

AN ABSTRACT OF THE THESIS OF

Samantha J. Pack for the degree of Master of Science in Rangeland Science presented on June 9, 2015.

Title: Canyon Grasslands of the Hells Canyon National Recreation Area: How have they changed over time and what is their future trajectory?

Abstract approved: _____

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The canyon grasslands of the Hells Canyon National Recreation Area (HCNRA) are a unique ecosystem within the Pacific Northwest Bunchgrass Region (PNWBR) with a long history of natural and anthropogenic disturbances including fire, invasive species introduction, historical livestock grazing, and cultivation. Even with this history, these canyon grasslands contain some of the last remnants of the Pacific Northwest Bunchgrass Region. For thousands of years, these grasslands were occupied by the Nez Perce Tribe and have been grazed since the 1700s. In addition to grazing, settlers cultivated many parts of the HCNRA and some of these homesteads can still be seen today. Both historical and current land uses are strongly influenced by the natural topography of these canyon grasslands, with the highest concentration of land use centered on benchlands while steep canyon slopes avoided cultivation and were used less by livestock. The different plant associations of these grasslands are also influenced by the unique topography of the HCNRA due to the relationships between soil moisture and depth and abrupt alterations in aspect, slope, and elevation. Very few studies have examined the plant associations of the canyon grasslands of the HCNRA, even fewer have asked how they have changed over time, and there are no studies looking into their future trajectory by assessing the seed bank.

The first study in my thesis (Chapter 2) focused on how canyon grasslands have changed over time using a repeated survey of vegetation from four different plant associations within the Lower Innaha Subbasin. From the original study conducted in 1981, a total of 19 different plots in four plant associations were chosen to be resampled in 2014. Since the original study was used to classify seral stages within the plant associations, these successional stages were used to determine if the plant communities had transitioned between the seral classes over the 33 year-time-period. In addition, given the importance of topography to these grasslands, elevation, slope, and aspect were evaluated for their relationship to successional changes. Both Nonmetric Multidimensional Scaling (NMS) and Indicator Species Analysis were used to verify the seral stage classifications for each plot in 1981 and 2014. To evaluate how each association had changed between sampling years, Multi-response Permutation Procedures (MRPP) and NMS were used. Most of these plant associations were relatively stable and had, for the most part, remained at the same seral stage or transitioned to a later seral stage. Among the plant associations, slope was the topographical variable that appeared most related to the transitions in seral stages. Steeper slopes either remained at the same seral stage or transitioned to a later one, while gentler slopes (< 20%) tended to shift from later to earlier seral stages. A relatively new introduced annual grass to the region, *Ventenata dubia* (not present in the 1981 sampling), was found in three of the four plant associations and was most abundant on the benchlands. The results of this resurvey suggest that topography is related to both the distribution of plant associations and which sites will shift in seral stage over time across the canyon grasslands of the Lower Innaha Subbasin.

The second study of my thesis (Chapter 3) focused on using a seed bank study as one of the many ways to examine the future trajectory of the plant communities in the canyon

grasslands of the Lower Innaha Subbasin, with a particular focus on the benchlands. The seed bank contains the regenerative pool for plant communities and represents the potential for a community to respond to disturbances. The seed bank from benchland sites in one plant association was evaluated in relation to the standing vegetation, successional stage, and historical cultivation. To my knowledge, this was the first seed bank study for the grasslands of this region. Vegetation cover and soil samples were collected from 8 sites, including two previously cultivated and two reference noncultivated sites. NMS was used to extract the strongest community gradients, which naturally separated out the seral stage classifications of the vegetation. To evaluate differences between the vegetation and the seed bank, between successional stages, and between cultivation histories, MRPP was used. Results from the seed bank study are consistent with many other studies around the world in perennial grasslands showing that the vegetation and seed bank are often dissimilar. Similarities between the vegetation and seed bank were highest in the annual grass dominated stage compared to the early seral stage. The effects of cultivation appear to still be evident in the seed bank, where cultivated sites have significantly more introduced grasses compared to noncultivated sites ($p < 0.05$). There was an overall greater abundance of introduced annual forb and grass species in the seed bank on these benchland sites, suggesting that they may be native seed limited and could easily shift to invasive species dominance after further disturbance, especially on previously cultivated areas. The results of both of these studies suggest that benchlands and lower sloped sites surrounding them in the canyon grasslands of the Lower Innaha Subbasin may be less resistant and resilient to disturbance. Priorities for future research and management may also need to focus on the plant communities of benchlands in these unique grasslands.

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Canyon Grasslands of the Hells Canyon National Recreation Area: How have they changed over time and what is their future trajectory?

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Chapter 1: History of the Hells Canyon National Recreation Area

1.1 Introduction

Canyon grasslands of the Hells Canyon National Recreation Area (HCNRA) are a unique ecosystem type within the Pacific Northwest Bunchgrass Region (PNWBR) (Evans and Tisdale 1972). The PNWBR once extended from southeastern Oregon to British Columbia, including parts of Idaho, Montana and Washington (Evans and Tisdale 1972). Due to the steep topography of HCNRA, anthropogenic disturbances have been limited and some of the last intact stands of the PNWBR can only be found within this canyon grassland (Tisdale 1986; Lichthardt and Moseley 1997). The representative bunchgrass species within these grasslands include Sandberg's bluegrass (*Poa secunda*), Idaho fescue (*Festuca idahoensis*), prairie junegrass (*Koeleria macrantha*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) (Johnson and Swanson 2005). These native bunchgrass species form different plant associations with a distribution that is strongly related to topo-edaphic patterns (Tisdale 1986; Johnson and Simon 1987). In addition, topography has largely influenced the extensive land-use history of the HCNRA and has shaped the canyon grassland vegetation found there today (Tisdale 1986; Johnson and Simon 1987; Lichthardt and Moseley 1997; Ecovista 2004; Johnson and Swanson 2005).

The canyon grasslands of the HCNRA were originally set aside as a Forest Reserve in 1907, until Congress established the HCNRA in 1975 (USDA Forest Service 2003; USDA Forest Service 2014). Managed by the Wallowa-Whitman National Forest (WWNF), the HCNRA consists of approximately 264,052 hectares with 5% under private land ownership, 18% owned by the Nez Perce Tribe, and the remainder as public lands (USDA Forest Service 2003).

Prior to European settlement, the HCNRA was occupied by the Nez Perce for thousands of years (USDA Forest Service 2014). The Nez Perce were known to have manipulated the vegetation of the HCNRA through fire and grazing (USDA Forest Service 2014). Cattle and horses were obtained by the Nez Perce during the 1700s and were grazed throughout the HCNRA during the spring and summer months (Bartuszevige et al. 2012). Early explorers used the various pathways created by the Nez Perce to navigate the rough terrain of the HCNRA while surveying the land, hunting for furs, and searching for gold (Idaho State Historical Society 1992). In 1862, the Homestead Act encouraged settlement and cultivation of the HCNRA (Idaho State Historical Society 1992). Benchlands within the HCNRA were heavily used by settlers for cultivation and livestock grazing (Ecovista 2004).

By the 1880s, many portions of the HCNRA, including the Lower Imnaha Subbasin, had been settled with ranches and farms (Buckendorf et al. 2001), but grazing regulations were not established until these areas had become a part of the Imnaha Forest Reserve in 1907 (USDA Forest Service 2014). Soon after World War I, most of the region's mining operations began to shut down due to a sudden drop in ore prices. The farming industry was hit with grasshopper outbreaks, forcing many residents to relinquish their lands, abandon their homesteads, or seek work in nearby towns (Buckendorf et al. 2001). The Federal New Deal programs in the 1940s brought new roads and recreational opportunities to parts of the HCNRA, and boosted the local economy through the creation of new jobs (Buckendorf et al. 2001). After World War II, sheep numbers declined due to the intensive and costly management of large-scale sheep ranching (Daubenmire 1940). At the same time, cattle numbers continued to increase throughout the

HCNRA as the demand for beef increased (Daubenmire 1940). From 1940-1970, cattle numbers steadily increased and were grazed on both private and public lands within the HCNRA (Buckendorf et al. 2001). As cattle numbers plateaued around the middle of the century, farmland continued to be abandoned in the region (Bartuszevige et al. 2012). Remnants of these homesteads can still be found throughout the HCNRA including orchards, abandoned fields, and equipment (Buckendorf et al. 2001). Cattle are still grazed in many parts of the HCNRA, although their numbers are considerably lower than that of the early 1900s (USDA Forest Service 2014).

In the latter half of the 20th century, several studies focused on classifying grassland associations within the HCNRA (Evans and Tisdale 1972; Tisdale 1986; Johnson and Simon 1987). While there has been some research to assess and understand relics of the PNWBR on the plateaus, (Aller et al. 1981; Lichthardt and Moseley 1997; Endress et al. 2007; Hanson et al. 2008; Bartuszevige et al. 2012), only a few have studied the vegetation within the canyon grasslands of the HCNRA (Evans and Tisdale 1972; Tisdale and Bramble-Brodahl 1983; Callihan et al. 1993; Wallace et al. 2008). Around the world, many studies have evaluated the distribution of grasslands based upon topography (Perring 1959; Tisdale and Bramble-Brodahl 1983; Lieffers and Larkin-Lieffers 1986; Gong et al. 2008; Rodhouse et al. 2014) and the effects of grassland vegetation change in response to disturbance (Bennie et al. 2006; Wellstein et al. 2007), as well as the interactions between topography and disturbance (Defosse et al. 1997; Carmel and Kadmon 1999; Amezaga et al. 2004; Wellstein et al. 2007). Likewise, there are many studies world-wide that have addressed grassland seed banks, their relationship to

successional status, as well as their relationships to various disturbances (Thompson and Grime 1979; Henderson et al. 1988; Bertiller 1992; Eriksson and Ehrlén 1992; Russi et al. 1992; Peco et al. 1998; Hild et al. 2001; Luzuriaga et al. 2005; Cox and Allen 2008; Scott and Morgan 2012; Ma et al. 2013; Pekas and Schupp 2013; Bertiller and Carrera 2015). However, within the canyon grasslands of the HCNRA, few have examined changes in grassland vegetation over time (Gucker and Bunting 2011), none have addressed the relationship of topography to these changes, and none have examined seed banks within the canyon grasslands in the HCNRA. This thesis will address two overarching questions using sites within the Lower Imnaha Subbasin of the HCNRA:

- 1) How have the canyon grassland communities changed over time?
- 2) What is the potential successional trajectory of these grasslands, specifically on the heavily used benchlands?

To address how canyon grasslands are changing, I conducted a repeat study of data collected in 1981 from four different plant associations (Chapter 2). I expected that plots located on benchlands and more gentle slopes (< 20%) would be more likely to have remained in earlier seral stages or have transitioned from later to earlier stages due to the long-term effects of past land uses (Johnson and Simon 1987). The potential future trajectory of canyon grasslands was evaluated using a seed bank study on eight different benchlands within the same plant association (Chapter 3). Specifically, I asked how the seed bank related to vegetation, successional status, and historical cultivation. Knowing already that many of these benchlands contain a high abundance of annual species, I hypothesized that the seed bank and vegetation

would be more similar at the earliest seral stages and that there would be differences in the seed bank of cultivated sites vs. noncultivated sites. I anticipated that the results of these studies could be useful in future management of canyon grasslands within the study area, in addition to contributing valuable information about these unique and understudied plant associations and informing future state-and-transition models. Since the HCNRA consists of private, public, and tribal land ownership, the future of these grasslands affects a wide variety of people and their future cultural land-use practices.

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Chapter 2: How Have Canyon Grasslands in the Hells Canyon National Recreation Area Changed Over Time?

2.1 Introduction

Background Information

Topography has a well-known and widely studied influence upon the distribution of plant communities (Perring 1959; Tisdale and Bramble-Brodahl 1983; Lieffers and Larkin-Lieffers 1986; Gong et al. 2008; Rodhouse et al. 2014). Within grasslands, topographical variation can create differences in plant communities and associations that are related to elevation, slope, and aspect (Perring 1959; Tisdale and Bramble-Brodahl 1983; Lieffers and Larkin-Lieffers 1986; Bennie et al. 2006; Gong et al. 2008). Where grasslands occur within steep canyons and mountains, such as the coulees of Alberta (Canada), Northern Galilee Mountains (Israel), Basque Country (Spain), Patagonian grasslands (Argentina), and British chalk grasslands (Europe) there is particular interest in how topography interacts with disturbances to influence long-term vegetation change (Lieffers and Larking-Lieffers 1986; Defosse et al. 1997; Carmel and Kadmon 1999; Amezaga et al. 2004; Bennie et al. 2006). These relationships between disturbance and topography can be related to edaphic factors (Defosse et al. 1997; Amezaga et al. 2004; Wellstein et al. 2007; Gong et al. 2008), changes in nutrient depositions (Amezaga et al. 2004; Wellstein et al. 2007; Gong et al. 2008), and livestock distribution and use of the landscape (Defosse et al. 1997; Carmel and Kadmon 1999; Amezaga et al. 2004). Because these topo-edaphic characteristics and their relationship to contemporary and historical disturbances can play an important role in grassland resistance and resilience to future disturbances, understanding these relationships is becoming an important priority for both conservation and restoration (Bennie et al. 2006; Rodhouse et al. 2014).

Canyon grasslands of the Hells Canyon National Recreation Area (HCNRA) represent some of the last intact grassland communities of the Pacific Northwest Bunchgrass Region (PNWBR), in large part because the unique topography of canyon grasslands has left many of these associations untouched by cultivation (Tisdale and Bramble-Brodahl 1983; Tisdale 1986). The original range of the PNWBR extended from eastern Oregon, parts of Idaho and Montana, and up to northeastern Washington and British Columbia (Evans and Tisdale 1972). Today only a few small isolated patches of the original bunchgrass communities exist. The unique landscape of these canyon grasslands is due in part to breakdown of Paleozoic and Mesozoic rocks (Ecovista 2004), as well as the natural weathering of Columbia basalt formations (Tisdale 1986). The grasslands of the HCNRA include green fescue (*Festuca viridula*), Idaho fescue (*Festuca idahoensis*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) associations (Johnson and Simon 1987). Topo-edaphic patterns contribute strongly to the distribution of canyon grassland associations within the HCNRA, and abrupt changes in composition can occur on different aspects at the same elevation with the same soil parent material (Tisdale 1986). In turn, the interactions between topography and grassland associations have influenced the distribution of the many cultural land uses of canyon grasslands throughout history (Tisdale 1986; Ecovista 2004).

In concert with topography, natural and anthropogenic disturbances have shaped the canyon grassland vegetation over time (Tisdale 1986; Johnson 1994; Ecovista 2004; USDA Forest Service 2014). Historically, fire was frequent and heterogeneous across the different landscape types (Johnson 1994). Many plant communities within the canyon grasslands of the PNWBR are

considered relatively stable because species composition changes very little over time in response to natural disturbances (Daubenmire 1975; Tisdale 1986; Johnson 1994; Gray and Lichthardt 2003; Johnson and Swanson 2005; Gucker and Bunting 2011). However, exotic species have altered plant community composition, and exotic annual grasses may have changed the natural fire regimes by allowing fires to become more intense and homogenous across the landscape (Johnson 1994; Gray and Lichthardt 2003). Although canyon grasslands of the HCNRA have, for the most part, avoided extensive cultivation due to steep slopes and high relief (Tisdale and Bramble-Brodahl 1983; Tisdale 1986), gentle sloping benchlands (< 20%) and ridgetops have been subject to many different agricultural practices (Tisdale 1986; Johnson 1994; USDA Forest Service 2014). Benchlands were also favored for cultivation and grazing because their deep clayey soils are able to retain moisture later in the growing season (Johnson 1994). Heavy use of these benchlands for cultivation, livestock grazing, and by wildlife are believed to have reduced most of the native bunchgrass species and replaced them with exotic grasses and forbs (Johnson 1994). Intact stands of native bunchgrasses within the HCNRA can still be found on areas of steep slopes, where plant communities were less accessible to grazing ungulates (Mancuso and Mosley 1994). Due to the rapid conversion of the PNWBR to agriculture, little is actually known about the original grasslands (Bartuszevige et al. 2012).

There have been several early studies that identified plant associations within the HCNRA canyon grasslands (Evans and Tisdale 1972; Tisdale 1986; Johnson and Simon 1987). Plant associations represent discrete community types that develop and persist within particular environments (Johnson and Simon 1987). Tisdale (1986) categorized canyon grassland

association series of western Idaho based on their relationship to environmental factors such as climate, topography, edaphic, and biotic properties. Tisdale (1986) identified both bluebunch wheatgrass and Idaho fescue series, and further categorized associations within each series. Parallel work done by Johnson and Simon (1987) identified both bluebunch wheatgrass and Idaho fescue series and their corresponding associations. These vegetation studies were done at different locations in canyon grasslands within the PNWBR, but each of the studies resulted in similar plant association findings. Johnson and Simon (1987) took the identification of the bluebunch wheatgrass and Idaho fescue series and plant associations further by classifying their seral stages. Seral stages were thought to be the steps that lead to the climax community, a final stable state of species composition (Huschle and Hironaka 1980; Johnson and Simon 1987). Disturbances, such as fire and grazing, were associated with shifts from later to earlier seral stages (Huschle and Hironaka 1980; Johnson and Simon 1987).

Few studies have looked at the role disturbances play on plant succession within the bunchgrass communities of canyon grasslands within the HCNRA (Johnson and Simon 1987; Johnson 1994) and even fewer have examined changes in these unique sites (Gray and Lichthardt 2003). Only one study has revisited the early survey sites established by Tisdale (1986) in the canyon grasslands of western Idaho (Gray and Lichthardt 2003). These permanent plots were relocated in 1994 and resurveyed 8 years later. This study concluded, like others before it, that native bunchgrass communities in this system were relatively stable over an 8 year period (Gray and Lichthardt 2003). However, as in the 1980s, there was concern over the increase in exotic invasive species (Tisdale 1986; Johnson and Simon 1987; Gray and Lichthardt 2003). Currently,

there are no studies that have examined how canyon grassland communities are changing over the long term and how topography relates to these changes in the vegetation. It is critical to study the role of long term secondary succession in canyon grasslands to better understand the relationship of these successional trajectories to topography and disturbance for conservation and management of these systems (Huschle and Hironaka 1980; Johnson 1994; Bennie et al. 2006; Rodhouse et al. 2014).

