory vegetation may translate to increases in bare ground where the impacts of erosion can be severe (Davenport et al. 1998, Pierson et al. 2008). Soil conservation in arid landscapes where *J. occidentalis* occurs is essential if productivity and resistance to weed invasion is to be maintained. Lastly, preservation of biodiversity has become an important societal value. As the theories of integrated ecosystem management, which often strive to increase biodiversity, become more developed (i.e. Sheley et al. 1999, Schmandt 2006, Wang et al. 2006, Nunan 2006), land managers will be better equipped to employ management strategies that satisfy societal demands.

Seed Bank Ecology in Semi-arid Environments

Review of the Literature

Unfortunately, research pertaining to seed bank dynamics in *J. occidentalis* communities is restricted. Though still somewhat limited, far more literature has been generated when the scope is expanded semi-arid environments such the Great Basin in the U.S., and the shrublands of Australia. What follows is a review of some of the relevant contributions.

As one might expect, seeds in the seed bank are not randomly distributed. Rather, they follow patterns often associated with the established vegetation. Several studies illustrate this relationship. Young and Evans (1975) examined the germinability of seed reserves collected beneath and between shrubs in a big sagebrush community. It was found that seeds collected from beneath the shrub canopy were more likely to germinate than those collected in the interspace. Another study (Strickler and Edgerton 1976) found that more seeds emerged from litter samples than in mineral soil in mixed conifer forest (interestingly, no conifer seeds germinated). These patterns demonstrate that the presence of woody species may affect the spatial distribution of

both interspecific and intraspecific seeds. Everett (1986) concurs that woody species can affect seed distribution. This study recorded the seed rain under tree-harvested and un-harvested *Pinus monophylla*-*Juniperus osteosperma* (singleleaf pinyon-Utah juniper) woodland for four consecutive years. Seed bank input was higher in harvested plots; this relatively reduced seed rain in un-harvested plots agrees with the idea that the presence of trees may have the potential to reduce the quantity of seeds stored in the seed bank.

Other factors such as seed shape and soil characteristics can have an influence on seed distribution as well. Chambers (2000) followed the movements of seeds during a restoration experiment. Soil surface characteristics were examined and correlated to seed type. It was found that seeds with no appendages showed little horizontal movement away from the parent plant. Seeds with appendages were also non-randomly redistributed, and large soil depressions trapped seeds more readily than small ones. Coffin and Lauenroth (1989) evaluated seed bank variability across differing soil textures at different time intervals. The authors concluded that temporal variation had a greater influence on seed bank distribution than spatial variability because site differences tended to be a result of fluctuations in seed bank inputs from annuals that produced transient, as opposed to persistent seed. Beatty (1991) examined the seed banks of several different communities in a mosaic landscape. She found that species composition of standing vegetation differed from community to community but that differences among seed bank composition varied less. This may indicate that seed banks are relatively stable when compared to standing vegetation or that seeds are more uniformly distributed across the landscape than standing vegetation. Davies (2008) found that seeds of *Taeniatherum caput-medusae* (medusahead) were less likely to be found in stands of tall grasses than in stands of annual grasses indicating that vegetation structure may also have an influence in seed distribution.

Similarity between standing vegetation and the seed bank does not always exist. Everett (1986) found that proportions of seed bank species were not equivalent to the

proportions of species in the standing vegetation but did reflect the current vegetation more closely than the predicted potential (climax) vegetation. Marlette and Anderson (1986) found that in stands of *Agropyron cristatum* (crested wheatgrass), which can be highly stable, *A. cristatum* seeds dominated the seed bank. Where it was present, *Artemisia tridentata* (big sagebrush) seeds were co-dominant with *A. cristatum*. In this case, the species dominant in the vegetation were also dominant in the seed bank. However, seeds of *Elymus elymoides* (squirreltail) were also tracked and despite an abundant seed source, dispersal into crested wheatgrass stands for this species was exceptionally low.

Peco et al. (1998) attempted to locate a measure that predicted the similarity between the species composition of the seed bank and standing vegetation. Germination was used as a proxy for seed counts. The standing vegetation appeared to be determined by elevation, topography, and grazing intensity, but the seed bank was not. It was proposed that the perennial to annual ratio and the proportion of bare soil in October be used to predict the level of similarity between the composition of the standing vegetation and the seed bank. It appears that as the number of annuals and amount of bare ground increases, standing vegetation to seed bank similarity increases.

Disturbance may exaggerate differences between the standing vegetation and the seed bank but the relationship may not be linear. Osem et al. (2006) examined the effects of grazing on the similarity between species in the seed bank versus established vegetation. Peak-standing biomass of annuals was used as a measure of annual productivity. They concluded that at low levels of net primary productivity (as measured by peak standing biomass) where soil water and nutrients are limiting, the relationship between seed bank to standing vegetation similarity is positive. At high levels of net primary productivity, where space and light are limiting, the reverse is true. Above this range soil resource availability is no longer the factor limiting plant density. It was hypothesized that grazing encouraged recruitment from the seed bank

by diminishing vegetation cover and litter accumulation that could constrain germination, seedling emergence, and plant survival.

Invasive species such as *Bromus tectorum* (cheatgrass) have the potential to be over represented in the seed bank. Clements et al. (2007) published a study investigating the seed banks of both native and invasive species in the semi-arid shrub-steppe region of British Columbia, Canada. Of the 39 species found in the seed bank, six species accounted for 85% of the seed bank and were the most common in the standing vegetation (*Purshia tridentata* (antelope bitterbrush), *Bromus tectorum* (cheatgrass), *Sporobolus cryptandrus* (sand dropseed), *Polygonum douglasii* (Douglas' knotweed), *Centaurea diffusa* (diffuse knapweed), and *Hesperostipa comata* (needle-and-thread)). *B. tectorum* possessed a seed bank density surpassing all others by at least ten fold at 233 seeds m⁻² potentially increasing the challenge to restore the site. Hassan and West (1986), in the sagebrush region of Utah, examined vegetation establishment from the seed pool at two points in time (fall and spring) in burned and unburned plots. It was found that the viable soil seed pool was less dense in burned plots than in unburned plots and that seed pools were dominated by *Bromus tectorum*. The viable soil seed pool was larger under shrubs than in the interspace in unburned plots and smaller under shrubs in the burn plots, which typically burn hotter than the shrub interspace. They concluded a rather dismal outlook for restoration for this study area. *B. tectorum* was dominant before fire and was, unfortunately, even more dominant afterwards making the reestablishment of other plants extremely difficult. Thresholds such as this one may be important for plant communities experiencing change whether the changes are incurred via small scale management practices or through large scale climate change.

In a more broad attempt to examine seed ecology, Chambers et al. (1999) reviewed the reproductive ecology, seed dispersal, post-dispersal seed mortality, seed dormancy, seed germination requirements, and seedling establishment of pinyon and juniper species of the western US. Included were seed and seedling fate diagrams that helped

to put seed bank dynamics into perspective. Further research in this direction would significantly advance the knowledge base and modeling capacity of the field of vegetation science.

Seed Bank Relevance to Restoration

Van der Valk and Peterson (1989) reviewed the possibility of exploiting seed banks for management purposes (including restoration) and made three simple but important points. First, if management is to be successful, the seeds of desired species must be present in the seed bank. Second, undesirable species should be in low abundance and third, the proper environmental conditions for successful germination and establishment of desired species should be met. Seed banks containing disproportionately high numbers of undesirable species (i.e. Clements et al. 2007) or an underrepresentation of desirable species (i.e. Marlette and Anderson 1986) may not be useful; however, understanding how these compositions come to exist may lead to insights that can facilitate higher quality management of such systems. Understanding Van der Valk and Peterson's final point is essential to gaining the ability to accurately predict the path of species regeneration. Holding species availability and species performance constant, successional changes cannot occur without site availability (Pickett 1987).

If restoring the native vegetation of sagebrush steppe communities associated with *J. occidentalis* is the objective, it is important to understand understory population dynamics. A central component of this is the seed bank (Venable 1989). Though the seed bank represents an important source of plant population regeneration, it is often overlooked because it is difficult to observe (Kalisz and McPeck 1992, Brown and Venable 1986). This is a significant oversight because the seed bank provides a genetic reserve distinct from the standing population, accordingly natural selection has the opportunity to operate on a separate set of traits (germination time, seed persistence, etc.) consequently producing a better adapted population (Templeton and Levin 1979). Further, this reserve may at times be the only source of recruitment for a

population. For example, disturbances such as intense fire, severe freezing events, and prolonged drought may partially remove standing vegetation. This would effectively reduce the current year's seed crop and lower possible recruitment from vegetative reproduction.

The seed bank is also important during less severe disturbance. The process of woody plant encroachment has the potential to negatively affect both the seed bank and standing vegetation. The following discusses four studies (Table 1.1) investigating these relationships.

Koniak and Everett (1982) conducted an observational field study that recovered soil samples from beneath four successional stages of *Pinus monophylla* (singleleaf pinyon). It was found that soil seed reserves became increasingly depleted as the *P. monophylla* canopy closed. It is possible that this trend may be generalized to other arid land conifer expansions, including that of *J. occidentalis* as the climate is similar, but further research is required. Contrary to the findings of Koniak and Everett (1982), Allen & Nowak (2008) found that seed bank density and species diversity did not differ between high, medium, and low *Pinus monophylla*/*Juniperus osteosperma* cover treatments. Reasons for the disparity between these findings are unclear. Site dissimilarity and temporal variation related to climatic conditions are possibilities. Also, patch characteristics play a role in determining seed bank composition (Caballero et al. 2008). The patch size of dense tree stands may impose a limit on outside seed sources. The larger the stand, the smaller the probability that outside seed will be deposited deep within the stand.

In an Australian *Eucalyptus camaldulensis*/*Leptospermum scoparium* stand, Price & Morgan (2008) showed that species richness decreased with increasing *L. scoparium* abundance. Similarly, Bakker et al. (1996) revealed that as time passed the number of species in the seed bank decreased during *Juniperus communis* (common juniper) encroachment. They concluded that once juniper has encroached into an area,

successful regeneration of the previous vegetation cannot rely on the seed bank alone. This illustrates that understanding the relationship between seed bank composition and degree of disturbance may aid in categorizing restoration potential.

Table 1.1. Seed bank studies addressing woody species encroachment in semi-arid environments

Citation	Plant Community	Study Design	Duration	Results
Koniak & Everett (1982)	<i>Pinus monophylla</i> ; CA	1 site containing 4, 900m ² plots in each of 4 treatments (early, mid-1, mid-2, and late seral)	One Year	Seed density and species diversity decreased from early to late successional stages
Bakker et al (1996)	<i>Juniperus communis</i> ; Baltic Islands	1 site containing 10, 4m ² plots in each of 3 treatments (beneath juniper, interspace, and ungrazed interspace)	One Year	Number of species in the seed bank decreased during juniper encroachment Seed bank density and species diversity did not differ between high, medium, and low tree cover treatments
Allen & Nowak (2008)	<i>Pinus monophylla</i> / <i>Juniperus osteosperma</i> ; NV	3 sites containing 3, 1963m ² plots in each of 3 treatments (high, medium, and low juniper cover)	One Year	
Price & Morgan (2008)	<i>Eucalyptus camaldulensis</i> / <i>Leptospermum scoparium</i> ; Australia	1 site containing a total of 100, 0.25m ² plots divided among 3 treatments (interspace, beneath single tree, and beneath thicket)	One Year	Species richness decreased with increasing <i>L. scoparium</i> abundance

The studies cited here were single year samples. Understanding the relationship between seed bank composition and the degree of *J. occidentalis* invasion at multiple

sites and across years may illuminate whether or not a site is restorable without additional human input. If the number of seeds comprising the seed bank of understory species is related to *J. occidentalis* cover then it is possible that a threshold may be identified beyond which the understory vegetation is unable to recover. Understanding this relationship will increase the potential for success in restoration and other land management activities associated with the *J. occidentalis* expansion.

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Chapter 2: Survivors of Invasion; Seed Bank Response to Juniper Expansion in the Sagebrush Steppe

Abstract

Expansion of *Juniperus occidentalis* into the sagebrush steppe has resulted in significant changes in understory composition. A consequence of increased *J. occidentalis* dominance may be a depletion of the seed bank. Depletion is problematic because it has the potential to lower site resiliency through a reduction of species availability. This research evaluated the affects of the relative abundance of *J. occidentalis* on the soil seed bank. Questions addressed were: 1) is species richness negatively correlated with *J. occidentalis* abundance; 2) does the number of weedy species increase along a gradient of *J. occidentalis* abundance; and 3) does seed density decrease as *J. occidentalis* abundance increases? Two eastern Oregon sagebrush steppe sites were chosen to represent the juniper woodland-sagebrush steppe region. These sites displayed a range of *J. occidentalis* canopy cover. Samples were collected in the fall of 2006 and 2007 and subjected to both cold-wet and warm-dry stratification. Germination occurred over a period of eight months under greenhouse conditions. Linear and Poisson regression techniques were used to evaluate relationships. No statistically significant relationships were detected between *J. occidentalis* cover and species richness or weedy species diversity at either site in either year, with one exception; Bridge Creek in 2007 showed a positive correlation between *J. occidentalis* cover and seed species diversity. For seed density the results were more complicated. In 2006, *J. occidentalis* cover was strongly related to seed density at Devine Ridge but in 2007 there was no evidence of a correlation. At Bridge Creek in 2006, seed density decreased as *J. occidentalis* cover increased but in 2007 the opposite relationship appeared; however, this relationship was only weakly significant. This variability in results suggests a complex relationship between *J.*

occidentalis cover and seed bank composition that may partially depend on weather conditions.

Introduction

Woody plant expansion is occurring in many places across North America and throughout the world (Archer et al. 1995, Van Auken 2000, Briggs et al. 2005). Of concern in the northwestern Great Basin is *Juniperus occidentalis* Hook. (western Juniper) (Miller and Rose 1995). Expansion of *J. occidentalis* into sagebrush steppe has resulted in significant changes in understory composition (Burkhardt and Tisdale 1969, Knapp and Soule 1998, Miller et al. 2000). A potential consequence of increased *J. occidentalis* dominance may be a depletion of the seed bank. The potential for depletion is problematic because a reduction in amount of species available from the seed bank may compromise site resiliency. During disturbances that disrupt current vegetation, a reduction in recruitment from the seed bank could make the site more susceptible to colonization by weedy species or could lead to a reduction in the amount of cover protecting the soil surface and thus increase site susceptibility to erosion. The range of *J. occidentalis* has varied considerably over the past 12,000 years (Miller and Wigand 1994). Today the species occupies the northwestern portion of the Great Basin covering 3.6 million hectares in east-central Oregon, northeastern California, northwestern Nevada, and southwestern Idaho (Miller et al. 2005). Establishment rates for *J. occidentalis* during the past 130 years have been unusually high and likely contributes to the observed expansion (Miller and Wigand 1985, Miller and Rose 1995). The cause of this expansion has been primarily attributed to decrease in fire occurrence caused by a reduction in fine fuels due to heavy grazing and active fire suppression (Burkhardt and Tisdale 1976). Optimal climatic conditions for reproduction and heavy grazing (Miller and Rose 1995, Archer et al. 1995) may also be contributing factors. Grazing is related to reductions in fire occurrence because it reduces the abundance and continuity of fine fuels (Miller and Rose 1999).

