

RESTORATION OF PLANT COMMUNITIES TO RED-BURNED SOILS

by

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## Abstract

Fire, natural or anthropogenic, is a common occurrence in the open forests and grasslands of Western North America. The effects of fire on soil and vegetation depend largely on the soil temperatures and the residence time of the burn. Generally, the more severe the fire, the more significant the changes are to soil and vegetation. The relationship between the most severe fires, or where the soil has been oxidized to a red colour, and invasive species is unknown. Resource availability may increase on these soils, leading to favourable conditions for invasive species, or the disturbance may be so severe that nothing is able to grow indefinitely.

I performed two studies to investigate the relationship between invasive species and red-burned soil. To reduce the threat of interface fires near Kamloops, BC, excess timber was harvested, piled and burned on site (pile burning), created multiple burn scars denuded of vegetation and large areas of red soil. In the first study, I investigated soil nutrient flux differences between red-burned and unburned soil using ion-exchange resin technology. I also investigated three restoration methods to control invasive species: the addition of agronomic or native seed, the addition of arbuscular mycorrhizal fungi (AMF) inoculum, and the addition of soil cover. Non-native species cover was high on red soil 2 years post-burn, which may be linked to measured increased nutrients. Only the addition of agronomic seed was successful at suppressing non-native species cover.

The second study compared the growth of native, agronomic and invasive species on unburned and red-burned soil in a greenhouse study. Soil was collected in the field and transferred to a greenhouse. Treatments were soil burning, AMF, and watering. Burning increased aboveground biomass for the native species. AMF addition increased invasive species aboveground biomass for the invasive species, but decreased biomass for agronomic and native species. Watering increased aboveground biomass for the agronomic and invasive species.

The findings here suggest that pile burning creates areas that are susceptible to colonization of non-native species. Restoration efforts should be directed at these sites as soon as possible to ameliorate the effects of invasive species colonization.

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*To my family*

# 1 Introduction

Fire, natural or anthropogenic, is a common occurrence in the open forests and grasslands of Western North America. Historically, Aboriginal peoples used fire as a management tool to clear brush and other low vegetation, which promoted game and other food resources (Lewis 1973, Keeley 2002, Lepofsky et al. 2003). However, European colonization led to a cessation of this traditional practice. This management change has caused fuel accumulation in many forests, creating large areas prone to severe and uncontrollable wildfires (D'Antonio and Vitousek 1992). In interface areas, or those areas between the forest and urban zones, wildfires are particularly dangerous, posing real threat to homes and livelihoods, and potentially posing hazards to human safety.

The effects of burning on soil and vegetation depend largely on the soil temperatures and the duration or residence time of the burn (Certini 2005). These effects range from minor transient changes to soil and vegetation properties, to major changes that can render communities inhospitable to native biota indefinitely. The research reported here describes changes to soil and vegetation communities resulting from local severe fires and the potential of these areas to respond to restoration efforts.

Here I will describe the social and biological context of a burn program in the Kamloops area, British Columbia, the effects these burns have on the soil and vegetation, the potential for these burn areas to facilitate the invasion of unwanted plant species, and the application of restoration methods to these areas.

## **1.1 *Pine Beetle Outbreak and Forest Management Practices***

The forests surrounding many municipalities in BC have recently experienced high rates of tree mortality caused by insect outbreaks (e.g., Flint et al. 2009). Although downed woody debris provides important ecological functions (e.g., habitat, seed and fungal sources) forest managers have sought to remove it from the affected area rather than risk having it burn under uncontrolled conditions, particularly in the urban-forest interface.

This beetle-killed timber often has little market value, and the most efficient means of removal is to pile the downed trees on site and burn them under controlled conditions. This practice is referred to as pile burning, and creates denuded areas with highly altered soils (Figure 1-1). Under these pile burns, soil structure is dramatically changed: many soil nutrients are volatilized, soil water holding capacity is greatly reduced, soil pH and salinity dramatically increase, and above- and below-ground biota are greatly

reduced in diversity and abundance (Korb et al. 2004). The resultant soils are believed to be inhospitable to most plant species with the exception of unwanted exotic and invasive species (Dickinson and Kirkpatrick 1987, Allen 1989).



Figure 1-1. Example of pre-pile burn (left) and post-pile burn scar (right)

## **1.2 Fire and the Impacts of Pile Burning on Soils**

Physical, chemical, and biological soil properties are affected by fires. The effects are primarily a result of fire severity, which is a function of fire intensity (Keeley 2009). Fire intensity, also referred to as burn intensity, is defined as the energy output from the fire, and is measurable by temperature, residence time, and radiant energy (Keeley 2009). Fire severity, also referred to as burn severity, is defined as the aboveground and belowground organic matter consumption from fire (Keeley 2009). The resultant fires lead to ecosystem responses, which are functional processes that are altered by fire (Keeley 2009). Ecosystem responses may be measured as vegetative cover, seedling recruitment, plant community composition and diversity, and plant and animal regeneration or recolonization.

Low- to moderate-severity fires are typical of prescribed forest management. These fires typically have relatively low volumes of fuel, and are characterized by relatively low peak temperatures and/or short durations (i.e., generally a low fire intensity). Any changes to soil and vegetation properties are transient in nature; no irreversible ecosystem changes typically occur (Certini 2005).

Severe fires, such as wildfires or pile burns, generally have large-scale negative effects on soil and vegetation. Pile burning, in particular, creates areas of focus for heat. Often, felled trees and woody debris are in direct contact with the ground, creating large areas of soil that have been exposed to high temperatures for extended periods of time. Localized areas of high fire severity cause large ecosystem

responses such as significant removal of organic matter, deterioration of both soil structure and porosity, considerable loss of nutrients through volatilisation, nutrient leaching and soil erosion, and marked alteration of both quantity and specific composition of soil biotic communities (Certini 2005).

Fuel load influences both the intensity and severity of fires. Heavy fuel-loading can cause soil-surface temperatures to reach 500°C to 700°C, although instantaneous values of up to 850°C have been measured (DeBano et al. 1998, DeBano 2000). The degree of heating and the depth of heat are largely dependent on soil moisture and the duration of the burn. Steep temperature gradients are often measured; however, although heat is transported faster in moist soil and penetrates deeper than in dry soil, the latent heat of vaporization prevents soil temperatures from exceeding 95°C until the water completely vaporizes (Campbell et al. 1994).

### **1.2.1 Physical Effects on Soil**

Generally, fires with higher severity have more pronounced alterations on soil physical properties. Soil pH is increased because organic acids are denatured. Significant pH (>2 points) increases occur only at high temperatures (e.g., > 450°C to 500°C), or the temperatures observed in soil after pile burning (Certini 2005). Physical changes in soil caused by fire are summarized below (adapted from Certini 2005 unless otherwise noted):

1. Water repellency – physical changes in the soil create a water-repellent layer a few centimeters below the soil surface resulting in surface water runoff and soil erosion;
2. Structural stability – the combustion of organic elements reduces soil structure stability;
3. Bulk density – increases because of the collapse of aggregates and the clogging of voids; soil porosity and permeability decrease;
4. pH – increases due to release of alkaline cations, typically, the more severe the fire, the higher the resultant pH;
5. Colour – charring darkens soil at lower temperatures and formation of iron oxides reddens soil (Figure 1-2). Soil reddening can occur after 45 minutes of exposure to temperatures exceeding 600°C (Ketterings and Bigham 2000); and
6. Temperature regime – changes due to removal of aboveground vegetation and darkening of soil surface; for example, the range of soil temperatures experienced typically increases.

An example of physical changes in severely burned soil is provided by Creech et al. (2011) who followed the natural recovery of severely burned soil in Ponderosa Pine forests in the Northwest United States.

They reported differences in soil bulk density between burned and unburned soil six years post-burn, with lower bulk density in burned soils. Soil classification (sand or loamy sand) remained the same in burned and unburned areas, but burned areas had higher silt and clay fractions relative to unburned soils. Soil pH was significantly higher in burned compared to unburned soils, at both 0-10 cm and 10-20 cm deep, for all six years of the study, although this difference decreased over time.



Figure 1-2. Example of soil reddening created by direct soil contact of burning large woody debris (logs)

### 1.2.2 Chemical Effects on Soil

The degree of chemical alterations of soil is also directly proportional to the severity of the fire. For example, fire can volatilize nutrients, but can also cause chemical reactions that increase ephemeral soil nutrient availability. Chemical changes in soil caused by fire are summarized below (adapted from Certini 2005):

1. Organic matter – decreases immediately and after fire;
2. Availability of nutrients – increases, but change can be ephemeral:
  - a. Organic N – either volatilises or changes to more available forms; increased N – availability is ephemeral;
  - b. Organic P – mineralizes to orthophosphate, but can precipitate as slightly available mineral forms;
  - c. Other mineral nutrients – often dramatically increase, but ephemerally;

3. Exchange capacity – decreases with loss of organic matter; and
4. Base saturation – increases with combustion of organic matter.

An example of chemical changes in severely burned soil is provided by Rhoades et al. (2004), who investigated log burn-out openings from a forest fire. Log burn-out openings are created when smoldering downed woody debris remained in contact with the forest floor; these burns are similar to pile burn scars but generally have a smaller affected area. In these openings, soil chemical properties were significantly different than for the surrounding soil 3 years post-burn. Soil extractable  $P^+$ ,  $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$  were significantly higher in these burn-out openings, although most measures of extractable and available N were either not significantly different or significantly higher in the adjacent unburned forest floor.

### **1.2.3 Biological Effects on Soil**

The degree of biological alterations of soil is directly proportional to the severity of the fire, although the relationships tend to be less linear than those of fire and physical/chemical properties. This relationship is a result of soil biota being depleted at a certain fire severity, thus additional burning will have no incremental effect on soil biota as they are already absent. For example, the high severity fires resulting from slash burning negatively affects soil microbial and fungal communities (Esquilin et al. 2007). In addition, more severe pile-burning can eliminate both the mycorrhizal components of the soil as well as the soil seed bank (Korb et al. 2004), making post-fire colonization of native vegetation communities problematic. In log burn-out openings, post-fire patches were barren of vegetation even 3 years post-fire (Rhoades et al. 2004).

Biological changes in soil caused by fire are summarized below (adapted from Certini 2005 unless otherwise noted):

1. Microbial biomass – decreases; recovery is linked to vegetation colonization and recovery;
2. Composition of microbial community – generally fungi diminish more so than bacteria;
3. Invertebrate biomass – decreases, but mobility can buffer the degree of decrease;
4. Composition of invertebrates – changes because distinct phyla recover at different rates;
5. Soil seed bank – decreases, can be completely removed in high severity fires (Korb et al. 2004);  
and
6. Exotic species – establishment of exotic plant species often increases (Allen 1991).

An example of biological changes in severely burned soil is provided by Hebel et al. (2009), who reported that arbuscular mycorrhizal fungi (AMF) colonization of roots and soil microbial communities were greatly depleted in red soil, compared with less severely burned black soil. However, AMF abundance in soil was not found to be significantly different between the two burn severities. Red soil had 71% less soil C than black soil, strongly contributing to the microbial community differences between red and black soil. Similarly, total N of red soils was 69% less in red soil than in black soil.

### **1.3 Disturbance Theory**

The effect of fire on soil has consequences on the aboveground plant community via an increase in resources available to plants, e.g., increased light, water, and nutrients. These increases in resources create conditions that make communities invasible by novel species. This idea is referred to as the ‘fluctuating resource hypothesis’ (Davis et al. 2000). The fluctuating resource hypothesis acknowledges that, across multiple growth forms and broad taxonomic diversity, invasive species are generally more efficient than native species at using limiting resources in low resource systems on short timescales (Funk and Vitousek 2007). Given this assumption, it logically follows that any factor(s) that increase the availability of limiting resources will increase the vulnerability of a community to invasion.

### **1.4 Invasive Species**

Invasive species are defined as a subset of naturalized plants that produce reproductive offspring, often in large numbers, at considerable distances from parent plants, and thus have the potential to spread over a large area (Richardson and Pyšek 2006). Naturalized plants are those non-native plant species that form self-replacing populations for at least 10 years (Richardson and Pyšek 2006).

Invasive species are of world-wide ecological concern, causing widespread changes to biotic, abiotic and economic components of ecosystems. For example, invasive plant species can alter soil nutrient cycles (Evans et al. 2001, Ehrenfeld 2003), fire cycles (Billings 1994), biodiversity (Gurevitch and Padilla 2004), and belowground biotic communities (Richardson et al. 2000).

The invasion of an environment by new species is influenced by at least three factors: the number of propagules entering the new environment (propagule pressure), the characteristics of the new species, and the susceptibility of the environment to invasion by new species (invasibility) (Lonsdale 1999). Many weedy, non-native species perform well in disturbed environments because they produce an abundance of seed that may be highly persistent in the seed bank, or they are able to disperse great distances or have

minimal germination requirements (Haskins and Gehring 2004). Once established on burned sites, the high reproductive output of these species can allow them to effectively compete with native vegetation.

Invasive species are early colonizers of post-burn environments, across multiple environments and fire intensities (e.g., Fornwalt et al. 2010). Thus, pile burn scars may be susceptible to invasion (e.g. Haskins and Gehring 2004). However, alteration of the soil community may be so severe that recolonization of any species is delayed indefinitely (e.g., Rhoades et al. 2004).

### **1.4.1 Control of Invasive Species**

The most common technique used to control the emergence and spread of invasive species in a post-disturbance environment is the attempt to establish a non-invasive vegetative cover before invasive species arrive at the site. This established vegetative cover is thought to alter abiotic microsite conditions and/or the soil microbial community such that the post-disturbance resource increase is diminished and conditions no longer favour invasion. Dominant native, agronomic and other non-invasive, non-native species that produce abundant vegetative cover often have the greatest potential to deter establishment of invasive species at small scales (Hunter et al. 2006, Goergen and Chambers 2012).

The promotion of a native species cover into a disturbed area may be facilitated by the re-establishment of favourable soil biota. Although vegetation responses in these environments may be related to the near depletion of the entire soil biota (Esquilin et al. 2007), many restoration programs have only involved the re-introduction of arbuscular mycorrhizal fungi (AMF) (e.g., Korb et al. 2004). In nutrient-limiting environments, plants can benefit from the associations through improved acquisition of nutrients and water; in exchange, AMF receive carbon from the plants (Malloch et al. 1980). Additionally, AMF associations can provide plants with protection from drought, soil-borne pathogens and disease, and heavy metal toxicity (Tobar et al. 1994, Díaz et al. 1996, Augé 2001, Pozo et al. 2002).

Due to severe site alteration created by pile burning, many native plants may be unable to survive in the absence of AMF. However, many invasive species in semi-arid environments are non-mycotrophic (i.e., do not require a symbiotic association with AMF), and may have an advantage over native species in AMF-limited environments (Wicklow-Howard 1994).

## **1.5 Summary**

Pile burning in the dry interior grassland/open forests of British Columbia may create a “perfect-storm” for invasion. The clearing of vegetation removes competitive barriers to entry for these species, and the

burning creates nutrient pulses that invasive species are able to make use of more readily than native species. The reduction in symbiotic soil biota may prevent the re-establishment of native species. As well, the differential seed production rates between native and invasive species heavily favours invasive species.

