FIRST STEP RESTORATION TECHNIQUES IN INVADED GRASSLAND IN SOUTHERN BRITISH COLUMBIA

by

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ABSTRACT

Invasive species are considered the second greatest threat to biodiversity (after habitat loss) as they can alter ecosystem functioning, including nutrient cycling. Invasive plant species can be controlled using various methods and restoration is often attempted in degraded areas. Biological control temporarily eliminated diffuse knapweed from a site in Vernon, British Columbia, though the site remained completely dominated by other invasive species. Restoration was attempted using seed addition of native species and late summer and spring vegetation removal of invasive species. Seed addition did not result in increased native species abundance in the plots, likely because of abnormally low April precipitation. Vegetation removal in spring did not prevent the emergence of seedlings, and actually increased emergence of diffuse knapweed and thyme-leaved sandwort. Annual grasses on the other hand were more abundant in plots without vegetation removal. Removal of vegetation in the plots was not evident by biomass harvest in August, though it significantly increased diversity and the percentage of forbs in the total biomass. The plots with no vegetation removed had significantly greater percentage of grass in the total biomass and far greater litter mass. Comparing soil samples from two invaded ecosystems (diffuse knapweed and sulphur cinquefoil dominated) to one with few invasive species (bunchgrass dominated) resulted in finding that almost all nutrient levels measured and moisture were highest in the uninvaded ecosystem. As diffuse knapweed reacts positively to the removal of competition, vegetation removal should not be used as a restoration technique in invaded areas. In areas where there is no knapweed, however, vegetation removal may be beneficial to work against dominance by annual grass species. Soils of invaded ecosystems may also need to be considered, and only vegetation that can withstand drought and low levels of nutrients should be used.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

To my family.

INTRODUCTION

Ecosystems worldwide are being rapidly altered by development and agriculture, and are further
threatened by non-native invasive plants (Rubec and Lee 1997). Invasive species are considered
second only to habitat loss as the most harmful factor contributing to loss of biodiversity
(D'Antonio and Vitousek 1992, Rubec and Lee 1997, Wilcove *et al.* 1998, Mack *et al.* 2000,
Sakai *et al.* 2001, Strayer *et al.* 2006). Grasslands around the world have been particularly
impacted because they provide good agricultural land and they are easily developed for industry
and housing (Grassland Conservation Council 2004). Consequently, the dry interior bunchgrass
grasslands of British Columbia are one of the most endangered ecosystems in Canada.
Grasslands cover less than one percent of land area of British Columbia, but they supply critical
habitat for more than thirty percent of "species at risk" including species like the great basin
gopher snake and American badger (Grassland Conservation Council 2004, Conservation Data
Centre 2006). Studying invasive species in this ecosystem can improve understanding of
community dynamics. This understanding is crucial in restoration (Sakai *et al.* 2001) which is the
process of assisting with the recovery of an ecosystem that has been degraded, damaged or
destroyed by re-establishing its structural characteristics, species composition and ecological
processes (SERI 2004).

  Noxious weeds (species mandated under government legislation; in BC the *Weed Control
Act* 1996) and other non-native invasive species have led to economic loss by decreasing forage
and thus rangeland value (Strang *et al.* 1979, Olson *et al.* 1997), decreasing ecotourism
(Grassland Conservation Council 2004) and increasing fire risk (Mack *et al.* 2000, Link *et al.*
2006). In the most severe cases, non-native invasive species can completely alter the structure
and dynamics of an ecosystem (Hobbs 1999). The mechanisms for this include increasing

erosion (Lacey *et al.* 1989), altering nutrient cycling (Belnap and Phillips 2001, Rimer and Evans 2006), increasing incidence of plant diseases (Malmstrom *et al.* 2005), and potentially reducing or eliminating native populations (Mack *et al.* 2000, Masters and Sheley 2001, Bais *et al.* 2003). Sulphur cinquefoil (*Potentilla recta* L.) is one such plant that forms increasingly dense stands by producing numerous seeds that mostly drop next to the parent plant (Dwire *et al.* 2006). Some species of non-native invasive plants specifically alter soil properties (Gordon 1998, Van Riper and Larson 2008). For example, spotted knapweed (*Centaurea stoebe* L., often called *Centaurea maculosa* Lam.) elevates phosphorous within its rhizosphere (Thorpe *et al*. 2006) and cheatgrass (*Bromus tectorum* L.) may lower soil nitrogen by up to 50% by decreasing nitrogen available for microbial action (Rimer and Evans 2006). Alteration of soil nutrients may be an important aspect of invasion and may have long term effects even after an invasive species has been removed.