Decreases in understory vegetation are often associated with *J. occidentalis* encroachment into sagebrush steppe (Burkhardt and Tisdale 1969, Knapp and Soule 1998, Miller et al. 2000). Sustainable understory populations of *Artemisia tridentata* (big sagebrush) are important especially for sagebrush obligates such as *Centrocercus urophasianus* and *C. minimus* (sage grouse) (Crawford et al. 2004), and *Brachylagus idahoensis* (pygmy rabbit) (Paige and Ritter 1999). If restoration of sagebrush steppe communities associated with *J. occidentalis* encroachment is desired, it is important to understand understory population dynamics to develop effective management strategies. An important component of this is the seed bank (Venable 1989). Research indicates that soil seed reserves in semi-arid environments world-wide may become increasingly depleted as trees dominate (Koniak and Everett 1982, Bakker et al. 1996, Allen and Nowak 2008). This is troublesome because disturbances such as high severity fire, severe freezing events, and prolonged drought, may cause population recruitment to rely largely upon the seed bank. If reserves are low, species recovery will be slow, leaving the site open to ruderal species which are often undesirable. Seed bank relationship to *J. occidentalis* cover may also be important for categorizing restoration potential. Identifying the relationship between seed bank composition and the degree of encroachment (tree density, crown closure, or percent cover) may illuminate whether or not a species will recover without additional input of propagules. It may be possible that a threshold exists beyond which the understory vegetation is unable to recover without intensive inputs.

Several factors, including longevity of viability, seed predation, rate of seed decomposition, seed dissemination, animal manipulation of seed distribution (i.e. caching), and seed germination rates affect seed bank composition. These factors can be divided into two categories: seed bank input and seed bank losses (Simpson et al. 1989). Dormancy expression has a large influence on the rate of seeds exiting the seed bank. Some seeds may persist in the seed bank for long periods. As new seed is deposited each year, seeds begin to accumulate and thus increase the likelihood of

successful regeneration of vegetation after disturbance and possibly increasing site resilience. Other seeds do not exhibit dormancy and therefore do not contribute to the seed bank. A seed bank dominated by seeds lacking dormancy requires annual inputs to maintain site resilience. Under ordinary conditions (i.e. not having been recently disturbed and not experiencing extreme environmental conditions such as drought), the most important input to the seed bank is the level of seed production from mature plants on site (Parker 1989). Abundant seed crops are often related to favorable weather conditions. Sparse seed crops can be the result of herbivory, disease, or an increase in abundance of a dominant species, such as *J. occidentalis*, that introduces additional competition for resources. This research examines the effect of *J. occidentalis* cover on soil seed bank composition. Three questions were posed: 1) is species richness negatively correlated with *J. occidentalis* cover, 2) does the diversity of weedy species increase along a gradient of *J. occidentalis* cover, and 3) does seed density decrease as *J. occidentalis* cover increases?

Site Description and Methods

Site Description

Two study areas (Devine Ridge and Bridge Creek; Fig. 2.1) were selected to evaluate the relationship between *J. occidentalis* dominance and seed banks. The Devine Ridge site was located in the High Desert Ecological Province and Bridge Creek in the John Day Province. Both the High Desert and John Day provinces experience cold winters (Anderson et al.1998) and, as a consequence of the Cascade Range rain shadow, the precipitation regime at both sites is semi-arid (Orr et al.1992). A range of *J. occidentalis* cover varying from open to closed stands was captured at each location. The plots at Devine Ridge averaged 26% *J. occidentalis* cover, ranging from 2% to 55%. *J. occidentalis* cover was lower at Bridge Creek, the drier of the two sites, where the average cover was 11% with a range from 2% to 21%. The occurrence of *J.*

occidentalis expansion on the sites was verified using comparisons of 2005 and late 1950's aerial imagery (Fig. 2.2a and 2.2b). The Feature Analyst package for ArcGIS was used to obtain both contemporary (2005) and historical (1957 or 1958) estimates of percent cover values. Due to its distinctive dark color and shape, *J. occidentalis* is readily distinguishable from other vegetation on these sites. This method tends to underestimate cover values but adequately captures the direction of change. At Devine Ridge percent *J. occidentalis* cover increased 6.6% from 1958 to 2005. At Bridge Creek cover increased 4.3% between 1957 and 2005. Morphological characteristics (Miller et al. 2005) also suggest the majority of the trees have established since the late 1800s.

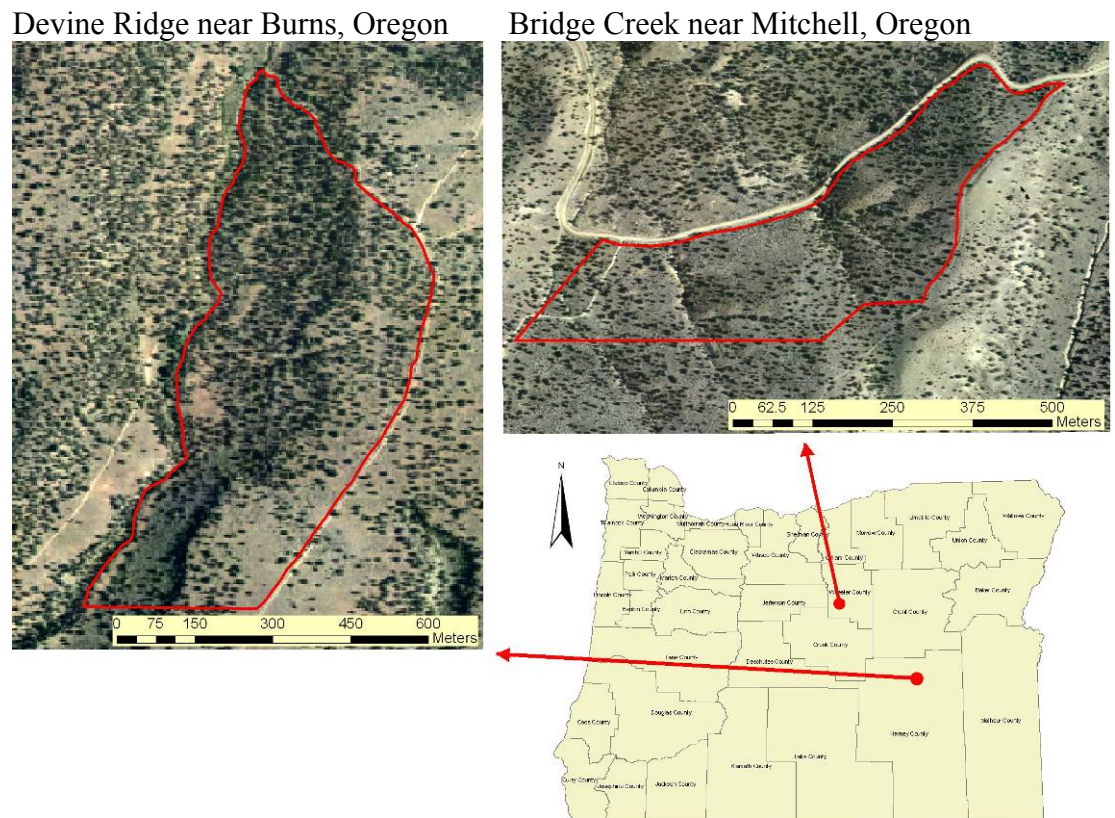
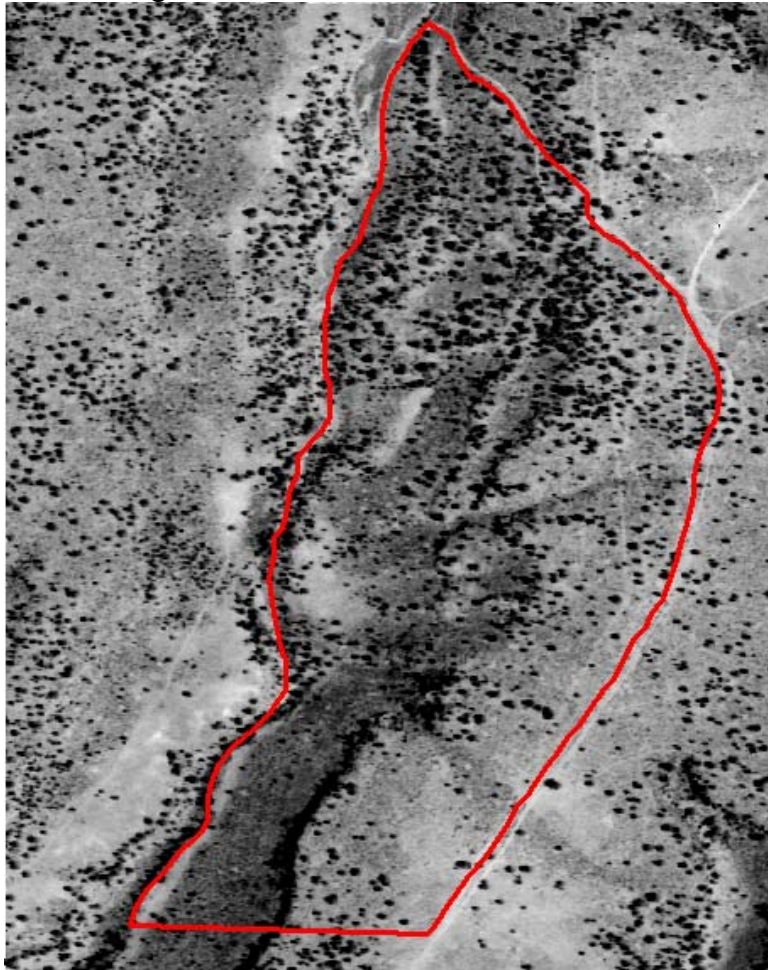


Figure 2.1. Study site maps of Bridge Creek and Devine Ridge, Oregon.

Devine Ridge 1958



Devine Ridge 2005

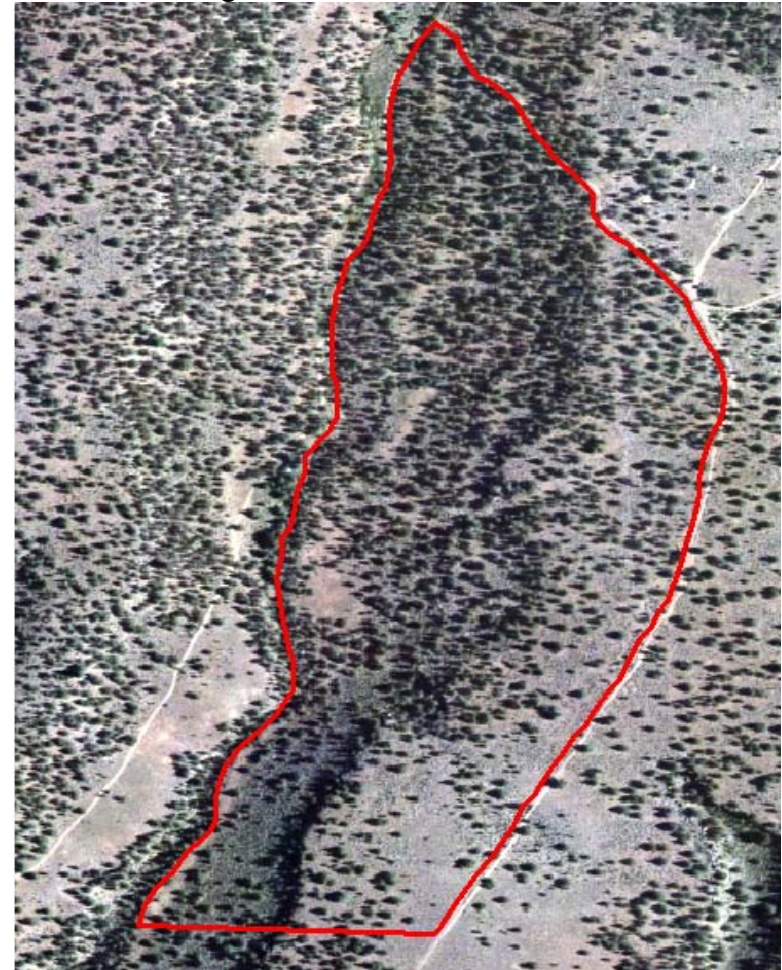
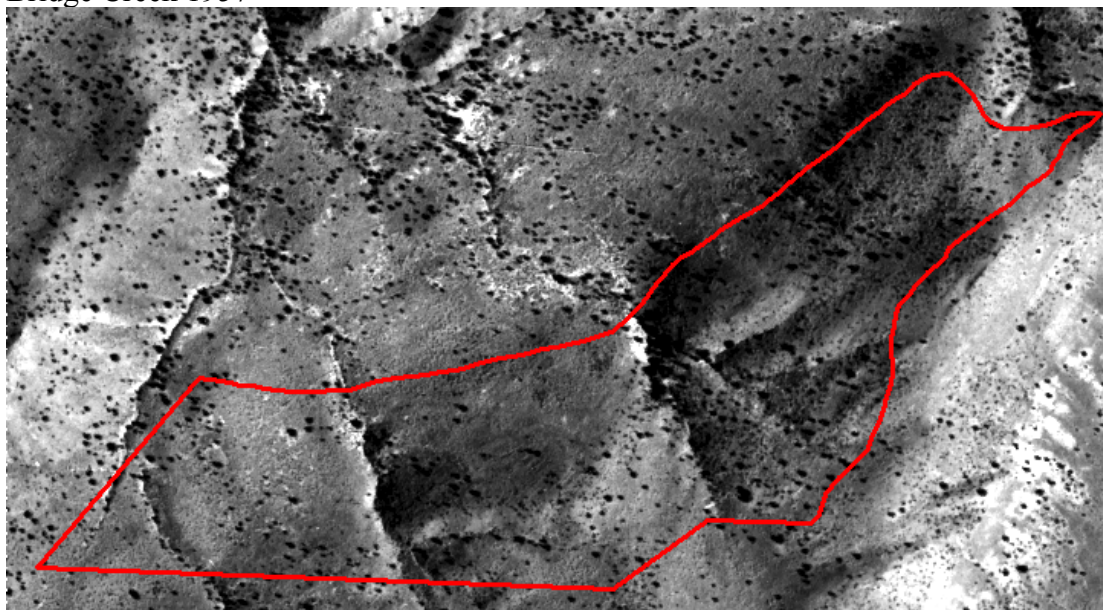


Figure 2.2a. Historical and contemporary images for Devine Ridge, OR.