In this thesis I describe two experiments performed to examine the effects of pile burning on vegetation composition, soil nutrient availability, the need for restoration, and the restoration potential of these highly disturbed sites. Chapter 2 describes the restoration potential of these areas, as well as the vegetation composition and soil nutrient availability on pile burn sites. Chapter 3 describes an experiment that investigates limiting factors to vegetation growth on these sites, as well as the different responses of plant groups on these soils.

## **2 Suppression of Non-Native Species on Pile Burn Scars**

### **2.1 Introduction**

Recent management programs to reduce the threat of interface fires (those occurring at the boundaries between wildlands and urban environments) involve the harvesting of both brush and mature trees. Unmarketable harvested large-diameter trees are piled on site and burned (pile burning), creating large areas of disturbed soils. Slash burns, different from pile burns, result when smaller diameter debris (e.g., branches and saplings) is piled and burned. While pile burning effects on soil are not well understood (but see Rhoades et al. 2004), a lot of research has been done on slash burn effects on soil (e.g., Haskins and Gehring 2004, Korb et al. 2004, Esquilin et al. 2007). In slash burns, soil properties are heavily altered, including increases in soil nutrient availability and hydrophobicity, decreases in soil organic carbon and biotic communities, and a general blackening of the soil (Certini 2005, Esquilin et al. 2007). In pile burns, soils experience exposure to higher temperatures for longer durations, and changes to soil properties are generally more severe than those under slash pile fires (Certini 2005, Hebel et al. 2009). The creation of the iron oxides result in soil reddening (Certini 2005).

An undesired consequence of these burns may be the opening of new areas that facilitate the spread of invasive plant species (Keeley 2000, Korb et al. 2004, Hunter et al. 2006). Invasive species are of world-wide ecological concern, causing widespread changes to biotic, abiotic and economic components of ecosystems. For example, invasive plant species can alter soil nutrient cycles (Evans et al. 2001, Ehrenfeld 2003), fire cycles (Billings 1994), biodiversity (Gurevitch and Padilla 2004), belowground biotic communities (Richardson et al. 2000), and abiotic conditions (Charles and Dukes 2007).

Invasive species are early colonizers of post-burn environments in many ecosystems (e.g., Fornwalt et al. 2010). Of particular concern is if these invaded pile burn scars become the sources of invasive species propagules and affect the surrounding, less disturbed vegetation. To prevent the spread of invasive species into surrounding vegetation, restoration efforts should be focused on the possible point source of invasive species: the pile burn scars. While no restoration efforts have been directed at pile burn scars, several techniques have been investigated to control invasive species in slash burn scars in general, but these have had limited success in restoring native species (Korb et al. 2004, Fornwalt and Rhoades 2011).

A common restoration technique aimed at reducing the establishment and spread of invasive species is to promote the growth of non-invasive species (D'Antonio and Meyerson 2002, Korb et al. 2004, Hunter et al. 2006, Peppin et al. 2010); the restoration of native communities is often a combined goal (Peppin et al. 2010). Slash scars (and thus, presumably, pile burn scars) are biotically depleted (Korb et al. 2004, Rhoades et al. 2004) - little to no seed bank or plant remnants remain in the soil to regenerate. In these biotically depleted environments, invasive species may establish more readily simply because they have highly efficient seed-dispersal mechanisms (Grime 1977). Native species can be highly competitive with invasive species in newly disturbed environments (Thomsen et al. 2005, Thomsen and D'Antonio 2007), and their rapid introduction may facilitate restoration. However, seeding native species may not be practical because they may not be available in sufficient quantities, and there may be concern over the suitability of available native genotypes (Weber et al. 1998). As such, many plant community restoration efforts involve the seeding of domesticated agronomic grasses (Eiswerth et al. 2009). Agronomic grasses can establish quickly, provide cover and stability for soils, and prevent the invasion of unwanted exotic species (Newman 2007). However, the use of these species in restoration is controversial. For example, many seed mixes are contaminated with the seeds of unwanted species (Newman 2007). Species that are regularly included in such mixes can establish self-sustaining monocultures (e.g., *Agropyron cristatum* (Bieb.) Tzvelev), creating biologically-impooverished areas that may result in the decline of endangered or rare species (Redente et al. 1989).

Next to seed limitations, soil mycorrhizal fungi may be the most important factor limiting native plant growth on highly disturbed soils (Skujinš and Allen 1986, Allen 1988, Allen 1989, Korb et al. 2004). Slash burning depletes the biotic components of the soil, including mycorrhizal fungi (Korb et al. 2004, Esquilin et al. 2007). In nutrient-limiting environments, plants may benefit from their association with arbuscular mycorrhizal fungi (AMF) through improved acquisition of nutrients and water. In exchange, AMF receive carbon from the plants (Malloch et al. 1980). Additionally, AMF associations may provide plants with protection from drought, soil-borne pathogens and disease, heavy metal toxicity, and high salinity (Tobar et al. 1994, Díaz et al. 1996, J. M. Ruiz-Lozano 1996, Augé 2001, Pozo et al. 2002). AMF abundance has been shown to promote vegetation diversity (van der Heijden et al. 2008). Thus, the re-establishment of a viable AMF community with seed treatment on scars may promote vegetation establishment.

“Live” soil containing mycorrhizal fungi, seeds, and other biotic components such as microfauna and flora have been experimentally added to disturbed areas and have had some success in restoring native

plant communities (e.g., Korb et al. 2004, Rowe et al. 2007). However, there are limitations to the practical application of this technique. Inoculated soil is expensive. Live soil may contain unwanted components (e.g., the seeds of invasive species, pathogens) that could adversely affect the restoration efforts. An alternative to the application of live soil inoculum is to use commercially-available sources of AMF, which have become more readily available in recent years (Gianinazzi and Vosátka 2004). Due to their ease of application and the assumed generalist nature of AMF associations, their use is becoming increasingly common in restoration efforts.

In warm dry climates, restoration efforts may be hampered by the lack of soil cover, typically provided by standing vegetation and litter. At mid-day during summer months, dark, exposed soils may become extremely hot, providing an inhospitable environment for seed germination and seedling growth (Drábek et al. 2007, Farrell et al. 2011). In warm climates, soil cover will increase soil moisture levels (Shay et al. 2001), reduce soil temperatures (Hogg and Lieffers 1991), and protect seedlings from the desiccating effects of wind (Facelli and Pickett 1991). Soil cover may also prevent soil nutrient loss caused by wind and water erosion (Li et al. 2007). The tempering effect of soil cover is magnified when the litter and vegetation layers as well as the forest cover are removed. Invasive species may preferentially establish on these exposed sites because they are often more tolerant of difficult growing conditions (Davis et al. 2000). The re-establishment of cover would remove this tolerance advantage of invasive species.

In this experiment I tested the following hypotheses:

- 1) Early establishment of native and agronomic species through seed addition will limit invasive species establishment and growth;
- 2) Commercially-available AMF inoculant will improve native species growth over invasive and agronomic species; and
- 3) The presence of soil cover (e.g. as straw) will preferentially improve native species growth over invasive and agronomic species.

## **2.2 Methods**

### **2.2.1 Study Site**

The experiment was conducted in three open parkland sites near Kamloops, British Columbia. These sites were located at the northern end of the Great Basin ecosystem. All three sites are in the Ponderosa Pine very hot, dry (PPxh) Biogeoclimatic subzone (Meidinger and Pojar 1991). This region has a semi-arid

continental climate with warm, dry summers and cool, dry winters. Mean annual precipitation ranges between 250 and 400 mm and the mean annual temperature ranges between 5.4 and 9.0 °C (Meidinger and Pojar 1991). Soils of this BEC Zone are typically Chernozemic or Brunisolic. Ecosystems in the PPxh subzone consist of Ponderosa pine (*Pinus ponderosa* C. Lawson), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love), rough fescue (*Festuca campestris* Rydb.) and big sagebrush (*Artemisia tridentata* Nutt.). Very dry sites within this subzone often have an association of arrow-leaved balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.) and prickly pear cactus (*Opuntia fragilis* (Nutt.) Haw.) (Meidinger and Pojar 1991). Common non-native species in this BEC zone are cheatgrass (*Bromus tectorum* L.), knapweed species (*Centaurea* spp.), Dalmatian toadflax (*Linaria genistifolia* spp. *Dalmatica* (L.) Marie & Petitmengen), sulphur cinquefoil (*Potentilla recta* L.), common houndstongue (*Cynoglossum officinale* L.), leafy spurge (*Euphorbia esula* L.), and Kentucky bluegrass (*Poa pratensis* L.)

The sites used in this experiment were chosen for their abundances of pile burn scars (Figure 2-1) created during the winter of 2007, and are summarized in Table 2-1. Burning occurred during the winter (December/January) of 2007/2008, when the soils were frozen and vegetation was senescent. At each site, large diameter ponderosa pine trees were harvested, arranged in discrete piles, and burned. The footprint of each burn measured approximately 30 to 60 m<sup>2</sup>, and each site has at least 8 piles that were burned. Combustion of organic material was near-complete; the post-burn scars were primarily composed of ash, black-burned soil and red-burned soil, with scattered pieces of charred debris (Figure 2-1). Post-pile-burn boundaries were easily distinguished visually, and the surrounding understory vegetation communities were relatively undisturbed.



Figure 2-1. An example of a pile burn scar at the Noble Creek site approximately 8 months after burning. Note the red soils indicating treatment areas. Posts indicate the corners of treatment plots.

Table 2-1. Geographic co-ordinates and elevation of the three study sites

Site	Northing	Easting	Elevation (masl)
Noble Creek	50°49'57"N	120°18'56"W	430
Heffley Creek	50°52'6.50"N	120°12'44.70"W	650
Barnhartvale	50°38'42.29"N	120°9'38.86"W	595

### 2.3 Experimental Design

The treatments (factors) investigated in this experiment were:

- 2 mycorrhizal fungi (AMF) levels - commercial inoculum added, no commercial inoculum added;
- 2 soil cover levels - present, absent; and
- 3 seed addition levels – native seed mix, agronomic seed mix, and no seed added.

The response variables measured were vegetation cover, species richness, species diversity, and soil nutrients.

### 2.3.1 Soil Nutrients

Over both study years soil nutrient availability was measured using Plant Root Simulator PRS™-probes (Western Ag Innovations, Saskatoon, SK). These probes were used in pairs: one probe measured plant-available cations ( $\text{NH}_4^+\text{-N}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ ,  $\text{Cu}^{2+}$ ,  $\text{Mn}^{2+}$ ,  $\text{Zn}^{2+}$ ,  $\text{Fe}^{3+}$ ,  $\text{Al}^{3+}$ ), and the other measured plant-available anions ( $\text{NO}_3^-\text{-N}$ ,  $\text{Cl}^-$ ,  $\text{SO}_4^-\text{-S}$ ,  $\text{H}_2\text{PO}_4^-\text{-P}$ ,  $\text{B}(\text{OH})_4^-\text{-B}$ ).  $\text{Pb}^{2+}$  and  $\text{Cd}^{2+}$  were also measured but excluded from the analysis for both study years because the majority of measurements were below the detection limits of  $0.2 \text{ mg}/10\text{cm}^2$  for both metals.  $\text{Cu}^{2+}$  was measured in both study years, but was excluded from the 2009 analysis for the same reason. During the 2008 growing season (end of May to end of July), 4 sets of probes were each placed in burned red soil, burned black soil at the edge of the burn (where soil was charred and denuded of vegetation, but where deep-rooted plants were re-emerging), and in unburned soil outside of the burn (12 sets per burn) at the Noble Creek Site. Pairs located in red-burned soil were placed at least 50 cm apart. Probes in black burned and unburned soil were placed at cardinal points of the burns. Probes in unburned soil were placed 3 m from the burn edge. A trench was dug around the probes and vegetation was cleared in the black burned and unburned soil (Figure 2-2). This was done at the recommendation of the manufacturer to avoid probes interacting with plant roots. During the 2009 growing season, 4 sets of probes were placed each in the red burned and unburned soil of a subset of burns investigated in 2008.



Figure 2-2. A pair of Plant Root Simulator<sup>TM</sup>-probes inserted, trenched, and cleared of vegetation in unburned soil

### 2.3.2 Applied Treatments

Treatments were established in May 2008, 5 months after burning occurred. At each of the three sites, a fully factorial stratified randomized experiment was established on red soil. Treatments were applied exclusively to continuous areas of red-burned soil. Each site had four replications of each treatment combination applied, for a total of 48 plots per site and 144 plots in total. Each plot was 1 m<sup>2</sup> and plots were separated by at least 50 cm. Treatment plots were randomized, except that treatments were distributed so as not to be clustered or duplicated within a single burn scar, to the extent possible.

Both the native and agronomic species mixes consisted of 1200 seeds per plot. The native seed mix was comprised of bluebunch wheatgrass, rough fescue, junegrass (*Koeleria macrantha* (Lebed.) Schult.), stiff needlegrass (*Achnatherum occidentale* (Thurb.) Barkworth), spreading needlegrass (*Achnatherum richardsonii* (Link) Barkworth), foxtail barley (*Hordeum jubatum* L.), yarrow (*Achillea millefolium* L.), brown-eyed susan (*Gaillardia aristata* Pursh), and old man's whiskers (*Geum triflorum* Pursh). These species were chosen because they produce high vegetation cover, and they represent dominant species in the areas surrounding the burn scars. I was unable to collect enough viable seed of bluebunch wheatgrass, rough fescue and junegrass in the field, and these species were purchased at Quality Seeds West (Surrey, BC). Seeds of all other species were hand-collected near Kamloops during the summer of 2007 and stored indoors in the laboratory in dry paper bags until needed. The agronomic species mix was also purchased

from Quality Seeds West and was comprised of creeping red fescue (*Festuca rubra* L.), hard fescue (*Festuca longifolia* auct. non Thuill), slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), tall wheatgrass (*Agropyron elongatum* (Host). Beauv), and annual ryegrass (*Lolium multiflorum* Lam.). These species were chosen because they all grow well on disturbed soils and typically do not invade native plant communities (Newman 2007).

Before being sown in the field treatment plots, native seeds were stratified by mixing them with wet sand and storing them at 4 °C for 10 days (Baskin and Baskin 2000).

The AMF inoculum used was purchased from BioOrganics™ (Santa Maria, CA) and consists of a mix of *Glomus aggregatum*, *G. clarum*, *G. deserticola*, *G. intraradices*, *G. monosporus*, *G. mosseae*, *Gigaspora margarita*, and *Paraglomus brasilianum* at a minimum of 50 spores/cm<sup>3</sup>. Each treatment consisted of 2 mL (~100 spores) of the inoculum, or approximately twice the rate of recommended application. Although the efficacy of commercially-available inoculum can be low, a similar product from BioOrganics™ has been shown to be viable in a greenhouse study (Cavender and Knee 2006).

The cover treatment was applied as straw (Figure 2-3), which was applied evenly to each plot so that it covered about 75% of the ground area to a depth of approximately 0.5 cm. The straw was held in place using 5 cm mesh wire, which was cut into 1 m<sup>2</sup> sections and stapled to the ground outside of the plot corners. Any germinating seedlings from seeds mixed in with the straw were removed immediately (< 5 germinating seedlings were identified during the course of the study).