Removing invasive species that have become community dominants can be difficult, and has often been accomplished through chemical control methods (Sheley *et al*. 2001). Chemicals are not permitted in many areas, such as near wetlands, and are not always effective in long term control, especially if an invasive seed bank has accumulated. A method that addresses some of these concerns is biological control. Biological control (biocontrol) of non-native invasive plants using natural predators of the invasive species has become a common practice and is based on the principle that invasive species are successful in part because they have escaped from their natural predators in their home range (Rubec and Lee 1997, Sakai *et al.* 2001). There have been a number of examples of successful biological control (Huffaker 1951, Zimmermann *et al*. 2001). However, the control of a non-native invasive species does not necessarily equate with restoration. An intriguing question is whether the seeding of native species can enhance

restoration success of a grassland following temporary eradication of diffuse knapweed by biocontrol agents.

The long term goal of ecological restoration is to increase land sustainability by enhancing its conservation values (Stein *et al*. 2008), land utilization value, and ecosystem processes. Success in restoration has been defined as creating a diverse assemblage of species similar to nearby reference sites without invasion, a significant presence of native species and few invasive species, and the presence of functional groups needed for long term stability (SERI 2004). More diverse systems are generally thought to be more stable (Tilman and Downing 1994, Ives and Carpenter 2007), and a goal of restoration is to create stable ecosystems, i.e. having the ability to return to a steady state after being affected by an outside force (Elton 1958, Piper *et al*. 2007). Piper *et al*. (2007) reported that the rate of establishment and species richness was higher when more species were planted up to a maximum of about eight added species. Recreating ecosystems through restoration provides opportunities to test approaches to restoration while serving conservation purposes (Piper *et al*. 2007). Because of the low dispersal capability of many native species (Bakker *et al*. 2003, Seabloom *et al*. 2003) it is likely that the bunchgrass ecosystem will be slow to self-restore. Therefore it is often necessary to intervene using other methods that may limit non-native species dominance, such as removal or clipping of these species. On the other hand, adding a higher richness of native species or functional groups may lead to faster establishment, thus invasive weed control may not be as important to restoration if more species are added (Piper *et al*. 2007).

While there are good arguments for using large-scale approaches along with long-term monitoring (Choi, 2004), mechanisms of invasion and restoration can be site-specific (D'Antonio *et al*. 1999) and can depend on soils, climate, and fauna (Hobbs 1999). Therefore,

valuable information can be gained by studying some of the individual components of specific communities.

For my study I chose a bunchgrass grassland site from which diffuse knapweed had been eradicated. The specific goal of my work was to increase the species richness and abundance of native species, and thereby determine the efficacy of seed addition and vegetation removal on my site. This study is part of an ongoing effort to apply theoretical knowledge about plant communities to restoration efforts. I address five questions:

(1) What is the species composition of the seed bank?

(2) Are the soils in areas invaded by sulphur cinquefoil and diffuse knapweed (both are non-native invasive species) different in nutrient, pH, conductivity or moisture levels from soils that have not been invaded?

(3) Can a bunchgrass community be restored by removal of diffuse knapweed alone, or is it also necessary to sow seeds of native grassland species to restore a diverse grassland community?

(4) Do species other than diffuse knapweed prevent the establishment of native species?

(5) Does increasing the number of native species added to an area increase the probability of restoration success?

METHODS

In addition to the following experiments, germination trials were carried out on the seeds used in the main field experiment. The methods for these appear in Appendix B.

Study site

The research was conducted on the grounds of the Vernon Military Camp (VMC) in Vernon, BC, Canada (lat 50.2325; long -119.2930). Vernon is located in the Interior Douglas-fir (IDF) biogeoclimatic ecosystem classification zone (Hope *et al.* 1991) and the VMC is located in the very dry hot sub-zone, Okanagan grassland variant (IDFxh1a) that is dominated by bunchgrass.

Along the roadsides there are high densities of cheatgrass (*Bromus tectorum* L.), diffuse knapweed (*Centaurea diffusa* Lam.), tall tumble-mustard (*Sisymbrium altissimum* L.), white sweet clover (*Melilotus alba* Desr.), wormwood (*Artemisia absinthium* L.) and dense patches of sulphur cinquefoil (*Potentilla recta* Linné), hound's-tongue (*Cynoglossum officinale* L.), Scotch thistle (*Onopordum acanthium* L.), Dalmatian toadflax (*Linaria dalmatica* (L.) Mill.), and Canada thistle (*Cirsium arvense* (L.) Scop.). These invasive species decrease in density away from the roadsides but they are at high densities in all disturbed areas. Dalmatian toadflax and diffuse knapweed were found almost everywhere at low densities, but in the less disturbed areas there was open ground covered by small xeric moss and lichens (cryptogamic crust) between bunchgrass clumps and many small forbs. Knopp and Larkin (2000) conducted an inventory of species in the area in 1999 and so there is some record of vegetation changes.