Study Objectives

In this study, we examined how the canyon grasslands of the Lower Imnaha Subbasin (located within the HCNRA) have changed over the long term by repeating the vegetation survey that Johnson and Simon (1987) completed in 1981, and comparing the results after the 33 year-time-period. Although the idea of linear succession has been replaced by state-and-transition models (Westoby et al. 1989), even within canyon grasslands (Johnson and Swanson 2005; USDA Forest Service 2014), this original seral classification system can provide a bench mark to examine the successional dynamics of these communities over time. Therefore, we first validated that the identified seral stages were different from one another in species composition in the original sampling year (1981). We then classified the current composition (2014) into seral stages and tested for differences in species composition between seral stages over time. Further, we asked how these seral stages were different in species composition between sampling years. Finally, given the importance of topography to the development of plant associations as well as land uses over time, we examined which topographical variables (elevation, aspect, and slope) were most related to the long-term changes in vegetation. Although our study does not test the

influence of any one particular land use (e.g., cultivation, livestock grazing, or wildlife herbivory), topography can serve as a proxy for the potential concentration of these land uses over time (Johnson 1994; Carmel and Kadmon 1999). We expected that plots located on benchlands and more gentle slopes (< 20%) would be more likely to have remained in earlier seral stages or have transitioned from later to early stages due to the long-term effects of past land uses (Johnson and Simon 1987).

2.2 Methods

Study Area

This research was conducted within the Lower Imnaha Subbasin of the HCNRA and included four major livestock grazing allotments: Toomey, Cow Creek, Lone Pine, and Rhodes Creek. As a temperate continental ecosystem, the Lower Imnaha Subbasin temperatures average 15.8 °C in the summer months and -2.6 °C in the winter months, and the mean annual precipitation is 473 mm (PRISM 2014). Elevation ranges from approximately 300 m (along the Imnaha River) to over 1000 m (ridgetops). As with other canyon grasslands, the microclimate is greatly affected by both aspect and elevation, especially at either extreme. Grasslands within our study area are primarily composed of green fescue, Idaho fescue, and bluebunch wheatgrass associations (Johnson and Simon 1987). The distribution of these different grassland types is largely due to the varying soil types, with Idaho fescue communities on deep loess soils and bluebunch wheatgrass communities on shallower soils (Johnson and Simon 1987). The many different plant

associations are linked to the numerous abiotic factors (Tisdale and Bramble-Brodahl 1983; Tisdale 1986).

Original Data

The original unpublished data from Johnson and Simon (1987) intensive plant study was obtained from the Wallowa-Whitman National Forest (WWNF) Supervisor's Office in Baker City, Oregon. In their study, Johnson and Simon (1987) visited over 250 different sites within the HCNRA conducting both reconnaissance and intensive plant surveys in 1980 and 1981. The purpose of their study was to identify and thoroughly describe the different plant associations located within the HCNRA. Their sites were chosen based on their physical characteristics, as well as evidence of few disturbances (e.g., grazing, fire, cultivation, and introduced species dominance). In the field, Johnson and Simon (1987) classified the soil types for each plot, which are known to covary with the different plant associations. For each plant association within the HCNRA, Johnson and Simon (1987) described the different seral stages (very early, early, mid, and late) and provided indicator species cover/frequency values for each seral stage.

Plot Selection

There were a total of 34 intensive survey sites found within 9 different plant associations throughout our study area. We wanted to resurvey sites in the plant associations that contained a range of seral stages. Therefore, to determine which plant associations to sample, we first classified the seral stages of the original 34 plots. Seral stages were classified by using a range of cover/frequency values established by Johnson and Simon (1987) to select the best match for each plot (A.1-A.4). Once the seral stages of each plot were established, the plots were grouped

by plant association to identify the ones that contained a range of seral stages. Since burned plots were limited in our study area, we only resurveyed plots that had not burned since 1981. A total of 19 plots within four different plant associations were chosen for re-sampling (Table 2.1).

Plant Associations

Our resurvey includes four different plant associations, three of which are bluebunch wheatgrass communities and one is an Idaho fescue community (Johnson and Simon 1987). The Idaho fescue community in our study is at the lowest end of its elevational range and is characterized by high productivity and northern facing aspects. Although named for the same dominant bunchgrass, each of the bluebunch wheatgrass associations are vastly different in their species composition and location within the study area. The bluebunch wheatgrass/Sandberg's bluegrass (*Poa secunda*)/Snake River phlox (*Phlox colubrine*) is one of the most productive bluebunch wheatgrass associations and occurs at the highest elevations with the wettest aspects. The bluebunch wheatgrass/Sandberg's bluegrass (granite) association is characterized by its quartz and diorite substrate and is considered a highly stable community. Finally, the bluebunch wheatgrass/sand dropseed (*Sporobolus cryptandrus*)/red three awn (*Aristida purpurea*) association is found almost exclusively on benchlands where multiple land uses (e.g., grazing and cultivation) have historically been highly concentrated. Nomenclature of plant species follows the USDA PLANTS Database (USDA, NRCS 2015).

Field Methods

The resurvey of each plot was completed as close as possible to the original date of collection and all sampling was completed by July 2014. Using GPS coordinates of plot locations, plot

photos, and field notes taken by Johnson and Simon (1987), we relocated the permanent metal stakes located at the ends and center of each transect. We were able to relocate the stakes for all but two of the 19 plots. We recorded the GPS coordinates of the location in which we sampled as close to photo point and field notes as possible. We then followed the field methods described for the original data collection to measure the plant attributes in 2014. Johnson and Simon (1987) used two permanently marked 30.5 m transects with 20-Daubenmire frames (20 cm x 50 cm) placed at 1.5 m intervals as subplots to record individual species percent canopy cover. Individual species frequency was calculated as the percentage of total frames within each transect where the species was present. Repeat photography was conducted at each transect to mimic the original plot photos taken in 1981. All data and photos are on file with the Wallowa-Whitman National Forest Supervisor's Office in Baker City, Oregon.

Data Analysis

Data from our resurveys was used to classify the seral stage of each plot in 2014 using the same methods previously described for the 1981 plots. All analyses were completed using PC-ORD software version 6.16 (McCune and Mefford 2011). To test for differences in species composition of seral stages between years and within years for each plant association, we used Multi-Response Permutation Procedures (MRPP). Sørensen distance measurement was used for each MRPP to test the null hypothesis of no difference between groups (Zimmerman et al. 1985). Within a plant association, we compared the chance-corrected within-group agreement (A-statistic), or effect size, of each comparison between years and within (McCune and Grace 2002). Likewise, for each of the four plant associations, Indicator Species Analysis (Dufrêne and

Legendre 1997) tests were done, with 4999 randomizations using the Monte Carlo test, to identify which species most strongly separated the groupings within the MRPP results. This test is based on the abundance/frequency of a species and the faithfulness of the species to a specific group (McCune and Grace 2002). All significant ($p < 0.05$) species identified in each sampling year were used to exclude those species that were not strong indicators of any one identified group. The indicator species analysis test results determine the indicator value for each species based on the exclusivity of that species towards an identified group. Between sampling years for all associations, we compared the indicator values for each species between the designated groupings (seral stages).

In order to evaluate changes in species composition between 1981 and 2014 (McCune and Grace 2002), we used Nonmetric Multidimensional Scaling (NMS) (Kruskal 1964) to extract the strongest composition gradients, allowing us to identify any separation of seral stage groupings within the species space. Species that were considered rare (< 5% of the data) were removed to decrease noise and enhance the natural relationships found within the dataset (McCune and Grace 2002). A generalized logarithmic transformation was used so that the dominate species would have more weight in the ordination (McCune and Grace 2002). Sørensen distance measurement was run using “auto-pilot” with the “slow and thorough” method and a random starting point. We chose this distance measurement because we were interested in the proportional differences in relative abundance compared to absolute differences (McCune and Grace 2002). The ordinations were graphed two-dimensionally because the first two axes explained the greatest portion of the variation for all plant associations. We evaluated separation

of plots in species space to identify if the patterns in plot placement were linked to the classified seral stage. To examine the relationship between seral stages and topographical variables, we overlaid a joint plot containing slope, aspect, and elevation for each association. Soil type was not used as a variable because it is known to covary with each plant association (Johnson and Simon 1987). Aspect was converted from degrees (measured in the field) to values ranging from 1-4, where 1 was the driest and 4 was the wettest (S=1, SW=1, W=2, NW=2, SE=3, N=4, NE=4) (B. McCune, Oregon State University, unpublished course packet).

2.3 Results

Classification of Seral Stages

Overall, most of the resurveyed plots either remained at the same seral stage or moved towards a later seral stage within the 33 year-time-period. Of the 19 plots sampled, seven plots remained at the same seral stage in 2014, eight transitioned to an earlier seral stage, and four transitioned to a later seral stage (Table 2.1). The bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association had the most plots that shifted from an earlier seral stage to a later seral stage. In contrast, the bluebunch wheatgrass/sand dropseed/red three awn association had the most plots that remained in early seral stages or transitioned into a new classification, "annual grass dominated." This new classification was necessary because of the high abundance of *Ventenata dubia*, which was not recorded in any plant association in 1981 (Johnson and Simon 1987). Within a plant association, sites of the same seral stage tended to be more similar in species composition when compared to those of different seral stages (A5-A.12).

Idaho fescue/prairie junegrass (low elevation) association

Within this association, species composition between sampling years was the most similar in the mid seral plots ($A = 0.021$, $p < 0.001$) and the most different between late and very early seral plots ($A = 0.256$, $p < 0.001$) (Table 2.2). McCune and Grace (2002) described an effect size (A-statistic) greater than 0.200 indicating that the difference in species composition between the groups was very large. This cutoff point will be used as a guideline for each plant association. In general, a large effect size (A-statistic) indicates more variability in composition between groups (Abella and Covington 2004). In the later seral stages, the relationship of cover between *F. idahoensis* and *P. spicata* is typically 4:1 (Johnson and Simon 1987), making *P. spicata* an earlier seral species only in this association. The plots that change to early seral stages clearly showed a shift in the ratio between these two grasses. *Festuca idahoensis* was nearly absent from the very early seral stages (1981 and 2014), while the latest seral stages had the strongest indicator values for this late seral species (Table 2.3). Within this association, the shift from later to earlier seral stages occurred as axis 1 increased (Figure 2.1). When we examined the correlation between the main matrix (species) and each axis (analysis not shown in Figure 2.1), we found that later seral stages within this association were most correlated with high *F. idahoensis* ($r^2 = 0.782$) cover and low *P. spicata* ($r^2 = 0.471$) along axis 1. In addition, the shift in species composition as seral stages became earlier across axis 1, due to the increase in *P. spicata* and decrease in *F. idahoensis*. On the other hand, axis 2 was correlated with the transition between early and mid seral stages.

Bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association

For this plant association, the transition from early seral (1981) to mid seral (2014) showed the most similarities in species composition ($A= 0.069$, $p < 0.001$), whereas the transition from mid (1981) to early (2014) showed the least ($A= 0.172$, $p < 0.001$) (Table 2.2). Although both effect sizes are relatively weak (less than 0.200), the species composition between the early seral (1981) and mid seral (2014) was more similar compared to the transition from mid seral (1981) to early seral (2014). All comparisons of species composition within 1981 seral stages were similar since only mid and early seral stages were represented (Table 2.2). Compared to other plant associations in this study, this association contained the most late seral plots. The transition from earlier to later seral stages between sampled years within this association was related to increased *P. spicata* and *P. secunda* in addition of *P. columbrine* (Table 2.4). Whereas annual species such as *Artenaria serpyllifolia* and *B. tectorum* increased in cover from 1981 to 2014, they are still strong indicators for the early seral stage (Table 2.4). *Pseudoroegneria spicata* typically occurred within the drier plant communities of the Lower Imnaha Subbasin, although in this association it was known to thrive in the wetter sites (Johnson and Simon 1987). Within the ordination, *P. spicata* ($r^2= 0.335$) was correlated with axis 1, based on our results comparing the correlation of each species to the axes (analysis not shown in Figure 2.2). The increased cover of *P. spicata* along axis 1 was related to a wetter aspect (A.13). Later seral stages occurred along axis 1, where aspect was the wettest. Elevation and slope (A.13), however, were associated with axis 2, but in opposition to one another (Figure 2.2). Early seral species composition was

correlated with aspect becoming drier along axis 1, where exotic annual species such as *B. tectorum* ($r^2= 0.531$) and *A. serpyllifolia* ($r^2= 0.438$) were the greatest in cover.

Bluebunch wheatgrass/Sandberg's bluegrass (granite) association

Only two seral stages were represented in each year within this plant association. Between sampled years, the mid (1981) and early (2014) seral stages were more similar in species composition ($A= 0.051$, $p < 0.001$) than the sites that remained at very early seral stage ($A= 0.110$, $p < 0.001$) relative to the range in effect size within this association. *Pseudoroegneria spicata* was a strong indicator species for the early and mid seral stages (Table 2.5) and occurred on drier aspects within this association relative to the previous two associations (Johnson and Simon 1987). Therefore, as would be expected, the ordination showed *P. spicata* was correlated with the early and mid seral stages, which also occurred on the driest aspects (Figure 2.3). Very early seral stages were associated with an increase in *A. purpurea* and *S. cryptandrus*, species that tend to invade wetter sites within this association (Johnson and Simon 1987). Aspect was the most important correlate to the changes in seral stages compared to elevation and slope (A.13).

Bluebunch wheatgrass/sand dropseed/red three awn association

Between all of the associations sampled in this study, this one was the most unique because we had created a new seral stage classification to account for the presence of *V. dubia*, which was absent from the 1981 sampling. Species composition between sampled years was the most similar between the early seral stages ($A= 0.107$, $p < 0.001$) and very early vs. annual grass dominated seral stages ($A= 0.101$, $p < 0.001$). Conversely, *P. spicata* appeared to be the strongest indicator for the early seral stages in both years (Table 2.6). Perennial grasses such as

S. cryptandrus and *A. purpurea*, although native, were known to increase with disturbance within this association (Johnson and Simon 1987). All of the very early seral plots and one early seral plot from 1981 transitioned to annual grass dominated by 2014 (Table 2.1). This change in species composition between sampled years can be seen in the ordination results (Figure 2.4). Early seral stages between both years overlapped in species space, while there was a clear distinction between the very early and annual grass dominated seral stages. Slope was the strongest correlate for the transition from earlier to later seral stages (Figure 2.4) compared to aspect and elevation (A.13). In this plant association, more than any of the others, disturbances were highly concentrated on the shallowest slopes (Johnson and Simon 1987). Johnson and Simon (1987) noted that no late seral community within this association was found within the study area.

2.4 Discussion

This study indicates that the topography, which is known to contribute to the distribution of plant associations in the canyon grasslands of the Lower Imnaha Subbasin, may also influence how these associations change over time. In general, the seral stages within the plant associations sampled mostly remained in the same stage or moved to a later seral stage, with the exception of the bluebunch wheatgrass/sand dropseed/red three awn association. As we predicted, plots with more gentle slopes (< 20%) were most likely to remain in an early seral stage or move towards very early or annual grass dominated seral stages. Most of these were within the bluebunch wheatgrass/sand dropseed/red three awn association. This association is almost exclusively

found on the shallowest slopes and benchlands where land uses tended to be more concentrated since they are the most accessible topography of this study area (Johnson and Simon 1987). This is consistent with other grasslands around the world (Lieffers and Larkin-Lieffers 1987; Bennie et al. 2006). For example, in the British chalk grasslands, flatter sites showed the greatest magnitude of change in species composition in response to grazing, since grazing tends to be more concentrated on lower slopes (Bennie et al. 2006). The steeper slopes of the Idaho fescue/prairie junegrass (low elevation) and bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox associations make them largely inaccessible to grazing and cultivation (Johnson and Simon 1987). The plots that remained in early seral stages or transitioned to earlier seral stages in these associations were found on the driest aspects, with the only exception being the bluebunch wheatgrass/Sandberg's bluegrass (granite) association. In the bluebunch wheatgrass/Sandberg's bluegrass (granite) association plots tended to transition from later to earlier seral stage as aspect became wetter (Johnson and Simon 1987). Therefore, within a particular plant association, the importance of any one topographical feature can be related to succession in different ways because each one occurs in unique landscape positions throughout the Lower Imnaha Subbasin. The topographic differences in slope and aspect have been reported to affect the rate of vegetation change and can allow grassland associations to persist within larger grassland communities in many different regions (Lieffers and Larkin-Lieffers 1987; Carmel and Kadmon 1999; Amezaga et al. 2004; Bennie et al. 2006; Wellstein et al. 2007). The relationship between topo-edaphic patterns and the distribution of plant associations in canyon

grasslands may also play an important role in the introduction and spread of exotic species (Tisdale 1986).

Between the four plant associations, two distinct groups are represented; mesic associations and xeric associations. The Idaho fescue/prairie junegrass (low elevation) and bluebunch wheatgrass/ Sandberg's bluegrass/Snake River phlox associations occur within some of the most mesic grassland sites within the Lower Imnaha Subbasin (Johnson and Simon 1987). Transition from earlier to later seral stages within both of these plant associations appears to be associated with elevation and aspect more than slope, both of which influence temperature and moisture gradients (Tisdale 1986; Johnson 1994; Johnson and Swanson 2005). Similar to other studies in the region, wetter and higher elevation sites within these two plant associations contained more mid and late seral stages compared to the low and dry sites (Rodhouse et al. 2014). These highly productive associations are resilient to natural disturbances (Johnson and Simon 1987). It is no coincidence that the two most mesic plant associations contain the most plots that transitioned from earlier to later seral stages, or remained at the same seral stage. The combination of high native grass productivity and occurrence on steep slopes (average 55%) has discouraged most land-use practices (Tisdale 1986) and may have allowed communities similar to these to recover quickly following natural disturbances (Gucker and Bunting 2011). The connection between steep topography, resilience, and resistance to invasion in grassland communities has been previously reported (Bennie et al. 2006; Rodhouse et al. 2014). Steeper slopes, however, are susceptible to soil and plant displacement from heavy elk grazing (Johnson et al. 2013). Colluvial slopes, such as those in these two plant associations, are prone to

downslope movements, although most later seral communities are highly adapted to these annual movements (Johnson 1994). Both Tisdale (1986) and Johnson and Simon (1987) recorded exotic species within these two plant associations, but many of these species have become integrated into even the latest seral communities. The relationship between aspect and elevation to moisture and temperature is what allows some associations to exist in locations that would not normally support such mesic grassland communities (Johnson 1994).