Bridge Creek 1957



Bridge Creek 2005

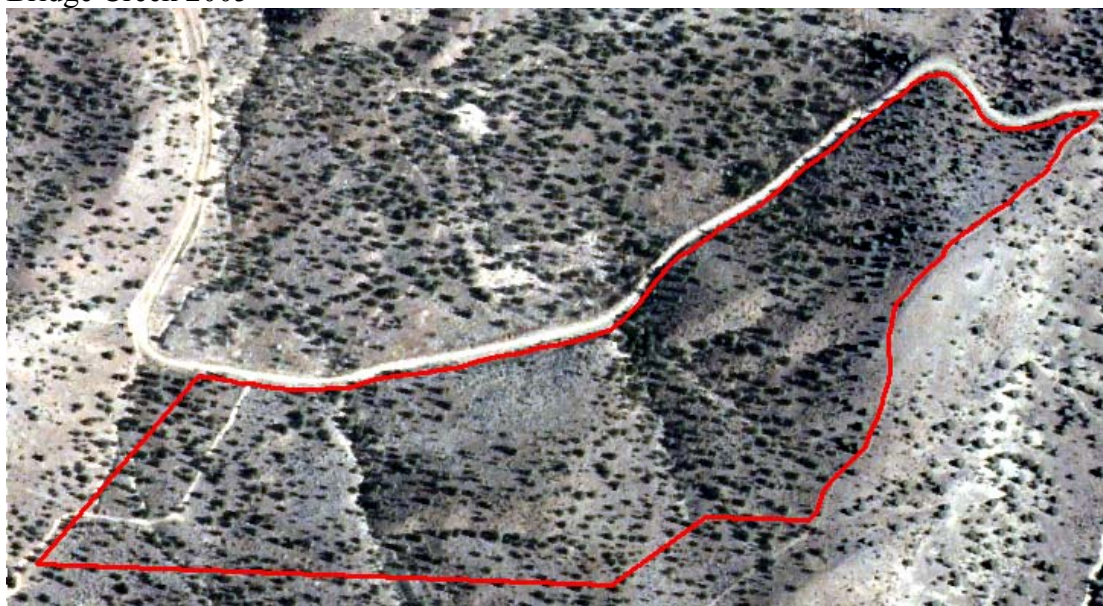


Figure 2.2b. Historical and contemporary images for Bridge Creek, OR.

Devine Ridge

The Devine Ridge site was located at the northern edge the High Desert Ecological Province. The High Desert Ecological Province is characterized by various volcanic formations and closed basins (Anderson et al. 1998). The 25 ha site was 16 km north of Burns Oregon at an elevation of approximately 1500 m, and was comprised of an *A. tridentata* ssp. *vaseyana*/*Festuca idahoensis* (mountain big sagebrush/Idaho fescue) plant association. Appendix B provides a species list and Table 2.1 describes the percent cover of vegetation by functional group across the study plots. As provided by the Natural Resources Conservation Service (NRCS) the ecological site description (SR Mountain North 12-16 PZ) gives the associated soils as loamy skeletal, mixed, superactive, frigid Pachic Haploxerolls (Westbutte series) and clayey-skeletal, smectitic, frigid Vitrandic Argixerolls (Erakatak series). A soil description done on site describes the soil as a relatively shallow (20-50 cm), course grained, sandy loam Mollisolls. Temperature extremes over the last 30 years range from 37.2°C to -33.3°C. Mean temperatures during the growing season were greater than the long term mean for both years (Fig. 2.3). Long term mean annual precipitation at the nearest weather station (Burns WSO, located 14.4 km south of and 238 m lower in elevation than Devine Ridge) was 28 cm on average; a value lower than the ecological site description describes (30.5-40.5 cm). The higher elevation and types of vegetation found on the site indicate that the study area receives more precipitation than the weather station; however, it is assumed that the patterns and trends at the weather station are similar to those at the site. 2006 experienced a wetter growing season than 2007 (Fig. 2.4). Total precipitation for the 2005-2006 and 2006-2007 water years were 41.8 cm and 22.5 cm, respectively.

Bridge Creek

The Bridge Creek site lies within the John Day Ecological Province that is characterized by easily erodible sedimentary buttes and plateaus capped with basalt (Anderson et al. 1998). Bridge Creek is located about 3 km northwest of Mitchell, Oregon at approximately 792 m. The site is 15 ha and occupied by the *A. tridentata*

ssp. *tridentata*/*Pseudoroegneria spicata* (basin big sagebrush/bluebunch wheatgrass) plant association. See Appendix B for a complete species list and Table 2.1 for percent cover of vegetation by functional group across the study plots. The NRCS has not yet conducted a soil survey, or compiled an ecological site description for this area, however the ecological site description would likely fall into the 10-12 in (254-305 mm) precipitation zone. The soils were described as course grained, loam to sandy loam mesic Typic Haploxerolls. Long term mean annual precipitation at the nearest weather station (Mitchell 2E, 2.7 km southeast and 16 m higher in elevation than Bridge Creek) is 29 cm. The 2006 growing season was wetter than that of 2007 (Fig. 2.4). Total precipitation for the 2005-2006 and 2006-2007 water years were 37.2 cm and 31.7 cm, respectively. Temperature extremes over the last 30 years range from 41.7°C to -32.8°C and temperatures were slightly below the long term average throughout the growing season (except for slightly above average temperatures in July) for both years (Fig. 2.3). Appendix A gives additional historical climate data and other site descriptors for both Devine Ridge and Bridge Creek.

Table 2.1. Percent cover of standing vegetation by functional group in 2006 for the two study locations

	Devine Ridge				Bridge Creek			
	Mean	Range			Mean	Range		
Juniper*	26.3	2	to	55	11.4	2	to	21
Shrubs	9.6	4	to	19	95.8	0	to	18
Perennial Grasses	22.7	8.3	to	33.7	34.2	16	to	53
Perennial Forbs	4.0	0.3	to	12.3	2.1	0	to	6
Annual Grasses	4.2	0	to	11.7	4.1	0	to	21
Annual Forbs	3.4	0.3	to	8	1.2	0	to	6.3

*Other trees negligible

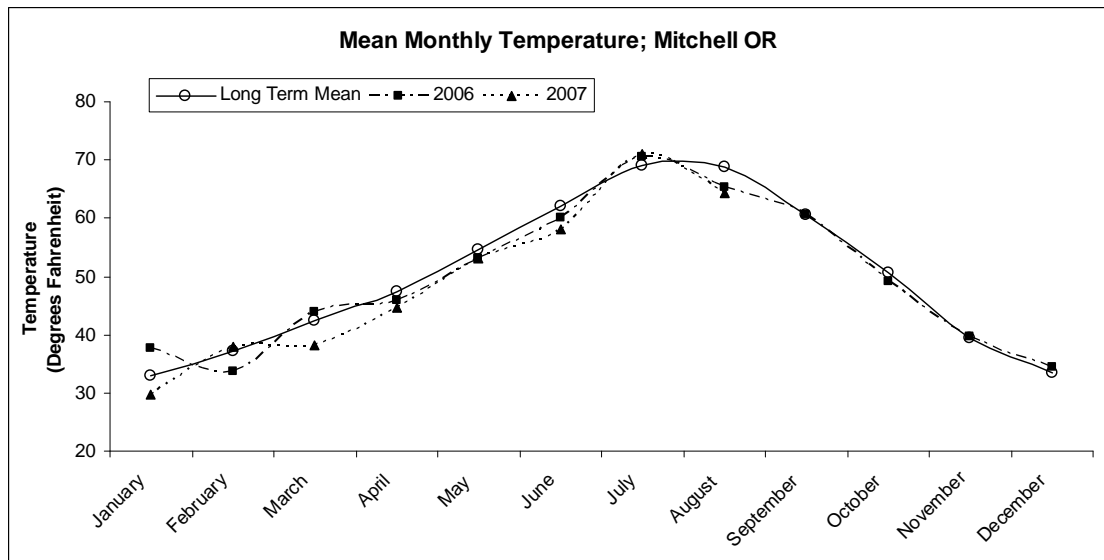
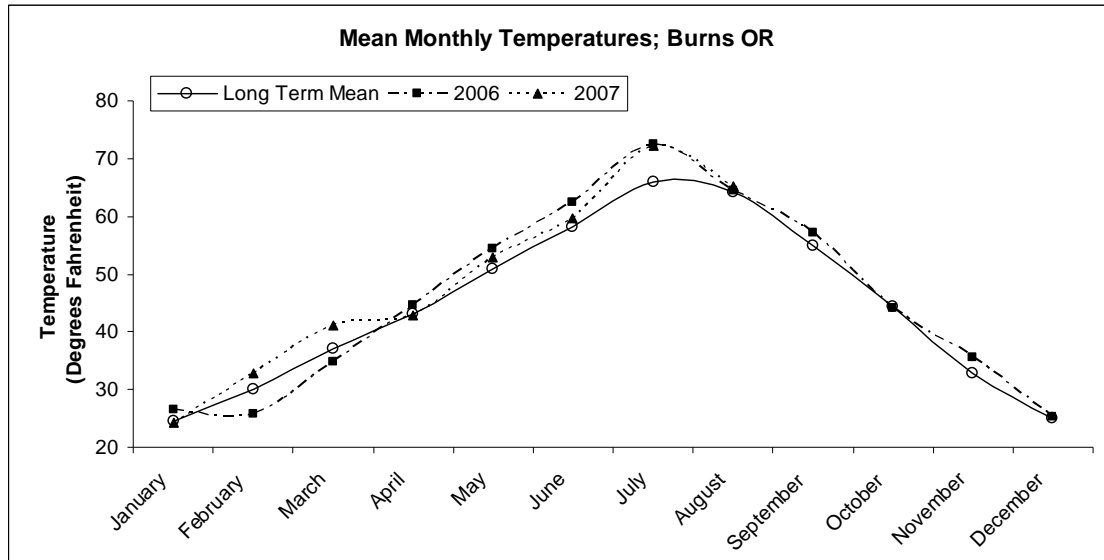


Figure 2.3. The 2006 and 2007 mean monthly temperatures and long term means from weather stations located near Burns and Mitchell, OR. Data from Burns represents Devine Ridge and data from Mitchell represents Bridge Creek. Note that data for 2007 was only available through August.

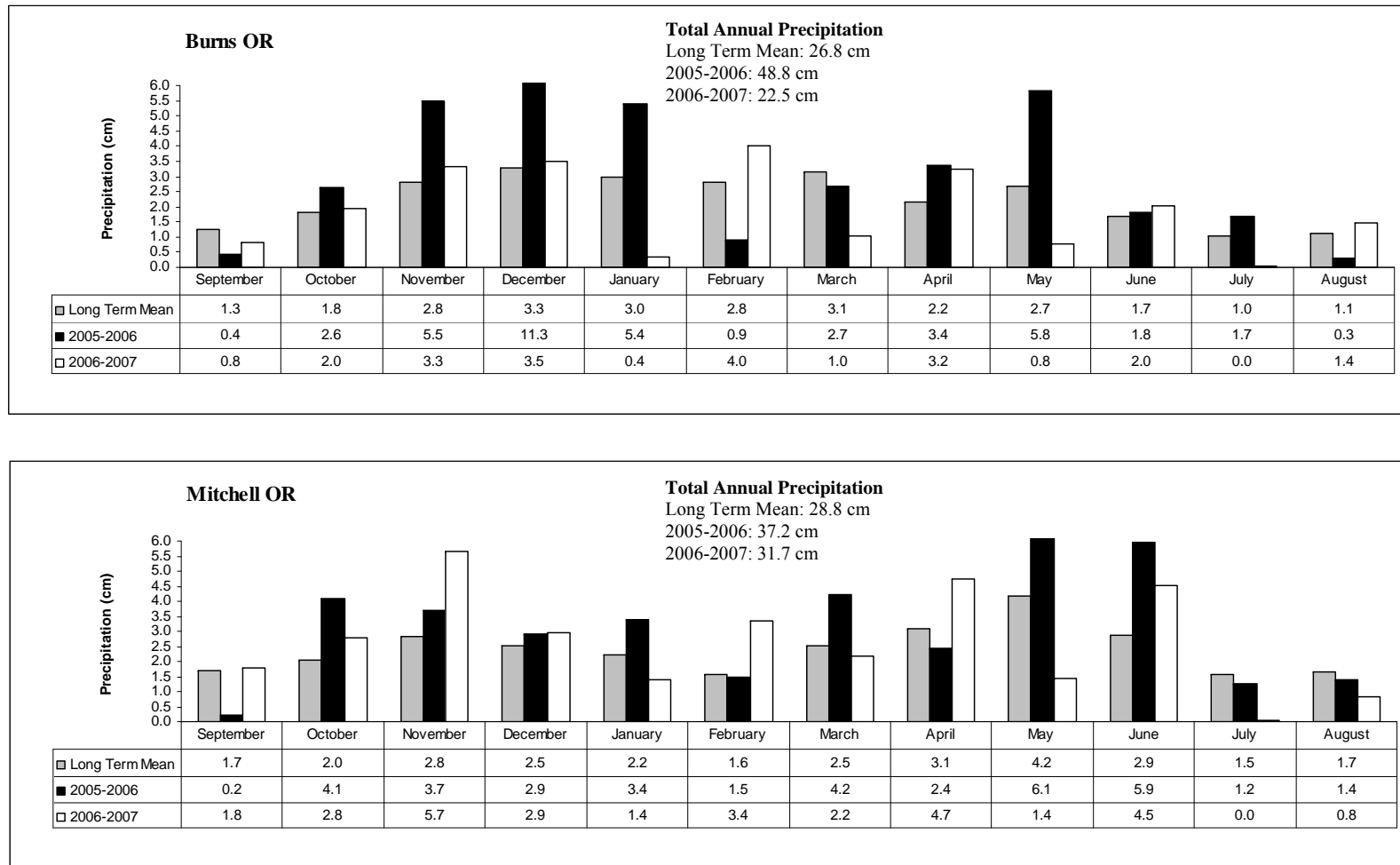


Figure 2.4. The 2005-2006 and 2006-2007 water year mean monthly precipitation and long term means from weather stations located near Burns and Mitchell, OR. Data from Burns represents Devine Ridge and data from Mitchell represents Bridge Creek.

Methods

Plot Selection

Seed bank and standing vegetation data were collected during 2006 and 2007 within 30 by 33 m (0.1 ha) plots randomly selected from point grids. Plots at Devine Ridge were selected from a 40 point grid covering about 25 ha with points spaced approximately 70 m apart. Plots at Bridge Creek were selected from a 28 point grid covering approximately 15 ha with spacing of about 67 m. Seventeen and 15 plots were established at Devine Ridge and Bridge Creek, respectively. At Devine Ridge one additional non-randomly chosen plot was selected to ensure adequate sampling in the low end of the range of *J. occidentalis* cover. During the fall of 2006, early snows prevented full sampling at Bridge Creek when only 9 of the 15 plots could be sampled. A full sampling was obtained in 2007.