The site had a history of disturbance, not only by the military, but also by cattle that were present on the site for many years, but have been excluded since 2005. Some areas of the VMC were previously irrigated with waste water and cut for hay, and while my study area was not irrigated, it may have been affected by run-off. Specific study plots were selected on a hillside where diffuse knapweed had previously been abundant, but in 2006, biological control agents had eliminated all knapweed plants including rosettes. This provided an excellent opportunity to investigate whether the natural bunchgrass community in the BC interior can be restored following the removal of knapweed, or if the removal of additional invasive species is also required.

Forty-eight 2 m x 2 m plots were placed haphazardly, their locations dependant on having a minimum 25% cover of diffuse knapweed in previous years as indicated by the dead stems from the previous year's mature plants. The sides of the plots were aligned with the cardinal compass points.

The dominant vegetation around the plots in 2006 consisted of tumble-mustard (*Sisymbrium altissimum*), bulbous bluegrass (*Poa bulbosa* L.), cheatgrass (*Bromus tectorum*), and horseweed (*Conyza nvisibili* (L.) Cronquist). In 2007, there were knapweed rosettes found in and around the plots, a small percentage of which bolted. All plants that bolted were observed to have biological control insects present, and were small with few flowering branches.

Soil samples

Soils were sampled from three types of areas on the site: (1) where knapweed was (and is) dominant (2) from bunchgrass dominated communities that resembled the goal of restoration, and (3) from sulphur cinquefoil dominated communities. At least two distinct areas (dense patches in the case of the invasive species) were used to obtain soil samples, and when multiple soil samples were taken from one area they had differing elevations, slopes, or aspects in an effort to get samples that would generalize the community and not the habitat. Six soil samples were taken from random locations in each site for a total of eighteen samples. The sample area was marked using a GPS unit as well as pink pin flags so that samples could be taken in the same location in both 2006 and 2007 to account for annual variation. Ten handfuls of soil were taken from the top 10 cm of soil within 1 m of the flag. The surface litter was brushed away and rocks over approximately 5 mm in diameter were removed. A minimum of 125 ml of soil was placed into labelled, sterile, collection bags. These samples were sent to Cantest (4606 Canada Way, Burnaby, BC Canada V5G 1K5) for analysis of moisture, total carbon, pH, conductivity, available nitrate, available phosphorus, total nitrogen, available calcium, available potassium, available magnesium, and organic matter.

Seed bank

A 10 x 10 x 10 cm sample of top soil was taken from the corner of each plot for seed bank analysis. These samples were collected in late summer (August 2006) and stored in a freezer to scarify the seeds. In the spring of 2007, the samples were planted into flats in a greenhouse. Sand (containing no seeds) mixed with 2 tablespoons of   nvisibilit was placed in a flat to a depth of 2 cm and the soil was spread evenly over the top of this mixture. The flats were watered every second day to encourage germination of the seeds and prevent the sand from drying out. The seedlings were allowed to grow and were counted once a month. A sample of the seedlings were transplanted into potting soil and allowed to grow so that they could be identified to species.

Main field experiment: seed addition and invasive removal

Three native seed mixtures containing different numbers of species (2, 4, or 8 species) and a vegetation removal regime were applied as treatments to the plots (Table 1); the control plots had no vegetation

removal or seed addition. A crossed design of these treatments resulted in eight different plot types that were each replicated six times for a total of forty-eight plots (Appendix A).

After the plots were established in July 2006, the vegetation removal treatments had all non-native species removed. Small plants and plants with small root systems were pulled directly from the soil. To minimize soil disturbance, larger plants and grasses were clipped off as close to the soil surface as possible. Vegetation was allowed to grow until seeds were to be added. At this stage, all plots were hand clipped on April 7 and 8, 2007 because annual grasses (mostly *Poa bulbosa* and *Bromus tectorum*) were well rooted and quite dense (50-90% cover) in all plots. Weeding (complete removal of the plant), as was done the previous year, would have led to excessive disturbance of the soil. The grasses and other non-native species were clipped to 1-2 cm depending on the surface topography. An attempt was made to avoid clipping the spring ephemeral native species. After this, vegetation was once more allowed to grow until the end of the experiment (August 2007) when all plots were clipped at ground level to collect biomass.

Table 1: The experimental design consisted of eight treatments (4 seed additions x +/0 vegetation removal) in 2 x 2 m plots, with species combinations as shown. A total of 1000 seeds/m² were added to each plot. Grass species are indicated by *. Species added were *Psuedoroegneria spicata*; *Gallardia aristata*; *Koeleria macrantha*; *Monarda fistulosa*; *Hesperostipa comata*; *Achnatherum occidentale*; *Heuchera nvisibilit*; *Geum trifolium*.