Figure 2-3. Example of cover treatment plot

The AMF and seed addition treatments were combined, if necessary, and mixed with 2 cups of slightly moistened sand. The mixture was then spread evenly on plots in May 2008. Seeds and inoculum were gently worked into the top surface of the soil. Control plots also had 2 cups of sand applied and this likewise was gently worked in to the top surface of the soil. The experiment failed that year, most likely due to unseasonably dry weather. The mean annual precipitation in Kamloops averages 35.2 mm in June and 29.5 mm in July. In 2008, Kamloops received 11.8 mm of precipitation in June and 13.8 mm in July (Environment Canada 2013). I reapplied the treatments in October of 2008 (seeds were not stratified prior to field application), and resampled in July of 2009.

Plant cover was estimated in the centre 50 cm x 50 cm of each plot, to minimize edge-effects. A 1 m x 1 m square grid was placed over the plot, with strings stretched across the grid every 10 cm in both directions. Plant cover was estimated to the closest 10% when cover was over 25%, and 0-1, >1-5, >5-10, >10-15, >15-20, >20-25% otherwise. Species nomenclature and origins followed Klinkenberg (2012) and Parish et al. (1999). Identification to genus was done when identification to species was not possible due to lack of reproductive structures (e.g., from insect grazing). The percent cover of bare ground, char, coarse woody debris, and rock were also estimated.

Using the same survey method as outlined above, the surrounding unburned vegetation was also surveyed in conjunction with the treatment surveys. Four each burn scar, 4 plots were located 3 m from the burn boundaries at the cardinal points.

### **2.3.3 Data Analysis**

Species were grouped into native, non-native (excluding agronomic), and agronomic species. Total species richness, non-native (excluding agronomic) species richness, and Shannon-Weiner diversity indices ( $H'$ ) were also calculated to compare community indices. Data were analyzed using the aov function in R x64 v2.14.2, and Tukey's post-hoc test for differences among treatments if there were more than 2 treatments. Paired t-tests were performed on soil nutrient data within years. If necessary, data were transformed using  $\log(n+1)$  and tested for normality and equivalence of variance. Data were blocked by pile burn identity and site. Significance level was set at  $\alpha=0.05$ .

## 2.4 Results

### 2.4.1 Nutrients

In this experiment I found that red-burned soil had higher plant-available nutrients than the surrounding unburned soil for both the first and the second year after burning. Nutrient supply values for the unburned soil were different between years (Table 2-2); for example, NO<sub>3</sub>-N supply rates were an order of magnitude higher in unburned soil in 2009 compared to 2008 (Table 2-3 and 2-4). Thus, only the relative differences in supply values between unburned and red burned soil are comparable between years, not the absolute differences. Generally, nutrient supply values increased with increasing severity of burn (Table 2-2). Specifically, in 2008 black-burned soils had higher nutrient supply than unburned soil for NO<sub>3</sub><sup>-</sup>-N, B(OH)<sub>4</sub><sup>-</sup>-B, Fe<sup>3+</sup>, Mn<sup>2+</sup>, and SO<sub>4</sub><sup>-</sup>-S (Table 2-3). Red-burned soils had higher nutrient supply than black-burned soils in 2008 for NH<sub>4</sub><sup>+</sup>-N, K<sup>+</sup>, Fe<sup>3+</sup>, Mn<sup>2+</sup>, and SO<sub>4</sub><sup>-</sup>-S (Table 2-3). Over both study years, red-burned soils always had higher nutrient supply than unburned soil, with the exception of B(OH)<sub>4</sub><sup>-</sup>-B (Tables 2-3 and 2-4). Ammonium was approximately five times higher in the red-burned soil than in unburned soil in 2008 and approximately three times higher in 2009. Nitrate was almost nine times higher in red burned soil than unburned soil in the first year, but this increased to nearly 19 times higher two growing seasons after burning. Boron was the only nutrient to have higher supply in red-burned soil in 2008 but lower supply in 2009.

Table 2-2. Summary of 2008 and 2009 ANOVA for burned versus unburned nutrient supply values at Noble Creek site. Values are significant at p<0.05 (bold).

Nutrient	Df	2008		Df	2009	
		F-value	Pr(>F)		F-value	Pr(>F)
NH <sub>4</sub> <sup>+</sup> -N	2	11.1	<b>&lt;0.001</b>	1	17.14	<b>&lt;0.001</b>
NO <sub>3</sub> <sup>-</sup> -N	2	8.441	<b>0.002</b>	1	102.8	<b>&lt;0.001</b>
B(OH) <sub>4</sub> <sup>-</sup> -B	2	8.311	<b>0.002</b>	1	11.91	<b>0.002</b>
Mg <sup>2+</sup>	2	4.691	<b>0.018</b>	1	35.63	<b>&lt;0.001</b>
Ca <sup>2+</sup>	2	3.479	<b>0.046</b>	1	9.13	<b>0.006</b>
K <sup>+</sup>	2	12.9	<b>&lt;0.001</b>	1	31.16	<b>&lt;0.001</b>
H <sub>2</sub> PO <sub>4</sub> <sup>-</sup> -P	2	4.533	<b>0.021</b>	1	49.89	<b>&lt;0.001</b>
Fe <sup>3+</sup>	2	11.88	<b>&lt;0.001</b>	1	36.89	<b>&lt;0.001</b>
Cu	-	-	-	1	43.81	<b>&lt;0.001</b>
Mn <sup>2</sup>	2	60.06	<b>&lt;0.001</b>	1	106	<b>&lt;0.001</b>
SO <sub>4</sub> <sup>-</sup> -S	2	56.03	<b>&lt;0.001</b>	1	65.55	<b>&lt;0.001</b>
Al <sup>3+</sup>	2	4.5	<b>0.021</b>	1	19.56	<b>&lt;0.001</b>
Residuals	26			26		

Table 2-3. Mean ( $\pm 1$  SE) nutrient supply values (mg/10cm<sup>2</sup>) for 2008, Noble Creek site. Nutrients with the same letters indicate no significant difference between treatments at  $p < 0.05$ . Multiplication factor indicates the ratio in nutrient supply values (red-burned/unburned soil).

Nutrient	Unburned (mg/10cm <sup>2</sup> )	Black-burned (mg/10cm <sup>2</sup> )	Red-burned (mg/10cm <sup>2</sup> )	Multiplication factor (red-burned/unburned)
NH <sub>4</sub> <sup>+</sup> -N	3.45 (0.66) a	3.41 (1.04) a	17.36 (2.32) b	5.0
NO <sub>3</sub> <sup>-</sup> -N	6.40 (1.43) a	58.48 (34.0) b	55.96 (27.78) b	8.7
B(OH) <sub>4</sub> <sup>-</sup> -B	1.10 (0.04) a	1.44 (0.08) b	1.44 (0.10) b	1.3
Mg <sup>2+</sup>	201.64 (17.57) a	235.60 (25.83) ab	363.80 (60.07) b	1.8
Ca <sup>2+</sup>	910.96 (73.40) a	1123.86 (126.11) ab	1368.71 (144.30) b	1.5
K <sup>+</sup>	163.48 (17.95) a	223.56 (27.41) a	398.27 (50.52) b	2.4
H <sub>2</sub> PO <sub>4</sub> <sup>-</sup> -P	6.43 (1.73) a	6.20 (0.96) ab	14.16 (3.81) b	2.2
Fe <sup>3+</sup>	3.19 (0.37) a	7.12 (2.97) b	11.49 (1.64) c	3.6
Mn <sup>2+</sup>	1.58 (0.17) a	4.12 (1.10) b	29.24 (5.14) c	18.5
SO <sub>4</sub> <sup>-</sup> -S	12.66 (0.88) a	45.64 (8.64) b	201.60 (33.01) c	15.9
Al <sup>3+</sup>	14.33 (0.51) a	16.34 (0.82) ab	17.29 (0.77) b	1.2

Table 2-4. Mean ( $\pm 1$  SE) nutrient supply values (mg/10cm<sup>2</sup>) for 2009, Noble Creek site. All values are significantly different between treatments,  $p < 0.05$  (Table 2). Multiplication factor indicates the ratio in nutrient supply values (red-burned/unburned soil).

Nutrient	Unburned (mg/10cm <sup>2</sup> )	Red-burned (mg/10cm <sup>2</sup> )	Multiplication factor (red-burned/unburned)
NH <sub>4</sub> <sup>+</sup> -N	1.67 (0.24)	4.97 (1.12)	3.0
NO <sub>3</sub> <sup>-</sup> -N	18.53 (3.22)	348.80 (61.10)	18.8
B(OH) <sub>4</sub> <sup>-</sup> -B	1.29 (0.10)	1.88 (0.14)	0.7
Mg <sup>2+</sup>	327.37 (24.08)	580.29 (40.03)	1.8
Ca <sup>2+</sup>	1389.97 (62.80)	1790.91 (129.64)	1.3
K <sup>+</sup>	224.91 (16.62)	494.94 (50.79)	2.2
H <sub>2</sub> PO <sub>4</sub> <sup>-</sup> -P	8.40 (1.28)	25.74 (2.81)	3.1
Fe <sup>3+</sup>	5.34 (1.13)	19.13 (3.20)	3.6
Cu <sup>2+</sup>	0.29 (0.09)	1.16 (0.15)	4.0
Mn <sup>2</sup>	4.50 (0.83)	39.57 (4.63)	8.8
SO <sub>4</sub> <sup>-</sup> -S	37.58 (26.55)	296.70 (46.15)	7.9
Al <sup>3+</sup>	32.60 (0.81)	40.63 (1.77)	1.2

## 2.5 Experimental Treatments

Cover and seed treatments significantly affected the total vegetation cover (Table 2-5), where total vegetation cover was higher for the agronomic seed addition than for no seed addition or native seed addition (Figure 2-3), and total vegetation cover was increased by the cover treatment (Figure 2-4). The only significant main effect on non-native vegetation cover was the seed treatment (Table 2-5), where the

agronomic seed addition had lower non-native vegetation cover than either native seed addition or no seed addition (Figure 2-3). For non-native vegetation cover, cover and AMF treatment also interacted to promote non-native ground cover in the presence of cover and AMF (Figure 2-5). The only significant effect on native vegetation cover was the seed treatment (Table 2-5), where native seed addition had higher native vegetation cover than either the agronomic seed addition or no seed addition. The cover and seed treatments affected agronomic vegetation cover (Table 2-5), where agronomic vegetation cover was higher for agronomic seed addition than for no seed addition or native seed addition (Figure 2-3), and total vegetation cover was increased by the cover treatment (Figure 2-4). Figures of non-significant findings are presented in Appendix A.

Table 2-5. Summary of 3-way ANOVA for total vegetation cover, non-native vegetation cover, native vegetation cover, and agronomic vegetation cover. Data were blocked by site (Site) and individual burn scar (Pile Burn). Values are significant at  $p < 0.05$  (bold).

	Vegetation cover by groups of interest								
	Total vegetation cover			Non-native vegetation cover		Native vegetation cover		Agronomic vegetation cover	
	Df	F value	Pr(>F)	F value	Pr(>F)	F value	Pr(>F)	F value	Pr(>F)
Site	2	4.302	<b>0.016</b>	3.579	<b>0.032</b>	0.852	0.430	0.95	0.390
Pile Burn	34	1.052	0.412	1.508	0.064	0.882	0.653	1.227	0.221
Cover	1	8.539	<b>0.004</b>	1.386	0.242	1.557	0.215	4.981	<b>0.028</b>
Seed	2	18.950	<b>&lt;0.001</b>	4.179	<b>0.018</b>	135.246	<b>&lt;0.001</b>	163.629	<b>&lt;0.001</b>
AMF	1	0.352	0.554	0.204	0.653	1.184	0.279	0.095	0.759
Cover x Seed	2	1.518	0.225	1.529	0.222	0.033	0.967	1.552	0.217
Cover x AMF	1	1.021	0.315	5.427	<b>0.022</b>	2.355	0.128	1.605	0.209
Seed x AMF	2	1.065	0.349	0.062	0.940	1.140	0.324	0.282	0.755
Cover x AMF x Seed	2	1.195	0.308	0.654	0.523	0.645	0.527	0.396	0.674
Residuals	90								

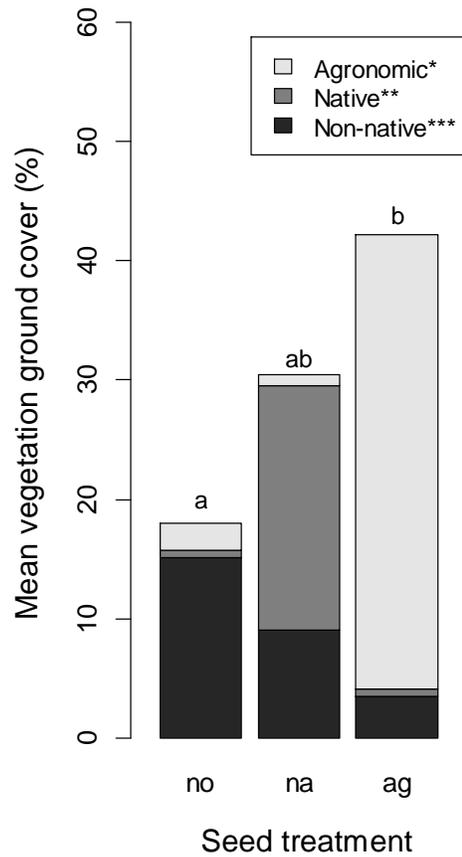


Figure 2-3. The effect of seed addition on total vegetation cover. Bars with the same letters indicate no significant difference among treatments for total vegetation cover ( $p < 0.05$ , Tukey's post-hoc test). \*Agronomic vegetation cover is higher for agronomic seed added than the no seed and native seed added ( $p < 0.05$ , Tukey's post-hoc test). \*\*Native vegetation cover is higher for the native seed added than the no seed and agronomic seed added ( $p < 0.05$ , Tukey's post-hoc test). \*\*\*Non-native vegetation cover is significantly different between no seed and agronomic seed only ( $p < 0.05$ , Tukey's post-hoc test). no=no seed added; na= native seed added; ag= agronomic seed added.

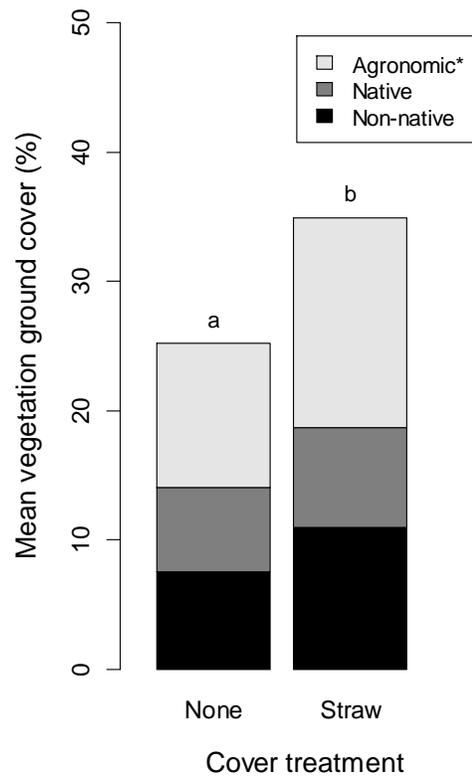


Figure 2-4. The effect of cover treatment on total vegetation cover. Bars with the same letters indicate no significant difference between treatments for total cover ( $p < 0.05$ ). \*Agronomic vegetation cover is significantly different between treatments ( $p < 0.05$ ).