Vegetation Sampling

Vegetation data within plots was obtained from the Joint Fire Science (JFS) SageSTEP Project (www.sagestep.org), which is concurrently taking place at each site. Tree canopy, shrub, and herbaceous cover by species were measured in all plots during the spring and summer months. Cover of individual understory species, bare-ground, rock and litter in the understory were measured using the line-point intercept method (Herrick et al. 2005) along four, 30 m transects in each plot. Tree canopy cover was estimated measuring the longest width (D_1) and the width perpendicular to the longest width (D_2). Canopy cover across the entire plot is the sum of the canopy area calculated for each tree rooted within the plot: $\pi[(D_1 + D_2)/4]^2$.

Seed Bank Sampling

The seed bank was sampled in late October or early November. This timing was selected so that collection took place after most plants had shed their seeds and before field germination began. Ten cores along each of 4, 30 m transects were collected at 3 m intervals (Fig. 2.5). These 40 samples were then consolidated into one composite sample for each plot. At the appropriate location, a 5 cm diameter PVC coupling was

pounded approximately 5 cm into the soil using a plywood slab and a rubber mallet (see Appendix C for a full equipment list). Litter was included in the sample. A depth of 5 cm was chosen because studies measuring depth to viable seed (Chippindale and Milton 1934, Strickler and Edgerton 1976, Russi et al. 1992, Traba et al. 2004) have found that the majority lies above that depth. This produced a soil sample of 98 cm³ of soil per core. The core was extracted and placed into a labeled plastic zip lock bag. If sampling at the exact specified transect mark was not feasible (too rocky, woody plant base, etc.) then the sampling took place at the nearest feasible location within 0.5 m.

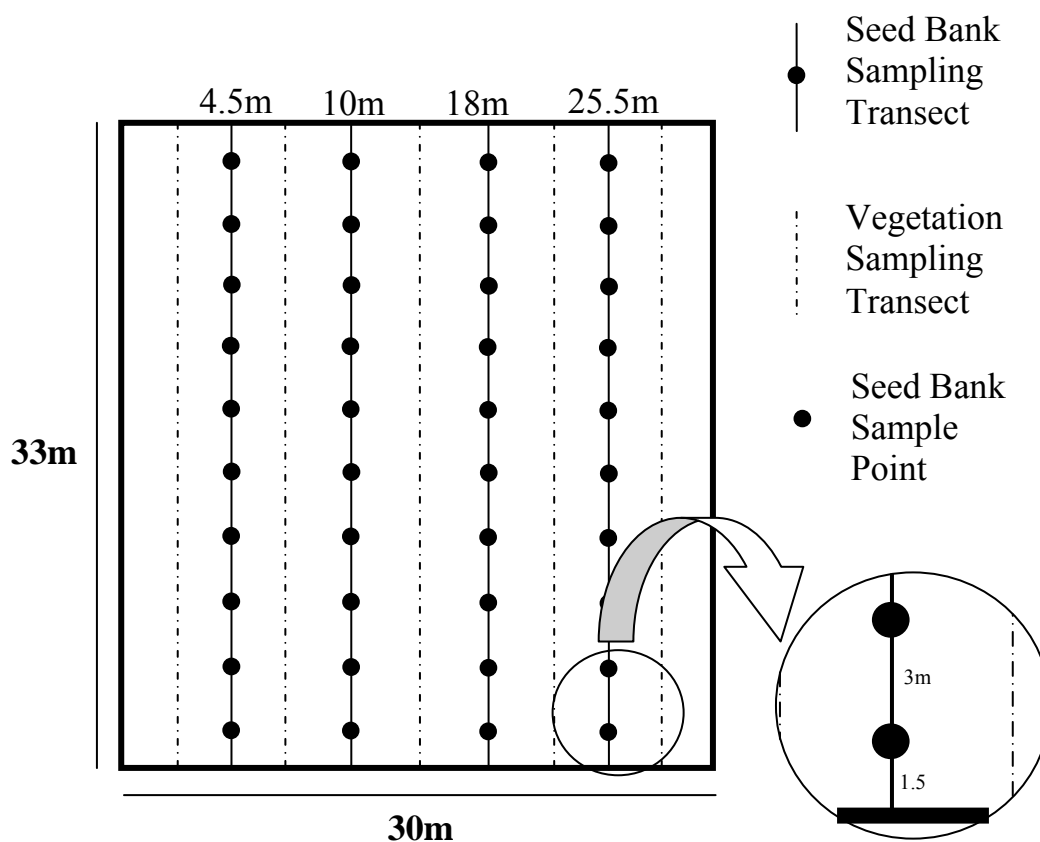


Figure 2.5. Seed bank sampling layout diagram at Devine Ridge and Bridge Creek, OR for 2006 (Not to scale)

Greenhouse Germination

Direct seed counts and seed identification are not feasible for the large sample sizes necessary for seed bank sampling. Germination was used as a proxy for direct counts to obtain seed bank composition information. To increase the probability of breaking dormancy, cold-wet, and warm-dry stratifications were employed.

Consolidated soil core samples from each plot were wet to field capacity and transferred within three days to a refrigerator held at 1°C for a 60-day cold-wet stratification. Once stratification was complete, the soil samples were each spread over sterile sand in 25 by 50 cm flats for germination. The resulting soil layer over the sand was approximately 2 cm thick. Germination took place in a greenhouse located on the Oregon State University campus in Corvallis, Oregon, which was held at a temperature of around 21°C. Each flat, which represented a single plot, were randomly placed on benches. Two control flats were added to check for possible contamination from windborne seed or seed in the sterilized sand. Samples were then watered to initiate germination and subsequent seedlings were checked twice per day and watered with a misting nozzle as needed. As soon as seedlings could be identified to the most specific level of classification feasible (genus or species) they were removed to reduce the possibility of germination suppression of other seeds due to competition. If seedlings proved difficult to identify, they were marked as unknowns and a selection were potted separately and allowed to grow until identifying characteristics developed. A small amount of vegetative germination (bulbs, etc.) was present. Each individual was counted as a seedling. After germination appeared to have ceased, which was after about four months, samples were put through a warm-dry stratification for a period of 14 days. Samples were then remixed and watering was reinitiated for a second germination period, again lasting approximately four months. The total germination period occurred January through August.

Nomenclature, as well as information on functional group designation, life duration (annual or perennial), nativity (native or introduced), and weed status (weedy or non-weedy), were obtained from the NRCS Plants Database (USDA, NRCS 2008).

Description of Analysis

Due to differences in site-to-site variability of soils and *Artemisia tridentata* subspecies, Devine Ridge and Bridge Creek were analyzed separately (S-PLUS v. 7.0. 2005. Insightful Corp. Seattle, WA). Seed density correlation to *J. occidentalis* cover was analyzed using linear regression. Both sites and years, warranted log-log transformation. Poisson regression was used to analyze both total species diversity and weedy species diversity responses. These data did not require transformation and overdispersion parameters were unnecessary. Unknown species, which accounted for a negligible portion (averaging 1% and 2% at Devine Ridge in 2006 and 2007, respectively and less than 1% at Bridge Creek both years), were ignored for the weedy species diversity analysis.

Results

No seedlings germinated in any of the control trays and so it was assumed that seed contamination in the greenhouse was insignificant. Fewer species were identified in the seed bank than were reported for the standing vegetation and only about half of the species found in the seed bank were found in the standing vegetation for both sites and years (Table 2.2). Appendix D gives a listing of all species identified from the seed bank by year and site. Appendix E lists the functional group designation, life duration, and weed status for these species.

Table 2.2. Number of species in the seed bank and standing vegetation across years and sites

	Devine Ridge		Bridge Creek	
	2006	2007	2006	2007
Standing Vegetation				
(# of species)	87	99	48	62
Seed Bank (# of species)	48	37	33	32
Proportion Common*	48%	57%	48%	56%

* The "Proportion Common" is the ratio of the number of species common between the seed bank and the standing vegetation over the number of species in the seed bank.

At Devine Ridge, approximately half of the seeds identified from the seed bank were annuals in both 2006 and 2007 (Fig. 2.6). At Bridge Creek the seed bank was dominated by annuals in both years.

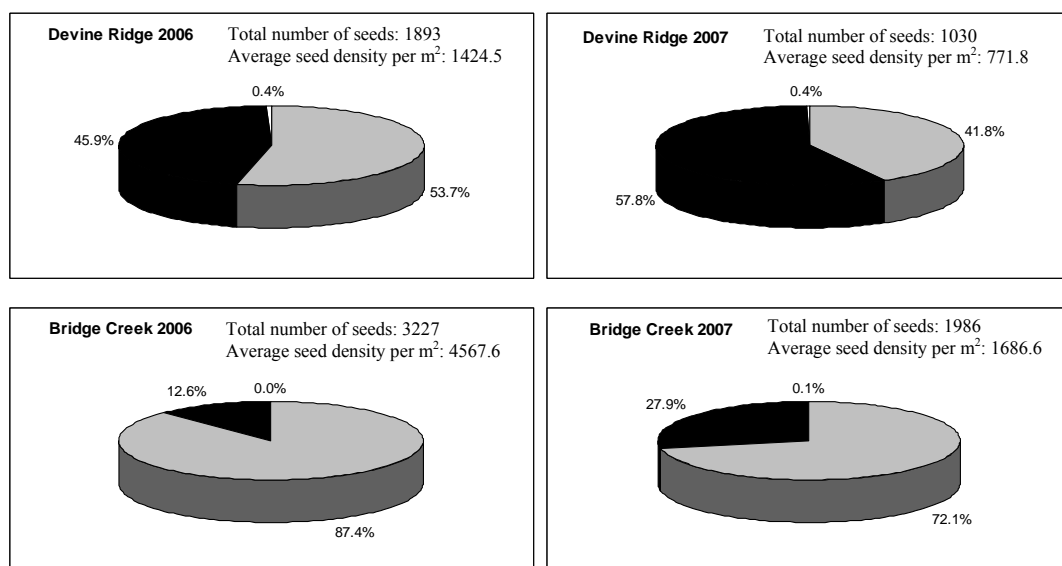


Figure 2.6. Percentage of seed bank composed of perennials (black), annuals (grey), and unknowns (white).

When comparing within the same year, Devine Ridge and Bridge Creek had similar levels of species diversity (Table 2.4). Although not tested for statistical significance, species diversity appeared lower in 2007 than in 2006. For species diversity in 2006,

there was no evidence for a relationship with *J. occidentalis* cover at either Devine Ridge ($p = 0.99$) or Bridge Creek ($p = 0.83$). In 2007, Devine Ridge again showed no evidence of a correlation between *J. occidentalis* cover and species diversity ($p = 0.71$). However, in 2007 Bridge Creek showed a positive correlation between *J. occidentalis* cover and seed species diversity ($p = 0.04$). It was estimated that for each 10% increase in *J. occidentalis* cover, seed diversity increased 39.7%. Results from all statistical analyses are shown in Table 2.3.

Table 2.3. P-values indicating strength of relationship between *J. occidentalis* cover and the response variables

Response Variable	Devine Ridge		Bridge Creek	
	2006	2007	2006	2007
Species Diversity	0.99	0.71	0.83	0.04* (+)
Weed Species Diversity	0.84	0.18	0.94	0.5
Seed Density	<.001** (-)	0.32	0.08* (-)	0.15* (+)

(+) indicates positive relationship
(-) indicates negative relationship

Table 2.4. Average number of seed bank species per plot

	2006		2007	
	Mean	Range	Mean	Range
Devine Ridge	13.5	8 to 19	8.8	4 to 13
Bridge Creek	13.2	8 to 17	9.1	4 to 13

Within the same year, the number of weedy species was similar between sites but the number of weedy species appeared to decrease at both sites in the second year. There were a total of 11 and 10 weedy species at Devine Ridge and Bridge Creek, respectively in 2006. In 2007, there were 7 weedy species at Devine Ridge and 8 and Bridge Creek. Though not tested statistically, both weedy and non-weedy densities were higher at Bridge Creek on average (Table 2.5). There was no evidence that the number of weedy species was related to *J. occidentalis* percent cover in either year at

Devine Ridge (2006, $p = 0.84$; 2007, $p = 0.18$) or Bridge Creek (2006, $p = 0.94$; 2007, $p = 0.50$).

Table 2.5. Density of weedy and non-weedy species (seeds/m²)

	Weedy Species		Non-weedy Species	
	2006	2007	2006	2007
Devine Ridge	52.4	33.0	1358.6	715.1
Bridge Creek	126.0	56.9	4423.2	1601.7

Again, though not tested for statistical significance, mean total seed densities appeared to be higher at Bridge Creek than Devine Ridge (Table 2.6). Total seed densities are plotted against percent *J. occidentalis* cover in Fig. 2.7 (note differences in scale between sites). At Devine Ridge *Lithophragma glabrum* (bulbous woodland-star) was present at the highest density across the site in both years (37.8% and 34.6% of the total seeds collected from the site in 2006 and 2007, respectively). At Bridge Creek *Draba verna* (spring draba) was present at the highest density (65.6% and 57.1% of the total seeds collected from the site in 2006 and 2007, respectively). The five most abundant species within sites were the same in both years though their order differs (Table 2.7). Of the top five at Devine Ridge, *Lithophragma glabrum* and *Poa secunda* (Sandberg bluegrass) are perennials, the remaining three are annuals. At Bridge Creek *Lithophragma glabrum* and *Sporobolus cryptandrus* (sand dropseed) are perennials while the others annuals.

The majority of the species in the seed bank on these sites are native (14.5% and 19.4% were introduced species at Devine Ridge and 27.8% and 24.2% at Bridge Creek in 2006 and 2007) but at Bridge Creek introduced species contribute disproportionately higher to the total number of seeds (79.6% and 65.6% in 2006 and 2007 respectively). *Draba verna* and *Holosteum umbellatum* (jagged chickweed) account for the majority of these seeds. *Draba verna* alone accounts for the highest proportion of those seeds (82.4% and 87.1% in 2006 and 2007 respectively). Both

Draba verna and *Holosteum umbellatum* are considered naturalized and are not considered to be weedy species.

In 2006, *J. occidentalis* cover was strongly related to seed density at Devine Ridge ($p < 0.01$). It was estimated that for each doubling in *J. occidentalis* percent cover, seed density decreased by 21% (95% confidence interval: 15 to 27%). In 2007, there was no evidence of a correlation ($p = 0.32$). At Bridge Creek in 2006, *J. occidentalis* cover was weakly correlated with a decrease in seed density ($p = 0.08$). It was estimated that every doubling of *J. occidentalis* percent cover was associated with a 40% decrease in seed density. In the second year, the pattern was reversed at Bridge Creek. A very weak positive correlation appeared between *J. occidentalis* cover and seed density ($p = 0.15$). It was estimated that every doubling in juniper cover was associated with a 34% increase in seed density (11% decrease to 101% increase).