		0 spp.	2 species (500 seed/m² each)	4 species (250 seed/m² each)	8 species (125 seed/m² each)
Weeds removed	No seed addition		*P. spicata* *G. aristata*	*P. spicata* *K. macrantha* *G. aristata* *M. fistulosa*	*P. spicata* *K. macrantha* *H. comata* *A. occidentale* *H. nvisibilit* *G. trifolium* *G. aristata* *M. fistulosa*
Weeds not removed	No seed addition (control)		*P. spicata* *G. aristata*	*P. spicata* *K. macrantha* *G. aristata* *M. fistulosa*	*P. spicata* *K. macrantha* *H. comata* *A. occidentale* *H. nvisibilit* *G. trifolium* *G. aristata* *M. fistulosa*

The species added were forb and grass pairings and these were added to all plots on the same day. A seeding rate of 1000 seeds/m² was used after a literature search for common experimental seeding rates

and effectiveness (Sheley *et al*. 1999, Warren *et al*. 2002, Bakker *et al*. 2003, Seabloom *et al*. 2003, Hofmann and Isselstein 2005, Sheley and Half 2006, Thomsen *et al*. 2006). The number of seeds of each species decreased with increasing species richness in the mixture so that the total number of seeds in each plot was held constant at 4000 (Table 1). This ensured that the treatment was number of species and not seeding rate, but assumed all seeds added had approximately the same germination rate.

All but two of the species were collected on site during the summer of 2006. The remaining two species (*Pseudoroegneria spicata* (Pursh) Á. Löve and *Koeleria macrantha* (Ledeb.) Schult) were purchased from seed suppliers Briteland Agricultural Services and Supplies Ltd. (Vernon, BC, Canada) and Prairie Seeds (Nisku, AB, Canada) respectively. The seeds that were collected in the field had been kept in the freezer for a period of two months while purchased seeds were known to be germination ready and purchased just prior to planting. All seeds were further stratified by being kept wet in the refrigerator for seven days, and then kept at room temperature during the two days of plot preparation. Many of the species had begun to show radical emergence, though in most species this occurred in a very low percentage of seeds. However, at least 25% of bluebunch wheatgrass seeds showed radical emergence, the sizes of which ranged from 1-10 mm. On April 9, 2007, the seeds for each plot (4000 seeds total) were mixed with 250 ml of sand to ensure even coverage when spread into the plot as the damp seeds would have clumped. An equal amount of sand was added to plots that did not receive seeds. A problem with the seeds of *Geum triflorum* (Pursh.) was that their long, feathery styles clumped together, were difficult to separate, and got caught up on other vegetation (mostly in plots with no vegetation removal), which may have hindered the seeds' contact with soil.

There was rain for a short period (0.7 mm) on the day the seeds were planted (April 9, 2007), and the day following (0.8 mm), and the 13th (0.3 mm), but only occasional trace amounts of rain after that until April 24 (Environment Canada 2008).   The entire month had 3.5 mm of rain; very low compared to the monthly average of 27.2 mm (Environment Canada 2008). Temperatures dropped to -3.5 °C at night on the 11th, -0.5°C on the 12th, and below 0°C once for three hours on April 18th (Environment Canada 2008).

Decoy food to attract herbivores away from the plots (60 ml of rabbit food, 18% fibre, from Briteland Agricultural Services and Supplies Ltd.) was placed 3 m east (downhill) from each plot, and 3 m west (uphill) of each plot (Longland and Bateman 1998). This was done because the distribution of plots was uneven and many plots were too close together for the consistent placement of decoys. If plots were 6 m or more east/west from the next set of plots, decoy food was placed between the two sets.

Species in the plots were identified on July 13, 2006 (including previous knapweed cover estimated by viewing the remains of knapweed stems), May 20, 2007, and July 17, 2007. Species that appeared to be common in plots were collected (from outside the plots) and pressed so that unknown species could be identified and catalogued; specimens were also photographed. In May 2007, all unknown and knapweed seedlings were counted, and all species recorded in the centre 1 m² of each plot. The presence of rodents as indicated by mounds, tunnels, and holes was recorded for each plot.

On August 14, 2007, the above-ground biomass was collected from all plots. To avoid edge effects the centre 1 m² of above-ground biomass was clipped, collected, dried, identified, and separated into native and invasive species. The litter was also collected that day. The litter removed from plots with the vegetation removal treatment was generally a small amount of annual grass from the previous year (distinguishable as it was grey and partially degraded). The litter removed from plots with untouched vegetation was composed mostly of knapweed and tumble mustard from previous years, which was also grey coloured but woody (heavy) and largely not degraded.

Granivory bioassay

To determine the potential impact of granivory, a bioassay was carried out three times; June 27, July 17, and August 13, 2007. A Petri dish was prepared for each of the plots, containing ten seeds of each of the eight species. Open Petri dishes were placed at a random corner of each plot, dug slightly in to be even with the soil surface and to maximize access for rodents. The dishes were left out for one night only, and collected the next day to reduce possible loss of seeds by wind.