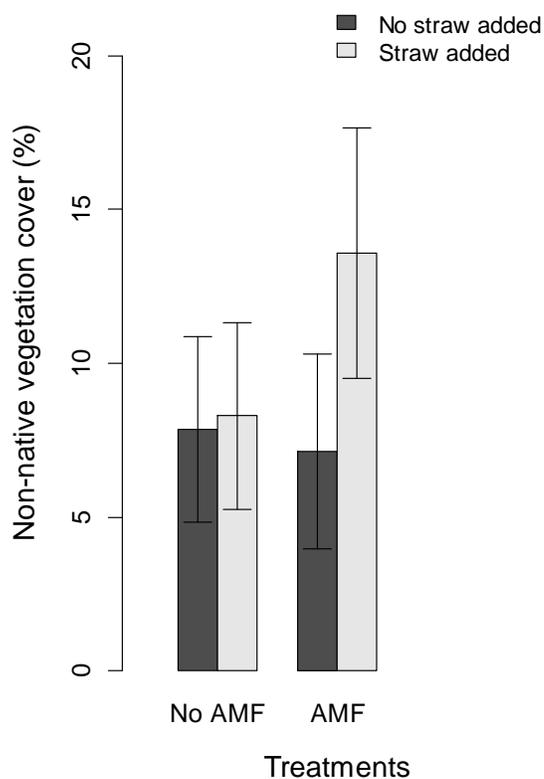


Figure 2-5. Non-native vegetation cover interaction between soil cover and addition of AMF. Data displayed as mean ( $\pm 1$  SE). Cover and AMF addition combine to increase non-native vegetation cover.

Total vegetation cover (Figure 2-6a) and non-native vegetation cover (Figure 2-6b) also varied significantly among sites, with the Barnhartvale site having the highest total vegetation cover and non-native vegetation cover, and the Noble Creek site having the lowest.

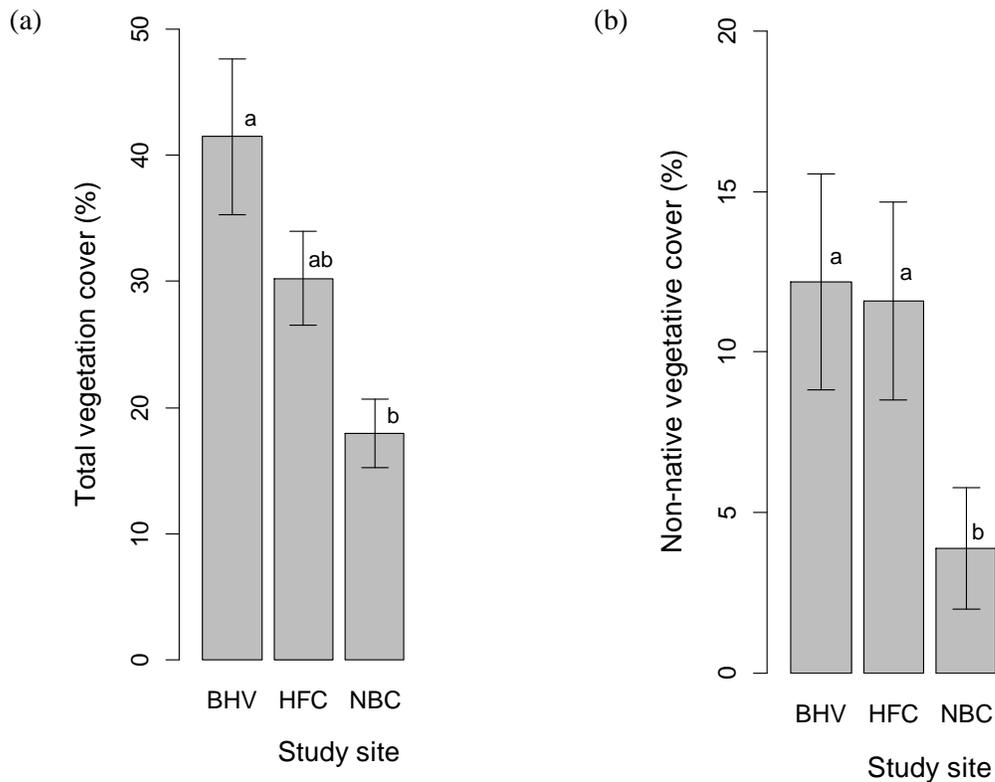


Figure 2-6. Mean ( $\pm 1$  SE) (a) total vegetation cover, and (b) non-native vegetation over study sites. Bars with the same letter indicate no significant difference among treatments ( $p < 0.05$ ). BHV=Barnhartvale site, HFC=Heffley Creek site, NBC=Noble Creek site.

The cover and seed treatments significantly affected the total species richness (Table 2-6), where total species richness was higher when straw cover was added than when it was not (Figure 2-7a), and total species richness was higher with the agronomic and native seed added than when no seed was added (Figure 2-7b). The only treatment to affect non-native species richness was seed addition (Table 2-6), with only the agronomic seed addition reducing non-native species richness (Figure 2-8). Shannon-Weiner diversity ( $H'$ ) was significantly affected by cover and seed treatments (Table 2-6), where  $H'$  followed the same pattern as total species richness, being higher when cover was added than when it was not (Figure 2-9a), and being higher when agronomic and native seed were added than when no seed was added (Figure 2-9b). The Shannon-Weiner diversity index also had a 3-way interaction for cover x AMF x seed treatments (Table 2-6).

Table 2-6. Summary of 3-way ANOVA for total species richness, non-native species richness, Shannon-Weiner diversity ( $H'$ ). Data were blocked by site (Site) and individual burn scar (Pile Burn). Values are significant at  $p < 0.05$  (bold).

	Total species richness			Non-native species richness		Shannon-Weiner diversity ( $H'$ )	
	Df	F value	Pr(>F)	F value	Pr(>F)	F value	Pr(>F)
Site	2	0.933	0.397	0.037	0.964	0.274	0.761
Pile Burn	34	1.599	<b>0.041</b>	1.880	<b>0.010</b>	1.508	0.064
Cover	1	10.777	<b>0.001</b>	3.588	0.061	6.022	<b>0.016</b>
Seed	2	38.768	<b>&lt;0.001</b>	5.317	<b>0.007</b>	30.769	<b>&lt;0.001</b>
AMF	1	0.191	0.663	0.102	0.750	0.140	0.709
Cover x Seed	2	2.105	0.128	2.036	0.137	2.296	0.107
Cover x AMF	1	0.318	0.574	3.624	0.060	0.038	0.845
Seed x AMF	2	1.181	0.313	0.338	0.714	0.636	0.532
Cover x AMF x Seed	2	2.852	0.063	1.073	0.346	3.152	<b>0.048</b>
Residuals	90						

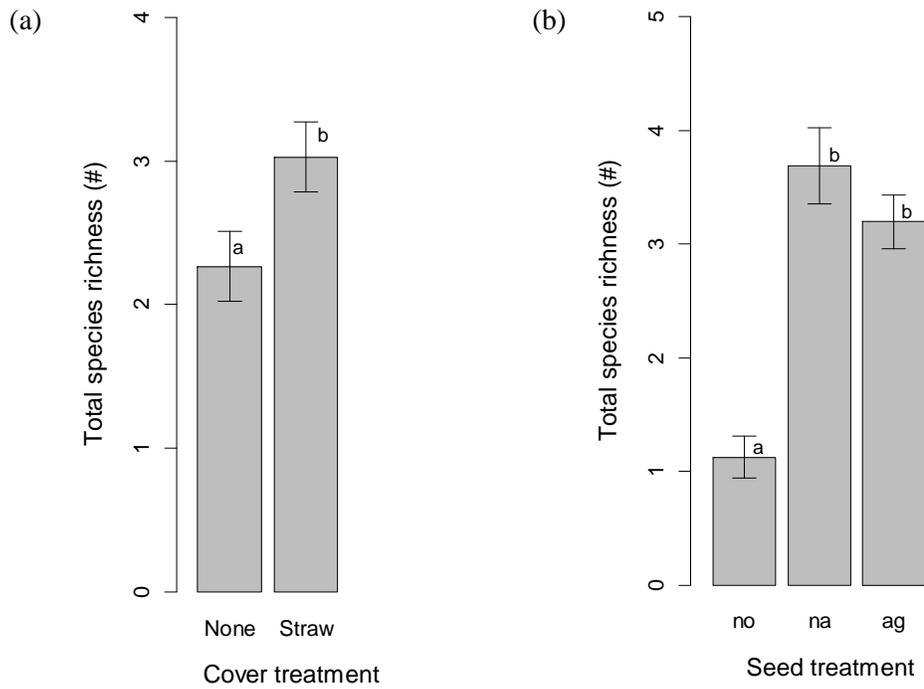


Figure 2-7. (a) The effect of cover treatment on total species richness (mean  $\pm$  1 SE), and (b) the effect of seed addition on total species richness (mean  $\pm$  1 SE). Bars with the same letter indicate no significant difference between treatments for species richness ( $p < 0.05$ ). no=no seed added; na= native seed added; ag=agronomic seed added.

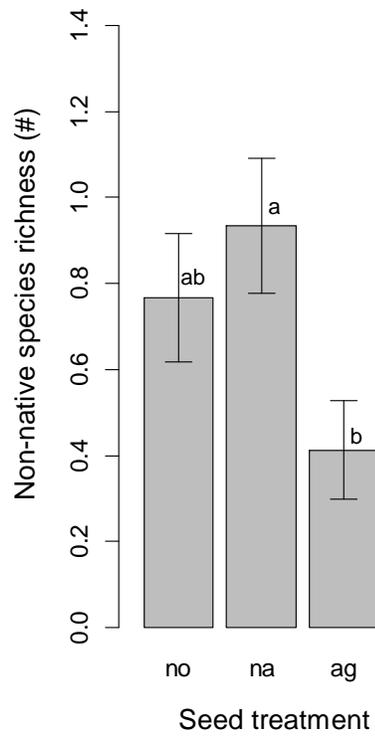


Figure 2-8. The effect of seed addition on non-native species richness (mean  $\pm$  1 SE). Bar with the same letters indicate no significant difference between treatments for total cover ( $p < 0.05$ ). no=no seed added; na=native seed added; ag=agronomic seed added.

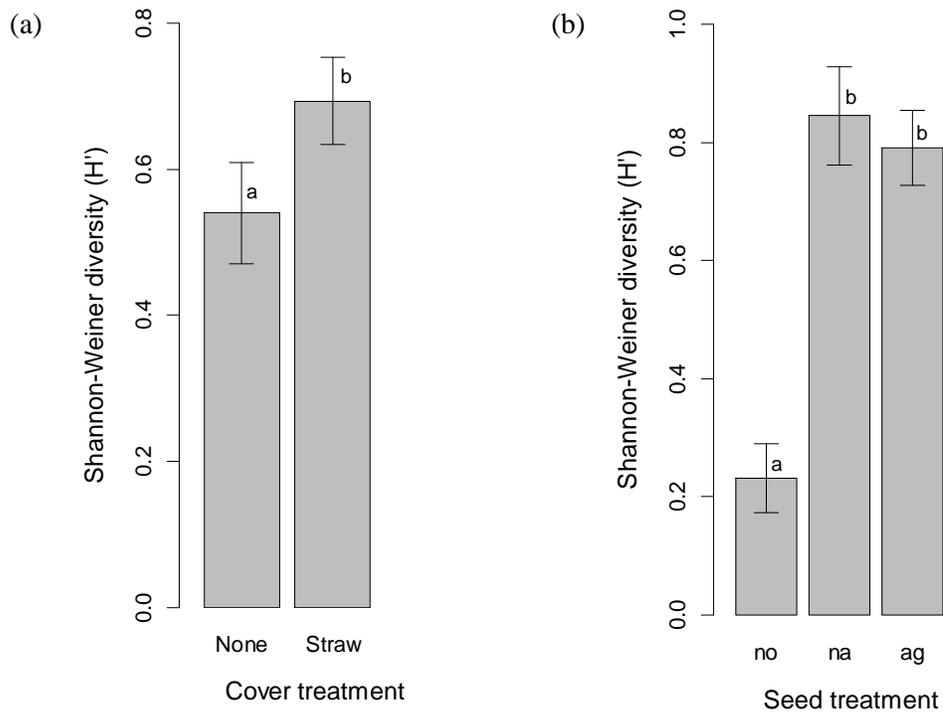


Figure 2-9. (a) The effect of cover treatment on Shannon-Weiner diversity ( $H'$ ) (mean  $\pm$  1 SE), and (b) the effect of seed addition on  $H'$  (mean  $\pm$  1 SE). Bars with the same letters indicate no significant difference between treatments for  $H'$  ( $p < 0.05$ ). no=no seed added; na=naive seed added; ag=agronomic seed added.

Photographic examples of sampled treatment plots are shown in Figures 2-11 through 2-15.



Figure 2-10. Native seed treatment plot, with straw added but no AMF inoculum, July 2009



Figure 2-11. Agronomic seed treatment plot, with cover and AMF inoculum addition, July 2009. Note the large-stature *B. tectorum* (brown) surrounding treatment vegetation (green).



Figure 2-12. Native seed treatment plot, no cover or AMF inoculum added, July 2009. Orange colours on post indicate outer edges/corner of plot.



Figure 2-13. Native seed treatment plot, cover added but no AMF inoculum, July 2009



Figure 2-14. AMF inoculum added treatment plot, no straw or seeds added, July 2009

### 2.5.1 Species

Forty-four species were identified in the unburned areas, and 36 species, including those which were seeded, were identified in treatment plots (Table 7; Appendix A). Twenty-two species were common between unburned areas and treatment plots. Many of these species were non-native including cheatgrass, Japan brome (*B. japonicus* Thunb.), and corn brome (*B. squarrosus* L.). While Japan brome was relatively uncommon in the study area (2.5% of unburned plots), both corn brome and cheatgrass were widespread (46.3% and 35.0% of unburned plots respectively, compared with 7.2% and 11.6% of all treatment plots). However, the growth form of these species varied between unburned and burned areas. In the unburned plots, these *Bromus* spp. were mostly very short plants with few inflorescences; i.e., they did not visibly comprise a large portion of the ecosystem. In the burned soils, independent of treatment type, species' cover was typically one or two large plants with many inflorescences (Figure 2-16).



Figure 2-15. Tall stature *Bromus tectorum* plant on red-burned soil, control plot

The remaining non-seeded species identified only in the treatment plots were non-native. These included species from the Brassicaceae or Chenopodiaceae family including Russian thistle (*Kochia scoparia* (L.) Schrad.), tall tumble-mustard (*Sisymbrium altirrsum* L.), and Loesel's tumble-mustard (*Sisymbrium loeselli* L.). Multiple non-native species were identified in the unburned areas, but not in treatment plots, including species from the Poaceae and Asteraceae family such as smooth brome (*Bromus inermis* Leyss.), diffuse knapweed (*Centaurea diffusa* Lam.), oxeye daisy (*Leucanthemum vulgare* Lam.), and Dalmation toadflax (*Linnaria genistifolia* subs. *dalmatica* (L.) Maire& Petitmengin).

## **2.6 Discussion**

Pile burning created soil with elevated nutrient levels, and vegetation communities initially devoid of vegetation. Both factors have implications for restoration of vegetation communities, and the susceptibility of these communities to colonization by non-native species.