Table 2.6. The 2006-2007 mean seed density of the seed bank per plot (seeds/m²)

	2006				2007			
	Mean	Range			Mean	Range		
Devine Ridge	1424	777	to	3108	771	178	to	1337
Bridge Creek	4567	1082	to	10242	1686	356	to	4152

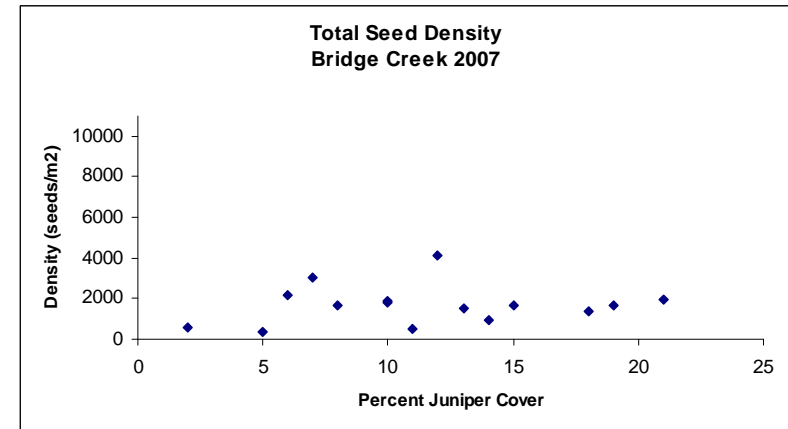
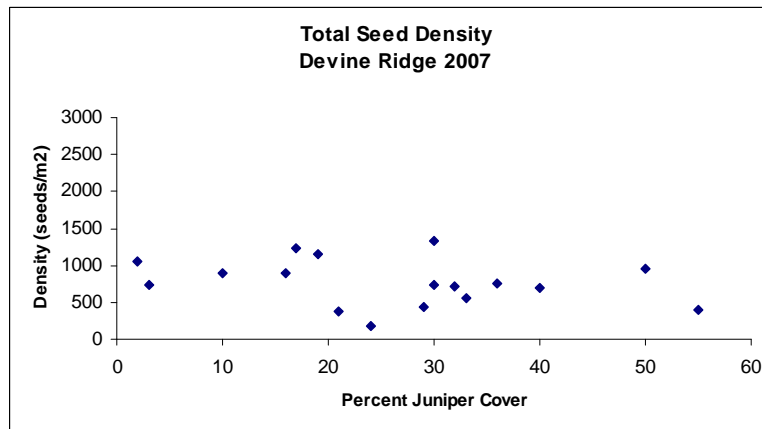
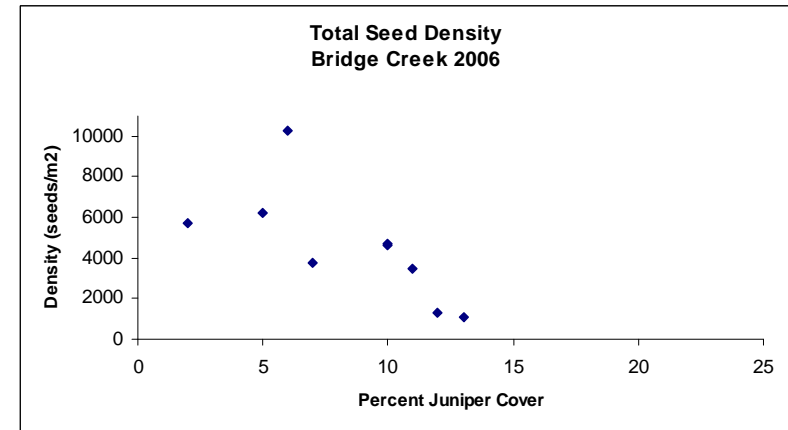
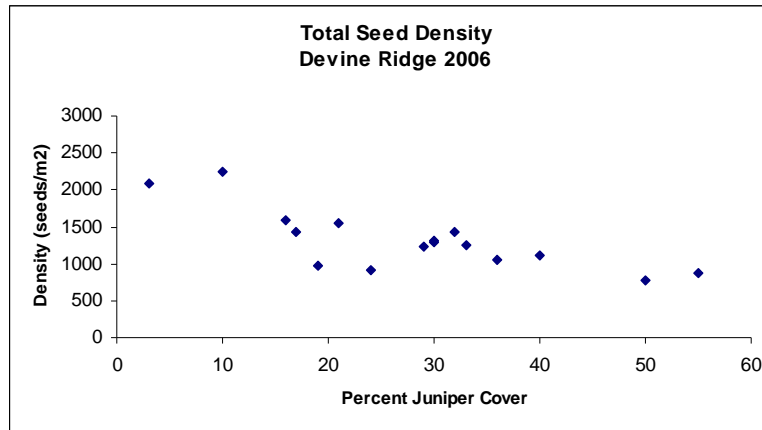


Figure 2.7. Total seed density as a function of percent *J. occidentalis* cover.

Table 2.7. The five most abundant seed bank species by site and year as measured by seed density (seeds/m²)

Devine Ridge 2006		Bridge Creek 2006	
Species	Seed Density	Species	Seed Density
<i>Lithophragma glabrum</i>	538.3	<i>Draba verna</i>	3000.0
<i>Collinsia parviflora</i>	463.2	<i>Holosteum umbellatum</i>	558.1
<i>Microsteris gracilis</i>	71.4	<i>Stellaria nitens</i>	304.5
<i>Draba verna</i>	69.9	<i>Sporobolus cryptandrus</i>	245.0
<i>Poa secunda</i>	50.4	<i>Lithophragma glabrum</i>	226.6
Devine Ridge 2007		Bridge Creek 2007	
Species	Seed Density	Species	Seed Density
<i>Lithophragma glabrum</i>	267.7	<i>Draba verna</i>	961.0
<i>Collinsia parviflora</i>	178.2	<i>Sporobolus cryptandrus</i>	191.5
<i>Poa secunda</i>	75.2	<i>Lithophragma glabrum</i>	178.0
<i>Draba verna</i>	74.4	<i>Stellaria nitens</i>	98.3
<i>Microsteris gracilis</i>	48.9	<i>Holosteum umbellatum</i>	61.9

Discussion

The relationship between *J. occidentalis* cover and both seed bank diversity and density were not consistent across years at each site. Reasons for these results are important to discuss because seed bank species diversity and density are related to site resiliency and thus the capacity for successful restoration after disturbance.

Diversity

Total Species Diversity

Except for a weak ($p = 0.04$), correlation to juniper cover at Bridge Creek in 2007, species diversity was not related to *J. occidentalis* cover at either site in either year. These results are in contrast to other studies. In Australia, Price & Morgan (2008)

found that species diversity decreased with increasing abundance of the encroaching woody species *L. scoparium*. Similarly, Bakker et al. (1996) showed that the number of species in the seed bank decreased during *Juniperus communis* (common juniper) encroachment on the Baltic Islands. In duff and transition zones from duff to interspace in a *Pinus monophylla* (singleleaf pinyon) woodland, Koniak and Everet (1982) found that species diversity tended to decrease from grass-forb, shrub-tree, tree-shrub to tree dominated sites. Detecting no change in diversity may be a result of seeds that persist for long periods of time in the seed bank.

An obvious first guess as to why species diversity increased at Bridge Creek during the second year would be an increase in weedy species; however, the analysis did not support this hypothesis.

Weedy Species Diversity

No relationships between weedy species diversity and *J. occidentalis* cover were detected. Though weedy species were present in the standing vegetation at both sites, their presence did not appear to be problematic because they were in low abundance. This low abundance suggests that these sites may be relatively resistant to weed invasion at least during gradual disturbance.

Seed Bank Similarity to Standing Vegetation

Though they cannot be quantitatively compared in this study due to differences in sampling technique, some comments can be made about the relative resemblance of the seed bank to the standing vegetation. About half of the species found in the seed bank were also found in the standing vegetation. Clements et al. (2007) found similar results. All of the species most common in the seed bank were also present in the standing vegetation. For both sites during both years, the five most common species consisted of one perennial grass and four annual spring forbs. Annual forbs were expected to be in high abundance because of their tendency toward a high capacity to

produce seed but the reason for the low occurrence of a perennial grass in the seed bank is unclear.

Many of the perennial grasses abundant in the standing vegetation were not present (or at least did not germinate) in the seed bank even in low numbers. These included *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Koeleria macrantha* (prairie junegrass). Allen and Nowak (2008) also found this to be true for *Pseudoroegneria spicata*. Reasons for this are unclear. Possible causes are lack of inputs to the seed bank during the study period (perennial plants do not need to produce seed each year to maintain their population) or the possibility that seed dormancy of these species was not broken during greenhouse germination.

Although the study areas were typical semi-arid upland locations, several riparian species were recovered from the seed bank that were not found in the standing vegetation. Unsurprisingly, the frequency of their occurrence appeared to be related to their distance from the nearest water source. Most riparian species were recovered from plots at Devine Ridge where a perennial spring lies just outside the northwest boundary of the site. Riparian species (including *Typha sp.* (Cattail)) also were found at Bridge Creek. The closest perennial water source to this site is Bridge Creek at a distance of 1.5 km. Aerial images from 1958 suggest the possibility of the existence of a water development about a 1 km northeast of the site. If water was available there during that time, it seems reasonable for seeds of *Typha sp.* to reach the site via the wind. Seeds may also have reached the site more recently through active movement by animals such as birds, cattle, humans, or by water during spring runoff. These riparian species are unlikely to establish on the site but their presence indicates that seed dissemination for some species are relatively high.

Density

Overall Seed Density

Seed density decreased as a function of increasing *J. occidentalis* at both sites the first year (though at Bridge Creek the relationship was weak, $p = 0.08$). Similar results did not occur in the second year.

In agreement with first year findings, Koniak and Everett (1982) found that seed bank density decreased as *P. monophylla* cover increased. In contrast, Allen & Nowak (2008) found that seed bank density and species diversity did not differ between high, medium, and low *Pinus monophylla/Juniperus osteosperma* cover treatments. This is in agreement with second year findings. Reasons for the disparity between these studies are unclear. Site dissimilarity and temporal variation in seed crops related to climatic conditions are possibilities. Also, patch characteristics play a role in determining seed bank composition (Caballero et al. 2008). Patch size and configuration may be a large factor determining the spatial homogeneity or heterogeneity of the seed bank. The patch size of dense tree stands may impose a limit on outside seed sources. The larger the patch, the smaller the probability that outside seed will be deposited deep within the patch especially for seeds characterized by short distance dispersal. Conversely, a stand intermingled with open canopy patches is more likely to contain seeds of species from open canopy patches.

It was thought annuals and perennials might respond differently to encroachment of *J. occidentalis*. To investigate this, total seed density was separated into annual seed density and perennial seed density. Several regression models were explored but none showed significant results. Even after removing the effect of density by relativising annual and perennial seed density no relationships were detected. At least under some situations, it appears that over all seed density is more strongly related to *J. occidentalis* cover than either annual or perennial seed density separately.

Species of Interest

Because it is such a predominant weedy species in the Great Basin, analysis of *Bromus tectorum* in isolation was attempted but was unsuccessful due to very high variability of seed distribution across plots. This indicates a clumped distribution of *B. tectorum* seed. Other species, including *Purshia tridentata* (bitterbrush) and *Vulpia bromoides* (brome fescue) also appeared to have a clumped distribution. Vegetation structure can impact seed distribution. For instance, a patchy distribution of the standing vegetation could lead to a patchy seed distribution, or the presence of one species may have an effect on the seed distribution of another. In one study, *B. tectorum* was found to occur more frequently under shrubs than in interspaces (Young and Evans 1975). Another study investigating *Taeniatherum caput-medusae* (medusahead), a weedy species sharing many characteristics with *B. tectorum*, showed that tall grasses limited *T. caput-medusae* seed dispersal (Davies 2008). Animals can also play a role in causing clumped seed distributions. *Purshia tridentata* is cached by rodents and there is some evidence that the distribution of *B. tectorum* seed is affected by ants (Mull and MacMahon 1994). It could be the case that this study area has an especially high frequency of plants that produce seed whose seed bank follows a clumped distribution and, in fact, the literature suggests that the spatial distribution of seeds in the Great Basin tends toward a clumped pattern (Kemp 1989). If many seeds exhibit this characteristic, this level of sampling intensity may not capture enough variation to accurately represent the nature of the seed bank. Inadequate sampling intensity could especially be the case at Bridge Creek during the first year of the study when only 9 of 15 samples were collected. However, it should be noted that as compared to other seed bank studies sampling intensity of this study at the plot level was high.

Another species of particular interest in this system is *Artemisia tridentata*. It has been documented that *A. tridentata* density and cover declines as *J. occidentalis* colonizes an area (Burkhart and Tisdale 1969, Miller et al. 2000). With about 50 million seeds per ha in mature stands (Young and Young 1992) and germination rate not being a limiting factor (Harniss and McDonough 1976), it was expected that a decrease in

abundance with increasing *J. occidentalis* would be detected in the seed bank if such a relationship existed. However, this could not be tested due to the low amount of *A. tridentata* germination. In 2006 at Devine Ridge only five seeds germinated and in 2007 only two germinated. At Bridge Creek, no *A. tridentata* seeds germinated in either year. Such low germination was unexpected. Further research revealed two possible reasons for this. First, *A. tridentata* seeds are very small, between 3500-3800 seeds per gram (Young and Young 1992). Because of this seeds must be located either very shallow in the soil profile, or at the soil surface for germination to occur (Jacobson and Welch 1987). Our germination procedure may not have met this requirement. Secondly, *A. tridentata* fruits in late summer or early fall and seed reaches maturity in early winter (Young and Young 1992). Soil samples for this study were collected in the fall, probably before maturity of the current year's seed crop. Also, germination from the previous year's seed crop could have reduced seed numbers. These factors may explain the low number of *A. tridentata* detected. A study by Young and Evans (1989) agrees with this logic by showing no germinable *A. tridentata* seeds from their fall samples. However, Allen and Nowak (2008) also took fall samples and were able to detect enough *A. tridentata* to establish a negative relationship with juniper cover. Differences in seed viability between the subspecies of *A. tridentata* and specific environmental conditions during the studies may account for this discrepancy.

Conclusions

The results of this study suggest a complex relationship between *J. occidentalis* cover and seed bank composition. Due to the high temporal variability inherent in both the weather conditions typical of Great Basin ecosystems and the high variability in seed production of Great Basin plants, longer time scales and *in situ* seed bank measurements are required to obtain more accurate predictions about vegetation response.

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Chapter 3: Quantitative Evaluation of a Seed Bank Threshold during Juniper Expansion

Abstract

The ability to apply the threshold concept to seed bank dynamics in systems experiencing woody plant expansion would be useful for categorizing restoration potential. This study identified and evaluated the strength of seed bank depletion thresholds associated with *Juniperus occidentalis* (western juniper) expansion in eastern Oregon. In 2006 and 2007, soil seed density and *J. occidentalis* cover were measured at two eastern Oregon sagebrush-steppe sites each displaying an array of *J. occidentalis* abundance. A non-parametric deviance reduction approach was used for threshold detection. A recently developed threshold strength index evaluated the strength of the identified thresholds. For both years and sites seed bank depletion thresholds were identified but their strength was very weak. These findings indicate that a reliable seed bank depletion threshold, as defined in this study, may not exist for these sites at least over the course of this study. Though these results were negative, the approach was useful and pursuit of its further development is suggested for evaluation of other suspected thresholds.