In contrast to the two mesic plant associations, the bluebunch wheatgrass/Sandberg's bluegrass (granite) and bluebunch wheatgrass/sand dropseed/red three awn associations occur on the driest sites sampled within this study. These two plant associations contained the most plots that transitioned from later to earlier seral stages. As has been reported, both aspect and slope can influence the transition in species composition within semi-arid grasslands (Carmel and Kadmon 1999; Amezaga et al. 2004; Gong et al. 2008), where species such as *B. tectorum* tend to be associated with the drier more southern facing aspects (Rodhouse et al. 2014). Both of these plant associations occur on typical xeric bluebunch wheatgrass areas within the Lower Imnaha Subbasin. However, their response to topographical variables was different due to the differences in plant association characteristics. The wetter sites within the bluebunch wheatgrass/Sandberg's bluegrass (granite) have a higher potential for the establishment of early seral native bunchgrass species such as *A. purpurea* and *S. cryptandrus* (Johnson and Simon 1987). Conversely, the wetter sites within the bluebunch wheatgrass/sand dropseed/red three awn association tends to have higher cover of later seral native species. These associations typically occur on shallower slopes within the study area (Johnson and Simon 1987) and are more susceptible to concentrated

land uses such as grazing and cultivation (Tisdale 1986; Johnson and Simon 1987; Johnson 1994; Ecovista 2004; USDA Forest Service 2014).

Exotic grasses are of increasing concern on shallow slope sites within the Lower Imnaha Subbasin (Johnson 1994; USDA Forest Service 2014). The bluebunch wheatgrass/sand dropseed/red three awn association was the most unique of all associations sampled because of the high abundance of *V. dubia*. The abundance of this newly dominant introduced annual grass necessitated the creation of an annual grass dominated stage. However, since very little is known about this species within the HCNRA or across the entire region, it is unknown where this seral stage would fit into successional classifications generated by Johnson and Simon (1987).

Ventenata dubia was not recorded in the Johnson and Simon (1987) sampling, however it has been observed in other studies within the HCNRA (Tisdale 1986; Gray and Litchardt 2003; Johnson and Swanson 2005; Johnson et al. 2013). The increase in exotic annual grasses within the HCNRA is a threat to native plant communities (Tisdale 1986; Johnson and Simon 1987; Johnson 1994; Mancuso and Mosley 1994; Ecovista 2004; USDA Forest Service 2014), particularly those on benchlands. In addition, the introduction of *V. dubia* in the HCNRA is of increasing concern for land managers (Johnson and Swanson 2005; Johnson et al. 2013). Our findings suggest that sites on the driest aspects may be less resistant and resilient post-disturbance due to naturally low productivity and extensive land-use history.

The presence of *V. dubia* in the bluebunch wheatgrass/sand dropseed/red three awn association has greatly altered the community composition based on our study results. According to Northam and Callihan (1994) this exotic annual grass was first found in northern Idaho in

1956. Since then it has spread into eastern Washington, Oregon and seven of the western states (USDA, NRCS 2015). Very little is known about the basic ecology, life history, and the factors that assist invasion of *V. dubia* within canyon grasslands (Johnson and Swanson 2005; Johnson et al. 2013). Some studies suggest that this species is more abundant on sites that are heavily impacted by elk, especially from trampling (Johnson et al. 2013). Other studies suggest that elk are capable of spreading this and other exotic species throughout adjacent grasslands (Sheehy and Vavra 1996; Vavra et al. 2007; Johnson et al. 2013), although cattle have been shown to transmit more exotic species compared to elk in adjacent bunchgrass prairies (Bartuszevige and Endress 2007). Our study results suggest that *V. dubia* is not limited to a particular grassland association, although it is found in highest abundance within the bluebunch wheatgrass/sand dropseed/red three awn association on benchlands. Although this exotic annual grass tended to occur in the earliest seral plots within each of the plant associations, it was present in one late seral plot within the bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association. While *V. dubia* was mostly present in the earliest seral stages within three of the four associations sampled, other exotic annual grasses are typically found in all seral stages of each association (A.1-A.4).

Study Limitations

There are a few limitations to this kind of retrospective study. First, since this dataset includes only two sampling years that are 33 years apart, several factors we did not measure could be related to the changes in these communities, including temperature and precipitation. The mean annual precipitation in 1981 was higher than in 2014 (difference of 126 mm, Figure 2.5),

although the mean annual temperature in 2014 (10.7 °C) was greater than that of 1981 (9.8 °C) (PRISM 2014). This difference in precipitation and temperature between sampling years could explain why Johnson and Simon (1987) found more annual forb species than we did in 2014. Second, Johnson and Simon (1987) stratified their original plot selection to avoid disturbances such as fire, grazing, and cultivation. Their stratification meant to ensure they selected plots that best represented the various seral stages within each plant association. Because these types of sites were avoided, we are limited in our interpretation of the impact directly from these disturbances to the changes we see between sampled years. Finally, although we resurveyed plots within the fullest range of seral stages in four very common plant associations within our study area, they still only represent 55% of the 34 intensive survey plots that Johnson and Simon (1987) sampled in the early 1980s.

Future Research

There is potential for further repeat studies using our dataset as well as including more plots and more sampling years. Although this study used seral stages, the data itself can also provide valuable information to populate future state-and-transition models of canyon grasslands. Future studies could also look at the implications of the introduction of *V. dubia* over time. More research is needed to understand the full range of dynamics within canyon grassland plant associations, including how increasing exotic species cover affects them. Continuing to resample the plots from this study in the future at regular intervals would provide additional valuable information about the successional dynamics within this system. Finally, there are over 250 plots

within the HCNRA across multiple plant associations that should be revisited and evaluated for change over time in relation to topography, climate, and land-use history.

2.5 Conclusion

The canyon grasslands of the HCNRA represent a unique ecosystem type and contain some of the last remnants of the larger PNWBR. This study was the first to identify how these canyon grasslands have changed over a decadal time scale (> 30 years) and how topography may be associated with these changes. Our findings are consistent with others that suggest these native bunchgrass communities change little over time in the absence of disturbance (Tisdale 1986; Johnson and Simon 1987; Johnson 1994; Gray and Lichthardt 2003). Overall, 58% of our plots stayed in the same seral stage or transitioned into later ones. The results of this resurvey suggest that topography patterns may not only be related to the distribution of plant associations across the canyon grasslands of the Lower Imnaha Subbasin, but may also influence which sites change most over time. Our results are also consistent with other grassland studies around the world concluding that topo-edaphic patterns affect both the distribution of communities and the shift in vegetative composition following disturbance (Defosse et al. 1997; Carmel and Kadmon 1999; Amezaga et al. 2004; Bennie et al. 2006; Wellstein et al. 2007). Overall, the plots that remained as early seral or transitioned from later to early seral stages were found on more shallow slopes. In addition, elevation and aspect, both of which are known to affect precipitation and soil moisture potential, appeared to be relevant to transition from later to earlier seral stages in two of our plant associations. This suggests that the drier aspect sites within plant associations may have

lower resiliency following disturbances. The increasing abundance of exotic annual grasses and the introduction of *V. dubia* are of great concern to management. More research is needed to understand this increase, how to contain it, and how to restore areas that are already highly invaded (Hanson et al. 2008).

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Chapter 2: Figures

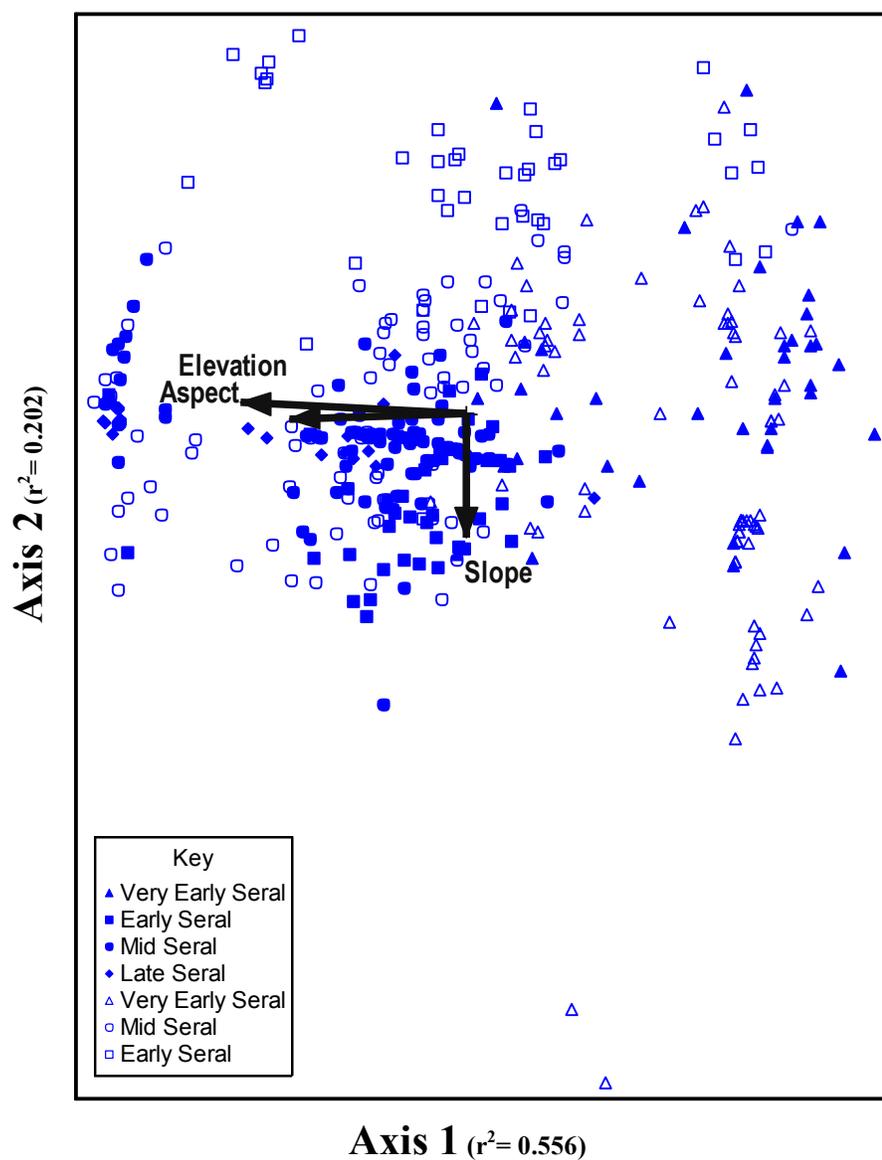


Figure 2.1 NMS results showing 2-dimensional ordination for the 1981 and 2014 sampling together with joint plot overlay within the Idaho fescue/prairie junegrass (low elevation) association. This ordination shows the individual species composition for 1981 (closed symbols) and 2014 (open symbols) sampling. Values for each joint plot variable increases in the direction of the vector.

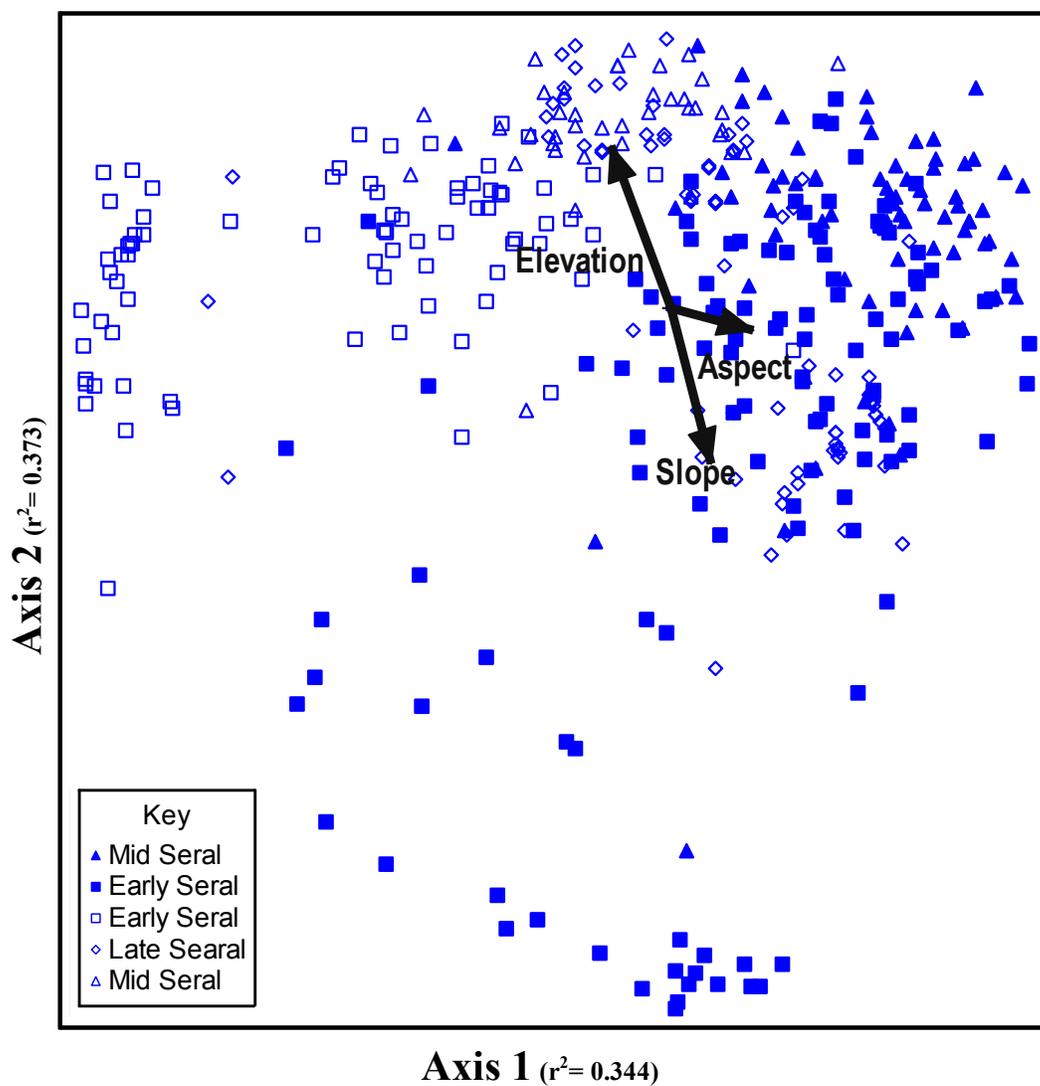


Figure 2.2 NMS results showing 2-dimensional ordination for the 1981 and 2014 sampling together with joint plot overlay within the bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association. This ordination shows the individual species composition for 1981 (closed symbols) and 2014 (open symbols) sampling. Values for each joint plot variable increases in the direction of the vector.

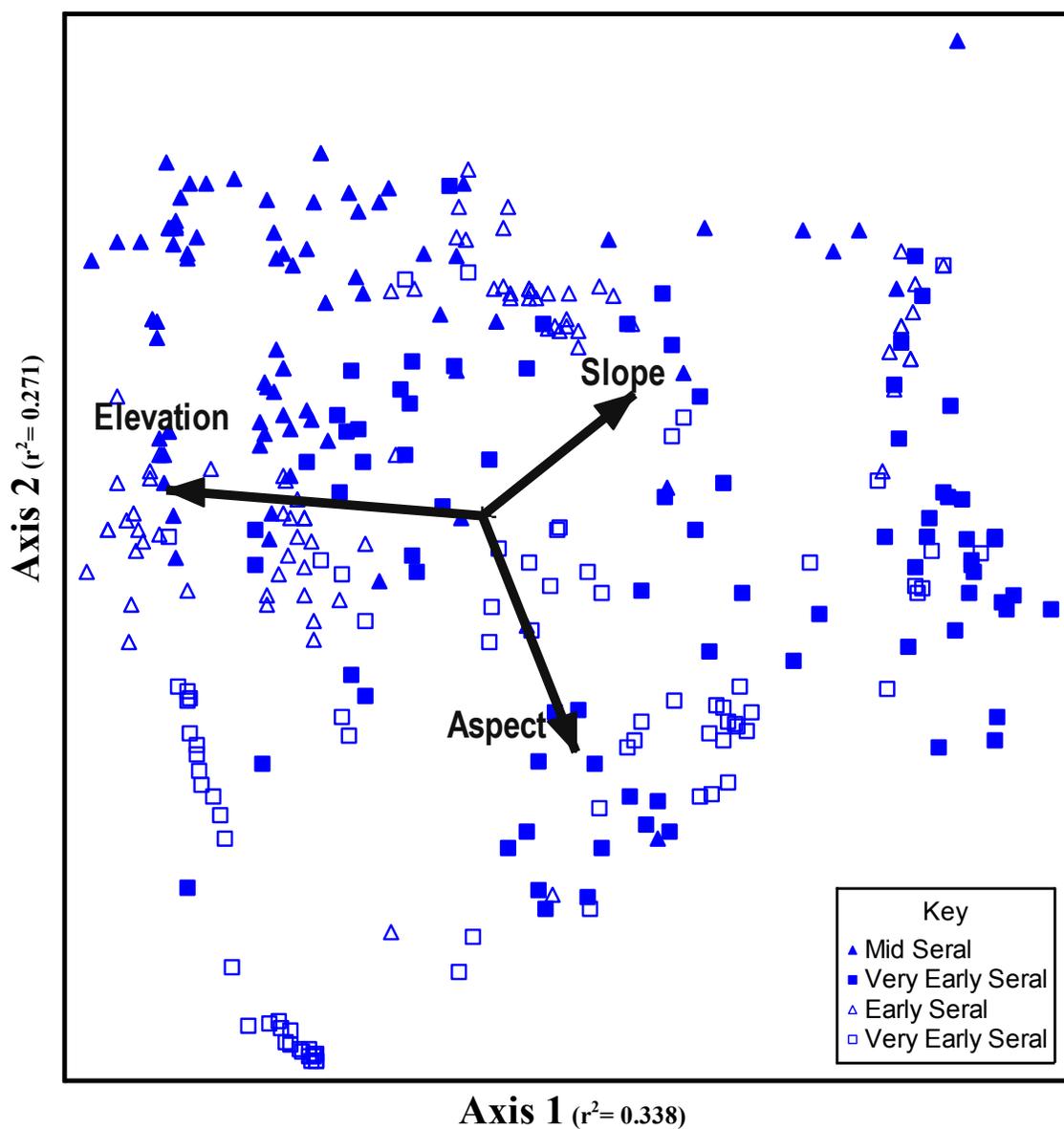


Figure 2.3 NMS results showing 2-dimensional ordination for the 1981 and 2014 sampling together with joint plot overlay within bluebunch wheatgrass/Sandberg's bluegrass (granite) association. This ordination shows the individual species composition for 1981 (closed symbols) and 2014 (open symbols) sampling. Values for each joint plot variable increases in the direction of the vector.