Immediate increases to soil nutrients are commonly observed after burning (Certini 2005), caused largely by the combustion of organic matter. While soil nutrients may eventually reach or fall below pre-burn levels due to nutrient loss primarily through leaching and erosion (Creech et al. 2011), this temporary pulse would make systems more susceptible to invasion (Davis et al. 2000). However, nutrients are

increasingly volatilized with increasing burn severity, and red-burned soils may not have sufficient nutrients to make them susceptible to invasion. Here I showed that red-burned soil had higher plant-available nutrients than the surrounding unburned soil for both the first and the second year after burning. In particular, nitrate was almost nine times higher in red-burned soil than unburned soil in the first year, but this increased to nearly 19 times higher two growing seasons after burning. Soil nitrate typically increases after burning, but can lag for weeks or months as nitrifying bacteria respond to the increase in ammonium and soil pH (Certini 2005). The relative difference in soil potassium also increased approximately 50% from 2008 to 2009, possibly resulting from potassium becoming more available as sodium leaches from the soil. Only the relative levels of boron did not follow this trend, with boron being higher in burned than unburned soils in 2008 but lower in 2009. Boron can be a limiting growth factor in many soils in the interior of British Columbia (Carter and Brockley 1990). That it is depleted from the soil so quickly after burning may restrict native plant long-term recovery to severely burned soils.

These findings differ from Hebel et al. (2009), who found that black-burned soil had higher nutrient levels than red-burned soil. Here, I found that nutrient values were either higher in red-burned soil or did not differ from the black-burned soil. One cause for this discrepancy may be the time of burn (i.e., summer vs. winter). Frozen soils during winter may provide some protection from nutrient loss during burning. The latent heat of vaporization of water would temper the heat-induced soil changes. Another possible explanation for this discrepancy would be differing fuel loads between this study and those of Hebel et al. (2009). The red soil of that study was most likely created from single, fallen logs. The red soil of my study was created during larger pile burns with heavier fuel loading. Heavier fuel loading can lead to greater increases of released nutrients, as a result of burning increasing pH and available forms of cations (Feller 1988, DeBano et al. 1998, Certini 2005, Creech et al. 2011). These two hypotheses are potentially conflicting and would require further investigation.

The immediate increases to soil nutrients and the resultant susceptibility to invasion would indicate that restoration efforts are warranted. My treatments had mixed success in reducing the colonization of burn scars by invasive species. My findings supported the hypothesis that the early establishment of agronomic species, but not the early establishment of native species, limited non-native species establishment and growth, although there was no significant difference between native and agronomic vegetation cover. The broad scale seeding of agronomic species post-wildfire is a common restoration or rehabilitation technique, although these programs have had mixed success in suppressing invasive species (Peppin et al.

2010). However, agronomic species generally tend to be more effective than native species, particularly when the seeded species produce high cover, a finding that is supported here.

As a management tool, agronomic species are much more easily obtained than native species, and will not contaminate the native gene pool (Knapp and Rice 1994). Currently, there are no native seed nurseries in British Columbia; any native seed used in restoration projects would either need to be collected onsite prior to disturbance, or would have to be purchased from a native seed nursery located elsewhere. The first restoration technique would require advanced knowledge of the disturbance, plus significant effort to collect the seed.

My findings tentatively support the hypothesis that the presence of soil cover will improve plant establishment and growth. The presence of soil cover increased plant cover for agronomic species and for total cover, and increased species richness and the Shannon-Weiner diversity index. These results suggest that soil cover creates conditions that are unfavourable to native and non-native species, but favourable to agronomic species. This finding is counter to those of multiple other studies suggesting that plant litter is highly important in the structure and function of grassland communities (e.g., Lamb 2008). While these studies investigated multiple aspects of plant litter (nutrient cycling, carbon, etc.), my finding suggests that the cover aspect of litter is not a significant contributor to native or invasive plant community composition and aboveground cover, at least on soils affected by intense heat due to pile burning. This result is somewhat surprising but may suggest that other abiotic or biotic conditions limit growth, rather than soil cover. There are two possible explanations for this finding. The first is that the amelioration provided by cover was insufficient to affect the establishment and growth of native and non-native species. The second is that establishment and growth of these plant groups was independent of affects that soil cover would ameliorate, such as high soil temperatures, high solar insolation, and desiccating effects of wind.

My findings do not support the hypothesis that commercial AMF inoculum would improve the establishment and growth of native species. The addition of commercial AMF did not have any significant effect on cover estimates for any of the three plant groups tested, species richness or diversity, although it did interact with cover to promote non-native vegetative cover. The commercial inoculant had a non-significant positive trend in non-native cover and a non-significant negative trend in native and agronomic cover. Several mechanisms may explain this lack of significant response: (1) AMF inoculum did not contain active spores; (2) spores migrated off-plot during the winter season; (3) AMF spores did not survive the winter season; and (4) the AMF inoculum used was inappropriate for the soil conditions.

Results from Chapter 3 suggest that the AMF inoculum did contain active spores, and the secure cover would have prevented some of the spores from migrating off-plot. Of the remaining possible explanations, the last is most likely. While the death or grazing of spores cannot be ruled out, other studies have also found that commercial AMF inoculum is not always effective when used in a field setting (Rowe et al. 2007, White et al. 2008), possibly because AMF is less generalist in nature than previously assumed.

The use of commercial AMF inoculum is controversial (Schwartz et al. 2006). This technology generally involves the application of, at most, a few AMF species with little to no intra-specific genetic variability. This technology also assumes a highly generalist mutualism between AMF and their host plant species, when the relationship between AMF and their host plant species varies from highly mutualistic to neutral to highly parasitic (Klironomos 2003). The broad-scale application of limited AMF species and genomes may therefore have positive, neutral, or negative effects on any species. Individual plant responses to the inoculum are difficult to predict prior to investigation. Controlled experiments have shed doubt on the efficacy of commercially-available AMF inoculum (e.g., Rowe et al. 2007, e.g., White et al. 2008), even hypothesizing that commercial AMF mixes are enhanced with nutrients.

Researchers have also raised the concern over the global movement of mycorrhizal fungi (Schwartz et al. 2006). They argue that the movement of mycorrhizal fungi can potentially introduce new invasive species into ecosystems, and that the consequences of these introductions are poorly understood. Instead, they recommend using native inoculum whenever possible. In the research described here, the introduction of novel AMF genotypes and species into a restoration system did not have any discernible effect on plant cover. However, the presence of native inoculum has been shown to be beneficial to restoration projects where it has been available (Korb et al. 2004, White et al. 2008). Given the short turn-around time of some restoration work (e.g., restoring vegetative cover to disturbed areas to prevent erosion and invasive species spread) it may be prudent to consider creating a stockpile of native AMF.

The species that naturally regenerated on burns were largely non-native, primarily composed of non-mycorrhizal (Brassicaceae, Chenopodiaceae) and facultative mycorrhizal (*Bromus* spp.) species (Wang and Qiu 2006). Those from non-mycorrhizal families were primarily found only on treatment plots. Multiple non-native species, primarily from the Poaceae and Asteraceae families, were found only in the unburned surrounding area, suggesting that the burns are host to some, but not all, non-native species. Other research has found that mycorrhizal colonization of roots can be low in post-slash burn

environments (Korb et al. 2004; Esquilin et al. 2007), and, combined with my findings here, would suggest that post-pile burn colonization would favour non- and facultative-mycorrhizal species.

Percent vegetation cover of treatment plots was generally higher than what was observed in similar studies (Haskins and Gehring 2004, Korb et al. 2004, Creech et al. 2011). Although differences in climatic regimes and site factors such as soils and slope among the study sites may contribute to some of this difference, the most likely higher contributing may be the presence of an 'intact' vegetation cover in the areas surrounding the burns providing a ready seed source, possibly combined with the sharp increases to soil nutrients created when burning frozen soils. Disturbed areas are often seed-limited (Korb et al. 2004, White et al. 2008), and the ready supply of propagules from surrounding vegetation contributes to rapid recolonization. The surrounding vegetation in similar studies was burned along with the slash piles; hence, there were fewer recruitment opportunities.

## **2.7 Conclusion**

The findings here, in comparison with similar studies of restoration of pile burn scars suggests that pile burning during winter, along with the non-burning of surrounding vegetation, creates areas that are susceptible to high cover of non-native species. Restoration efforts should be directed at these sites as soon as possible after burning to ameliorate the effects of invasive species colonization.

The amelioration treatments tested in this research had mixed success in reducing non-native species cover on the red soil of pile burn scars. The most effective treatment in reducing non-native species cover was the seeding of agronomic species, although the high seeding density used may prevent these findings from being applicable in larger disturbed areas. Commercial AMF inoculum was an ineffective treatment, and its use should be avoided in field environments until a better understanding of host specificity is attained.

## 3 Exploring Limiting Factors to Plan Growth on Red-burned Soil

### 3.1 Introduction

Fire, whether natural or anthropogenic, controlled or wild, is intrinsically linked with the vegetation communities where it occurs. In many vegetation communities, fire is also intrinsically linked to the spread and persistence of invasive species. Much research has been directed at understanding fire's effects on invasive species (e.g., Keeley 2000, e.g., Hunter et al. 2006, e.g., Fornwalt et al. 2010). Generally, medium to high severity fires can promote the spread and persistence of invasive species (Keeley 2000, Levine 2003, Brooks et al. 2004). The question remains whether the highest severity burns, those where oxidation has occurred to turn the soil red, are susceptible to invasion.

Invasive species are early colonizers of post-burn environments in many types of ecosystems and across fire intensities (e.g., Fornwalt et al. 2010). Thus, red-burned soil may be susceptible to invasion (Hebel et al. 2009). One possible mechanism for invasion on red-burned soils would involve increased nutrient availability (Chapter 2). The resource fluctuation hypothesis postulates that a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources (Davis et al. 2000). Invasive species, often R-type ruderals, are able to capitalize on these resource pulses more effectively than other species, which may be C-type competitors, or S-type stress-tolerators (Grime 1977). Relatively short-term nutrient increases in black-burned soil, primarily caused by the combustion of organic matter, are a well-known phenomenon (McNabb and Cromack Jr 1990, Neary et al. 1999, Certini 2005). Red-burned soils may also initially have high nutrient availability compared to unburned soils (Chapter 2), which may lead to increased success of invasive species.

Another possible mechanism for invasion on these soils, particularly in arid environments, may be water. Burned soils are hydrophobic, limiting water infiltration into the soil (Neary et al. 1999). The absence of living and dead vegetative cover can lead to increases in soil temperatures (Neary et al. 1999), and may increase evaporation/evapotranspiration rates (Wetzel and Chang 1987). Again, the resource fluctuation hypothesis (Davis et al. 2000) would predict that an addition of water (i.e., a resource pulse) in these conditions would favour invasive over native species.

The depletion of soil biota in post-burn environments may also contribute to vegetation community changes. Although vegetation responses in these environments may be related to the near depletion of the

entire soil biota (Esquelin et al. 2007), many restoration programs have only involved the re-introduction of arbuscular mycorrhizal fungi (AMF) (e.g., Korb et al. 2004), largely because the AMF-plant relationship is perceived to be a universally beneficial mutualism (Wang and Qiu 2006). Often, the goal of restoration programs in post-burn soils is to enhance native plant establishment and growth. However, over 80% of land plants form relationships with AMF (Malloch et al. 1980), and it is reasonable to assume this includes many invasive species. While research has compared the efficacy of AMF inoculum on unburned or black-burned soil (e.g., Rowe et al. 2007, e.g., White et al. 2008), none have evaluated inoculum efficacy on red-burned soil.

The experiment described in this chapter was designed to test the following hypotheses:

- 1) Different plant groups will show differential biomass responses to the increased nutrient supply available in red-burned soils because species with R-type characteristics (i.e., invasive) are able to capitalize on resource pulses better than species with C- or S-type characteristics (i.e., agronomic, native);
- 2) Different plant groups will show differential biomass responses to increased water on red-burned soil, again, because groups with R-type characteristics (i.e., invasive) are able to capitalize on resource pulses better than groups with C- or S-type characteristics (i.e., agronomic, native); and
- 3) AMF inoculum will increase aboveground plant biomass on red-burned soil because the addition of AMF will allow plants to more efficiently make use of resources.

## **3.2 Methods**

### **3.2.1 Experimental Design**

The experiment was carried out in the research greenhouse at Thompson Rivers University in Kamloops, British Columbia. The experiment was a full factorial design, with 2 levels of AMF addition (commercial inoculum added, no commercial inoculum added), 2 levels of water (high, low), and 3 levels of species (native, agronomic, and invasive), nested within 2 levels of burn severity (red burned soil, unburned forest floor). Each treatment had 6 replications for a total of 144 ten-cm<sup>2</sup> pots. Response variables were aboveground plant biomass.

For the burn severity treatment, a randomized block design was used to select soil from 6 pile burns (see Chapter 2). Soil was then brought to the greenhouse for application of remaining treatments. Each pile burn had 12 individual soil samples taken in red-burned soil and 12 individual soil samples taken in the

surrounding unburned soil. The AMF, water, and species treatment level were distributed evenly among individual pile burns (i.e., treatment replication within an individual pile burn was kept to a minimum to avoid bias).

### 3.2.2 Soil Collection

Soil was collected from a site located adjacent to the Noble Creek Site (NBC) described in Chapter 1; all burns were unseeded and undisturbed since burning occurred. The soil collection site was located at 50°50'40"N 120°18'30"W, 475 masl, and approximately 1.5 km N of NBC site, with an eastern aspect. This site was located in the Ponderosa Pine very hot, dry (PPxh) Biogeoclimatic Zone, which is characterized as a dry forest zone (Meidinger and Pojar 1991). This region has a semi-arid continental climate with warm, dry summers and cool, dry winters. Mean annual precipitation ranges between 250 – 400 mm and the mean annual temperature ranges between 5.4 and 9.0 °C (Lloyd et al. 1990). Soils of this BEC Zone are typically Chernozemic or Brunisolic (Soil Classification Working Group 1998). Ecosystems in the PPxh subzone consist of Ponderosa pine (*Pinus ponderosa* C. Lawson), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love), rough fescue (*Festuca campestris* Rydb.) and big sagebrush (*Artemisia tridentata* Nutt.).

During the winter of 2007/2008, the soil collection site was subject to a fuel thinning treatment in which mature trees were harvested, piled on site, and burned. Thinning and burn treatments occurred when the soils were frozen. Burn scars were left unseeded and undisturbed since time of burn.

Each pile burn had 12 individual soil samples taken in red-burned soil and 12 individual soil samples taken in the surrounding unburned soil. Soil was collected in a vertical column, leaving the soil profile intact, in June of 2008, and placed in 10 cm<sup>2</sup> pots. Soil was collected from randomized locations both inside and outside of burn scars (Figure 3-1); the soil vertical profile was left as intact as possible during soil collection. Inside the burn scars, soil was collected where the soil surface was red in colour. Undecomposed vegetative material was removed from the soil surface of the unburned soil treatment; otherwise, the organic layer was left intact. Both burned and unburned soil samples were collected at least 2 m from burn edges. Burned soil samples were collected at least 50 cm from other burned soil samples. Unburned soil samples were relatively evenly dispersed around the edge of each burn. All soil was collected in the same day, and stored in a cool, dry place until seeds were sowed, later that day.