Introduction

The use of state and transition modeling is becoming more popular in the field of applied ecology and are now a required part of the ecological site descriptions developed across the United States by the Natural Resources Conservation Service (USDA NRCS 1997). Thresholds are an important component of state and transition theory yet few studies have attempted to quantitatively address the threshold concept. Since its introduction to Rangeland Science, State and Transition Theory has undergone many advances (Briske et al. 2003, Bestelmeyer et al. 2003, Stringham et al. 2003, Briske et al 2008). The threshold concept has probably been the most controversial component of this theory. Thresholds, points where a small change in the system induces a disproportionately large response (Groffman et al. 2006), have the

potential to be useful tools for ecological management. Despite their potential usefulness, thresholds have rarely been quantitatively addressed. Chartier and Rostagno (2006) conducted one of the only rangeland studies to do so. Their research located a point along a gradient of vegetation cover where, during a rain event, the rate of soil erosion increased significantly. They termed this point the “soil conservation threshold” that can now be used to identify plant communities at risk of serious soil degradation.

Application of the threshold concept to seed bank dynamics may be similarly beneficial in systems experiencing woody plant expansion. In the Great Basin, it is hypothesized that as *J. occidentalis* begins to dominate a location, effective precipitation decreases both due to increased canopy interception of snow and rainfall (Larsen 1993, Young et al. 1984) and the large water uptake of *J. occidentalis* (Miller and Shultz 1987, Angell and Miller 1994). The resulting decrease in water availability for other species may cause the depletion of understory vegetation often associated with *J. occidentalis* expansion (Miller et al. 2000, Knapp and Soule 1998, Burkhardt and Tisdale 1969). Due to the reduction of seed producing plants, it is likely that replenishment of the seed bank is negatively affected by *J. occidentalis* expansion. Because of this relationship, it may be possible to identify a point along a gradient of *J. occidentalis* cover past which seed density drops off significantly termed the “seed bank depletion threshold.” Identification of such a threshold would aid in categorization of the restoration potential of sites affected by *J. occidentalis* expansion.

The relationship between percent cover of *J. occidentalis* and soil seed density was examined in an attempt to both identify and quantify a seed bank depletion threshold for sagebrush-steppe plant associations affected by *J. occidentalis* expansion.

Site Descriptions and Methods

Site Descriptions

Two study areas (Devine Ridge and Bridge Creek) were selected to determine if a threshold could be identified in seed banks along an increasing gradient of *J. occidentalis* dominance. The Devine Ridge site was located in the High Desert Ecological Province and Bridge Creek in the John Day Province. Both the High Desert and John Day provinces experience cold winters (Anderson et al. 1998) and as a consequence of the Cascade Range rain shadow, the climate at both sites is dry (Orr et al. 1992).

Both sites included a gradient of *J. occidentalis* cover from open to closed stands with at least some native understory characteristic of the sagebrush steppe. The plots at Devine Ridge averaged 26% *J. occidentalis* cover, ranging from 2% to 55%. *J. occidentalis* cover was lower at Bridge Creek where the average cover was 11% with a range from 2% to 21%. The occurrence of *J. occidentalis* expansion on the sites was verified using aerial imagery comparisons. Due to its distinctive dark color and shape, *J. occidentalis* is readily distinguishable from other vegetation on these sites. The Feature Analyst package for ArcGIS was used to obtain both contemporary (2005) and historical (1957 or 1958) estimates of percent cover values. This method tends to underestimate cover values but adequately captures the direction of change. Between the late 1950's and 2005, percent cover of *J. occidentalis* increased by 6.6% and 4.3% at Devine Ridge and Bridge Creek respectively. Morphological characteristics (Miller et al. 2005) also suggest the majority of the trees have established since the late 1800s.

Devine Ridge

Devine Ridge was located at the northern edge the High Desert Ecological Province. The High Desert Ecological Province is characterized by various volcanic formations and closed basins (Anderson et al. 1998). The site, which was 16 km north of Burns Oregon, was approximately 25 ha comprised of an *Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis* (mountain big sagebrush/Idaho fescue) plant association. The elevation of the site is approximately 1500 m. The ecological site description (SR

Mountain North 12-16 PZ) gives the associated soils as loamy skeletal, mixed, superactive, frigid Pachic Haploxerolls (Westbutte series) and clayey-skeletal, smectitic, frigid Vitrandic Argixerolls (Erakatak series). A soil description done on site describes the soil as a relatively shallow (20-50 cm), coarse grained, sandy loam Mollisolls. Temperature extremes over the last 30 years range from 37.2°C to -33.3°C. Annual precipitation at the nearest weather station (Burns WSO, located 14.4 km south of and 238 m lower in elevation than Devine Ridge) was 28 cm on average. That value is significantly lower than the ecological site description describes (30.5-40.5 cm). The higher elevation and types of vegetation found on the site indicate that the study area receives more precipitation than the weather station, but it is assumed that the patterns and trends at the weather station are similar to those at the site. 2006 experienced a wetter spring (218% of the long term mean in May) than 2007. In 2007 precipitation was only 29% of the long term mean in May, which is a critical month for seedling establishment.

Bridge Creek

The Bridge Creek site lies within the John Day Ecological Province, which is characterized by easily erodible sedimentary buttes and plateaus capped with basalt (Anderson et al. 1998). It is located about 3 km from Mitchell, Oregon at an elevation of 792 m and is approximately 15 ha of the *Artemisia tridentata* ssp. *tridentata*/*Pseudoroegneria spicata* (basin big sagebrush/bluebunch wheatgrass) plant association. The NRCS has not yet conducted a soil survey, or compiled an ecological site description for this area. The ecological site description would likely fall into the 10-12 PZ designation. The on site soils description describes a coarse grained, loam to sandy loam mesic typic haploxeroll. The site lies at an elevation of 792 m and under NRCS criteria would be mapped in the mesic temperature regime. Average annual precipitation at the nearest weather station (Mitchell 2E, located 2.7 km northwest and 16 m higher in elevation than Bridge Creek) is 29 cm. 2006 experienced a slightly wetter spring (146% and 207% the long term mean in May and June respectively) than

2007. In 2007 precipitation was 34% of the long term mean in May. Temperature extremes over the last 30 years range from 41.7°C to -32.8°C.

Refer to Duncan (Chapter 2, this volume) for detailed temperature and precipitation information. Appendix A gives additional historical climate data other site descriptors for both locations.

Methods

This study began in 2006 and was repeated in 2007. Plots (16 at Devine Ridge and 15 at Bridge Creek) were randomly selected from point grids at each location. In 2006, early snows prevented full sampling at Bridge Creek when only 9 of the 15 plots could be sampled; however, full sampling was obtained in 2007. The level of *J. occidentalis* cover was recorded for each plot during the spring of 2006. In the fall of 2006 and 2007, forty soil cores (98 cm³ of soil per core), collected along four transects at intervals of 3 m, were extracted from each plot. All cores from the same plot were consolidated into a single composite sample that was, after a 30 day cold-wet stratification period, germinated in a greenhouse to approximate the viable seed bank. Seedlings were counted and identified, then removed to prevent competition. After approximately 4 months when germination after the cold-wet stratification was complete, samples were dried down for a period of 14 days for warm-dry stratification to induce further germination. Germination continued for approximately 3 more months. The total germination period occurred January through August. For a more detailed description of the methodology see Duncan (Chapter 2, this volume).

Analysis

A non-parametric deviance reduction approach (Qian et al. 2003) was used for threshold detection. Uncertainty was estimated using the bootstrap method at 1000 iterations. After describing the data using non-parametric multiplicative regression (NPMR) (McCune 2006), threshold strength was evaluated using a newly developed index of threshold strength (Lintz H., unpublished 2008).

Results

At Devine Ridge in 2006 the threshold was estimated to occur between *J. occidentalis* cover values of 10 and 16% with an approximate 90% confidence interval between 2 to 21%. In 2007, the threshold occurred between *J. occidentalis* cover values of 19-21% (90% confidence interval from 0 to 32%). In 2006, at Bridge Creek the threshold was estimated to occur between *J. occidentalis* cover values of 6 and 7% with an approximate 90% confidence interval between 0 to 13%. In 2007, the threshold occurred between *J. occidentalis* cover values of 5-6% (90% confidence interval from 0 to 10%).

When compared to the threshold index value for a strong threshold (a perfect step, 0.93), no strong thresholds were identified. All threshold strength indexes were close to or below the value for a very weak threshold (a plane, 0.61) indicating that little change in seed density occurred as a result of a change in the level of *J. occidentalis* cover. NPMR model parameters are given in Table 3.1. The complete results of the threshold strength analysis are shown in Table 3.2.

Table 3.1. NPMR model statistics for threshold detection

	Devine Ridge		Bridge Creek	
	2006	2007	2006	2007
Fit xR2	0.5	-0.1	0.2	-0.2
N*	5.1	13.6	3.3	12.6
P-value	0.0	0.5	0.1	0.7
Tolerance	8.0	44.5	2.6	16.0
Sensitivity	0.7	1.0	1.1	1.0

Table 3.2. Threshold strength indices

	Threshold Strength Index	
	2006	2007
Devine Ridge	0.49	0.58
Bridge Creek	0.70	0.59
<i>For Comparison:</i>		
<i>Strong Threshold (Step)</i>	0.93	
<i>Weak Threshold (Plane)</i>	0.61	

Discussion

A seed bank threshold was suspected to exist in systems experiencing *J. occidentalis* expansion because it was possible that the reduction in understory cover often associated with *J. occidentalis* expansion was a result of lack of recruitment from the seed bank due to the negative affect *J. occidentalis* has on the amount of resources available to other plants. In this study, a reduction in seed density strong enough to be deemed an ecologically significant threshold was not detected. This could be due to the episodic nature of, or temporal variation in, seed crops. If such is the case then two years may not be an adequate length of time for detection of a threshold. It is also possible that *J. occidentalis* expansion does not have a negative effect on understory vegetation on the scale of these sites. Conditions of these particular sites may be such that they are more resilient to this type of disturbance. Generally speaking, thresholds may be more applicable to the abiotic characteristics of ecosystems. It could be that a seed bank depletion threshold occurs in conjunction with an erosion threshold associated with a lack of plants keeping soil on the site. Such a threshold would result in the washing away of seeds with sediment during erosion. If this is the case, this study did not identify a threshold because erosion did not appear to be a problem on either site.

The results of the threshold strength index analysis were at first counter intuitive. Because the data at Devine Ridge in 2007 most closely approximated a sigmoid curve, it was expected that this dataset would yield the strongest threshold index value. Surprisingly, it yielded the lowest value. The reason for this lies in the way in which the threshold strength index defines a threshold. This index weights a curve with a flat top and a flat bottom with a steep slope in between (a step shape) high. Only Bridge Creek in 2006 had a shape similar to this and it did indeed yield the strongest threshold index. A re-evaluation of whether this definition of a threshold is appropriate is necessary. Such concerns are not meant to suggest that this method should be discarded, but it does suggest that it should undergo further development. The value of the ability to numerically quantify thresholds and allow comparisons at similar scales is worth the effort that further research entails.

Conclusions

Quantitative verification of model parameters allows for greater predictive power and thus a greater propensity toward successful practical application of model outputs. The quantitative investigation of theoretical models also permits the opportunity to uncover inaccuracies in model structure. These results emphasize that the uncertainty associated with the existence of thresholds in particular systems, and the difficulty of their quantification when identified, are impediments to the practical application of ecological models that incorporate thresholds. For this reason, caution is advised when applying the threshold concept to ecological modeling.

The methods presented here have the potential to be used to quantitatively evaluate other suspected thresholds. Once they have undergone further development, using these methods for strength comparison between studies of similar scale may be especially useful and is encouraged.

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Chapter 4: General Conclusions

Improvements

As with most scientific endeavors, several things could be done to improve this research. Based upon the lessons learned during the execution of this thesis, these ideas are:

- A) Both of the studies presented, but the first especially, would benefit from an increase in the number of years allotted for sampling. The variability inherent in the climate of the Great Basin and therefore the vegetation response of plants (i.e. variation in seed crop size and viability) in this ecosystem cannot be adequately captured over the short time span of two years.
- B) To acquire a more accurate representation of the species in the seed bank, the timing of sampling could be adjusted. An early spring sampling regime could increase the representation of late maturing species (i.e. *Artemisia tridentata*). Such a shift would have the drawback of possibility losing seed to germination if sampling could not take place immediately after snow melt. Sampling on a quarterly or bimonthly basis may be the best solution. This method could provide interesting insights into the seasonal variability of the seed bank.
- C) An analysis of the effect of *J. occidentalis* patch size by cover class on seed bank composition would have been informative. It is likely that the effect on the seed bank is stronger when patch sizes, especially of dense stands, are large because the possibility of seed migration from outside the patch to the interior of the patch is reduced.

- D) Not having access to knowledge concerning the breaking of seed dormancy was also a limitation. In situ measurements of germination under field conditions over a long time period (10 years or more) would eliminate the problem of determining what dormancy breaking requirements are to be met in the greenhouse and would capture a greater percentage of variability at the site.

Future Research

Suggestions for future research include the production of a Great Basin seedling identification guide that includes dormancy breaking requirements, seed dissemination mechanisms, and physical seed characteristics, as well as information on seed predators. Another avenue for research is the exploration of the existence of local ecotypes. Though the studies presented in this thesis were not designed to evaluate differences in germination times, it was observed that some species that were located at both sites germinated at different times in the greenhouse depending on the site. This phenomenon, particularly apparent in *Collinsia parviflora*, may be evidence for the existence of local ecotypes. Revealing these types of site differences would increase our ability to predict site response and direct vegetation change.

An investigation into the reasons and implications of the dissimilarity often encountered between the seed bank and the standing vegetation would be valuable. According to the literature, it appears that dissimilarity between the seed bank and the standing vegetation is not unusual. For example, Pratt et al. (1984) observed that the seed bank under *Pinus ponderosa* (ponderosa pine) was dominated by annual forbs. However, these forbs were not abundant in the standing vegetation. In fact, the authors state that “species dominating the seed bank were generally unimportant in the standing vegetation.” Of the 57 species that germinated, only 21 were found in the standing vegetation. Additional research is needed to understand why Pratt et al. (1984) and others (Egan and Ungar 2000, Edwards and Crawley 1999, Peco et al.

1998, Coffin et al. 1989, Thompson and Grime 1979) have observed this standing vegetation-seed bank compositional discrepancy, however, possible reasons include episodic recruitment, an inability to meet dormancy breaking requirements during the experiment, an offset between seed sample collection and standing vegetation sampling at a particular site, plants producing low numbers of seed or having seeds that reach the seed bank in extremely low numbers for other reasons (susceptible to disease, predation, desiccation, etc.), seeds being non-randomly distributed in the seed bank (i.e. caching) causing them to go undetected in the sampling process, and the immigration of seed from outside sources that are non adapted to the locations of dissemination.