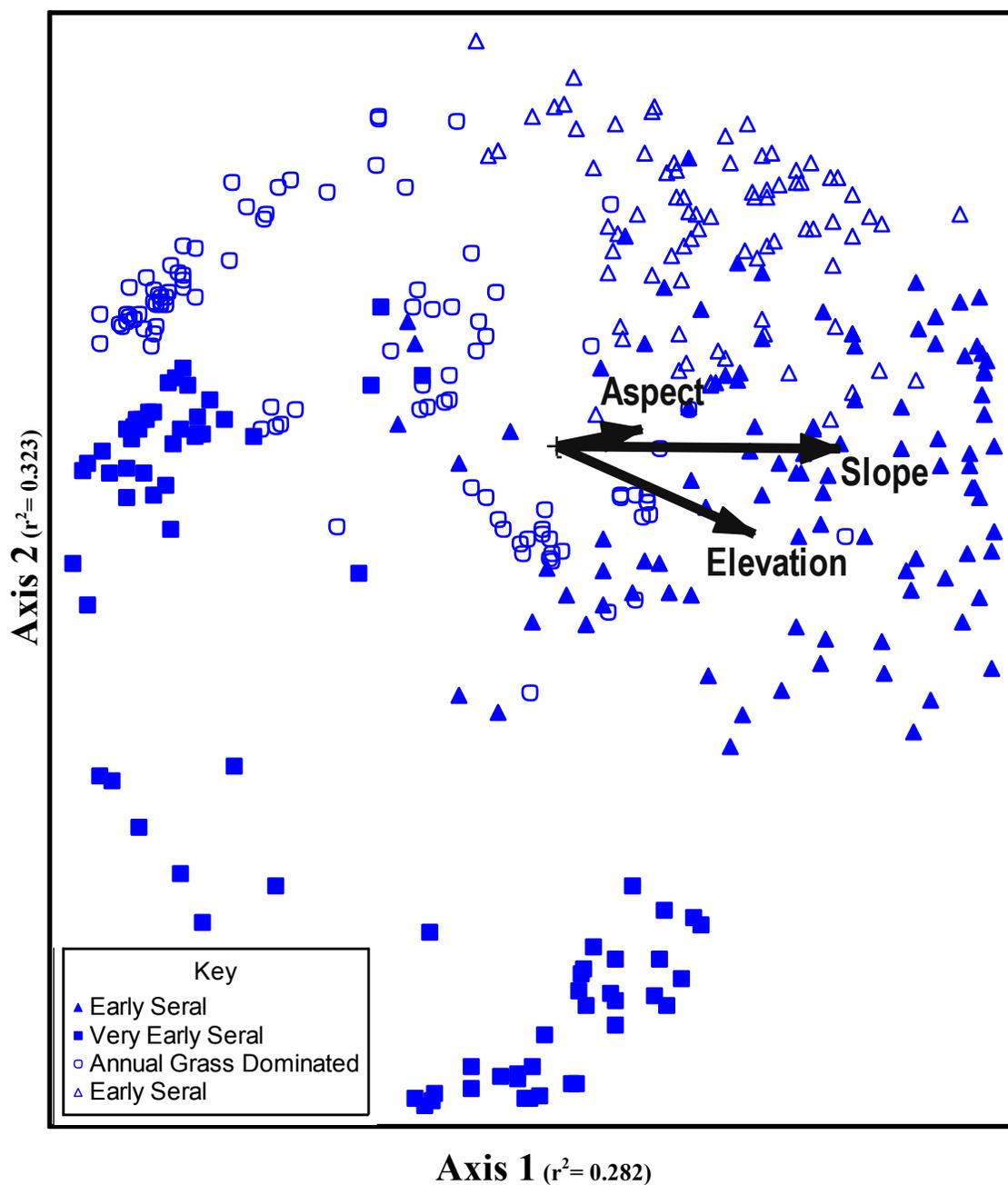


Figure 2.4 NMS results showing 2-dimensional ordination for the 1981 and 2014 sampling together with joint plot overlay within bluebunch wheatgrass/sand dropseed/red three awn association. This ordination shows the individual species composition for 1981 (closed symbols) and 2014 (open symbols) sampling. Values for each joint plot variable increases in the direction of the vector.

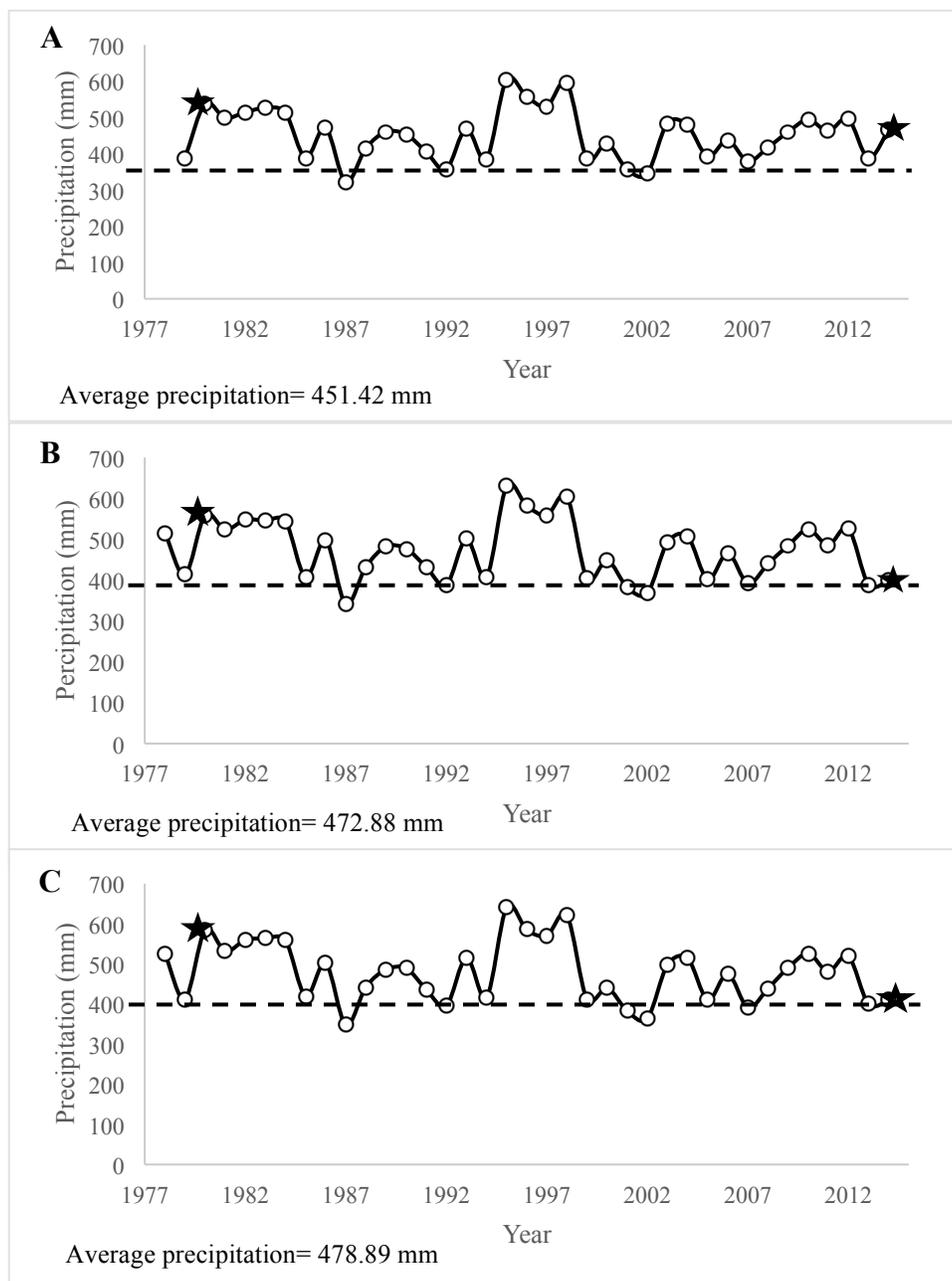


Figure 2.5 Precipitation data showing the variation in annual precipitation for three different elevational classes (low (A) = 518 m, mid (B) = 697 m, and high (C) = 929 m) for years 1978 to 2014 (PRISM 2014). The two sampling years (1981 and 2014) are emphasized with the star at each point. The dashed line represents the mean annual precipitation for each elevational class.

Chapter 2: Tables

Table 2.1 Characteristics of study plots by their plant association. Plant associations are based on Johnson and Simon (1987) classifications. Seral stages for both sampling periods were determined using individual species cover/frequency values for each association from Johnson and Simon (1987). The annual grass dominated seral stage was created in 2014 due to the presence of the new exotic species *Ventenata dubia* and the abundance of exotic annual grasses.

Plot Number	Slope	Aspect ¹	Elevation	Seral Stage 1981	Seral Stage 2014
Idaho fescue/prairie junegrass (low elevation)					
398	58%	4	823 m	Mid	Mid
417	54%	3	792 m	Late	Early
432	66%	4	930 m	Mid	Mid
348	67%	3	724 m	Early	Very Early
333	55%	3	692 m	Very Early	Very Early
bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox					
368	35%	3	732 m	Mid	Late
340	40%	2	777 m	Mid	Early
394	45%	1	762 m	Early	Early
396	58%	4	930 m	Early	Mid
541	67%	4	402 m	Early	Late
bluebunch wheatgrass/Sandberg's bluegrass (granite)					
399	7%	1	841 m	Mid	Early
587	50%	1	728 m	Mid	Early
405	34%	3	518 m	Very Early	Very Early
370	18%	3	698 m	Very Early	Very Early
bluebunch wheatgrass/sand dropseed/red three awn					
354	22%	1	707 m	Early	Early
349	15%	4	677 m	Early	Early
332	22%	1	640 m	Early	Annual Grass Dominated
338	10%	1	610 m	Very Early	Annual Grass Dominated
339	18%	1	732 m	Very Early	Annual Grass Dominated

¹ Aspect was converted from degrees (measured in the field) to values ranging from 1-4, where 1 was the driest and 4 was the wettest

Table 2.2 Multi-Response Permutation Procedures results for all plant associations. Seral stages for both sampling periods were determined using individual species cover/frequency values for each association from Johnson and Simon (1987). All comparisons were significant ($p < 0.001$).

Multiple Comparisons (Sørensen)	T	A
Idaho fescue/prairie junegrass (low elevation)		
1981 vs. 2014		
Mid vs. Mid	-7.20	0.021
Very Early vs. Very Early	-12.07	0.040
Late vs. Mid	-11.93	0.050
Early vs. Mid	-17.10	0.070
Early vs. Very Early	-33.28	0.111
Early vs. Early	-22.25	0.112
Mid vs. Early	-34.87	0.133
Very Early vs. Early	-29.88	0.151
Very Early vs. Mid	-47.98	0.194
Mid vs. Very Early	-67.19	0.204
Late vs. Early	-30.99	0.211
Late vs. Very Early	-57.71	0.256
bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox		
1981 vs. 2014		
Early vs. Mid	-28.48	0.069
Mid vs. Mid	-25.72	0.091
Early vs. Late	-52.61	0.108
Early vs. Early	-65.45	0.121
Mid vs. Late	-45.83	0.127
Mid vs. Early	-63.47	0.172
bluebunch wheatgrass/Sandberg's bluegrass (granite)		
Mid vs. Early	-21.23	0.051
Very Early vs. Early	-48.34	0.104
Very Early vs. Very Early	-50.64	0.110
Mid vs. Very Early	-21.23	0.173
bluebunch wheatgrass/sand dropseed/red three awn		
Very Early vs. Annual Grass	-48.67	0.101
Early vs. Early	-55.62	0.107
Early vs. Annual Grass	-70.93	0.123
Very Early vs. Early	-73.66	0.181

Table 2.3 Indicator species analysis results for the Idaho fescue/prairie junegrass (low elevation) association. Species listed are those with significant p-values (< 0.05). Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association.

	<u>Very Early</u> 1981	<u>Early</u> 1981	<u>Mid</u> 1981	<u>Late</u> 1981	<u>Very Early</u> 2014	<u>Early</u> 2014	<u>Mid</u> 2014
Later Seral Species							
<i>Festuca idahoensis</i>	1	13	24	28	0	8	22
<i>Koeleria macrantha</i>	0	22	2	0	0	0	30
<i>Poa secunda</i>	0	0	0	0	0	74	0
<i>Besseyia rubra</i>	0	0	2	0	24	0	10
Earlier Seral Species							
<i>Pseudoroegneria spicata</i>	15	18	10	4	21	13	9
<i>Archillea millefolium</i>	19	0	2	0	1	2	9
<i>Plantago aristata</i>	9	0	0	0	27	0	0
<i>Woodsia oregana</i>	0	0	0	0	20	0	2
<i>Phlox colubrine</i>	4	0	0	0	0	3	7
<i>Bromus tectorum</i>	0	0	0	0	0	35	0
<i>Bromus arvensis</i>	4	0	0	0	9	28	11
<i>Bromus briziformis</i>	33	0	0	0	0	0	1

Table 2.4 Indicator species analysis results for the bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association. Species listed are those with significant p-values (< 0.05). Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association.

	<u>Early</u> 1981	<u>Mid</u> 1981	<u>Early</u> 2014	<u>Mid</u> 2014	<u>Late</u> 2014
Later Seral Species					
<i>Pseudoroegneria spicata</i>	11	18	7	19	37
<i>Poa secunda</i>	0	1	14	4	45
<i>Plantago aristata</i>	0	0	36	0	5
<i>Phlox colubrine</i>	0	0	5	31	12
<i>Archillea millefolium</i>	2	15	2	0	4
<i>Cerastium glomeratum</i>	0	41	0	0	0
Earlier Seral Species					
<i>Astragalus inflexus</i>	16	0	1	0	0
<i>Bromus tectorum</i>	0	0	88	0	0
<i>Bromus arvensis</i>	5	0	0	46	0
<i>Arenaria serpyllifolia</i>	2	0	48	7	11

Table 2.5 Indicator species analysis results for the bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association. Species listed are those with significant p-values (< 0.05). Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association.

	<u>Very Early</u> 1981	<u>Mid</u> 1981	<u>Very Early</u> 2014	<u>Early</u> 2014
Later Seral Species				
<i>Pseudoroegneria spicata</i>	2	36	5	32
<i>Poa secunda</i>	0	1	63	10
<i>Plantago aristata</i>	13	2	30	17
<i>Lomatium spp.</i>	4	0	19	3
<i>Archillea millefolium</i>	1	5	1	13
<i>Vulpia microstachys</i>	15	5	0	0
Earlier Seral Species				
<i>Sporobolus cryptandrus</i>	11	0	12	0
<i>Aristida purpurea</i>	17	0	21	0
<i>Bromus tectorum</i>	2	0	25	20
<i>Erodium cicutarium</i>	1	0	46	0
<i>Veronica arvensis</i>	28	19	0	0
<i>Lepidium densiflorum</i>	3	10	0	0

Table 2.6 Indicator species analysis results for the bluebunch wheatgrass/sand dropseed/red three awn association. Species listed are those with significant p-values (< 0.05). Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association.

	<u>Very Early</u> 1981	<u>Early</u> 1981	<u>Annual Grass</u> 2014	<u>Early</u> 2014
Later-Seral Species				
<i>Pseudoroegneria spicata</i>	0	33	0	35
<i>Poa secunda</i>	0	1	5	74
<i>Calochortus macrocarpus</i>	0	0	0	8
<i>Plantago aristata</i>	0	7	3	60
Earlier-Seral Species				
<i>Sporobolus cryptandrus</i>	5	23	9	4
<i>Aristida purpurea</i>	41	0	12	0
<i>Bromus tectorum</i>	3	14	23	27
<i>Ventenata dubia</i>	0	0	51	1
<i>Tragopogon dubius</i>	0	0	27	0
<i>Erodium cicutarium</i>	0	1	16	34
<i>Hypericum perforatum</i>	40	0	0	0

Chapter 3: What is the Potential Future Trajectory of Benchlands within Canyon Grasslands?

3.1 Introduction

Background Information

The seed bank represents the plant community's past and where it will head in the future (Leck et al. 1989). A seed bank contains the regenerative pool for most plant communities (Henderson et al. 1988) and provides the potential for a community to respond to future disturbances (Coffin and Lauenroth 1989). Seed banks are typically classified into two categories, transient and persistent (Thompson and Grime 1979). The transient seed bank is defined as those seeds which germinate within one year following dispersal, while the persistent seed bank can remain longer than one year in the soil before germinating (Thompson and Grime 1979). In grassland ecosystems, perennial species have seeds that typically do not enter into dormancy and therefore contribute primarily to the transient seed bank (Pekas and Schupp 2013). Microsites within a plant community also play an important role in the ability of a seed to germinate and reach maturity (Eriksson and Ehrlén 1992). The distribution of a seed within a seed bank greatly affects the potential of the seed to establish (Thompson 1986). Even within the same community, different species may show notably different distribution patterns within the seed bank (Thompson 1986). In plant community ecology, therefore, understanding the role of the seed bank within a community is critical in determining ecosystem function and potential management (Luzuriaga et al. 2005).

Several biotic and abiotic factors can affect grassland seed banks including: grazing, predation, topography, fire, and cultivation. The impact of grazing on seed banks can be complex. In response to grazing, the seed bank composition can shift to include more forbs

(Russi et al. 1992; Peco et al. 1998; Hild et al. 2001) and a reduction in native grass seed density (Bertiller 1992; Bertiller and Carrera 2015). In some studies the total seed bank density was not affected by grazing (Kinucan and Smeins 1992; Milberg and Hansson 1994), although the species composition of the seed bank was almost always affected by grazing (Bertiller 1992; Kinucan and Smeins 1992; Russi et al. 1992; Milberg and Hansson 1994; Peco et al. 1998; Hild et al. 2001; Bertiller and Carrera 2015). Higher grazing stocking rates can also increase seed bank density (Russi et al. 1992). In addition to the effects of domestic livestock grazing, granivores are known to reduce the seed bank, especially in desert grasslands (Henderson et al. 1988). Likewise, the combined effects of grazing and topography on the grassland seed banks can be contradictory, with some independent of one another (Peco et al. 1998), while others are related to the differences in grazing regimes as influenced by topography (Bertiller 1992). Fire typically does not affect native seed banks in grasslands (Cox and Allen 2008). Conversely, the seed bank of exotic annual grasses in grasslands tends to decrease following fire (Humphrey and Schupp 2001; Cox and Allen 2008), but increase after several years or with multiple burns (Alexander and D'Antonio 2003). In addition to disturbances such as grazing and fire, the effects of cultivation can be evident decades later in the seed bank through the high density of exotic species (Scott and Morgan 2012; Ma et al. 2013).