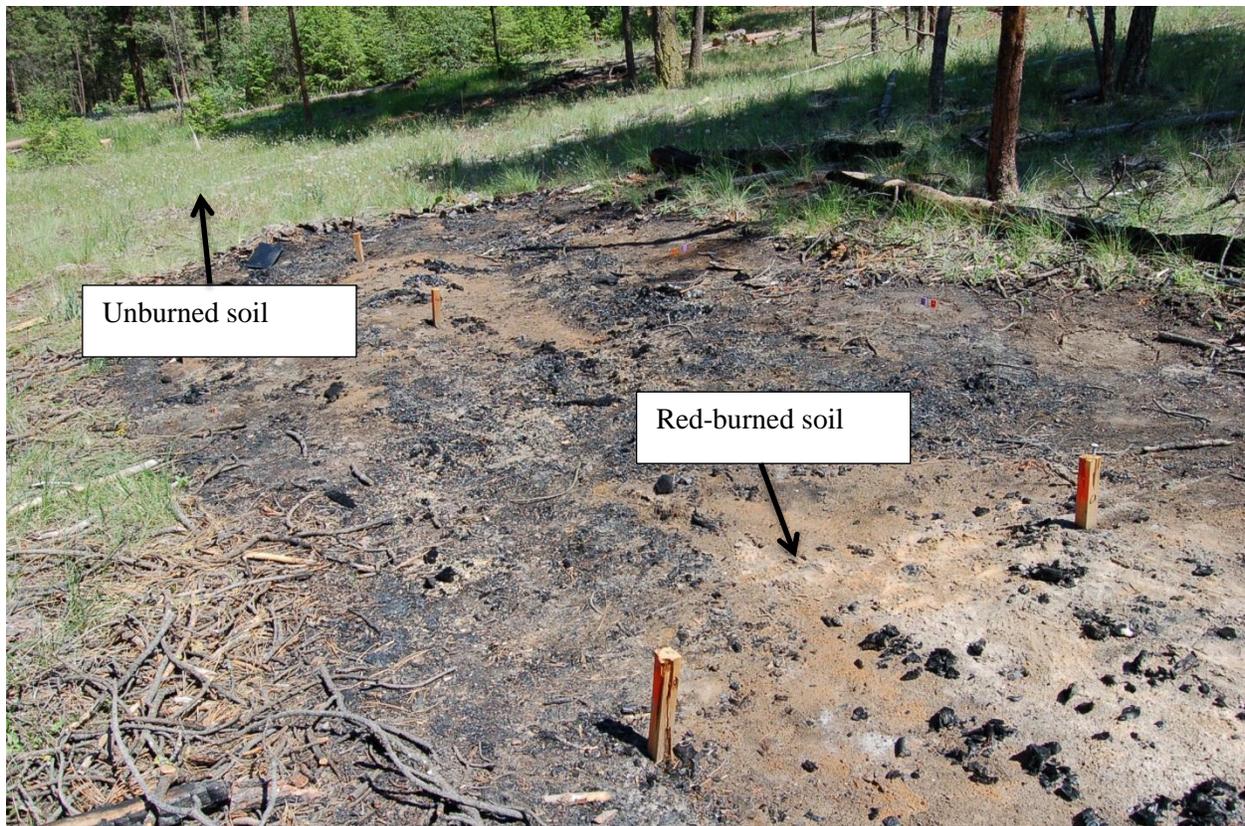


Figure 3-1. Example of soil sample site

### 3.2.3 Treatments - Plant species and AMF

The three species investigated were the native species rough fescue, the agronomic species annual ryegrass (*Lolium multiflorum* Lam.), and the invasive species cheatgrass (*Bromus tectorum* L.). These species were selected because they were either observed to grow on red-burned soil and were common components of the surrounding vegetation, or are used locally for reclamation of disturbed soils. Rough fescue and cheatgrass were both observed growing freely (i.e., self-seeded) on new pile burn scars. Annual ryegrass is known to grow under a wide range of edaphic conditions and is often used in post-wildfire reclamation seed mixes (e.g., Stella et al. 2010). Cheatgrass seeds were acquired from the general soil collection area in 2007 and stored indoors paper bags in a laboratory until sowed, and annual ryegrass and rough fescue seeds were purchased at Quality Seeds West (Surrey, BC).

The AMF inoculum was purchased from BioOrganics<sup>TM</sup> (Santa Maria, CA) and consisted of a mix of the AMF species *Glomus aggregatum*, *G. clarum*, *G. deserticola*, *G. intraradices*, *G. monosporus*, *G. mosseae*, *Gigaspora margarita*, and *Paraglomus brasilianum* at a minimum of 50 spores/cm<sup>3</sup>. The 0.5

mL of AMF application was approximately 100x higher than recommended by the manufacturer, but a higher level was chosen for practicality because it was too difficult to measure the recommended amount for 10 cm<sup>2</sup> pots. As well, the use of recommended concentrations of AMF inoculum has proven problematic in controlled greenhouse studies. One study found that using the recommended rate achieved colonization rates of 0.4 % of *Zea mays* roots, while using 10x the recommended application rate achieved colonization levels of 8.6% to 72.5% (Tarbell and Koske 2007). Therefore, a higher application rate may be more effective. AMF were added to the soil approximately one centimetre below the soil surface, and applied before the seeds were added to the pots for germination.

Two watering levels were used: 20 ml per day (Low) and at field capacity to saturation (High). These levels were observed to produce visible differences in soil moisture content.

For each seeding treatment, 10 seeds were added to each pot prior to the commencement of the watering treatment. The number of seeds that had germinated after 2 weeks were counted and everything except the 3 largest seedlings per pot were removed. If a given pot did not have 3 seedlings, then a seedling(s) was transplanted from a pot from one of its replicates. Pots were randomly placed in the temperature-controlled research greenhouse. Pot placements were re-randomized at week 2 and week 4. Temperature in the greenhouse was kept under 30°C, with average temperature being approximately 25°C. Light and humidity levels were natural; no supplemental lighting was used. Seeds were sown in June and harvested in July.

Treatments were continued for 6 weeks and then the aboveground biomass was harvested, dried in an oven at 75°C for 48 hours, and weighed. Plants were weighted individually. The response variable was aboveground biomass (per individual plant).

### **3.2.4 Data Analysis**

Data were analyzed using the aov function in R<sub>x64</sub> v2.14.2. If necessary, data were transformed using log(n+1) and tested for normality and equivalence of variance. Data were blocked by burn identity, and water level, AMF, and species identity treatments were nested within the burn treatment. The response variables were analyzed for all species considered together, and for each species individually.

Significance level was set at  $\alpha=0.05$ .

### 3.3 Results

Aboveground biomass was significantly different for water and species treatments (Table 3-1). All species had different biomass with annual ryegrass having the highest, and rough fescue having the lowest (Figure 3-2a). Watering also promoted aboveground biomass (Figure 3-2b). Interactions were observed among all factors. Because of the high degree of interaction, species' responses were individually analyzed.

Table 3-1. Summary of ANOVA for aboveground biomass. Data were blocked by individual burn scar (Pile Burn). Water, AMF, and species treatments were nested within burned or unburned status of soil (Burn). Data were considered significant at  $p < 0.05$  (bold).

	Df	F value	Pr(>F)
Pile Burn	5	0.376	0.865
Burn	1	2.705	0.865
Burn (Water)	2	32.949	<b>&lt;0.001</b>
Burn (AMF)	2	3.096	<b>0.047</b>
Burn (Species)	4	55.442	<b>&lt;0.001</b>
Burn (Water x AMF)	2	4.000	<b>0.019</b>
Burn (Water x Species)	4	8.325	<b>&lt;0.001</b>
Burn (AMF x Species)	4	5.175	<b>&lt;0.001</b>
Burn (Water x AMF x Species)	4	1.730	0.143
Residuals	305		

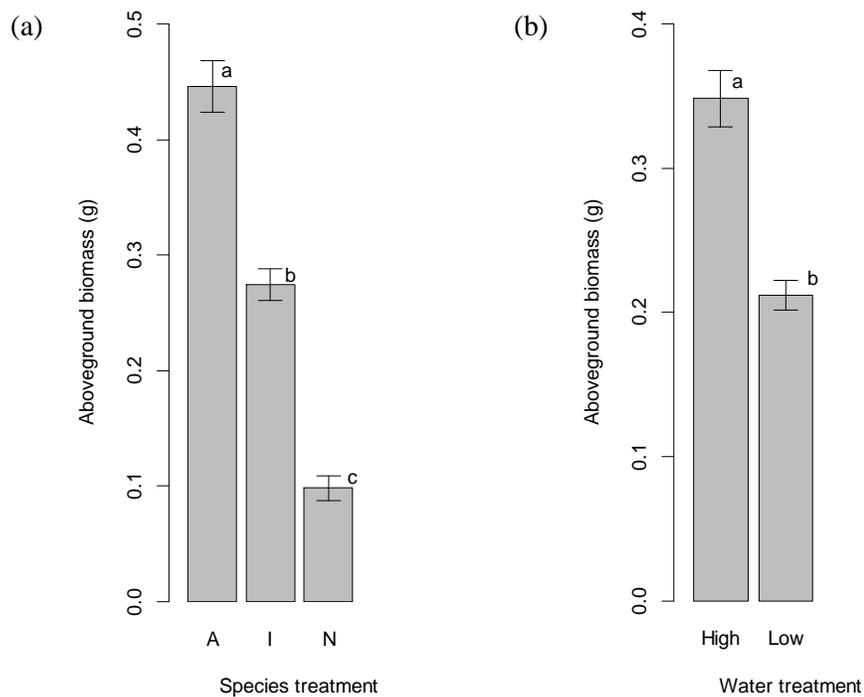


Figure 3-2. (a) Species differences in aboveground biomass (mean  $\pm$  1 SE), and (b) the effect of watering on aboveground biomass (mean  $\pm$  1 SE). Values with the same letters indicate no significant difference between treatments for aboveground biomass ( $p < 0.05$ ). A = agronomic species, annual ryegrass; I = invasive species, cheatgrass; N = native species, rough fescue.

The water and AMF treatments had significant effect on the aboveground biomass of annual ryegrass (Table 3-2), where watering increased aboveground biomass (Figure 3-3), and the addition of AMF decreased aboveground biomass (Figure 3-4a) when both factors were nested within burn treatment. Burned soil did not significantly affect annual ryegrass aboveground biomass. Water and AMF treatments interacted, where water appears to promote growth more when AMF is added to the soil than when it is not (Figure 3-5).

Both watering and AMF inoculum addition increased cheatgrass aboveground biomass (Figure 3-4 a and b).

The burn scar identity (Pile Burn), burning treatment (Burn), and AMF treatments had significant effects on the aboveground biomass of rough fescue (Table 3-2). Unique to the species investigated, burning

increased the aboveground biomass of rough fescue (Figure 3-4b). The addition of AMF decreased rough fescue aboveground biomass (Figure 3-4a).

Table 3-2. Summary of ANOVA for aboveground biomass. Data were blocked by individual burn scar (Pile Burn). Water and AMF treatments were nested within burned or unburned status of soil (Burn). Data were considered significant at  $p < 0.05$  (bold).

	Annual ryegrass aboveground biomass			Cheatgrass aboveground biomass			Rough fescue aboveground biomass		
	Df	F value	Pr(>F)	Df	F value	Pr(>F)	Df	F value	Pr(>F)
Pile Burn	5	1.708	0.137	5	0.6890	0.632	5	2.455	<b>0.037</b>
Burn	1	0.789	0.376	1	3.861	0.051	1	8.379	<b>0.005</b>
Burn(Water)	2	40.386	<b>&lt;0.001</b>	2	5.347	<b>0.006</b>	2	0.662	0.518
Burn(AMF)	2	3.593	<b>0.030</b>	2	3.924	<b>0.022</b>	2	3.402	<b>0.037</b>
Burn(Water x AMF)	2	3.149	<b>0.046</b>	2	2.458	0.089	2	0.007	0.993
Residuals	136			141			117		

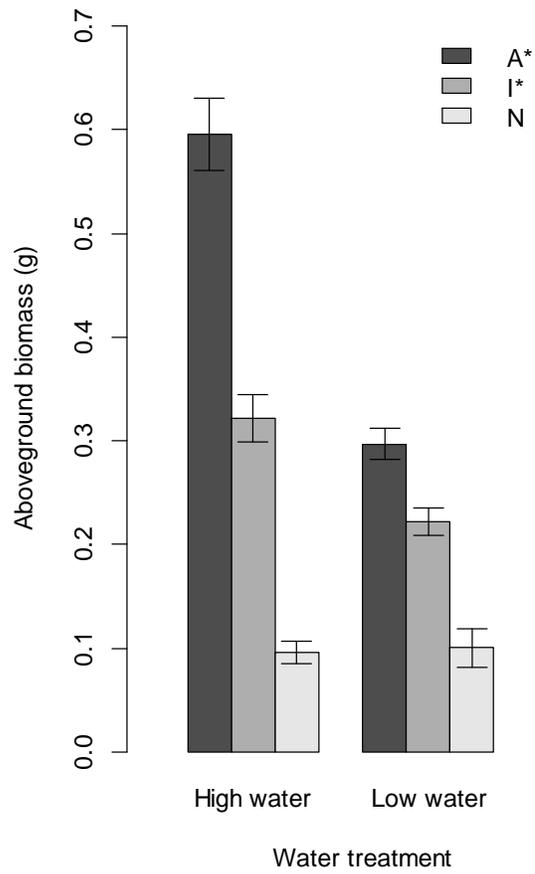


Figure 3-3. Mean ( $\pm$  1 SE) aboveground biomass by species for water treatment (mean  $\pm$  1 SE). \* in legend indicates species aboveground biomass is significantly different between treatments. A = agronomic species, annual ryegrass; I = invasive species, cheatgrass; N = native species, rough fescue.

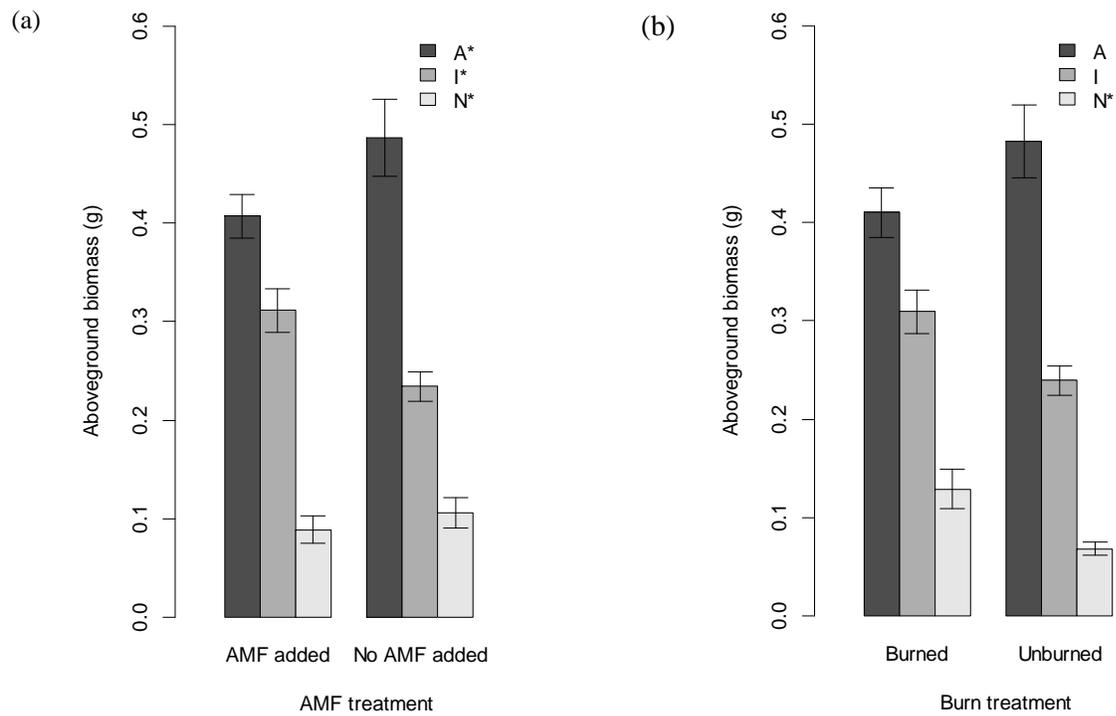


Figure 3-4 (a). Mean ( $\pm$  1 SE) aboveground biomass by species for (a) AMF treatment and (b) burn treatment. \* in legend indicates species aboveground biomass is significantly different between treatments. A = agronomic species, annual ryegrass; I = invasive species, cheatgrass; N = native species, rough fescue.