A comparison of the seed bank and standing vegetation is complicated because the standing vegetation is often measured using percent cover and the seed bank is measured using species counts. Yet even if measurements were taken differently, it is difficult to come up with an appropriate means of comparison. For example, a direct proportional comparison would not be an appropriate measure of similarity because it is known that some species inherently produce larger amounts of seed than others and some species produce seed only intermittently. It is possible that seeds from species not currently in the standing vegetation are present but are not currently under the appropriate conditions for germination and survival. Such seeds may be deposited either through long distance dispersal by wind, animals, etc. or deposited at some time during the past when the area supported a different plant community.

If seed bank-standing vegetation dissimilarity has characteristics that can be generalized then it may be possible to more accurately predict plant response after restoration. For simple example, a species that consistently requires fire scarification for germination will eventually be eliminated from the standing vegetation if fire suppression occurs over a long enough time period. If the seed of this species remains viable in the seed bank, fire can be reintroduced to stimulate reestablishment of this species. More complexly, it may be that seed banks generally have a higher proportion

of certain functional groups than is represented in the standing vegetation. Site modification to exploit this characteristic in favor of desired species could be conducted. With a better understanding of the relationship between the seed bank and the standing vegetation, such modification could become less risky.

Final Remarks

The most important contribution of both of the studies presented in this thesis is their relevance to restoration. Improving our understanding of variables that influence plant population dynamics, such as seed bank composition, will increase our ability to more accurately predict individual species or plant community response following disturbance. Seed banks represent an important ecosystem component because of their relevance to resilience and resistance and thus plant community maintenance and development. The seed bank is a last source for plant regeneration and therefore its condition is likely linked to the resiliency of the system that it belongs. Also, modeling of these systems can only be as accurate as the information put into them. Propagule input is one of the least understood stages of plant population dynamics and a stronger knowledge base concerning seed ecology would certainly be beneficial.

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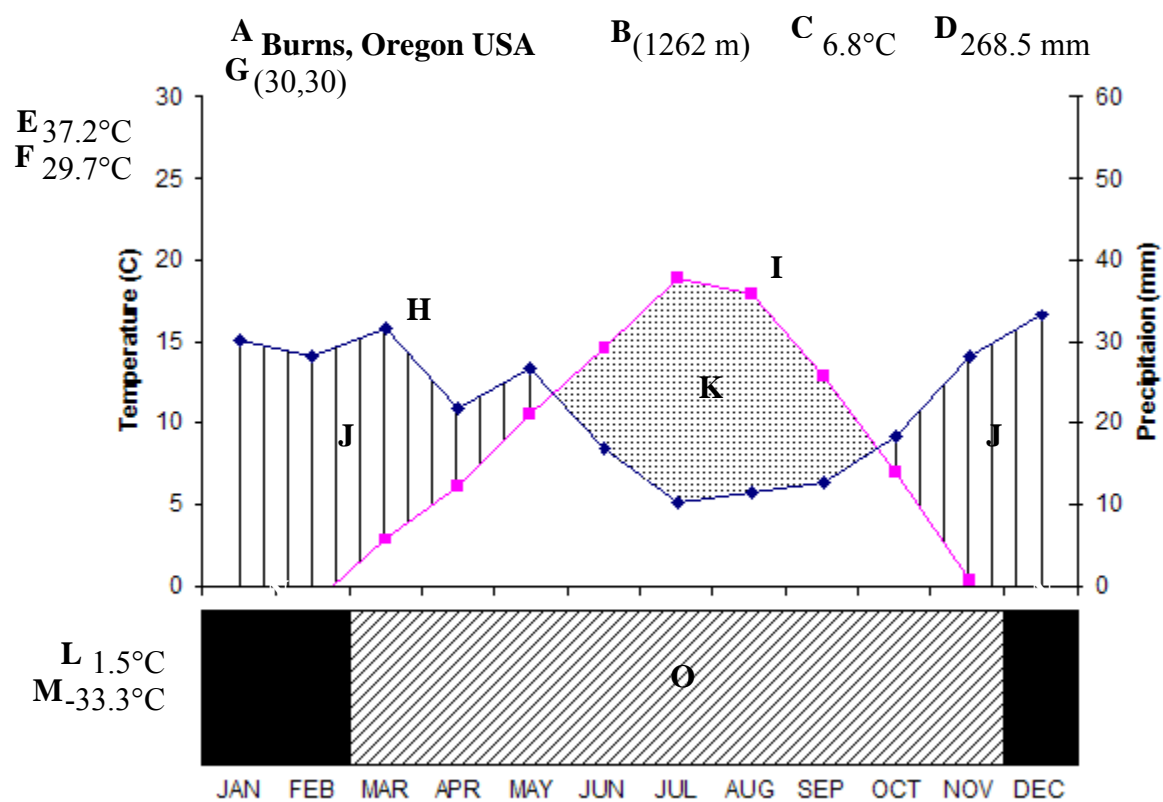
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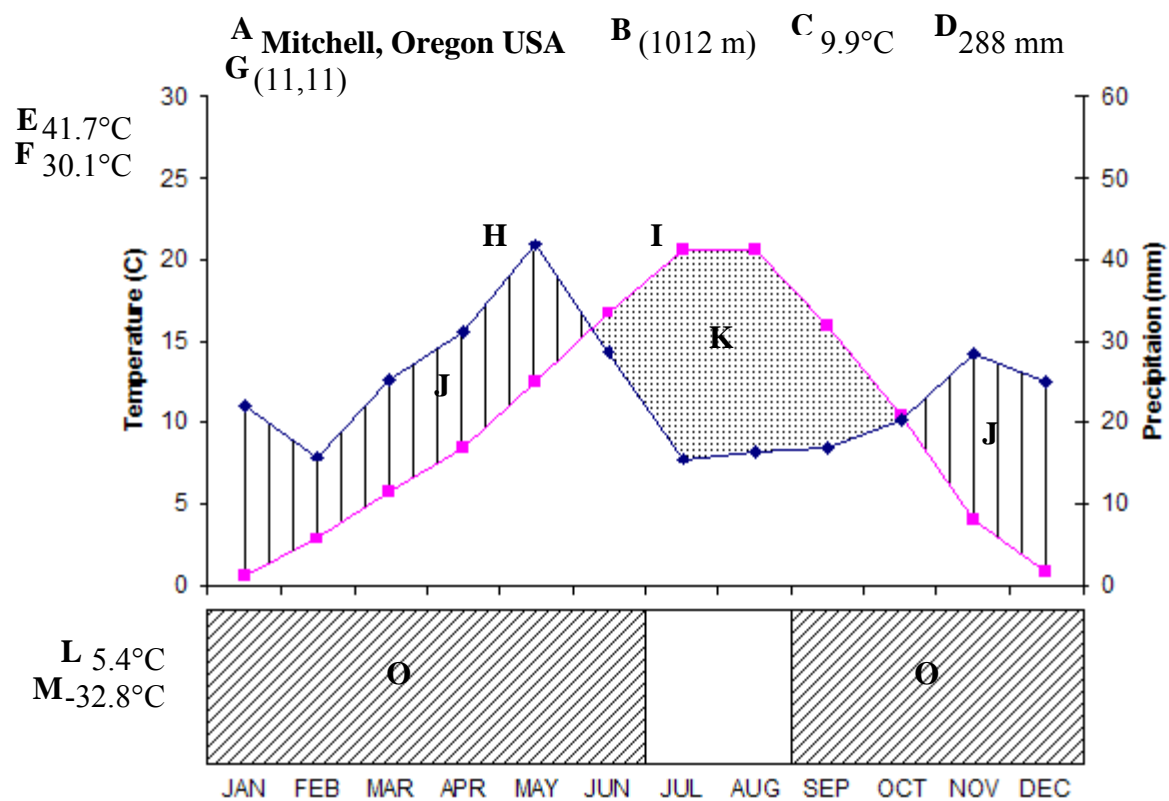
APPENDICES

Appendix A: Climatic Diagrams for Devine Ridge and Bridge Creek. OR

Key to Climatic Diagram

A	Station Name
B	Elevation (m)
C	Mean Annual Temperature (°C)
D	Mean Annual Precipitation (mm)
E	Absolute Maximum Temperature (°C)
F	Mean Daily Maximum of the Hottest Month (°C)
G	Number of Years of Observation (Temperature, Precipitation)
H	Monthly Means of Precipitation (mm)
I	Monthly Means of Temperature (°C)
J	Humid Period (lined)
K	Arid Period (dotted)
L	Mean Daily Minimum Temperature of Coldest Month (°C)
M	Absolute Minimum Temperature (°C)
N	Months with a Mean Daily Temperature below 0°C (darkened)
O	Months that can reach an Absolute Minimum below 0°C (hatched)





Appendix B: Standing Vegetation Species Lists

Species List for Standing Vegetation at Devine Ridge

2006

Note: 17 Unknowns

Achillea millefolium
Acnatherum lettermanii
Acnatherum thurberianum
Agoseris glauca
Agoseris grandiflora
Agoseris heterophylla
Allium acuminatum
Amelanchier alnifolia
Amsinckia tessellata
Antennaria dimorpha
Arabis drummondii
Arabis holboellii
Arabis sparsiflora
Artemisia tridentata ssp. *vaseyana*
Astragalus purshii
Bromus briziformis
Bromus tectorum
Calochortus macrocarpus
Castilleja glandulifera
Castilleja pilosa
Chrysothamnus viscidiflorus
Claytonia perfoliata
Collinsia parviflora
Collomia linearis
Corallorhiza maculata
Crepis intermedia
Crepis occidentalis
Cryptantha intermedia
Cryptantha torreyana
Delphinium andersonii
Descurainia pinnata
Elymus elymoides
Epilobium brachycarpum
Epilobium minutum
Eriastrum sparsiflorum
Ericameria nauseous
Erigeron filifolius
Erigeron linearis
Eriogonum corymbosus
Eriogonum heracleoides

2007

Note: 13 Unknowns

Achillea millefolium
Achnatherum thurberianum
Agoseris glauca
Agoseris heterophylla
Allium acuminatum
Alyssum alyssoides
Alyssum desertorum
Amelanchier alnifolia
Antennaria dimorpha
Artemisia arbuscula
Arabis drummondii
Arabis holboellii
Artemisia rigida
Arnica sororia
Arabis sparsiflora
Artemisia tridentata ssp. *vaseyana*
Astragalus purshii
Bromus tectorum
Carex filifolia
Calochortus macrocarpus
Castilleja pilosa
Ceratocephala testiculata
Chrysothamnus viscidiflorus
Claytonia perfoliata
Corallorhiza maculata
Collinsia parviflora
Crepis occidentalis
Cryptantha torreyana
Danthonia unispicata
Delphinium nuttallianum
Descurainia pinnata
Dodecatheon pulchellum
Draba verna
Elymus elymoides
Epilobium brachycarpum
Epilobium minutum
Erigeron corymbosus
Erigeron filifolius
Eriogonum heracleoides
Erigeron linearis

<i>Eriogonum ovalifolium</i>	<i>Ericameria nauseosa</i>
<i>Eriogonum sphaerocephalum</i>	<i>Eriogonum ovalifolium</i>
<i>Eriogonum strictum</i>	<i>Erigeron pumilus</i>
<i>Eriogonum umbellatum</i>	<i>Eriastrum sparsiflorum</i>
<i>Fescue idahoensis</i>	<i>Eriogonum sphaerocephalum</i>
<i>Fritillaria atropurpurea</i>	<i>Eriogonum strictum</i>
<i>Fritillaria pudica</i>	<i>Eriogonum vimineum</i>
<i>Gayophytum ramosissimum</i>	<i>Festuca idahoensis</i>
<i>Hydrophyllum capitatum</i>	<i>Fritillaria pudica</i>
<i>Juniperus occidentalis</i>	<i>Gayophytum racemosum</i>
<i>Koeleria macrantha</i>	<i>Gayophytum ramosissimum</i>
<i>Lewisia redivia</i>	<i>Hackelia cusickii</i>
<i>Lithophragma glabrum</i>	<i>Hydrophyllum capitatum</i>
<i>Lithophragma parviflorum</i>	<i>Juniperus occidentalis</i>
<i>Lithospermum ruderales</i>	<i>Koeleria macrantha</i>
<i>Lomatium macrocarpum</i>	<i>Leymus cinereus</i>
<i>Lomatium nevadense</i>	<i>Lewisia rediviva</i>
<i>Lomatium triternatum</i>	<i>Lithophragma glabrum</i>
<i>Lupinus argenteus</i>	<i>Lithophragma parviflorum</i>
<i>Lupinus caudatus</i>	<i>Lithospermum ruderales</i>
<i>Machaeranthera canescens</i>	<i>Lomatium cous</i>
<i>Melica bulbosa</i>	<i>Lomatium sp.</i>
<i>Microsteris gracilis</i>	<i>Lomatium nevadense</i>
<i>Microsteris gracilis</i>	<i>Lomatium triternatum</i>
<i>Nothocalais troximoides</i>	<i>Lupinus caudatus</i>
<i>Packera cana</i>	<i>Machaeranthera canescens</i>
<i>Penstemon speciosus</i>	<i>Melica bulbosa</i>
<i>Phacelia hastata</i>	<i>Microsteris gracilis</i>
<i>Phlox longifolia</i>	<i>Mimulus nanus</i>
<i>Phoenicaulis cheiranthoides</i>	<i>Myosotis stricta</i>
<i>Pinus ponderosa</i>	<i>Nothocalais troximoides</i>
<i>Plectritis macrocera</i>	<i>Packera cana</i>
<i>Poa cusickii</i>	<i>Penstemon deustus</i>
<i>Poa secunda</i>	<i>Penstemon speciosus</i>
<i>Polemonium micranthum</i>	<i>Phoenicaulis cheiranthoides</i>
<i>Polygonum douglasii</i>	<i>Phacelia hastata</i>
<i>Prunus virginiana</i>	<i>Phlox hoodii</i>
<i>Pseudoroegneria spicata</i>	<i>Phacelia linearis</i>
<i>Purshia tridentata</i>	<i>Phlox longifolia</i>
<i>Ranunculus glaberrimus</i>	<i>Pinus ponderosa</i>
<i>Ribes cereum</i>	<i>Plagiobothrys tenellus</i>
<i>Senecio integerrimus</i>	<i>Poa cusickii</i>
<i>Taraxacum officinale</i>	<i>Polygonum douglasii</i>
<i>Tetradymia canescens</i>	<i>Polemonium micranthum</i>
<i>Trifolium macrocephalum</i>	<i>Poa secunda</i>
<i>Zigadenus venuosus</i>	<i>Prunus emarginata</i>
	<i>Pseudoroegneria spicata</i>
	<i>Purshia tridentata</i>

Ranunculus glaberrimus
Ribes cereum
Senecio integerrimus
Silene douglasii
Nastotus stenophyllus
Taraxacum officinale
Tragopogon dubius
Trifolium macrocephalum
Viola bakeri
Vulpia octoflora
Zigadenus venenosus