In general, grasslands show a greater similarity between the seed bank and vegetation compared to forested ecosystems (Hopfensperger 2007), although many studies have shown relatively low correlation between perennial grassland seed bank and vegetation (Major and Pyott 1966; Thompson 1986; D'Angela et al. 1988; Coffin and Lauenroth 1989; Peco et al. 1998;

Stark et al. 2003; Caballero et al. 2008). Grasslands with high annual species cover tend to have more similarities between the seed bank and vegetation (Thompson and Grime 1979; Henderson et al. 1988), particularly at the functional group level (Pekas and Schupp 2013). Many perennial grass species contribute little to the seed bank (Major and Pyott 1966; D'Angela et al. 1988; Peco et al. 1998; Hild et al. 2001; Humphrey and Schupp 2001; Scott and Morgan 2012), since they do not rely on annual turnover (Major and Pyott 1966). More recently disturbed sites tend to show more similarities between the seed bank and vegetation compared to sites further along in succession, due to the presence of early successional species found in both the vegetation and seed bank (Grandin 2001; Caballero et al. 2008; Martinez-Duro et al. 2010; Scott and Morgan 2012; Auestad et al. 2013; Ma et al. 2013). Where cultivation has altered the vegetation and seed bank, the role of the seed bank is vital to the regeneration of grassland communities, in addition to playing an important role in management (Scott and Morgan 2012).

Grassland seed banks have been well studied around the world including the mesic grasslands of Europe (Thompson 1986; Milberg and Hansson 1994; Kalamees and Zoble 1997; Grandin 2001; Wellstein et al. 2007; Schmiede et al. 2009; Kalamees et al. 2012; Auestad et al. 2013) and North America (Stark et al. 2003), Mediterranean grasslands (Levassor et al. 1990; Russi et al. 1992; Lavorel et al. 1993; Peco et al. 1998; Luzuriaga et al. 2005; Caballero et al. 2008; Martinez-Duro et al. 2010), pampas of Argentina (D'Angela et al. 1988; Bertiller 1992; Bertiller and Carrera 2015), and the prairies of North America (Major and Pyott 1966; Templeton and Levin 1979; Coffin and Lauenroth 1989; Kinucan and Smeins 1992; Hild et al. 2001; Humphrey and Schupp 2001; Alexander and D'Antonio 2003; Cox and Allen 2008; Pekas

and Schupp 2013; Wallace et al. 2015). However, there are no studies that have examined the seed banks within the Pacific Northwest Bunchgrass Region (PNWBR) or the unique canyon grasslands within this region. The lack of seed bank studies within these grasslands may be due to the limited remaining intact ecosystems within this region. Historically, wide spread cultivation converted most of these PNWBR grasslands to croplands (Looney and Eigenbrode 2012). The canyon grasslands, like those within the Hells Canyon National Recreation Area (HCNRA), avoided these farming practices due to steep topography (Tisdale 1986). However, the few flat areas within the canyon grasslands of the HCNRA, known as benchlands, have a history of concentrated land use including grazing and cultivation that have left a lasting legacy (Johnson 1994). These benchlands are of conservation concern for management since many may have passed biotic thresholds for recovery (USDA Forest Service 2014). Following disturbances, such as plowing, the future vegetation may depend on the species represented in the seed bank (Levassor et al. 1990).

Study Objectives

The objectives of this study were to evaluate how the seed bank of the most common plant association found on the benchlands of canyon grasslands within the HCNRA relates to the vegetation on site, successional stage, and cultivation. Exotic annual grasses, such as *Bromus tectorum*, have been present in grasslands of the PNWBR since at least the 1970s (Johnson and Simon 1987). *Bromus tectorum* has already altered the composition and structure of Great Basin seed banks (Humphrey and Schupp 2001; Pekas and Schupp 2013), and we expected it to be a major component in the seed banks of the canyon grasslands in our study area. Much like other

grasslands where a large component of the vegetation is annual grasses (Henderson et al. 1988; Russi et al. 1992; Cox and Allen 2008; Scott and Morgan 2012), we expected the presence of annual species to generate more similarity between the vegetation and seed bank compared to communities dominated by perennial grasses (Major and Pyott 1966; Thompson 1986; D'Angela et al. 1988; Coffin and Lauenroth 1989; Peco et al. 1998; Stark et al. 2003; Caballero et al. 2008). Further, we expected the seed bank and vegetation of the earlier successional stages would be more closely related than those of the later successional stages (Grandin 2001; Caballero et al. 2008; Martinez-Duro et al. 2010; Scott and Morgan 2012; Auestad et al. 2013; Ma et al. 2013). Finally, we predicted that the cultivated sites in these canyon grasslands would follow other old-field studies, which report a tendency for long-term dominance of invasive species in the seed bank (D'Angela et al. 1988; Kalamees et al. 2012; Scott and Morgan 2012; Ma et al. 2013).

3.2 Methods

Study Area Description

Our research was conducted in the Lower Imnaha Subbasin of the HCNRA. Temperatures in the Lower Imnaha Subbasin average 15.8°C in the summer months and -2.6°C in the winter months with a mean annual precipitation of 473 mm (PRISM 2014). The grasslands of the study area are primarily composed of Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) associations (Johnson and Simon 1987). The focus of this project was in the bluebunch wheatgrass/sand dropseed (*Sporobolus cryptandrus*)/red three awn (*Aristida*

purpurea) association, which occurs almost exclusively on the benchlands in these canyon grasslands (Johnson and Simon 1987). Nomenclature of plant species follows the USDA PLANTS Database (USDA NRCS 2015).

Site Locations

Our study included 8 sites within the bluebunch wheatgrass/sand dropseed/red three awn association (Johnson and Simon 1987). These sites were classified into seral stages using cover/frequency values for each seral stage (Johnson and Simon 1987; A.4). Four of the sites were also selected based on their cultivation history. Two cultivated sites were located using homestead records, historical records, and aerial photographs (Morris 2012). Reference sites were selected from two adjacent benches that were not homesteaded and, to our knowledge, had not been cultivated. All four sites share a similar grazing history since the early 1900s (Johnson 1994), allowing us to study the impact of cultivation as our primary land-use variable. Several of the sites were given a new classification as “annual grass dominated,” rather than very early or early seral, because the newly introduced species *Ventenata dubia* was not present in the original surveys that defined the plant associations and their successional classes (Johnson and Simon 1987). Together, these 8 sites ranged from annual grass dominated to very early and early successional classes. There were no mid or later successional stages available to sample, as was the case in earlier studies (Johnson and Simon 1987).

Field Methods

All 8 sites were sampled using one 30.5 m transect running north to south placed at least 50 m from roads or fences to avoid any edge effects and with consideration not to cross topographical

changes. Along each transect, Daubenmire frames (20 cm x 50 cm) were placed at 3 m intervals, starting from zero, to record the percent canopy cover of each plant species. After the canopy cover of the vegetation had been recorded, four soil cores (located at each corner) were collected within each frame at 6 m intervals. The four soil cores (3 cm x 5 cm) were then combined to form a composite sample (five total per transect) for a total of 40 seed bank samples. All sampling was completed in June and July 2014.

Greenhouse Methods

Samples were refrigerated at 5 °C for 90 days in order to cold stratify the seeds (Gunnell 2009). All seed bank samples were then placed in their own germination trays and randomly assigned within the greenhouse. The germination trays (28 cm x 56 cm x 10 cm) contained a 6 cm sterile soil mixture layer over a 2 cm under-layer of sand (Pekas and Schupp 2013). The samples were spread in a very thin and even layer within germination trays and watered to field capacity. In order to mimic the natural high and low temperatures of the Lower Imnaha Subbasin, we used the average monthly highs and lows of May through August (Weatherbase 2015) in the greenhouse (May = 19.7 °C /1.8 °C, June =24.2 °C/5 °C, July = 29.7 °C/6.8 °C, and August = 29.8 °C/5.7 °C). Once a seedling was identified, it was counted and removed from the germination tray to avoid any competition between seedlings. All samples were grown for a period of 14 weeks when we quantified all species in each sample to determine species density (m⁻²). Identification of seedlings was aided by regional guides (Tveten and Asher 2011). If a seedling could not be identified to species, we transplanted several specimens into conetainers and allowed them to

grow until they could be confidently identified (Milberg and Hansson 1994; Stark et al. 2003; Caballero et al. 2008; Schmiede et al. 2009; Pekas and Schupp 2013).

Data Analysis

The seral stages of each site were classified following a system based on a species percent cover and frequency designed by the earlier ecologist who worked in our study area (Johnson and Simon 1987; A.4). All analyses were completed using PC-ORD software version 6.16 (McCune and Mefford 2011). Indicator species analysis (Dufrêne and Legendre 1997) was used to aid in the classification of the seral stages (A.14 and A.15), with 4999 randomizations for the Monte Carlo test. Indicator values are based on species abundance and frequency and are used to identify how faithful a species is to a specific group or seral stage in our case (McCune and Grace 2002). Johnson and Simon (1987) described indicator species for each seral stage within this plant association and, using this information, we compared their indicator species to those from our indicator species analysis results. All significant ($p < 0.05$) species indicator values were used to exclude those species that were not strong indicators of any one group. Nonmetric Multidimensional Scaling (NMS) (Kruskal 1964) was used identify any natural separation in seral stage groupings over a compositional gradient. Species that were considered rare (< 5% of the data) were removed to decrease noise and enhance any signal relating community composition within our environment (McCune and Grace 2002). A generalized logarithmic transformation was used on the dataset to ensure that the sub-dominant species would have weight in the ordination (McCune and Grace 2002). The Sørensen distance measurement was used and the data was run using “auto-pilot” with the “slow and thorough” method and a random

starting point. Finally, the ordination was graphed two-dimensionally since the first two axes explained the majority of the variation in the data. To further examine the relationship between species composition and the seral stages, we overlaid a joint plot containing the seral stage classification within the ordination to look for any correlations between seral stages. Multi-Response Permutation Procedures (MRPP) with a Sørensen's distance measurement was used to test for differences in species composition between successional stages of the vegetation, vegetation and seed bank within each successional stage, and between cultivated and noncultivated seed banks (Zimmerman et al. 1985). The chance-corrected within-group agreement (A-statistic), or effect size, for all comparisons was used to determine if the within-group homogeneity was greater than expected by chance for each comparison in our analyses (McCune and Grace 2002). Schmiede et al. (2009) also used the combination of NMS and MRPP to evaluate species composition of seed bank vs. vegetation and indicator species analysis to compare which species were more faithful to a specific treatment. Since the vegetation was measured in percent canopy cover of each species and the seed bank was measured as density of each species (m^{-2}), we converted the cover data into presence/absence values for each sample (Kalamees and Zoble 1997; Smith et al. 2002). This comparison should have a strong relationship because the seed bank samples were taken from within the frame used to quantify cover of vegetation. Differences between groups (introduced grasses, introduced forbs, native grasses, and native forbs) were tested between successional stages as well as between cultivated and noncultivated sites using nonparametric comparisons for each pair using the Wilcoxon

Ranked Sums method (Carr and Krueger 2012). All of these comparisons were completed using JMP 11.0 (SAS Institute Inc., Cary, NC).

3.3 Results

From a total of 40 samples, 33 different species were represented between the seed bank and the vegetation. A total of 19 species were found in the seed bank and 22 species were identified in the vegetation. Approximately 24% of the total species occurred in both the seed bank and the vegetation (Table 3.1). Of the 6,340 emerged seedlings, only five were unidentified (three forbs and two grasses). The seed bank composition consisted of 5% native grass, 21% native forb, 21% introduced grass, and 53% introduced forb species. In contrast, the vegetation species composition consisted of 18% native grass, 27% native forb, 23% introduced grass, and 32% introduced forb. Within the vegetation, perennial species were more abundant compared to annual species. However, in the seed bank, perennial species were nearly absent compared to annual species.

Vegetation

Successional classification of the vegetation (Table 3.3) showed that the early and very early seral stages were the most similar in species composition ($A = 0.057, p < 0.001$), whereas the early and annual grass dominated seral stages were the most different in species composition ($A = 0.146, p < 0.001$). Although both of these effect sizes were relatively weak for ecological data, the difference between the comparisons was still significant and A-statistics greater than 0.200 can be interpreted as large differences in composition between groups (McCune and Grace

2002). Early and very early seral stages were the most similar in species composition due to their overlap in species space compared to the annual grass dominated stage (Figure 3.1). Presence of native grass and forb species in the vegetation was the most similar between the very early and early seral stages (Table 3.2). Conversely, within the annual grass dominated stage, the species composition was very different between sites, shown by the two distinct clusters in the ordination (Figure 3.1). There was more variability in the species composition within the annual grass dominated stage compared to both the very early and early seral stages. In addition, the annual grass dominated stage contained the highest cover of introduced grasses and the lowest cover of native grasses and forbs (Figure 3.2). Cover of both native and introduced forbs was significantly higher in the very early seral stage (Figure 3.2).

Vegetation and Seed Banks

Results from the comparison of the vegetation to the seed bank showed that there was a significant difference in the species composition ($A = 0.265$, $p < 0.001$). Most of the species overlap between the vegetation and seed bank was introduced annual grasses and annual forbs (Table 3.1). Indicator species analysis comparing the vegetation and seed bank showed that native grasses and native forbs were strong indicators of the vegetation, while introduced forbs were strong indicators for the seed bank (Table 3.2). Introduced grasses were shared by both the vegetation and seed bank, where *V. dubia* was more faithful to the seed bank and *Bromus arvensis* was more faithful to the vegetation (Table 3.2).

Vegetation and Seed Banks Across Successional Stages

In the seed bank, native grasses and forbs were most abundant in the early seral stage (Figure 3.3). The early seral stage tended to contain more species in all categories compared to the annual grass dominated stage. Classification of the seed bank seral stages in relation to the vegetation seral stage showed a decrease in species composition similarity as seral stages transitioned from annual grass dominated to early seral (Table 3.3). The annual grass dominated stage showed more similarity in species composition between seed bank and vegetation ($A=0.288, p < 0.001$) compared to the early seral stage ($A=0.484, p < 0.001$).

Effects of Cultivation

There was a significant difference in the species composition between cultivated and noncultivated seed banks ($A=0.100, p < 0.05$; Table 3.3). The seedling density of introduced grasses was significantly higher in the cultivated sites compared to the noncultivated sites, while seedling density of introduced forbs was significantly higher on the noncultivated sites (Figure 3.2). There were no significant differences between seedling density of native grasses or forbs between cultivated and noncultivated sites.

3.4 Discussion

The successional status of the plant communities found on benchlands within the canyon grasslands of the Lower Imnaha Subbasin in our study were identified as either early seral, very early seral, or annual grass dominated. Due to the highly concentrated historical and contemporary land uses associated with these flatter areas within the canyons in our study, we

did not find any mid or late successional sites to sample (Johnson and Simon 1987). The classification of annual grass dominated was necessary because of the introduction of a relatively new invasive grass to the region, *V. dubia*. However, since we know relatively little about this species, it is not clear where the annual grass dominated stage fits into successional classifications generated by Johnson and Simon (1987). As was expected, the relationship between the vegetation and seed bank was strongest at what would be the earliest successional stages, where annual species dominated both the vegetation and seed bank. However, this relationship seemed to be more strongly related to *B. arvensis* and *V. dubia* than *B. tectorum*, even though *B. tectorum* did make up a major portion of the seed bank. Finally, as predicted, the seed bank within cultivated sites had significantly more introduced species than noncultivated sites. This difference was associated with introduced grasses and not introduced forbs. The native seed bank in both instances was extremely small and there were no differences explained by prior cultivation.

Since this was the first study to examine the seed bank of canyon grasslands, there are no direct comparisons available in the literature. However, our results are similar in many ways to the findings of other seed bank studies in the region and around the world. First, differences in species composition between the seed bank and vegetation are common within perennial grasslands (Major and Pyott 1966; Thompson 1986; D'Angela et al. 1988; Coffin and Lauenroth 1989; Peco et al. 1998; Stark et al. 2003; Caballero et al. 2008; Pekas and Schupp 2013) and, like in our study, perennial grass species tend to be underrepresented in the seed bank (Kalamees and Zobel 1997; Kalamees et al. 2012). Second, the decrease in similarity between vegetation and

seed bank with successional transition from annual dominated to early seral stages in our study has been reported by others (Grandin 2001; Caballero et al. 2008; Martinez-Duro et al. 2010; Scott and Morgan 2012; Auestad et al. 2013; Ma et al. 2013). Third, the similarities between the seed bank and vegetation in our study increased with the increasing dominance of annual species (Thompson and Grime 1979; Henderson et al. 1988; Pekas and Schupp 2013). Our results showed that nearly all shared species between the seed bank and vegetation were those of annual grasses and forbs. In addition, our 24% overlap of species between the germinated seed bank and vegetation was comparable to the 27% overlap in species reported by another study in the region (Pekas and Schupp 2013). Fourth, as in our study, it is not uncommon for forbs to dominate the seed bank (Russi et al. 1992; Peco et al. 1998; Hild et al. 2001; Alexander and D'Antonio 2003; Cox and Allen 2008; Gunnell 2009; Carr and Krueger 2012; Kalamees et al. 2012; Scott and Morgan 2012; Pekas and Schupp 2013). The most abundant forb species in our seed bank (*Arenaria serpyllifolia*) has been found to be abundant in seed bank studies around the world (Lavorel et al. 1993; Kalamees and Zobel 1997; Luzuriaga et al. 2005; Auestad et al. 2013) and is known to have a long seed lifespan (> 5 years) (Thompson et al. 1993). Fifth, as with studies within our region, exotic species in our study greatly outnumbered the native species in the seed bank (Humphrey and Schupp 2001; Gunnell 2009; Pekas and Schupp 2013). Finally, our results are consistent with others that show historical cultivation promotes dominance by early successional species in the seed bank (D'Angela et al. 1988; Kalamees et al. 2012; Scott and Morgan 2012; Ma et al. 2013).