An assumption that all granivores have an equal chance of finding and feeding upon the seed in the Petri dishes had to be made, though it may not be realistic (Kelrick *et al.* 1986). Only the first granivore reaching the dishes would have equal choice. This assumption had support because many dishes seemed untouched; therefore, it seemed reasonable to suggest that those that were discovered were only eaten by a single individual.

Statistical analyses

Both parametric and non-parametric statistics were used in the analysis of gathered data. In most cases, an attempt was made to normalize data and meet assumptions for a parametric test before non-parametric statistics were applied.

Soils

ANOVAs were used to determine if there was an interaction between year and community and if there were significant differences between years and between communities (overall and for each measured soil

characteristic). Potassium was close to being non-normal and so a Kruskal-Wallis test was used as well, to help determine if the ANOVA may have given faulty significance.

Vegetation

Because of the large numbers of empty cells in the data, Principal Components Analysis was not used (McCune and Grace 2002). Instead, analysis of dry mass of vegetation was carried out using non-metric multidimensional scaling (NMS) using a Sørensen distance measure. NMS has no assumptions and is able to cope with rare species data (McCune and Grace 2002). The Sørensen distance measure was used because it is non-metric, works with all types of data, does not assume that all variables are measured on the same scale, and is recommended for community data (McCune and Grace 2002). Data are compared to randomized data in a Monte Carlo test to determine dimensionality of the solution, and stress (departure from monotinocity) is calculated. NMS detects patterns in the data that form the basis of further testing. Cluster analysis was used to find groups of similar plots. NMS and cluster analysis were followed MRPP (multi-response permutation procedure), a non-parametric test that provides a significance level for groups identified by NMS, such as vegetation removal compared to no removal plots. MRPP not only indicates significant differences between groups, but also homogeneity within a group compared to random, and this statistic is called A (McCune and Mefford 1999). McCune and Mefford (1999) note that community ecology values for A are commonly below 0.1, and that an A value greater than 0.3 is high, which is logical because when A = 1 all items must be identical within groups. This statistic (A) allows the ecological importance of the significance to be considered by indicating how close to random the groups really are, because with large sample sizes significant values can be obtained regardless of the homogeneity of the groups (McCune and Mefford 1999). Finally indicator analysis was used to determine if any species typified any treatment. It was also used on the groups defined by cluster analysis to determine what species defined the groups. All analyses were carried out using PC-ORD4 (McCune and Mefford 1999).

McCune and Grace (2002) recommend removing all columns with only one or two occurrences of a particular species so original matrix of 38 species (34.3% of the cells filled), was reduced to 26 species (48% of the cells filled).

Variables in the second matrix, normally environmental variables, were largely calculated from the species biomass data. Plot total biomass, percent of forbs and grasses (by mass), litter mass, richness, evenness, and diversity were calculated for each plot. Plot distance from road and altitude of plot on the hillside were also included to determine if the location of the plots had an impact on the vegetation within them. In addition, categorical variables were added for treatment, removal compared to no removal, and

for location in groups that run up and down the hillside.

Sørensen's similarity index was used to compare removal treatments to ones with no removal. This is calculated by adding the number of species common to treatments I and dividing that by the

number of species in each treatment (S_1 and S_2).   Sørensen's similarity index:
$$\beta = \frac{2c}{S_1 + S_2}$$

As NMS only gives trends and does not provide significance levels between groups, normality of the variables in the second matrix were determined, as well as skew and kurtosis. Non-normal variables were identified using SYSTAT and log transformed to normalize the variance before doing parametric tests (ANOVAs) of difference between biomass and diversity attributes in removal plots and their control, plots with no removal. The factors that were successfully transformed were richness, evenness, and diversity. Some variables could not be transformed to meet assumptions for an ANOVA and so percent graminoid mass, total plot biomass, litter, and percent forb mass were subjected to Mann-Whitney U tests instead. Species that occurred in more than twelve plots were subjected to Mann-Whitney U tests of their biomass. Species that occurred in less plots than that commonly had too few individuals in one treatment, leading to large errors.

Granivory

The majority of the seeds were not eaten, making for a severely skewed data set. The simplest way to visualize the data was to use NMS, and MRPP was run on the months to verify that granivory was significantly different in each month and give some idea of the homogeneity of the data. Preference between seed species was analyzed using Mann-Whitney U tests. Indicator analysis was used to show which species had all ten seeds removed, so even if only one or two dishes were discovered by a species, that preference could be recorded for each month.

RESULTS

As with the previous section, any results associated with seed germination are given in Appendix B.