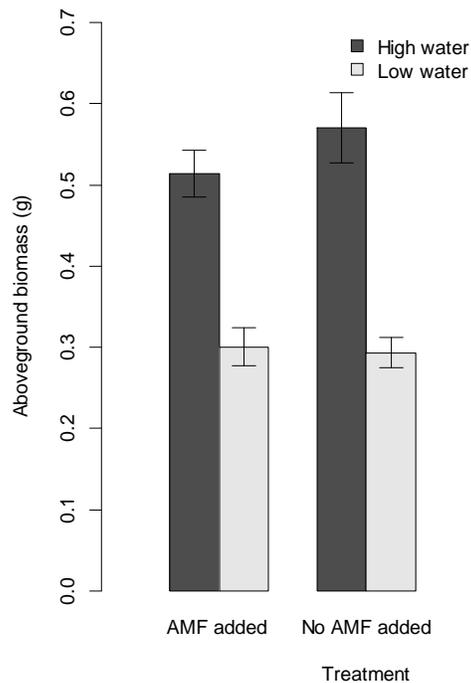


Figure 3-5. Mean ( $\pm$  1 SE) aboveground biomass interaction between AMF and water treatments.

Watering increases biomass more when no AMF inoculum is present.

### 3.4 Discussion

In general, my hypotheses were not supported. My findings did not support the hypothesis that red-burned soil would differentially promote invasive species aboveground biomass over other groups. Red-burned soil only created a significant increase in aboveground biomass for rough fescue. Given the higher levels of available nutrients in the red-burned soil over unburned soil (Chapter 2), it is somewhat surprising that neither cheatgrass nor annual ryegrass aboveground biomass responded positively to the red-burned soil. For these two species, other limiting soil factors, e.g., increased pH and salinity, or decreased exchange capacity may limit growth in these soils (Certini 2005, Hebel et al. 2009). However, annual ryegrass and cheatgrass are generally tolerant of a wide-range of abiotic conditions (Marcar 1987, Knapp 1996). A possible explanation is that belowground biomass, but not aboveground biomass, may increase with increasing nutrients (Aerts et al. 1991), and, thus, the response here to increased nutrients may have occurred belowground.

My findings somewhat supported the hypothesis that watering would differentially promote invasive species aboveground biomass over other species investigated. Both cheatgrass and annual ryegrass aboveground biomass responded positively to the high water treatment, although rough fescue did not. This finding was independent of the burn condition of the soil and supports and expands on those of Miller et al. (2006) who found that cheatgrass is water-limited in arid environments. However, these findings are counter to that of Condon et al. (2011), who found that cheatgrass was more successful under xeric conditions and a late-successional native species was more successful under mesic conditions. The water conditions tested here may not be considered xeric as the lower water treatment was 20 mL per day. The growth response of rough fescue would support this hypothesis. Rough fescue is sensitive to soil water content, except at the highest levels (Willms 1988). Thus, the lack of response of rough fescue to increases in soil water observed here may indicate that the low water treatment was not low enough to create a difference in aboveground biomass.

My findings did not support that hypothesis that AMF inoculum would promote the aboveground biomass for all species tested. Only the aboveground biomass of cheatgrass significantly increased with the addition of the inoculum. The aboveground biomass of annual ryegrass and rough fescue significantly decreased with the addition of the inoculum (i.e., the inoculum used appeared to be parasitic on the native and agronomic species, while mutualistic with the invasive species). These responses were independent of the burn condition of the soil (i.e., whether the soil would host a native AMF community) and suggest that the AMF inoculum used swamped the local biota. This range of responses support other research indicating that AMF does not universally promote plant growth (Klironomos 2003). The results may have been confounded by the use of commercial AMF inoculum rather than native. Commercial AMF inoculum can lead to distinct vegetation responses from those of native inoculum (e.g., Rowe et al. 2007, e.g., Tarbell and Koske 2007), and research suggests that commercial inoculum is not an appropriate tool in many restoration treatments as responses can be ineffective or detrimental to restoration efforts.

Relative aboveground biomass was consistent across all treatments, with annual ryegrass having the highest aboveground biomass, followed by cheatgrass, followed by rough fescue. Plant species with high initial cover can alter microsite conditions such that invasive species are no longer competitively superior (Hunter et al. 2006, Goergen and Chambers 2012). Both agronomic and native species can suppress invasive species in restoration seeding treatments (Davies et al. 2010), although agronomic species tend to be more successful than native species (Peppin et al. 2010; Chapter 2). My finding suggests the high

initial growth rate and germination rates of the agronomic annual ryegrass may contribute to potential suppression of the invasive cheatgrass (e.g., Chapter 2).

### **3.5 Conclusion**

The general lack of interaction at the species level observed here indicates that the treatment effects are additive rather than synergistic in nature. In particular, the responses to the addition of commercial AMF inoculum were independent of soil burning, indicating that findings here are applicable on a broader scale (i.e., not just burned soils).

The findings here, when compared to similar studies of restoration of pile burn scars would suggest that pile burning during winter (see Chapter 2), along with the non-burning of surrounding vegetation, creates areas that are susceptible to colonization of non-native species. Restoration efforts should be directed at these sites as soon as possible after burning to ameliorate the effects of invasive species colonization.

## Conclusions

In this research I showed that pile burning created soil with elevated nutrient levels, and vegetation communities initially devoid of vegetation. When representatives from the plant species groups of interest (native, invasive, agronomic) were investigated using soil taken from a pile burn site and grown in a greenhouse experiment, species displayed different responses to burning, water, and arbuscular mycorrhizal fungi (AMF) treatments. These findings have implications for restoration of vegetation communities on these soils, and the susceptibility of these communities to non-native and invasive species.

The ready colonization of new pile burn scars by non-native and invasive species observed during this study is problematic because the presence of invasive species often creates negative feedback effects on establishment and growth of native species (Jordan et al. 2011) and perpetuates the ongoing dominance of invasive species (Kulmatiski and Beard 2008). For example, the persistence of cheatgrass (*Bromus tectorum* L.) in the semi-arid regions of western North America is facilitated by its shifting of N-cycling to deeper layers of soil rather than at the soil crust where many native plants are adapted to access N (Sperry et al. 2006). These self-perpetuating communities may then act as a source of encroachment into the surrounding native vegetation.

A summary of my most relevant findings with respect to restoration work are:

- Although from a practical and human safety standpoint, burning in winter is preferable, this timing creates conditions that are susceptible to early colonization by invasive or non-native species. One possible explanation may be that the latent heat of vapourization of ice prevents nutrients from being lost from the site, which, when combined with the lack of competition from existing vegetation, creates conditions favourable for species with high seed output and efficient dispersal mechanisms (Moles et al. 2008), the majority of which are non-native and invasive in the study area.
- Pile burning creates conditions favourable for the establishment of some, but not all, invasive and non-native species. Non-native and invasive species that colonized burns were largely non-mycorrhizal or facultatively mycorrhizal, including multiple members of the Brassicaceae and Chenopodiaceae (Wang and Qiu 2006). Non-native species from obligate mycorrhizal families (e.g. Asteraceae, some Poaceae) were abundant in surrounding vegetation, but generally did not colonize the burn scars (Figure C-1).

- Manual seeding of burn scars with agronomic species reduced non-native species cover. In a comparison of invasive, agronomic and native species in a greenhouse experiment, the agronomic species had the highest aboveground biomass. This finding may explain the results of the field experiment where species that produce the highest cover (presumably related to biomass) are most effective at reducing non-native cover (Hunter et al. 2006, Goergen and Chambers 2012).
- Addition of AMF inoculum resulted in non-significant trends in non-native, agronomic and native species cover in the field experiment. However, in the greenhouse experiment, the addition of AMF inoculum resulted in significant increases in non-native species biomass, and significant decreases in native and agronomic species aboveground biomass. This finding is supported by many other studies (e.g., White et al. 2008) and suggests that commercial AMF inoculum is not an appropriate tool for field restoration treatments.



Figure C-1. *Centaurea* spp. on edge of pile burn scar. No *Centaurea* spp. were identified on the pile burn scars

These findings have implications for restoration practice:

- Pile burning should be avoided in the dry interior ecosystems of BC, where invasive species management is problematic.
- It may be preferable to perform pile burning when soils are not frozen.

- It may also be preferable to burn surrounding vegetation where possible, because this vegetation provides a ready invasive species seed supply to new burn scars. However, MacDougall et al. (2013) found that burning of previously-invaded grasslands, which had been subject to long-term (>100 years) fire suppression, may trigger ecosystem collapse. Thus, the need for broadscale burning should be made on a case-by-case basis.
- Seeding agronomic species at a high density can reduce non-native and invasive cover in the first 2 years after burning.
- The use of commercial AMF inoculum in a field environment is not recommended, as it had no effects on vegetation cover in the field and promoted invasive species growth in the greenhouse experiment.

While agronomic species may be an appropriate restoration tool for pile burn scars, the use of these species should only proceed after weighing the potential benefits against the potential costs. The use of agronomic species can be problematic because these species can self-seed into neighbouring communities and form self-sustaining populations. Although I avoided the use of known troublesome species in this research (e.g., crested wheatgrass (*Agropyron cristatum* (Bieb.) Tzvelev)), a species that currently does not display invasive tendencies may become invasive in the future (Moles et al. 2008). Many invasive species require “release” triggers to move from being simply non-native but not problematic, to being invasive. Changing climate combined with rapid land-use changes, may create conditions where non-problematic non-native species cross a biotic or abiotic barrier to become invasive (Moles et al. 2008). As well, agronomic seed mixes are often contaminated with other species. The seed mix used in this experiment, though purchased from a highly reputable source, had replaced one species listed on the packaging with another that we were unable to identify.

My research did not investigate the effect of pile burning of frozen soils on the microbial abundance and microbial community structure in the soil. While I hypothesize that the latent heat of vapourization may have protected the soil from nutrient loss, it may also have protected the soil microbial community. When soils are not frozen during burns, AMF colonization and soil microbial communities in red-burned soils are greatly depleted compared with less severely burned black soil (Hebel et al. 2009). Red soil had 71% less soil C than black soil, strongly contributing to the microbial community differences between red and black soil. Slash burning also depletes soil seed banks (Korb et al. 2004, Creech et al. 2011) and AMF communities (Korb et al 2004). However, the effect of high severity fires on the biotic communities in frozen soils is unknown, and warrants investigation.

Further research may also involve the possibility that the establishment of a protective barrier of non-invasive species may prevent the further spread of invasive species on to burn scars (Davies et al. 2010). Results from studies using this protective vegetation barrier technique found the cover and density of an invasive annual grass was lowered by a factor of greater than 40 compared with communities with no vegetation barrier. Species' movement across this barrier would be hindered by both competition and as a barrier to seed dispersion. Thus, rather than applying restoration treatments to entire disturbed areas, it may only be necessary to restore the edges, or the interfaces between the disturbed and undisturbed areas.

In summary, while pile burning is a cost-effective means of disposing of unwanted and unmarketable timber, the ecosystem consequences may be severe. Disposing of the timber away from sensitive grassland ecosystems is recommended for future work.

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# Appendices

## Appendix A – Figures for Non-Significant Findings

Figures A-1 through A-3 show non-significant treatment findings with respect to Chapter 2. Figure A-4 shows non-significant treatment findings with respect to Chapter 3.

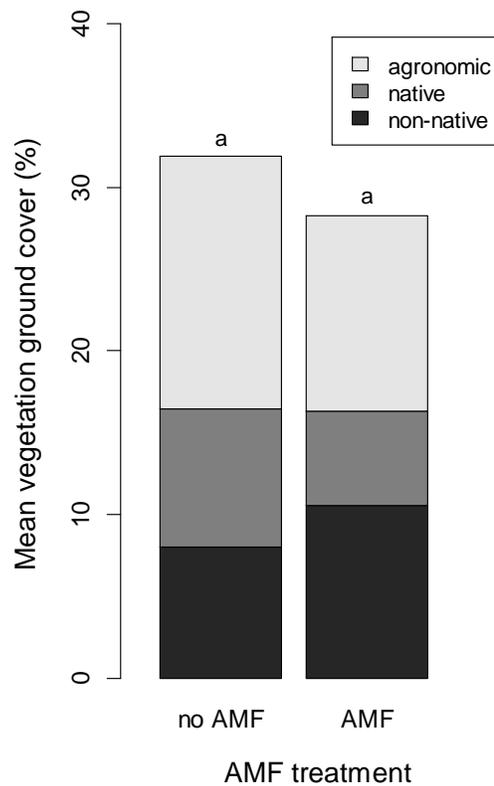


Figure A-1. Chapter 2. The effect of AMF addition treatment on total vegetation cover. Bars with the same letters indicate no significant difference among treatments for total vegetation cover ( $p < 0.05$ ). No significant differences were identified between treatment levels for agronomic, native, and non-native vegetation cover ( $p < 0.05$ ).

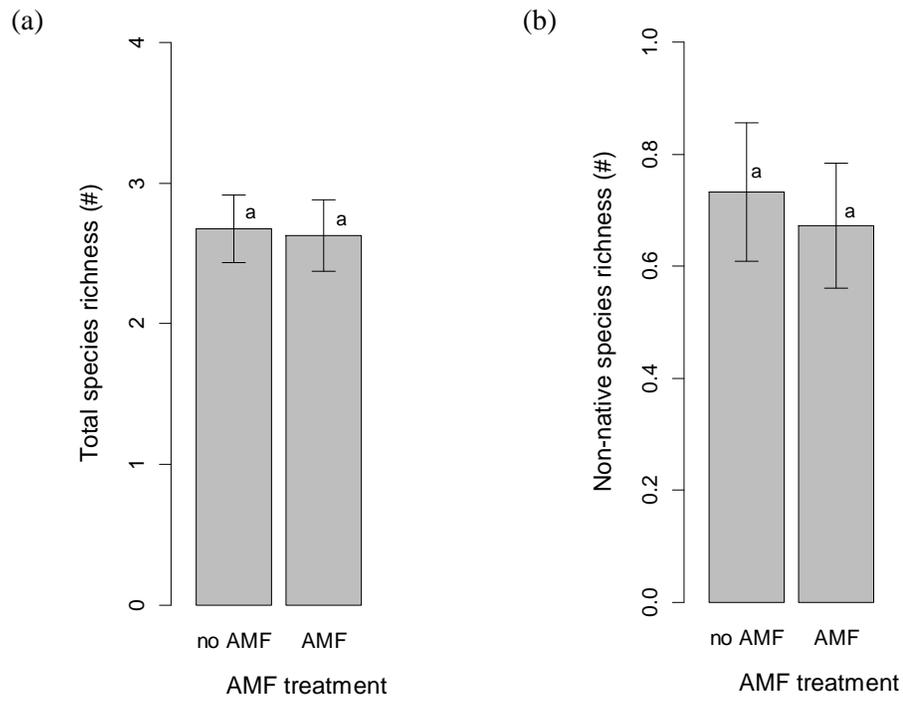


Figure A-2. Chapter 2. The effect of AMF addition on (a) total species richness, and (b) non-native species richness. Bars with the same letters indicate no significant difference between treatments ( $p < 0.05$ ).