Although seed bank studies typically underrepresent the perennial grass component of the community (Major and Pyott 1966; Thompson and Grime 1979; Coffin and Lauenroth 1989; Peco et al. 1998; Caballero et al. 2008), the lack of any *Poa secunda* emergence in our seed bank was surprising because it had the highest mean cover of any of the vegetation and was present at nearly every plot sampled. In addition, *P. secunda* is known to be a prolific seed producer (Karl et al. 1999) and other studies report high seedling emergence from the seed bank (Gunnell 2009; Pekas and Schupp 2013). There are several potential explanations for its absence in our seed bank including; sampling timing, methodology, phenology, seed distribution, and seed predation. In arid and semi-arid environments many perennial grass species typically make up the transient seed bank (Major and Pyott 1966; Thompson and Grime 1979; Pekas 2010). Gunnell (2009) sampled the seed bank in October and Pekas and Schupp (2013) sampled in August, both capturing the seeds of *P. secunda* and other perennial grass species while our sampling was completed by July. It is possible, therefore, that we did not capture the seed bank of this species if it is transient. In addition, both Gunnell (2009) and Pekas and Schupp (2013) wetted their samples before cold stratification. Also, Blaisdell (1958) identified the phenology stages of *P. secunda* within the canyon grasslands of Idaho and concluded that it did not begin to release seed until late June and was finished by late July. Seed bank sampling for our study did not begin until mid June and ended by early July, so it is possible that we did not capture the seed rain of *P. secunda* during our sampling. In addition, perennial grass species tend to have low seed dispersal and many seeds fall near the mother plant, making it difficult to capture this seed bank without destructive sampling of the plant (Major and Pyott 1966). Finally, seed predation from

ants can significantly affect the composition of the seed bank (Crist and MacMahon 1992). One of the most preferred plant species by harvester ants (*Pogonomyrmex occidentalis*) is *P. secunda* and its seed bank can be reduced 46% by them (Crist and MacMahon 1992). Although we did not test the effects of seed predation, it may have played an important role in the species composition of our sites.

Since our sampling was done early in the summer, it is possible that we did not capture the entire transient seed bank, particularly *P. secunda* and *P. spicata* whose seeds do not enter into dormancy (Hardegree et al. 1999). However, the findings of our study are consistent with results reported on the seed bank of persistent species, such as *S. cryptandrus* and *A. purpurea* (Henderson et al. 1988; Coffin and Lauenroth 1989; Hild et al. 2001; Humphrey and Schupp 2001). For example, the perennial grass *S. cryptandrus* is considered part of the persistent seed bank (Lippert and Hopkins 1950). *Sporobolus cryptandrus* was the most common native grass seedling in our study. Other seed bank studies have found similar amounts of *S. cryptandrus* (Henderson et al. 1988; Coffin and Lauenroth 1989; Hild et al. 2001; Humphrey and Schupp 2001) and it is a prolific seed producer with high germination rates (Lippert and Hopkins 1950). *Aristida purpurea*, in contrast, did not appear in our seed bank even though there was about 4% cover of this species in the vegetation. This is a common finding in other studies as well (Henderson et al. 1988; Robertson and Hickman 2012). Henderson et al. (1988) classified the seed bank of New Mexico desert grassland through seed identification, and although *A. purpurea* was found in the vegetation, it was not identified in the seed bank. It is possible that since our maximum greenhouse temperatures did not reach 40° C, the reported optimum for germination

(Evans and Tisdale 1979), we did not meet requirement for this species. However, given its reported absence in other studies and the fact that we reached germination requirements for the warm season grass (*S. cryptandrus*), we feel the conditions were satisfactory.

3.5 Conclusion

Without a full range of successional communities within this plant association to explore, including those in the mid and late seral stages, it is difficult to fully understand the future trajectory of this plant community from its seed bank. However, the relationship between standing vegetation and seed bank can aid in understanding how the community may respond to disturbances (Hopfensperger 2007). Our results suggest that the primary component of the seed bank on these sites is introduced annual grass and forb species. Therefore, based on what we have found in the germinated seed bank of these early successional stages, these sites may be native seed limited and could potentially shift to invasive species dominance after further disturbance, especially on previously cultivated areas. In addition, the highest representation of *S. cryptandrus* within the native perennial grass seed bank along with its tendency to colonize recently disturbed sites (Lippert and Hopkins 1950), suggests this species may be one of the first native grasses to establish after disturbance. It is also unclear how the newly introduced *V. dubia* will respond in these grasslands since there is very little known about its basic ecology, method of spread and interactions with other species (Wallace et al. 2015). More research should be done to examine the seed bank dynamics of this newly invading species and of the canyon grasslands in general.

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Chapter 3: Figures

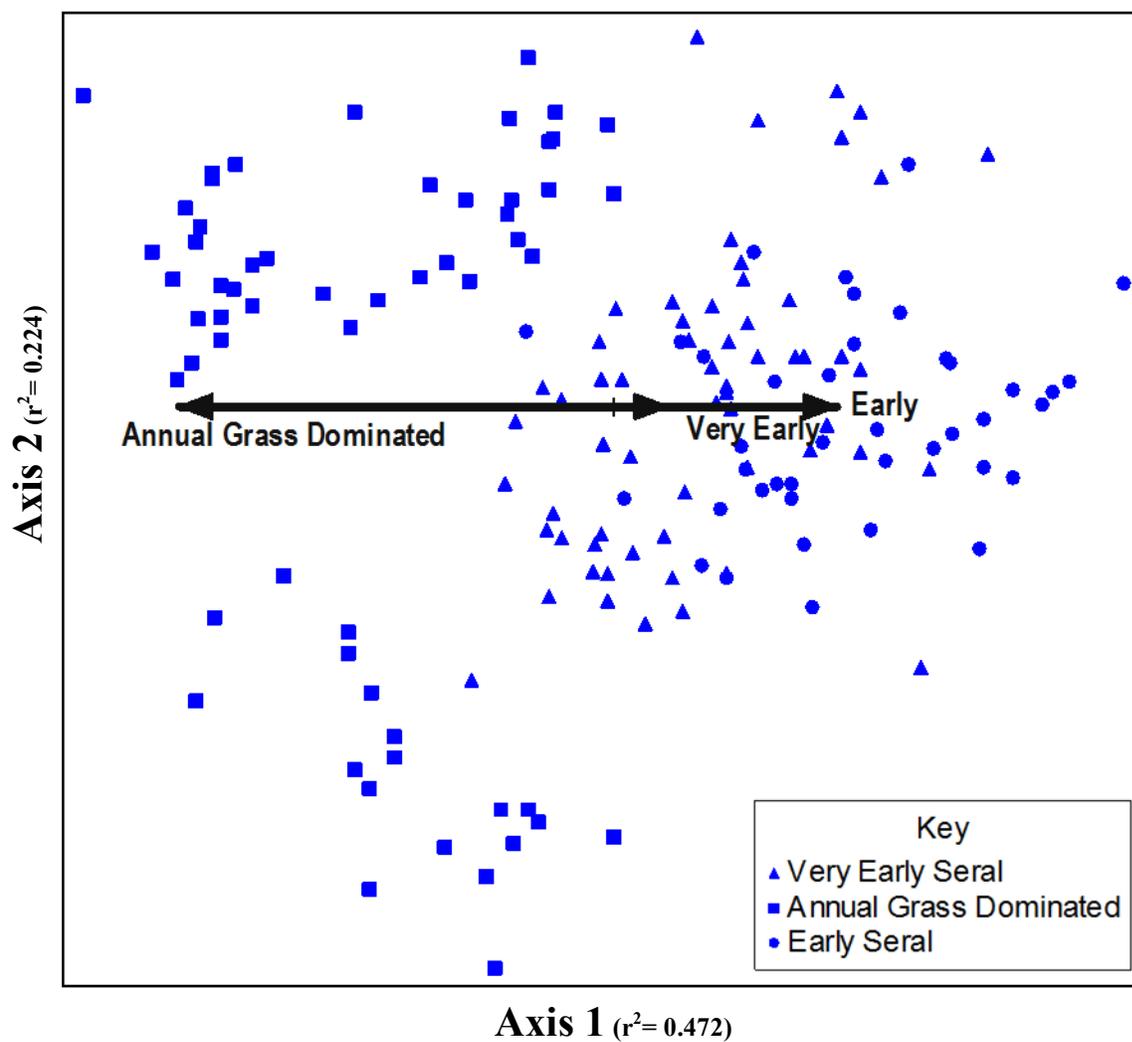


Figure 3.1 NMS results showing the 2-dimensional ordination comparing the vegetation species composition of all seed bank sites sampled in relation to the classified seral stages of each site. Values for the joint plot variables increase in the direction of the vector. Seral stage classifications are based on Johnson and Simon (1987) using species cover/frequency values.

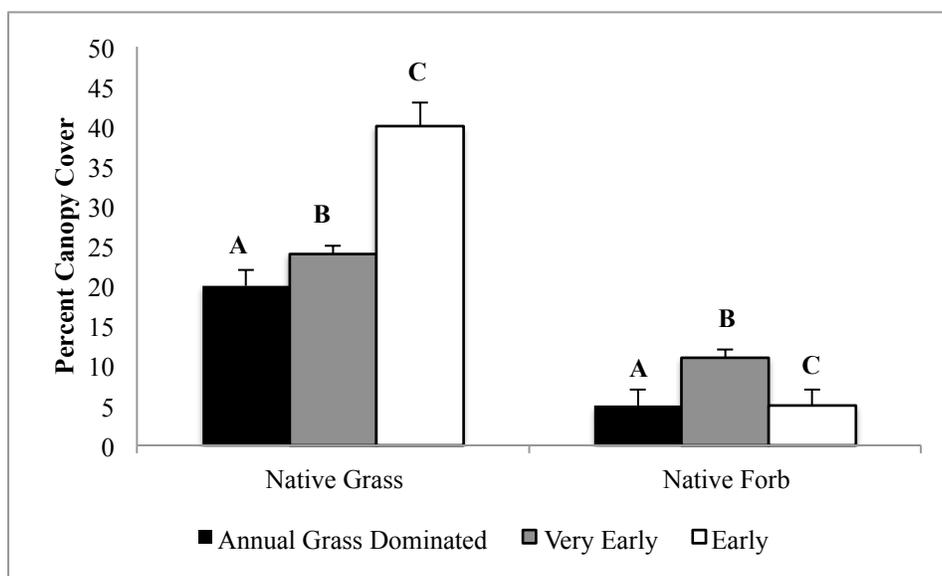
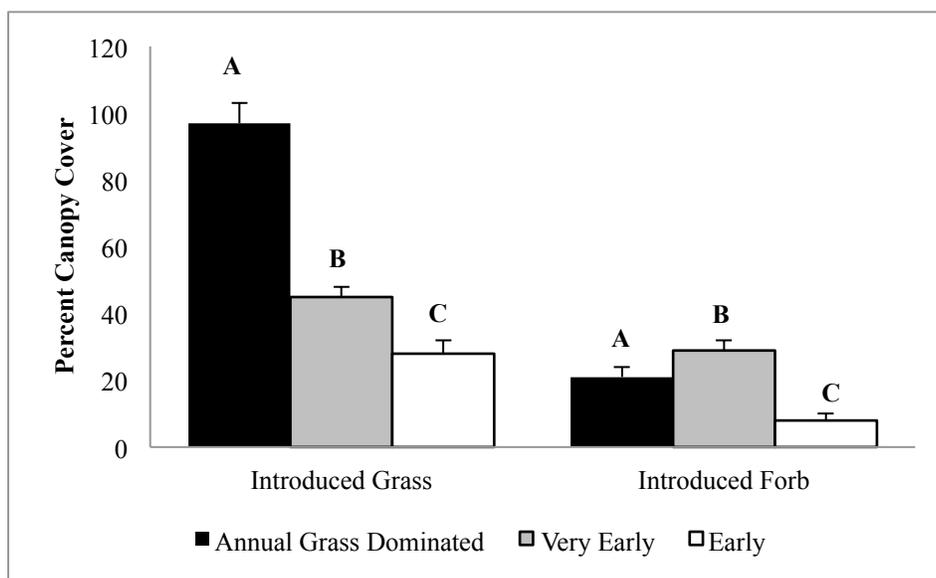


Figure 3.2 Percent canopy cover between seral stages based on species groupings. Species groups with different letters are significantly different ($p < 0.05$). Graphs show mean and standard error, analysis is nonparametric comparisons for each pair using Wilcoxon Rank Sums.

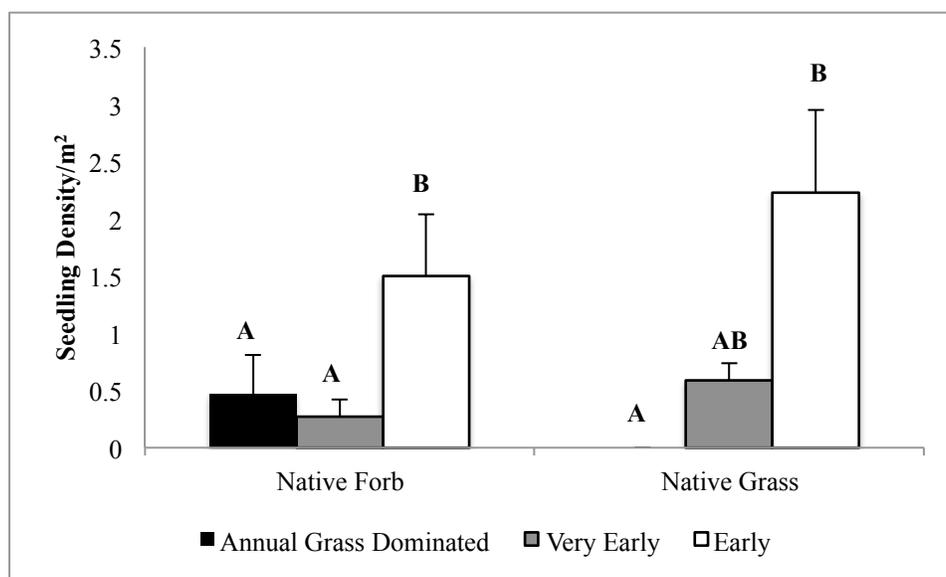
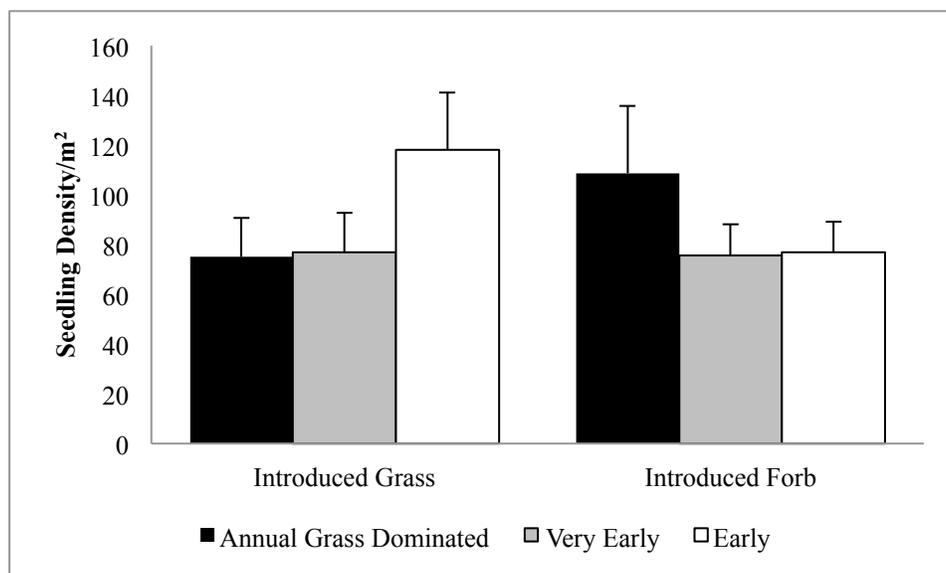


Figure 3.3 Seedling densities (m⁻²) between seral stages based on species groupings within the seed bank. Species groups with different letters are significantly different ($p < 0.05$). Graphs show mean and standard error, analysis is nonparametric comparisons for each pair using Wilcoxon Rank Sums.

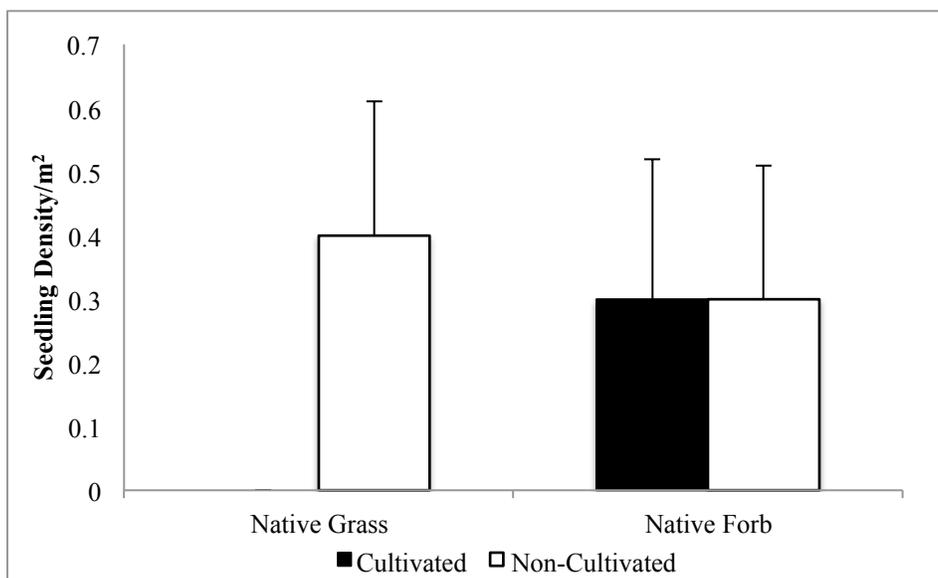
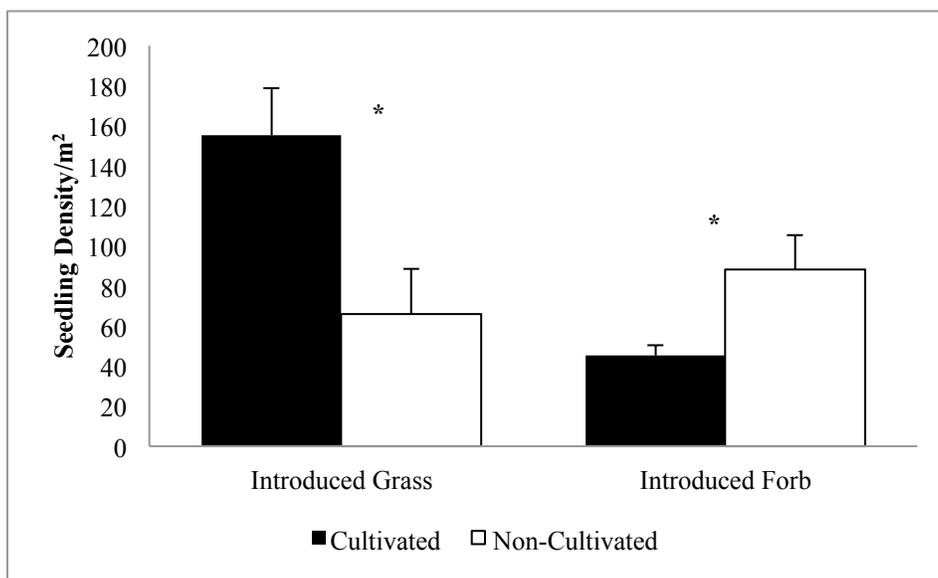


Figure 3.4 Seedling densities (m⁻²) between cultivated and noncultivated seed bank based on species groupings. Graphs show mean and standard error, analysis is nonparametric comparisons for each pair using Wilcoxon Rank Sums; * indicates $p < 0.05$.