Soil samples

There was no interaction between year and community (though both year and community were significantly different at $p \leq 0.05$) so data were pooled and factors examined by year and by community separately. Moisture, conductivity, total nitrogen, available phosphorous, available potassium, available calcium, and available magnesium were all significantly greater in 2007 than in 2006; only pH was significantly greater in 2006 than in 2007 (Table 2).

Table 2: Soil property values in 2006 and 2007. Factors with different letters are significantly different (ANOVA, $p \leq 0.05$) between years.

Factor	2006	2007
Moisture (%)	0.9 [a]	2.3 [b]
Total carbon (% dry weight)	4.0 [a]	3.7 [a]
pH	7.1 [a]	6.9 [b]
Conductivity (μS/cm)	58 [a]	321 [b]
Available nitrate (μg/g)	6.8 [a]	8.3 [a]
Available P (μg/g)	25 [a]	40 [b]
Total N (% dry weight)	0.215 [a]	0.361 [b]
Organic matter (%)	6.9 [a]	6.4 [a]
Available Ca (μg/g)	2421 [a]	3418 [b]
Available K (μg/g)	352 [a]	431 [b]
Available Mg (μg/g)	184 [a]	288 [b]

Knapweed-dominated communities had lower values for most soil factors than grass-dominated communities, with cinquefoil-dominated communities being intermediate and occasionally lower than grassland (Table 3).

Table 3: Mean values (ANOVA) for soil characteristics. Factors with different letters are significantly different (p ≤ 0.05) between the three community types, dominated either by grasses, cinquefoil or knapweed.

Factor	Grassland	Cinquefoil	Knapweed
Moisture (%)	2.4^a	1.5^{ab}	0.9^b
Total carbon (% dry weight)	5.8^a	3.5^b	2.3^c
pH	6.7^a	6.9^a	7.3^b
Conductivity (µS/cm)	236^a	182^a	152^a
Available nitrate (µg/g)	9.4^a	6.0^a	7.2^a
Available P (µg/g)	34^a	31^a	33^a
Total N (% dry weight)	0.421^a	0.267^b	0.176^b
Organic matter (%)	10.0^a	6.1^b	3.9^b
Available Ca (µg/g)	3724^a	2858^{ab}	2177^b
Available K (µg/g)	471^a	405^{ab}	298^b
Available Mg (µg/g)	323^a	306^a	79^b
C:N ratio	15.3^a	15.1^a	14.3^a

Cluster analysis did not provide strong evidence for the communities being different (Fig. 1). Groups chosen by cluster analysis included examples of at least two of the three communities and samples from the two years did not always group together (Fig. 1). However, ANOVA showed that community types were significantly different.
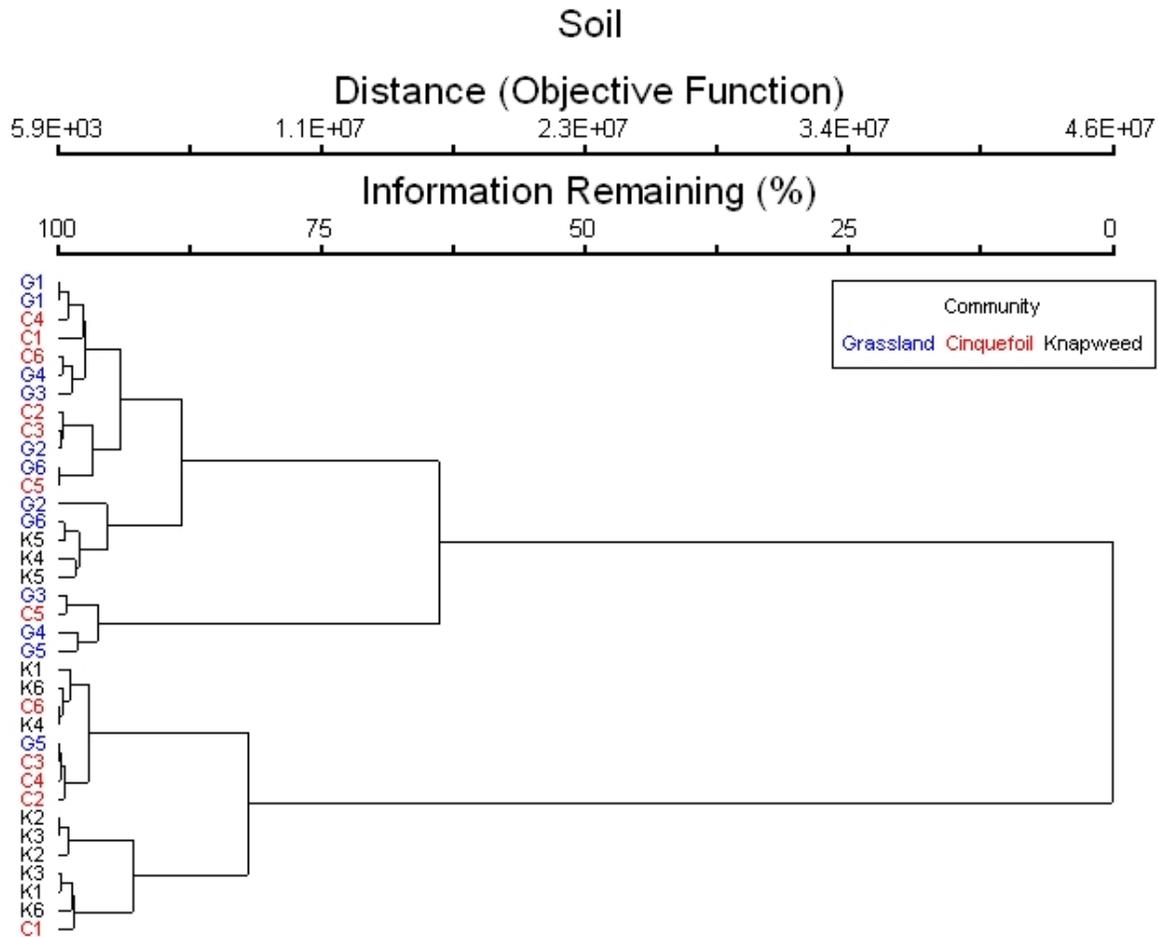
Figure 1: Cluster analysis of soil data using Eucledean/Ward's measures (2.94% chaining). Note that all groups include at least two communities (when groups are chosen that include at least 4 samples) and that measures between years do not always group together. Soils were from G = bunchgrass-dominated, C = sulphur cinquefoil-dominated, and K = diffuse knapweed-dominated sites.