Species List for Standing Vegetation at Bridge Creek

2006

Note: 15 Unknowns

Achillea millefolium
Acnatherum thurberianum
Agoseris glauca
Allium acuminatum
Alysum alyssoides
Antennaria dimorpha
Artemisia tridentata ssp. *tridentata*
Artemisia tridentata ssp. *vaseyana*
Astragalus purshii
Astragalus reventus
Blepharipappus scaber
Bromus briziformis
Bromus tectorum
Calochortus macrocarpus
Cercocarpus ledifolius
Chrysothamnus viscidiflorus
Collinsia parviflora
Cryptantha torreyana
Draba verna
Epilobium minutum
Eriastrum sparsiflorum
Erigeron filifolius
Erigeron linearis
Eriogonum ovalifolium
Eriogonum sphaerocephalum
Eriogonum strictum
Eriogonum vimineum
Erodium botrys
Fescue idahoensis

2007

Note: 9 Unknowns

Achillea millefolium
Achnatherum thurberianum
Agoseris heterophylla
Alyssum alyssoides
Alyssum desertorum
Antennaria dimorpha
Artemisia arbuscula
Artemisia tridentata ssp. *tridentata*
Astragalus conjunctus
Astragalus filipes
Astragalus purshii
Astragalus reventus
Bromus tectorum
Calochortus macrocarpus
Castilleja pilosa
Cercocarpus ledifolius
Chrysothamnus viscidiflorus
Collinsia parviflora
Crepis occidentalis
Dalea ornata
Descurainia pinnata
Draba verna
Epilobium brachycarpum
Epilobium minutum
Erigeron filifolius
Eriophyllum lanatum
Eriogonum microthecum
Ericameria nauseosa
Eriogonum ovalifolium

Gutierrezia sarothrae
Holosteum umbellatum
Juniperus occidentalis
Lactuca serriola
Lomatium macrocarpum
Lomatium nevadense
Lomatium sp.
Machaeranthera canescens
Opuntia fragilis
Penstemon speciosus
Poa cusickii
Poa secunda
Pseudoroegneria spicata
Purshia tridentata
Sporobolus cryptandrus
Taeniatherum caput-medusae
Tetradymia canescens
Tragopogon dubius
Vulpia octoflora

Eriogonum strictum
Festuca idahoensis
Fritillaria pudica
Galium aparine
Gutierrezia sarothrae
Hieracium albiflorum
Holosteum umbellatum
Juniperus occidentalis
Koeleria macrantha
Layia glandulosa
Lactuca serriola
Lomatium dissectum
Lomatium nevadense
Lomatium triternatum
Madia gracilis
Microsteris gracilis
Nothocalais troximoides
Opuntia fragilis
Penstemon eriantherus
Penstemon speciosus
Phacelia linearis
Pinus ponderosa
Plectritis macrocera
Plagiobothrys tenellus
Poa bulbosa
Poa cusickii
Poa secunda
Pseudoroegneria spicata
Purshia tridentata
Sporobolus cryptandrus
Taeniatherum caput-medusae
Tetradymia canescens
Vulpia octoflora

Appendix C: Equipment List

- 6, 3inch PVC Couplings
- 4 Rubber Mallets
- 6 Plywood Slats
- 150, 1 Gallon Plastic Bags
- 5, 30-M Field Measuring Tapes
- 10 Surveying Pins
- 4 Permanent Markers
- 1 GPS Unit (Batteries)
- 1 Compass
- 6 Oversized Coolers
- 100, 10 by 20" Greenhouse Flats
- 7, 5 Pound Bags Sterile Sand
- 70 Plant Tags
- 3 Rolls Paper Towels
- 1 Misting Nozzle
- 50 Seedling Pots
- 1, 5 Pound Bag Potting Soil
- 1 Digital Camera
- 1, 1 Pound Bag Vermiculite
- 4 Plastic Storage Containers
- 4 Gallons Distilled Water

Appendix D: Seed Bank Species Lists

Species List for Seed Bank at Devine Ridge

* Also found in the standing vegetation.

2006

*Achillea millefolium**
Achnatherum occidentale
*Allium acuminatum**
*Antennaria dimorpha**
*Arabis sp.**
*Artemisia tridentata**
*Bromus tectorum**
Castilleja tenuis
Cirsium arvense
Claytonia rubra
*Collinsia parviflora**
Collomia grandiflora
*Cryptantha torreyana**
*Delphinium sp.**
*Descurainia pinnata**
Draba verna
*Elymus elymoides**
Epilobium brachycarpum
*Epilobium ciliatum**
*Ericameria nauseosa**
Gayophytum diffusum
Gnaphalium palustre
Holosteum umbellatum
Juncus bufonius
Juncus ensifolius
Juncus sp.
*Juniperus occidentalis**
Lactuca saligna
Lactuca serriola
*Lithophragma glabrum**
*Melica bulbosa**
*Microsteris gracilis**

2007

*Achnatherum thurberianum**
*Alyssum alyssoides**
*Arabis sp.**
*Artemisia tridentata**
*Bromus tectorum**
Carex rossii
Claytonia rubra
*Collinsia parviflora**
*Cryptantha torreyana**
*Descurainia pinnata**
*Draba verna**
*Elymus elymoides**
*Epilobium brachycarpum**
Epilobium ciliatum
*Ericameria nauseosa**
*Erigeron filifolius**
Gnaphalium palustre
Holosteum umbellatum
Juncus nodosus
*Juniperus occidentalis**
Lactuca serriola
Linaria dalmatica
*Lithophragma glabrum**
*Microsteris gracilis**
*Poa secunda**
*Polygonum douglasii**
*Purshia tridentata**
Stellaria nitens
Symphyotrichum frondosum
Tragopogon dubius *
Woodsia oregana
 Note: 5 Unknowns

Mimulus breviflorus
Mimulus guttatus
Mimulus nanus
Myosotis stricta
*Pinus ponderosa**
*Poa secunda**
*Polemonium micranthum**
*Polygonum douglasii**
Polygonum heterosepalum
Ranunculus glaberrimus
Salix lucida
Senecio sylvaticus
Stellaria nitens
Symphyotrichum frondosum
*Trifolium macrocephalum**
Vulpia octoflora
 Note: 7 Unknowns

Species List for Seed Bank at Bridge Creek

* Also found in the standing vegetation.

2006

*Achillea millefolium**
*Achnatherum thurberianum**
*Alyssum alyssoides**
*Antennaria dimorpha**
*Astragalus sp.**
*Bromus tectorum**
Chamaesyce serpyllifolia
Chamerion angustifolium
Cirsium arvense
Conyza canadensis
Descurainia pinnata
*Draba verna**
Epilobium brachycarpum
Epilobium ciliatum
Galium aparine
*Gutierrezia sarothrae**

2007

*Achillea millefolium**
*Alyssum alyssoides**
Amaranthus albus
*Antennaria dimorpha**
*Bromus tectorum**
Ceratocephala testiculata
Chamaesyce serpyllifolia
Chamerion angustifolium
Cirsium arvense
Claytonia rubra
*Collinsia parviflora**
*Cryptantha torreyana**
*Descurainia pinnata**
*Draba verna**
Eriogonum niveum
*Eriogonum strictum**

*Holosteum umbellatum**

*Lactuca serriola**

Lithophragma glabrum

Microsteris gracilis

Plagiobothrys tenellus

Plectritis macrocera

*Poa secunda**

*Pseudoroegneria spicata**

*Purshia tridentata**

*Sporobolus cryptandrus**

Stellaria nitens

*Tragopogon dubius**

Senecio sylvaticus

Verbascum thapsus

Vulpia bromoides

*Vulpia octoflora**

Note: 3 Unknowns

*Gutierrezia sarothrae**

Holosteum umbellatum

Juncus nodosus

*Juniperus occidentalis**

Lithophragma glabrum

*Lomatium sp.**

*Microsteris gracilis**

*Poa secunda**

*Purshia tridentata**

*Sporobolus cryptandrus**

Stellaria nitens

Tragopogon dubius

Verbascum thapsus

Vulpia bromoides

Woodsia oregana

Note: 1 Unknown

Appendix E: Weed Status, Growth Habit, Nativity, and Functional Group Designation for Seed Bank Species.

Species	Weedy?	Duration	Functional Group	Nativity
<i>Achillea millefolium</i>	YES	Perennial	Forb	Native
<i>Achnatherum occidentale</i>	NO	Perennial	Bunchgrass	Native
<i>Achnatherum thurberianum</i>	NO	Perennial	Bunchgrass	Native
<i>Allium acuminatum</i>	NO	Perennial	Forb	Native
<i>Alyssum alyssoides</i>	YES	Annual	Forb	Introduced
<i>Amaranthus albus</i>	YES	Annual	Forb	Introduced
<i>Antennaria dimorpha</i>	NO	Perennial	Subshrub	Native
<i>Arabis</i> sp.	UNK	Annual/Biennial	Forb	UNK
<i>Artemisia rigida</i>	NO	Perennial	Subshrub	Native
<i>Artemisia tridentata</i>	YES	Perennial	Shrub	Native
<i>Astragalus</i> sp.	UNK	Perennial	Forb	Native
<i>Bromus tectorum</i>	YES	Annual	Annual Grass	Introduced
<i>Carex rossii</i>	NO	Perennial	Graminoid	Native
<i>Castilleja tenuis</i>	NO	Annual	Forb	Native
<i>Ceratocephala testiculata</i>	YES	Annual	Forb	Introduced
<i>Chamaesyce serpyllifolia</i>	NO	Annual	Forb	Native
<i>Chamerion angustifolium</i>	NO	Perennial	Forb	Native
<i>Cirsium arvense</i>	YES	Perennial	Forb	Introduced
<i>Claytonia rubra</i>	NO	Annual	Forb	Native
<i>Collinsia parviflora</i>	NO	Annual	Forb	Native
<i>Collomia grandiflora</i>	NO	Annual	Forb	Native
<i>Conyza canadensis</i>	YES	Annual/Biennial	Forb	Native
<i>Cryptantha torreyana</i>	NO	Annual	Forb	Native
<i>Delphinium</i> sp.	UNK	Perennial	Forb	UNK
<i>Descurainia pinnata</i>	NO	Annual/Biennial	Forb	Native
<i>Draba verna</i>	NO	Annual	Forb	Introduced
<i>Elymus elymoides</i>	NO	Perennial	Bunchgrass	Native
<i>Epilobium brachycarpum</i>	NO	Annual	Forb	Native
<i>Epilobium ciliatum</i>	NO	Perennial	Forb	Native
<i>Ericameria nauseosa</i>	YES	Perennial	Shrub	Native
<i>Erigeron filifolius</i>	NO	Perennial	Forb	Native
<i>Eriogonum niveum</i>	NO	Perennial	Subshrub	Native
<i>Eriogonum strictum</i>	NO	Perennial	Subshrub	Native
<i>Galium aparine</i>	YES	Annual	Forb	Native
<i>Gayophytum diffusum</i>	NO	Annual	Forb	Native
<i>Gnaphalium palustre</i>	YES	Annual	Forb	Native
<i>Gutierrezia sarothrae</i>	YES	Perennial	Shrub	Native
<i>Holosteum umbellatum</i>	NO	Annual	Forb	Introduced
<i>Juncus bufonius</i>	YES	Annual	Graminoid	Native
<i>Juncus effusus</i>	NO	Perennial	Graminoid	Native
<i>Juncus ensifolius</i>	NO	Perennial	Graminoid	Native
<i>Juncus nodosus</i>	NO	Perennial	Graminoid	Native
<i>Juniperus occidentalis</i>	YES	Perennial	Tree	Native

<i>Lactuca saligna</i>	NO	Annual/Biennial	Forb	Introduced
<i>Lactuca serriola</i>	YES	Annual/Biennial	Forb	Introduced
<i>Linaria dalmatica</i>	YES	Perennial	Forb	Introduced
<i>Lithophragma glabrum</i>	NO	Perennial	Forb	Native
<i>Lomatium sp.</i>	UNK	Perennial	Forb	UNK
<i>Melica bulbosa</i>	NO	Perennial	Graminoid	Native
<i>Microsteris gracilis</i>	NO	Annual	Forb	Native
<i>Mimulus breviflorus</i>	NO	Annual	Forb	Native
<i>Mimulus guttatus</i>	NO	Perennial	Forb	Native
<i>Mimulus nanus</i>	NO	Annual	Forb	Native
<i>Monolepis nuttalliana</i>	NO	Annual	Forb	Native
<i>Myosotis stricta</i>	NO	Annual	Forb	Introduced
<i>Pinus ponderosa</i>	NO	Perennial	Tree	Native
<i>Plagiobothrys tenellus</i>	NO	Annual	Forb	Native
<i>Plectritis macrocera</i>	NO	Annual	Forb	Native
<i>Poa secunda</i>	NO	Perennial	Bunchgrass	Native
<i>Polemonium micranthum</i>	NO	Annual	Forb	Native
<i>Polygonum douglasii</i>	NO	Annual	Forb	Native
<i>Polygonum heterosepalum</i>	NO	Annual	Forb	Native
<i>Pseudoroegneria spicata</i>	NO	Perennial	Bunchgrass	Native
<i>Purshia tridentata</i>	NO	Perennial	Shrub	Native
<i>Ranunculus glaberrimus</i>	NO	Perennial	Forb	Native
<i>Salix lucida</i>	NO	Perennial	Tree/shrub	Native
<i>Senecio sylvaticus</i>	NO	Annual	Forb	Introduced
<i>Sporobolus cryptandrus</i>	NO	Perennial	Bunchgrass	Native
<i>Stellaria nitens</i>	NO	Annual	Forb	Native
<i>Symphyotrichum frondosum</i>	NO	Annual	Forb	Native
<i>Tragopogon dubius</i>	YES	Annual/Biennial	Forb	Introduced
<i>Trifolium macrocephalum</i>	NO	Perennial	Forb	Native
<i>Typha sp.</i>	UNK	Perennial	Forb	Native
<i>Verbascum thapsus</i>	YES	Annual/Biennial	Forb	Introduced
<i>Vulpia bromoides</i>	NO	Annual	Annual Grass	Introduced
<i>Vulpia octoflora</i>	YES	Annual	Annual Grass	Native
<i>Woodsia oregana</i>	NO	Perennial	Forb	Native
UNK02	UNK	Annual/biennial	Forb	UNK
UNK04	UNK	Annual/biennial	Forb	UNK
UNK05	UNK	Perennial	Forb	UNK
UNK06	UNK	Annual/biennial	Forb	UNK
UNK07	UNK	Perennial	Tree/shrub	UNK
UNK08	UNK	Annual/biennial	Forb	UNK
UNK20	UNK	Perennial	Forb	UNK
UNK22	UNK	Annual	Forb	UNK
UNK23	UNK	Annual/biennial	Forb	UNK
UNK30	UNK	Perennial	Bunchgrass	UNK
UNK31	UNK	Perennial	Bunchgrass	UNK
UNK32	UNK	Perennial	Bunchgrass	UNK
UNK33	UNK	Perennial	Bunchgrass	UNK