Chapter 3: Tables

Table 3.1 List of all species present in the seed bank and vegetation organized by growth form and native/introduced status. Seed bank values are presented as density counts (m^{-2}) and vegetation values were calculated as the average percent canopy cover of each species.

	Seed Bank	Vegetation
Native Grass		
<i>Aristida purpurea</i>	0	4
<i>Poa secunda</i>	0	16.4
<i>Pseudoroegneria spicata</i>	0	3
<i>Sporobolus cryptandrus</i>	17	2.9
Native Forb		
<i>Amsinckia menziesii</i> ¹	7	2
<i>Astragalus inflexus</i>	0	0.4
<i>Lomatium spp.</i>	0	0.4
<i>Opuntia polyacantha</i>	0	0.6
<i>Plantago aristata</i> ¹	18	2.5
<i>Pseudognaphalium stramineum</i> ¹	3	0
<i>Sedum stenopetalum</i>	0	0.3
<i>Silene antirrhina</i> ¹	4	0
Introduced Grass		
<i>Bromus arvensis</i> ¹	109	9.3
<i>Bromus tectorum</i> ¹	358	12.7
<i>Poa bulbosa</i>	4	0
<i>Poa compressa</i>	0	0.5
<i>Thinopyrum intermedium</i>	0	1.7
<i>Ventenata dubia</i> ¹	2292	10.5
Introduced Forb		
<i>Arenaria serpyllifolia</i> ¹	1314	5.3
<i>Convolvulus arvensis</i>	0	0.2
<i>Draba verna</i> ¹	673	0
<i>Erodium cicutarium</i> ¹	98	12.1
<i>Holosteum umbellatum</i> ¹	369	0
<i>Hypericum perforatum</i>	81	0
<i>Lamium amplexicaule</i>	735	0
<i>Lepidium perfoliatum</i>	6	0
<i>Medicago lupulina</i>	0	0.1
<i>Medicago sativa</i>	0	0.3
<i>Myosotis arvensis</i> ¹	181	0
<i>Sisymbrium altissimum</i>	9	0
<i>Thlaspi arvense</i> ¹	0	0.3
<i>Tragopogon dubius</i> ¹	0	1
<i>Verbascum blattaria</i>	62	0

¹Indicates annual species, all other species are perennial.

Table 3.2 Indicator species analysis results for the comparison of the vegetation to the seed bank using presence/absence data. Species listed are those with significant p-values (< 0.05). Abbreviations for seral stages are: annual grass dominated (A.G.), very early (V.E.), and early (E.).

	<u>Vegetation</u> (A.G.)	<u>Seed Bank</u> (A.G)	<u>Vegetation</u> (V.E.)	<u>Seed Bank</u> (V.E)	<u>Vegetation</u> (E.)	<u>Seed Bank</u> (E.)
Native Grasses						
<i>Pseudoroegneria spicata</i>	1	0	0	0	64	0
<i>Poa secunda</i>	5	0	43	0	43	0
<i>Sporobolus cryptandrus</i>	1	0	26	2	5	9
<i>Aristida purpurea</i>	60	0	0	0	0	0
Native Forbs						
<i>Amsinckia menziesii</i>	19	2	3	0	8	0
<i>Plantago aristata</i>	0	0	10	1	30	17
<i>Sedum stenopetalum</i>	0	0	3	0	39	0
Introduced Grasses						
<i>Bromus arvensis</i>	25	16	11	7	16	1
<i>Thinopyrum intermedium</i>	0	0	33	0	0	0
<i>Ventenata dubia</i>	10	22	17	22	0	22
Introduced Forbs						
<i>Arenaria serpyllifolia</i>	9	20	2	24	0	15
<i>Draba verna</i>	0	25	0	25	0	38
<i>Holosteum umbellatum</i>	0	20	0	37	0	37
<i>Hypericum perforatum</i>	0	40	0	0	0	10
<i>Lamium amplexicaule</i>	0	17	0	39	0	32
<i>Myosotis arvensis</i>	0	50	0	9	0	9
<i>Verbascum blattaria</i>	0	54	0	1	0	0

Table 3.3 Multi-Response Permutation Procedures results comparing; vegetation species composition between seral stages; vegetation vs. seed bank for each seral stage, and species composition of cultivated and noncultivated seed bank. All seral stage classifications are based on the vegetation species cover/frequency values using Johnson and Simon (1987) classifications.

Multiple Comparisons (Sørensen)	<i>T</i>	<i>P</i>	<i>A</i>
Vegetation			
Annual Grass Dominated vs. Very Early	-8.500	6.15×10^{-6}	0.140
Very Early vs. Early	-3.114	0.009	0.057
Annual Grass Dominated vs. Early	-7.677	1.01×10^{-5}	0.146
Vegetation vs. Seed Bank			
Annual Grass Dominated	-15.70	$<1.0 \times 10^{-8}$	0.288
Very Early	-17.27	$<1.0 \times 10^{-8}$	0.362
Early	-12.18	4.7×10^{-6}	0.484
Cultivated vs. Noncultivated Seed Bank	-4.372	0.003	0.100

Chapter 4: Final Conclusions

4.1 Conclusion

The Hells Canyon National Recreation Area (HCNRA) contains a unique ecosystem type for the Pacific Northwest Bunchgrass Region (PNWBR) and many of these communities can be found nowhere else in the world (Lichthardt and Moseley 1997). Since much of these canyon grasslands are largely inaccessible to both humans and livestock, many of these native communities have faced minimal anthropogenic disturbances (Tisdale 1986; Mancuso and Moseley 1994). Topo-edaphic patterns are known to affect the distribution of plant associations within canyon grasslands of the HCNRA (Tisdale and Bramble-Brodahl 1983; Tisdale 1986; Johnson and Simon 1987; Johnson 1994) and other grasslands around the world (Defosse et al. 1997; Carmel and Kadmon 1999; Bennie et al. 2006; Wellstein et al. 2007; Gong et al. 2008). In addition to the distribution of plant associations, topography has affected the distribution of historical land uses throughout the HCNRA (Tisdale 1986; Johnson 1994; Ecovista 2004; USDA Forest Service 2014). For example, the distribution of land uses within the HCNRA is strongly related to slope, where gentle-sloping benchlands have incurred more concentrated land use (e.g., livestock grazing and cultivation) compared to steeper and rocky slopes (Johnson 1994; Ecovista 2004; USDA Forest Service 2014). These gentle-sloping benchlands are of concern for management (USDA Forest Service 2014), but there has been no prior research that examined how they have changed in the long term (> 30 years) or what the future trajectory may be for these grasslands, especially on the benchlands.

In this thesis, I examined how canyon grasslands of the Lower Imnaha Subbasin have changed over time by resurveying plots that were established in 1981 in four different plant

associations (Chapter 2). Overall, the results showed several plant associations within these canyon grasslands are relatively stable plant communities over a 33 year-time-period. As predicted, plant associations on the steepest slopes were more likely to transition to a later seral stage or remain the same, while plant associations on the shallowest slopes tended to move towards earlier seral stages. This finding is consistent with other grassland studies around the world showing the topo-edaphic patterns affect both the distribution of communities and the shift in vegetative composition following disturbance (Defosse et al. 1997; Carmel and Kadmon 1999; Amezaga et al. 2004; Bennie et al. 2006; Wellstein et al. 2007). In addition, elevation and aspect, which both correspond to precipitation and soil moisture potential, were relevant to transitions from later to earlier seral stages. Also as predicted, the bluebunch wheatgrass (*Pseudoroegneria spicata*)/sand dropseed (*Sporobolus cryptandrus*)/red three awn (*Aristida purpurea*) association, found primarily on benchlands, had the most sites where successional status remained in early stages or transitioned to a new classification, “annual grass dominated.” This new classification had to be created because of the introduction and dominance of *Ventenata dubia*, a species that was not present in the plots during the original data collection in 1981 (Johnson and Simon 1987). This plant association is found on drier aspects and lower slopes in canyon grasslands in my study area, suggesting that these communities may have lower resistance and resilience to disturbance.

I also examined the potential future trajectory of the plant association most commonly found on benchlands within the Lower Imnaha Subbasin by examining the seed bank (Chapter 3). Specifically, I looked at how the seed bank related to the vegetation, successional status, and

cultivation history in my study area. The results showed that the annual grass dominated stage was the most similar between the vegetation and seed bank. This finding was consistent with other studies showing a greater similarity between vegetation and seed bank in grasslands with high annual species cover (Thompson and Grime 1979; Henderson et al. 1988). By far, the primary component of the seed bank in this study was introduced annual grasses and introduced forb species. The seed bank from cultivated sites had significantly more introduced species than native species compared to noncultivated sites, especially introduced grasses. The newest introduced annual grass, *V. dubia*, made up the highest proportion of the total seed bank, an unexpected result given *Bromus tectorum* has been a dominant species in the canyon grasslands for a longer period of time (Tisdale 1986; Johnson and Simon 1987; Johnson 1994; Gray and Lichthardt 2003; Gucker and Bunting 2011). The highest representation of native perennial grasses in the seed bank was from *S. cryptandrus*. The benchlands in my area did not include any mid or late seral communities. My sampling only represents the annual grass dominated, very early, and early seral stages of this plant association, making it difficult to explore the full range of potential successional trajectories that could be expected in this plant association. However, my findings suggest that these early successional seed banks at these sites could be native seed limited and potentially shift to exotic annual species dominance with further disturbance, especially on previously cultivated areas. Since there is very little known about the newly introduced *V. dubia*, it is unclear how this species will interact with disturbances.

Taken together, the results from both studies highlight the importance of topography in the distribution of land uses and its relationship to the changes and future trajectories of these

plant associations. The rugged topography of the HCNRA presented challenges to those who lived there historically as well as those who make their living there today. All of the people who have lived in these canyon grasslands left imprints on the contemporary landscape. Benchlands and lower slopes have faced the most concentrated land use compared to steeper areas within the HCNRA because both cultivation and livestock grazing are topographically restricted as slope increases. Both studies emphasize the priority for research and management on these benchlands since the plant association of these benchlands was generally more altered than those on the steeper slopes, especially where there was historical cultivation. More research is needed to understand how and where canyon grasslands respond to different types of disturbances including cultivation, livestock grazing, changing fire regimes, and changes in climate over time. More work could be done to map the distribution of these land uses (especially cultivation) in connection with topography. Finally, the presence of the relatively new exotic annual grass, *V. dubia*, further emphasizes the need to study the unique remnants of these grasslands since they represent some of the last intact plant associations of their type.

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APPENDICES

A.1 Range of values used to classify the seral stages of each plot for both sampling years within the Idaho fescue/prairie junegrass (low elevation) association. The very early, early, mid, and late values are written as cover/frequency was recorded from Johnson and Simon (1987) indicator species for this association. The range of values for each seral stage was created based on the same indicator species for this association; these values are also written as cover/frequency.

Plant Code ^a	Very Early	Very Early Range	Early	Early Range	Mid	Mid Range	Late	Late Range
FEID	4/30	1-10/25-75	20/100	11-25/100	32/100	26-52/100	53/100	53-75/100
KOMA	3/40	3-7/35-45	2/70	1-2/68-84	2/85	2-3/85-100	2/50	2-3/46-55
PSSPS	27/100	27-35/95-100	21/90	17-26/85-94	26/100	27-30/100	12/78	10-16/65-84
BRBR	8/20	6-9/10-25	10/50	10-19/35-55	6/65	3-6/56-75	3/28	1-3/26-34
PHCO10	1/60	1-2/40-59	2/60	1-2/60-66	1/69	1-2/67-72	1/72	1-2/72-90
HIAL2	1/30	1-2/20-45	3/60	3-7/53-60	2/50	1-2/46-52	2/61	1-2/61-78
BRAR5	12/40	5-12/30-55	15/10	13-20/2-10	1/19	1-2/19-29	2/11	1-2/11-18

^a Plant codes represent the following species: FEID- *Festuca idahoensis*, KOMA- *Koeleria macrantha*, PSSPS- *Pseudoroegneria spicata*, BRBR5- *Bromus brizaeformis*, PHCO10- *Phlox colubrine*, HIAL2- *Hieracium albiflorum*, and BRAR5- *Bromus arvensis*.

A.2 Range of values used to classify the seral stages of each plot for both sampling years within the bluebunch wheatgrass/Sandburg's bluegrass/Snake River phlox association. The very early, early, mid, and late values are written as cover/frequency was recorded from Johnson and Simon (1987) indicator species for this association. The range of values for each seral stage was created based on the same indicator species for this association; these values are also written as cover/frequency.

Plant Code ^a	Early	Early Range	Mid	Mid Range	Late	Late Range
PSSPS	29/100	28-32/100	26/100	18-27/100	33/100	33-40/100
POSE	2/75	1-2/55-77	3/80	3-4/78-95	5/100	5-8/96-100
ASIN5	8/75	7-10/60-77	5/80	3-6/78-90	1/50	1-2/40-59
PHCO10	5/50	3-7/45-65	1/70	1-2/66-75	1/75	1-2/76-85
CEGL	2/38	1-2/28-45	3/50	3-5/46-60	3/25	3-5/18-27
ERCOC	1/88	1-2/75-95	2/70	1-2/50-74	1/25	1-2/20-49
OPPO	5/63	4-6/50-66	3/90	3-4/80-95	2/75	1-2/67-79

^a Plant codes represent the following species: PSSPS- *Pseudoroegneria spicata*, POSE- *Poa secunda*, ASIN5- *Astragalus inflexus*, PHCO10- *Phlox colubrine*, CEGL2- *Cerastium glomeratum*, ERCOC3- *Erigeron concinnus*, and OPPO- *Opuntia polyacantha*.

A.3 Range of values used to classify the seral stages of each plot for both sampling years within the bluebunch wheatgrass/Sandberg's bluegrass (granite) association. The very early, early, mid, and late values are written as cover/frequency was recorded from Johnson and Simon (1987) indicator species for this association. The range of values for each seral stage was created based on the same indicator species for this association; these values are also written as cover/frequency.

Plant Code ^a	Very Early	Very Early Range	Early	Early Range	Mid	Mid Range	Late	Late Range
PSSPS	5/100	1-12/100	17/100	13-24/100	29/100	14-29/100	32/100	30-45/100
POSE	1/50	1-2/30-55	6/67	4-8/56-75	2/86	1-2/76-88	3/100	2-4/89-100
BRTE	4/100	2-4/100	5/100	4-5/100	6/100	6-8/100	1/67	1-2/65-98
LOMA	7/100	6-10/85-100	3/67	3-5/60-84	1/57	1-3/45-59	3/33	2-4/30-44
ERCOC3	2/100	1-2/100	2/100	2-3/80-100	2/71	1-2/65-79	1/33	1-2/25-64
OPPO	4/100	3-4/100	5/100	5-8/65-98	2/43	1-2/40-64	1/33	0-1/25-39
SPCR	10/50	7-15/40-62	3/67	2-6/63-78	--	--	1/33	1-2/28-39

^a Plant codes represent the following species: PSSPS- *Pseudoroegneria spicata*, POSE- *Poa secunda*, BRTE- *Bromus tectorum*, LOMA- *Lomatium macrocarpum*, ERCOC3- *Erigeron concinnus*, OPPO- *Opuntia polycantha*, and SPCR- *Sporobolus cryptandrus*.

A.4 Range of values used to classify the seral stages of each plot for both sampling years within the bluebunch wheatgrass/sand dropseed/red three awn association. The very early, early, mid, and late values are written as cover/frequency was recorded from Johnson and Simon (1987) indicator species for this association. The range of values for each seral stage was created based on the same indicator species for this association; these values are also written as cover/frequency.

Plant Code ^c	Very Early	Very Early Range	Early	Early Range	Mid	Mid Range
SPCR	19/86	19-30/70-90	11/100	10-18/91-100	7/67	1-9/40-69
ARPUL	15/93	15-25/50-100	13/43	7-14/40-49	5/33	1-6/20-39
PSSPS	4/86	0-18/50-88	23/100	19-40/100	45/100	41-60/100
POSE	3/64	1-3/40-65	4/86	4-6/86-100	2/67	1-2/65-85
BRTE	18/100	16-50/100	10/100	7-15/100	2/100	1-6/100
ERCOC3	2/21	1-2/15-70	3/100	3-5/71-100	1/100	1-2/100
HYPE	4/43	1-4/36-50	6/57	6-10/51-80	5/33	5-6/15-35
ARSE2	5/50	4-6/45-75	3/29	1-3/20-32	10/33	7-15/33-44
ERCI6	5/93	1-5/80-100	6/71	6-13/40-79	15/33	14-25/25-39

^a Plant codes represent the following species: SPCR- *Sporobolus cryptandrus*, ARPUL- *Aristida purpurea*, PSSPS- *Pseudoroegneria spicata*, POSE- *Poa secunda*, BRTE- *Bromus tectorum*, ERCOC3- *Erigeron concinnus*, HYPE- *Hypericum perforatum*, ARSE2- *Arenaria serpyllifolia*, and ERCI6- *Erodium cicutarium*.

A.5 Multi-Response Permutation Procedures results for the Idaho fescue/prairie junegrass (low elevation) association with individual plot comparisons for each sampling year (1981 and 2014). Seral stage codes are: (V.E.) very early, (E.) early, (M.) mid, and (L.) late. All comparisons were significant ($p < 0.05$).