Seed bank

The following species emerged from the seed bank soil samples and grew to adults in the greenhouse: *Hesperostipa comata, Vicia   nvisibil, Tragopogon dubius, Potentilla recta, Sisymbrium altissimum, Taraxacum officinale, Conyza   nvisibili, Centaurea diffusa, Myosotis verna, Sonchus arvensis, Lactuca serriola, Chenopodium album, Stellaria media, Bromus* spp., and *Poa bulbosa* (from bulblets in soil). Other species never obtained sufficient growth for identification, dying after being transplanted.

Bromus spp. Were most abundant and emerged before any of the forbs. Comparison of abundances could not be made, however, because the seedlings dried out and died before obtaining sufficient growth to be identifiable to species. Approximately 70% of the species identified above

occurred in more than 20% of the plots (Table 4). Several of the remaining species were locally abundant in one area (*Vicia Americana* abundant in plots labelled 1, and *Hesperostipa comata* and *Chenopodium album* in plots closest to the road).

Main field experiment: seed addition and invasive removal

Seed addition did not result in any additional germination in the plots, though germination trials were successful for all but one species (Appendix B). Seedlings of invasive species were found in all the plots. There was a highly significant (p<0.0001) difference in the number of diffuse knapweed seedlings between removal treatments (mean of 16 plants per plot) and controls (mean of 4 plants per plot).

Native species other than *Achnatherum occidentale* were rare on the hillside (as found from seed bank analysis and plot biomass) and did not change in abundance between years with the exception of silky lupine (*Lupinus sericeus* Pursh.). Silky lupines were present in ten plots in 2006, and 17 plots in 2007.

Bromus tectorum was the only plant that occurred in all plots, though *Sisymbrium altissimum* and *Poa bulbosa* were in the centre 1 m^2 of all plots but one (Table 4). Most biomass in the plots came from *Sisymbrium altissimum* as these were one of the largest plants, but *Bromus tectorum* was by far the most abundant in numbers. Only nine species occurred in more than fifty percent of the plots (Table 4). Relative frequency of species in the plots followed a the classic reverse-J pattern, with thirteen species occurring in less than three percent and five species occurring in more than ninety percent of the plots (Fig. 2).

Table 4: Mean biomass of species per plot, average number of individuals in plots at harvest in 2007 (nearest whole number), and the percentage of plots in which each was found. Perennials indicated by *.