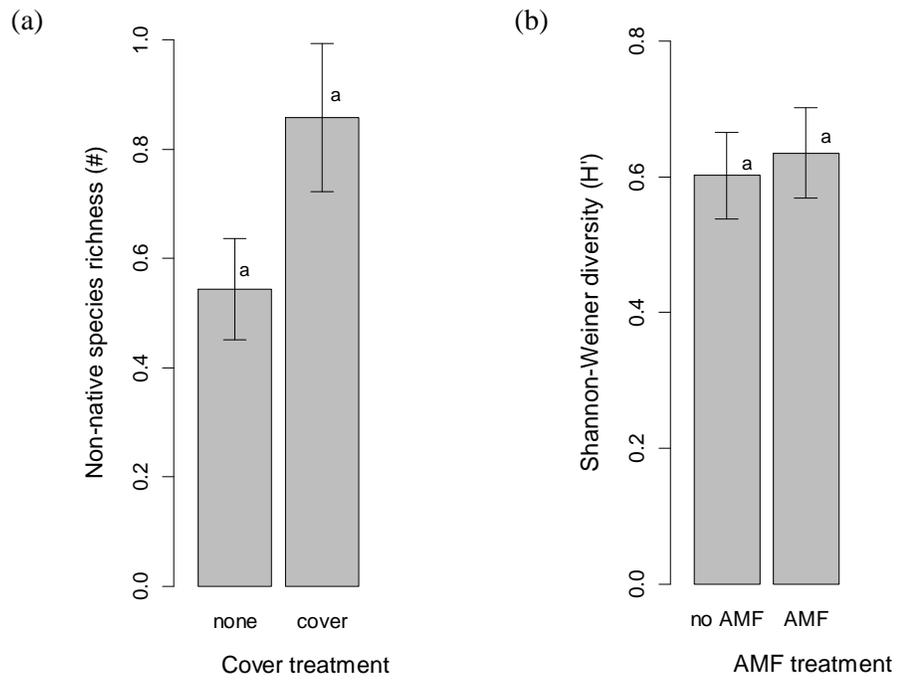


Figure A-3. Chapter 2. (a) The effect of cover treatment on non-native species richness, and (b) The effect of AMF treatment on Shannon-Weiner diversity index ( $H^2$ ). Bars with the same letter indicate no significant difference between treatments ( $p < 0.05$ ).

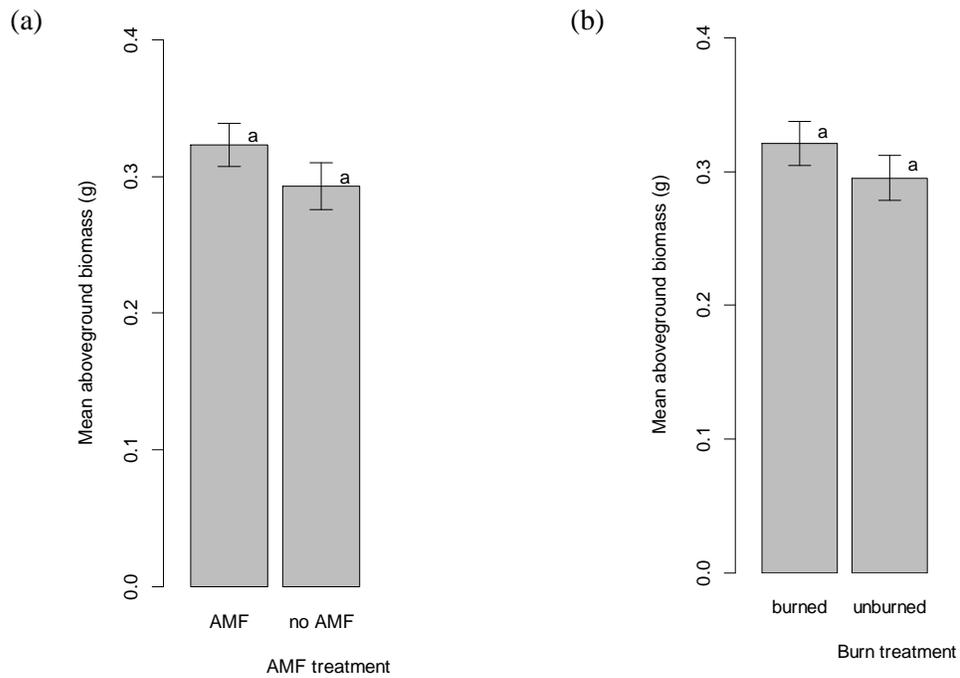


Figure A-2. Chapter 3. (a) Total aboveground biomass differences for AMF addition treatment differences in aboveground biomass, and (b) total aboveground biomass for burn treatment. Bars with the same letters indicate no significant difference between treatments for aboveground biomass ( $p < 0.05$ ).

## Appendix B – Species Identified in Chapter 2

Table B-1 lists the frequencies of occurrences of species identified in treatment plots and in unburned areas.

Table B-1. Frequency (%) of identified species in burn treatments and in unburned surrounding plots. Species with an \* indicates those that were seeded in the treatments.

Family	Species	Common name	Status <sup>1</sup>	No treatment	Agronomic seed	Native seed	No seed	Cover	No cover	AMF	No AMF	All treatment plots	All unburned plots
Asteraceae	<i>Achillea millefolium</i> *	yarrow*	Na	7.7	-	22.2	2.1	5.7	10.3	7.5	8.5	8.0	16.3
Poaceae	<i>Achnatherum occidentale</i> *	stiff needlegrass*	Na	-	2.2	42.2	6.4	22.9	10.3	14.9	18.3	16.7	18.8
Poaceae	<i>Achnatherum richardsonii</i> *	spreading needlegrass*	Na	-	-	22.2	-	8.6	5.9	6.0	8.5	7.2	11.3
Rosaceae	<i>Amelanchier alnifolia</i>	saskatoon	Na	-	-	-	-	-	-	-	-	-	2.5
Asteraceae	<i>Antennaria</i> spp.	pussytoes	Na	-	-	-	-	-	-	-	-	-	13.8
Brassicaceae	<i>Arabis holboellii</i>	holboell's rockcress	Na	-	-	-	-	-	-	-	-	-	2.5
Asteraceae	<i>Artemisia frigida</i>	pasture sage	Na	-	-	-	-	-	-	-	-	-	5.0
Fabaceae	<i>Astragalus collinus</i>	hillside milkvetch	Na	-	-	-	-	-	-	-	-	-	3.8
Fabaceae	<i>Astragalus miser</i>	timber milkvetch	Na	-	2.2	4.4	4.3	2.9	4.4	3.0	4.2	3.6	12.5
Asteraceae	<i>Balsamorhiza sagittata</i>	arrow-leaf balsamroot	Na	-	-	-	-	-	-	-	-	-	8.8
Poaceae	<i>Bromus inermis</i>	smooth brome	NN	-	-	-	-	-	-	-	-	-	1.3
Poaceae	<i>Bromus japonicus</i>	Japanese brome	NN	-	-	-	2.1	1.4	-	-	1.4	0.7	2.5
Poaceae	<i>Bromus squarrosus</i>	corn brome	NN	-	4.3	8.9	8.5	7.1	7.4	6.0	8.5	7.2	46.3
Poaceae	<i>Bromus tectorum</i>	cheatgrass	NN	15.4	8.7	8.9	17.0	14.3	8.8	13.4	9.9	11.6	35.0
Asteraceae	<i>Centaurea diffusa</i>	diffuse knapweed	NN	-	-	-	-	-	-	-	-	-	2.5
Chenopodiaceae	<i>Chenopodium album</i>	lamb's quarters	NN	-	2.2	-	-	-	1.5	-	1.4	0.7	1.3

Family	Species	Common name	Status <sup>†</sup>	No treatment	Agronomic seed	Native seed	No seed	Cover	No cover	AMF	No AMF	All treatment plots	All unburned plots
Asteraceae	<i>Cirsium arvense</i>	Canada thistle	NN	7.7	-	-	2.1	-	1.5	-	1.4	0.7	-
Asteraceae	<i>Crepis</i> spp.	hawksbeard	Unk	-	-	4.4	-	2.9	-	-	2.8	1.4	-
Poaceae	<i>Elymus trachycaulus</i> *	Slender wheatgrass*	Ag	-	82.6	2.2	6.4	34.3	26.5	31.3	29.6	30.4	-
Asteraceae	<i>Erigeron corymbosus</i>	long-leaved fleabane	Na	-	-	-	-	-	-	-	-	-	1.3
Asteraceae	<i>Erigeron filifolius</i>	thread-leaved fleabane	Na	-	5.0	-	-	-	-	-	-	-	1.3
Poaceae	<i>Festuca campestris</i> *	rough fescue*	Na	-	-	20.0	-	8.6	4.4	9.0	4.2	6.5	35.0
Poaceae	<i>Festuca ovina</i> *	sheep fescue*	Ag	-	13.0	-	-	5.7	2.9	4.5	4.2	4.3	-
Poaceae	<i>Festuca rubra</i> *	red fescue*	Ag	-	50.0	-	2.1	15.7	19.1	14.9	19.7	17.4	-
Liliaceae	<i>Fritillaria pudica</i>	yellow bell	Na	-	-	-	-	-	-	-	-	-	3.8
Asteraceae	<i>Gaillardia aristata</i> *	brown-eyed susan*	Na	-	2.2	13.3	-	7.1	2.9	6.0	4.2	5.1	-
Asteraceae		unkown daisy	Unk	-	-	2.2	-	1.4	-	1.5	-	0.7	3.8
Poaceae	<i>Hesperostipa comata</i> *	needle-and-thread grass*	Na	-	-	6.7	-	2.9	1.5	4.5	-	2.2	10.0
Poaceae	<i>Hordeum jubatum</i> *	foxtail barley*	Na	-	-	15.6	-	5.7	4.4	4.5	5.6	5.1	-
Poaceae	<i>Hordeum vulgare</i>	common barley	Ag	-	6.5	4.4	2.1	5.7	2.9	7.5	1.4	4.3	-
Chenopodiaceae	<i>Kochia scoparia</i>	summer-cypress	NN	-	2.2	4.4	-	2.9	1.5	3.0	1.4	2.2	-
Poaceae	<i>Koeleria macrantha</i> *	junegrass*	Na	-	-	-	-	-	-	-	-	-	8.8
Asteraceae	<i>Lactuca serriola</i>	prickly lettuce	NN	-	4.3	4.4	10.6	1-	2.9	6.0	7.0	6.5	6.3
Asteraceae	<i>Leucanthemum vulgare</i>	oxeye daisy	NN	-	-	-	-	-	-	-	-	-	2.5
Scrophulariaceae	<i>Linnaria genistifolia</i> subs. <i>damlatica</i>	Dalmation toadflax	NN	-	-	-	-	-	-	-	-	-	1.3
Boraginaceae	<i>Lithospermum ruderale</i>	lemonweed	Na	-	-	-	-	-	-	-	-	-	5.0
Poaceae	<i>Lolium multiflorum</i> *	Italian ryegrass*	Ag	-	52.2	-	2.1	18.6	17.6	16.4	19.7	18.1	-

Family	Species	Common name	Status <sup>†</sup>	No treatment	Agronomic seed	Native seed	No seed	Cover	No cover	AMF	No AMF	All treatment plots	All unburned plots
Poaceae	<i>Lolium perenne</i> *	perennial ryegrass*	Ag	-	8.7	-	-	4.3	1.5	3.0	2.8	2.9	-
Berberidaceae	<i>Mahonia aquifolium</i>	tall Oregon-grape	Na	-	-	-	-	-	-	-	-	-	1.3
Asteraceae	<i>Matricaria discoidea</i>	pineapple weed	Unk	-	-	-	-	-	-	-	-	-	1.3
Fabaceae	<i>Medicago lupulina</i>	black medic	NN	-	-	2.2	-	1.4	-	1.5	-	0.7	6.3
Fabaceae	<i>Medicago sativa</i>	alfalfa	Ag	-	2.2	-	-	1.4	-	-	1.4	0.7	6.3
Fabaceae	<i>Melilotus alba</i>	white sweet-clover	NN	-	2.2	2.2	2.1	2.9	1.5	1.5	2.8	2.2	1.3
Pinaceae	<i>Pinus ponderosa</i>	ponderosa pine	NA	-	-	-	-	-	-	-	-	-	1.3
Plantaginaceae	<i>Plantago patagonica</i>	woolly plantain	Na	-	-	-	-	-	-	-	-	-	1.3
Poaceae	<i>Poa secunda</i>	Nevada bluegrass	Unk	-	2.2	53.3	4.3	22.9	16.2	16.4	22.5	19.6	-
Poaceae	<i>Poa compressa</i>	Canada bluegrass	Ag	-	-	-	-	-	-	-	-	-	8.8
Poaceae	<i>Poa pratensis</i>	Kentucky bluegrass	NN	-	-	4.4	6.4	4.3	2.9	3.0	4.2	3.6	27.5
Polygonaceae	<i>Polygonum</i> sp.		Unk	-	2.2	-	-	1.4	-	-	1.4	0.7	1.3
Poaceae	<i>Pseudoroegneria spicata</i> *	bluebunch wheatgrass	Na	-	-	53.3	2.1	17.1	19.1	17.9	18.3	18.1	33.8
Rosaceae	<i>Rosa nutkana</i>	Nootka rose	Na	-	-	-	-	-	-	-	-	-	2.5
Brassicaceae	<i>Sisymbrium altissimum</i>	tall tumble-mustard	NN	-	2.2	4.4	2.1	4.3	1.5	4.5	1.4	2.9	-
Brassicaceae	<i>Sisymbrium loeselli</i>	loesel's tumble-mustard	NN	-	2.2	6.7	2.1	2.9	4.4	4.5	2.8	3.6	-
Asteraceae	<i>Taraxacum officinale</i>	common dandelion	NN	7.7	8.7	22.2	17.0	17.1	14.7	17.9	14.1	15.9	52.5
Asteraceae	<i>Tragopogon dubius</i>	yellow salsify	NN	7.7	-	17.8	4.3	10.0	4.4	3.0	11.3	7.2	51.3
Poaceae	unknown <i>Elymus</i> *		Ag	-	56.5	-	4.3	22.9	17.6	22.4	18.3	20.3	2.5
Fabaceae	<i>Vicia americana</i>	American vetch	Na	-	-	2.2	-	-	1.5	1.5	-	0.7	5.0
Poaceae	<i>Vulpia octoflora</i>	six-week fescue	Na	-	-	-	-	-	-	-	-	-	11.3

<sup>†</sup>Na – native; NN – non-native; Ag – agronomic; Unk – unknown