Multiple Comparisons (Sørensen)	<i>T</i>	<i>A</i>
<u>1981</u>		
333 (V.E.) vs. 348 (E.)	-37.69	0.216
333 (V.E.) vs. 398 (M.)	-39.64	0.212
333 (V.E.) vs. 417 (L.)	-41.05	0.312
333 (V.E.) vs. 432 (M.)	-38.01	0.237
348 (E.) vs. 398 (M.)	-16.51	0.086
348 (E.) vs. 417 (L.)	-22.69	0.168
348 (E.) vs. 432 (M.)	-16.18	0.096
398 (M.) vs. 417 (L.)	-18.22	0.110
398 (M.) vs. 432 (M.)	-16.48	0.086
417 (L.) vs. 432 (M.)	-5.08	0.040
<u>2014</u>		
333 (V.E.) vs. 348 (V.E.)	-38.30	0.260
333 (V.E.) vs. 398 (M.)	-36.06	0.220
333 (V.E.) vs. 417 (E.)	-34.58	0.187
333 (V.E.) vs. 432 (M.)	-36.45	0.204
348 (V.E.) vs. 398 (M.)	-36.54	0.310
348 (V.E.) vs. 417 (E.)	-38.57	0.275
348 (V.E.) vs. 432 (M.)	-44.02	0.325
398 (M.) vs. 417 (E.)	-33.53	0.196
398 (M.) vs. 432 (M.)	-25.22	0.138
417 (E.) vs. 432 (M.)	-29.98	0.419

A.6 Indicator species analysis for species within the Idaho fescue/prairie junegrass (low elevation) association. Species listed are those with significant p-values (< 0.05). Values are written as 1981 seral stage/2014 seral stage. Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association. Dash marks indicate that the species did not occur in that particular plot.

	<u>Plot 333</u>	<u>Plot 348</u>	<u>Plot 398</u>	<u>Plot 417</u>	<u>Plot 432</u>
Later Seral Species	V. Early/V. Early	Early/ V. Early	Mid/Mid	Late/ Early	Mid/ Mid
<i>Festuca idahoensis</i>	0/1	9/0	18/17	19/5	15/13
<i>Koeleria macrantha</i>	-----	14/0	6/27	-----	0/12
<i>Poa secunda</i>	0/1	10/0	-----	0/71	-----
<i>Vulpia microstachys</i>	20/0	-----	-----	-----	-----
<i>Frasera albicaulis</i>	13/0	-----	-----	-----	-----
<i>Besseyia rubra</i>	0/47	-----	4/20	-----	-----
<i>Lupinus caudatus</i>	-----	-----	37/0	-----	-----
Earlier Seral Species					
<i>Pseudoroegneria spicata</i>	11/15	12/13	6/4	3/9	7/9
<i>Archillea millefolium</i>	14/0	0/2	3/3	0/2	1/10
<i>Plantago aristata</i>	5/58	-----	-----	-----	-----
<i>Woodsia oregana</i>	-----	0/28	0/4	-----	-----
<i>Phlox colubrine</i>	3/0	-----	0/15	-----	-----
<i>Bromus tectorum</i>	0/1	-----	-----	0/33	-----
<i>Bromus arvensis</i>	2/24	-----	-----	0/19	0/31
<i>Arenaria serpyllifolia</i>	-----	-----	38/0	-----	-----
<i>Tragopogon dubius</i>	17/3	-----	-----	-----	-----
<i>Bromus briziformis</i>	27/0	-----	-----	-----	0/2
<i>Amsinckia menziesii</i>	20/0	-----	-----	-----	-----
<i>Veronica arvensis</i>	-----	-----	-----	13/0	-----
<i>Bromus hordeaceus</i>	-----	-----	-----	1/0	1/0

A.7 Multi-Response Permutation Procedures results for the bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association with individual plot comparisons for each sampling year (1981 and 2014). Seral stage codes are: (V.E.) very early, (E.) early, (M.) mid, and (L.) late. All comparisons were significant ($p < 0.05$).

Multiple Comparisons (Sørensen)	<i>T</i>	<i>A</i>
<u>1981</u>		
340 (M.) vs. 368 (M.)	-11.91	0.061
340 (M.) vs. 394 (E.)	-31.83	0.148
340 (M.) vs. 396 (E.)	-23.90	0.118
340 (M.) vs. 541 (E.)	-21.39	0.122
368 (M.) vs. 394 (E.)	-20.21	0.086
368 (M.) vs. 396 (E.)	-21.72	0.105
368 (M.) vs. 541 (E.)	-23.46	0.128
394 (E.) vs. 396 (E.)	-12.83	0.055
394 (E.) vs. 541 (E.)	-21.04	0.104
396 (E.) vs. 541 (E.)	-17.62	0.095
<u>2014</u>		
340 (E.) vs. 368 (L.)	-41.93	0.303
340 (E.) vs. 394 (E.)	-36.96	0.211
340 (E.) vs. 396 (M.)	-42.77	0.292
340 (E.) vs. 541 (L.)	-48.64	0.447
368 (L.) vs. 394 (E.)	-33.21	0.198
368 (L.) vs. 396 (M.)	-22.42	0.132
368 (L.) vs. 541 (L.)	-45.91	0.334
394 (E.) vs. 396 (M.)	-38.43	0.247
394 (E.) vs. 541 (L.)	-49.68	0.413
396 (M.) vs. 541 (L.)	-48.81	0.389

A.8 Indicator Species Analysis for species within the bluebunch wheatgrass/Sandberg's bluegrass/Snake River phlox association. Species listed are those with significant p-values (< 0.05). Values are written as 1981 seral stage/2014 seral stage. Later seral and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association. Dash marks indicate that the species did not occur in that particular plot.

	<u>Plot 340</u>	<u>Plot 368</u>	<u>Plot 394</u>	<u>Plot 396</u>	<u>Plot 541</u>
Later Seral Species	Mid/Early	Mid/Late	Early/Early	Early/Mid	Early/Late
<i>Pseudoroegneria spicata</i>	10/1	8/20	6/7	9/10	2/17
<i>Poa secunda</i>	0/23	2/11	1/2	0/30	-----
<i>Calochortus</i>	-----	-----	-----	-----	-----
<i>macrocarpus</i>	0/72	-----	1/0	-----	0/9
<i>Plantago aristata</i>	-----	0/15	0/11	0/19	0/2
<i>Phlox colubrine</i>	-----	0/8	-----	0/12	-----
<i>Lomatium spp.</i>	-----	-----	-----	-----	0/18
<i>Sedum stenopetalum</i>	17/0	1/8	0/3	1/0	-----
<i>Archillea millefolium</i>	-----	-----	-----	-----	26/0
<i>Phacelia linearis</i>	52/0	12/0	-----	-----	-----
<i>Cerastium glomeratum</i>	1/0	10/0	22/1	-----	-----
<i>Erigeron concinnus</i>	-----	-----	-----	-----	-----
Earlier Seral Species					
<i>Astragalus inflexus</i>	-----	-----	25/0	-----	5/0
<i>Bromus tectorum</i>	0/24	-----	0/69	0/1	-----
<i>Bromus arvensis</i>	-----	-----	2/0	2/0	3/79
<i>Arenaria serpyllifolia</i>	0/19	0/24	1/33	3/4	-----
<i>Sporobolus cryptandrus</i>	0/38	-----	-----	-----	-----
<i>Erodium cicutarium</i>	0/15	-----	-----	-----	-----
<i>Amsinckia menziesii</i>	-----	-----	0/55	-----	-----
<i>Ventenata dubia</i>	-----	-----	-----	-----	-----
<i>Veronica arvensis</i>	-----	-----	22/0	23/0	-----

A.9 Multi-Response Permutation Procedures results for the bluebunch wheatgrass/Sandberg's bluegrass (granite) association with individual plot comparisons for each sampling year (1981 and 2014). Seral stage codes are: (V.E.) very early, (E.) early, (M.) mid, and (L.) late. All comparisons were significant ($p < 0.05$).

Multiple Comparisons (Sørensen)	<i>T</i>	<i>A</i>
<u>1981</u>		
399 (M.) vs. 587 (M.)	-24.85	0.129
399 (M.) vs. 405 (V.E.)	-45.54	0.371
399 (M.) vs. 370 (V.E.)	-33.50	0.227
587 (M.) vs. 405 (V.E.)	-35.66	0.120
587 (M.) vs. 370 (V.E.)	-27.48	0.136
405 (V.E.) vs. 370 (V.E.)	-41.31	0.235
<u>2014</u>		
399 (E.) vs. 587 (E.)	-34.71	0.206
399 (E.) vs. 405 (V.E.)	-46.14	0.369
399 (E.) vs. 370 (V.E.)	-46.68	0.328
587 (E.) vs. 405 (V.E.)	-42.61	0.297
587 (E.) vs. 370 (V.E.)	-44.74	0.329
405 (V.E.) vs. 370 (V.E.)	-34.73	0.231

A.10 Indicator Species Analysis for species within the bluebunch wheatgrass/Sandberg's bluegrass (granite) association. Species listed are those with significant p-values (< 0.05). Values are written as 1981 seral stage/2014 seral stage. Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association. Dash marks indicate that the species did not occur in that particular plot.

	<u>Plot 399</u>	<u>Plot 587</u>	<u>Plot 405</u>	<u>Plot 370</u>
Later Seral Species	Mid/Early	Mid/Early	V. Early/V. Early	V. Early/V. Early
<i>Pseudoroegneria spicata</i>	26/21	12/12	1/2	1/3
<i>Poa secunda</i>	3/20	-----	0/20	0/46
<i>Erigeron concinnus</i>	-----	7/10	0/1	-----
<i>Plantago aristata</i>	1/2	1/17	4/41	9/2
<i>Lomatium spp.</i>	0/2	-----	8/1	-----
<i>Archillea millefolium</i>	0/26	9/0	0/1	3/0
<i>Vulpia microstachys</i>	-----	11/0	29/0	-----
<i>Scutellaria angustifolia</i>	-----	23/0	-----	-----
Earlier Seral Species				
<i>Sporobolus cryptandrus</i>	-----	-----	-----	22/24
<i>Aristida purpurea</i>	-----	-----	33/41	-----
<i>Bromus tectorum</i>	-----	0/39	4/51	-----
<i>Erodium cicutarium</i>	-----	-----	0/1	1/68
<i>Arenaria serpyllifolia</i>	-----	0/2	-----	6/8
<i>Taeniatherum caput-medusae</i>	-----	-----	0/1	0/9
<i>Veronica arvensis</i>	15/0	6/0	-----	47/0
<i>Lepidium densiflorum</i>	-----	21/0	6/0	-----

A.11 Multi-Response Permutation Procedures results for the bluebunch wheatgrass/sand dropseed/red three awn association with individual plot comparisons for each sampling year (1981 and 2014). Seral stage codes are: (A.G) annual grass dominated, (V.E.) very early, (E.) early, (M.) mid, and (L.) late. All comparisons were significant ($p < 0.05$).

Multiple Comparisons (Sørensen)	<i>T</i>	<i>A</i>
1981		
332 (V.E.) vs. 338 (V.E.)	-34.53	0.349
332 (V.E.) vs. 339 (V.E.)	-28.32	0.228
332 (V.E.) vs. 349 (E.)	-7.000	0.049
332 (V.E.) vs. 354 (E.)	-19.98	0.165
338 (V.E.) vs. 339 (V.E.)	-47.30	0.362
338 (V.E.) vs. 349 (E.)	-45.52	0.306
338 (V.E.) vs. 354 (E.)	-49.80	0.420
339 (V.E.) vs. 349 (E.)	-41.24	0.227
339 (V.E.) vs. 354 (E.)	-46.55	0.316
349 (E.) vs. 354 (E.)	-20.19	0.110
2014		
332 (A.G.) vs. 338 (A.G.)	-30.42	0.234
332 (A.G.) vs. 339 (A.G.)	-35.08	0.329
332 (A.G.) vs. 349 (E.)	-29.80	0.243
332 (A.G.) vs. 354 (E.)	-32.75	0.289
338 (A.G.) vs. 339 (A.G.)	-51.45	0.421
338 (A.G.) vs. 349 (E.)	-51.68	0.436
338 (A.G.) vs. 354 (E.)	-52.06	0.422
339 (A.G.) vs. 349 (E.)	-46.26	0.304
339 (A.G.) vs. 354 (E.)	-49.04	0.359
349 (E.) vs. 354 (E.)	-31.98	0.209

A.12 Indicator Species Analysis for species within the bluebunch wheatgrass/sand dropseed/red three awn association. Species listed are those with significant p-values (< 0.05). Values are written as 1981 seral stage/2014 seral stage. Later and earlier seral stage species are organized based on Johnson and Simon (1987) classifications for this association. Dash marks indicate that the species did not occur in that particular plot.

	<u>Plot 332</u>	<u>Plot 338</u>	<u>Plot 339</u>	<u>Plot 349</u>	<u>Plot 354</u>
	Early/A.	V. Early/A.	V. Early/A.	Early/Early	Early/Early
Later-Seral Species	Grass	Grass	Grass		-----
<i>Pseudoroegneria spicata</i>	8/0	-----	-----	8/7	23/24
<i>Poa secunda</i>	0/35	-----	-----	0/43	1/16
<i>Calochortus macrocarpus</i>	0/28	-----	-----	-----	-----
<i>Plantago aristata</i>	5/3	-----	0/2	2/13	4/42
<i>Astragalus inflexus</i>	-----	-----	0/18	-----	-----
Earlier-Seral Species					
<i>Sporobolus cryptandrus</i>	27/7	-----	5/9	7/5	3/0
<i>Aristida purpurea</i>	0/1	60/24	1/0	-----	-----
<i>Bromus tectorum</i>	6/18	5/28	-----	13/11	1/8
<i>Ventenata dubia</i>	0/28	0/60	-----	0/1	-----
<i>Tragopogon dubius</i>	1/5	0/3	0/20	-----	-----
<i>Erodium cicutarium</i>	-----	-----	1/44	1/42	0/2
<i>Hypericum perforatum</i>	-----	-----	76/1	-----	-----

A.13 Joint plot results showing the correlation of the second matrix (topographical variables) with the first matrix (individual species cover) by plant association.

	Axis	Elevation	Aspect	Slope
Idaho fescue/prairie junegrass (low elevation)				
	1	0.264	0.203	0.000
	2	0.013	0.008	0.145
	3	0.004	0.029	0.030
bluebunch wheatgrass/Sandberg's bluegrass/Snake River Phlox				
	1	0.084	0.114	0.054
	2	0.227	0.031	0.216
	3	0.029	0.000	0.026
bluebunch wheatgrass/Sandburg's bluegrass (granite)				
	1	0.495	0.147	0.237
	2	0.042	0.371	0.193
	3	0.025	0.004	0.007
bluebunch wheatgrass/sand dropseed/red three awn				
	1	0.300	0.130	0.428
	2	0.134	0.030	0.003
	3	0.031	0.017	0.002

A.14 Indicator species analysis results comparing the species composition of the vegetation using the percent cover values of each species measured in the field. Species listed are those with significant p-values (< 0.05). Abbreviations for seral stages are: annual grass dominated (A.G.), very early (V.E.), and early (E.).

	<u>Haas</u> <u>Homestead</u> <u>(V.E.)</u>	<u>Haas</u> <u>Reference</u> <u>(V.E.)</u>	<u>Johnson</u> <u>Reference</u> <u>(V.E.)</u>	<u>Plot</u> <u>332</u> <u>(A.G.)</u>	<u>Plot</u> <u>338</u> <u>(A.G.)</u>	<u>Plot</u> <u>339</u> <u>(A.G.)</u>	<u>Plot</u> <u>349</u> <u>(E.)</u>	<u>Plot</u> <u>354</u> <u>(E.)</u>
Native Grasses								
<i>Pseudoroegneria spicata</i>	0	0	0	1	0	0	37	37
<i>Poa secunda</i>	14	14	12	14	0	0	15	12
<i>Sporobolus cryptandrus</i>	0	19	24	10	0	0	2	1
<i>Aristida purpurea</i>	0	0	0	1	50	15	0	1
Native Forbs								
<i>Amsinckia menziesii</i>	14	0	0	1	0	17	0	2
<i>Plantago aristata</i>	0	17	14	1	0	0	16	32
<i>Sedum stenopetalum</i>	0	14	0	0	0	0	0	42
<i>Lomatium</i>	68	0	0	0	0	0	0	0
Introduced Grasses								
<i>Bromus arvensis</i>	13	1	6	10	10	21	3	10
<i>Bromus tectorum</i>	12	13	6	14	17	9	6	12
<i>Thinopyrum intermedium</i>	100	0	0	0	0	0	0	0
<i>Ventenata dubia</i>	18	6	13	29	30	0	0	0
Introduced Forbs								
<i>Arenaria serpyllifolia</i>	0	0	41	32	14	0	0	0
<i>Brassica rapa</i>	0	0	0	24	0	21	0	0
<i>Erodium cicutarium</i>	16	10	16	0	0	15	11	3
<i>Thlaspi arvense</i>	0	2	0	0	0	0	23	0
<i>Tragopogon dubius</i>	0	3	3	6	5	16	0	0

A.15 Indicator species analysis results comparing the species composition of the seed bank vegetation using the density of each species measured as the number of seedlings m⁻². Species listed are those with significant p-values (< 0.05). Abbreviations for seral stages are: annual grass dominated (A.G.), very early (V.E.), and early (E.).

	<u>Haas</u> <u>Homestead</u> <u>(V.E.)</u>	<u>Haas</u> <u>Reference</u> <u>(V.E.)</u>	<u>Johnson</u> <u>Reference</u> <u>(V.E.)</u>	<u>Plot</u> <u>332</u> <u>(A.G.)</u>	<u>Plot</u> <u>338</u> <u>(A.G.)</u>	<u>Plot</u> <u>339</u> <u>(A.G.)</u>	<u>Plot</u> <u>349</u> <u>(E.)</u>	<u>Plot</u> <u>354</u> <u>(E.)</u>
Native Grasses								
<i>Sporobolus cryptandrus</i>	0	0	7	0	0	0	1	42
Native Forbs								
<i>Amsinckia menziesii</i>	2	0	0	27	0	0	0	0
<i>Plantago aristata</i>	0	1	1	0	1	0	9	49
Introduced Grasses								
<i>Bromus tectorum</i>	10	13	4	17	25	2	3	12
<i>Ventenata dubia</i>	11	12	2	17	5	1	19	9
Introduced Forbs								
<i>Arenaria serpyllifolia</i>	0	2	14	52	18	0	0	3
<i>Draba verna</i>	1	9	21	10	6	0	34	14
<i>Holosteum umbellatum</i>	2	55	4	0	13	4	14	4
<i>Hypericum perforatum</i>	0	0	0	5	0	72	0	6
<i>Lamium amplexicaule</i>	19	5	19	10	7	0	3	34
<i>Myosotis arvensis</i>	4	0	0	51	30	5	1	1
<i>Sisymbrium altissimum</i>	4	0	1	2	1	7	0	0
<i>Verbascum blattaria</i>	1	0	0	1	10	77	0	0