Scientific name	Common name	Avg. Biomass / plot (g)	Avg. Plants / plot	Plots present (%)
Achnatherum occidentale*	Stiff Needlegrass	7.45	4	10
Antennaria sp.*	Pussytoes	0.24	2	2
Arenaria serpyllifolia	Thyme-leaved Sandwort	0.90	36	40
Bromus sp.	Brome sp.	1.13	27	54
Bromus tectorum	Cheatgrass	6.20	122	100
Camelina microcarpa	Littlepod false flax	0.08	1	6
Centaurea diffusa	Diffuse knapweed	21.18	26	92
Chenopodium alba	Lamb's quarters	5.08	6	17
Conyza canadensis	Horseweed	10.16	3	52
Epilobium sp.	Willowherb	2.31	1	6
Erodium cicutarium	Stork's bill	0.99	1	8
Gaillardia aristata*	Brown-eyed Susan	25.66	3	2
Hesperostipa comata*	Needle and thread grass	1.56	1	15
Lactuca serriola	Prickly Lettuce	25.55	4	75
Lithospermum arvense	Field Gromwell	0.07	1	4
Lupinus sericeus*	Silky lupine	5.91	1	33
Medicago lupulina	Black medic	2.31	6	8
Melilotus alba	White sweet-clover	15.42	1	2
Myosotis verna	Spring forget-me-not	0.05	25	27
Poa bulbosa	Bulbous bluegrass	2.49	47	98
Poa pratensis*	Kentucky bluegrass	3.11	13	6
Polygonum sp.	Knotweed sp.	5.82	6	90
Potentilla recta*	Sulphur cinquefoil	3.44	1	2
Salsola kali	Russian thistle	23.08	3	33
Sisymbrium altissimum	Tall tumble-mustard	70.07	11	98
Stellaria media	Common chickweed	0.02	1	2
Taraxacum officinale*	Dandelion	0.07	2	4
Tragopogon dubius	Yellow salsify	9.77	13	73
Verbascum thapsus	Mullein	1.16	1	2
Vicia sp.	Vetch	3.83	1	13

Relative Frequency of Species
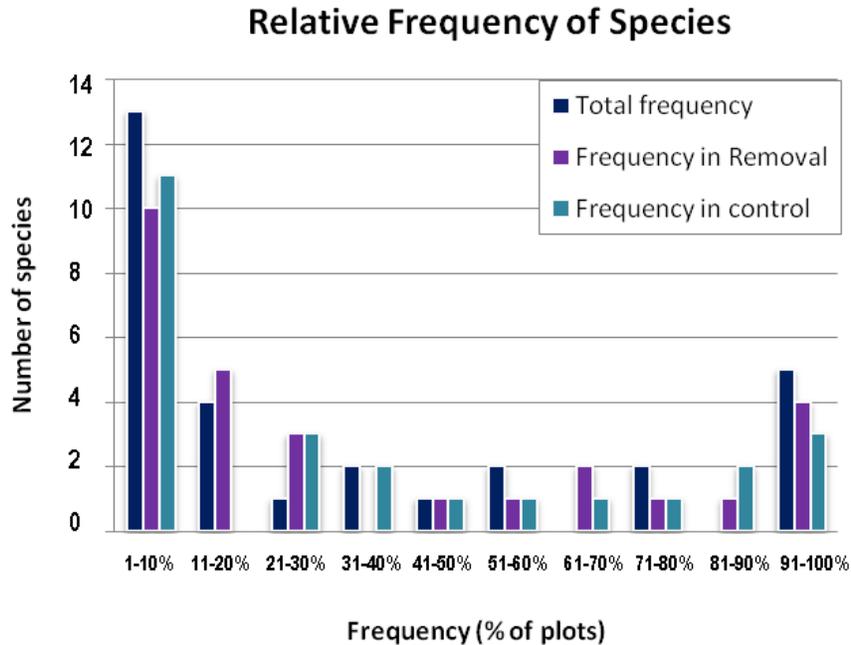
Figure 2: Frequency of species in the vegetation removal (and its control, no removal) treatments.

Because there was no germination of added seeds in the plots, data analysis was based on the remaining treatment; removal of vegetation. NMS came to a 2 dimensional solution (Fig. 3) with a final stress (departure from monotinocity) of 15.73716, a value deemed acceptable for ecological data by McCune and Grace (2002). The total R^2 (measure of fit) was 0.842 (axis 1 = 0.586, axis 2 = 0.255) with an orthogonality of 99.9 and final instability of 0.00001, indicating an effective ordination (McCune and Grace 2002). On the NMS graph, most of the plots outside the centre cluster did not have vegetation removed (Fig. 3).

Eleven variables (including the 3 categorical variables) were included in the second matrix: plot total biomass, percent of forbs and grasses (by mass), litter mass, richness, evenness, diversity, plot distance from road, treatment (of the eight combinations), vegetation removal treatment, and location in groups that run up and down the hillside. The main matrix included all species present in at least two plots (McCune and Mefford 1999), though the removal of the eleven least common species did not seem to impact the solution.

Sisymbrium altissimum, *Lactuca serriola*, and *Tragopogon dubious* had the best fit to the axes of the ordination (Table 5). Only diffuse knapweed (greater in removal) and miscellaneous grass (species unidentifiable due to lack of seed, genus *Poa*) biomass (greater in control) were significantly different between vegetation removal and non-removal control (p<0.0001 and 0.001 respectively).

17
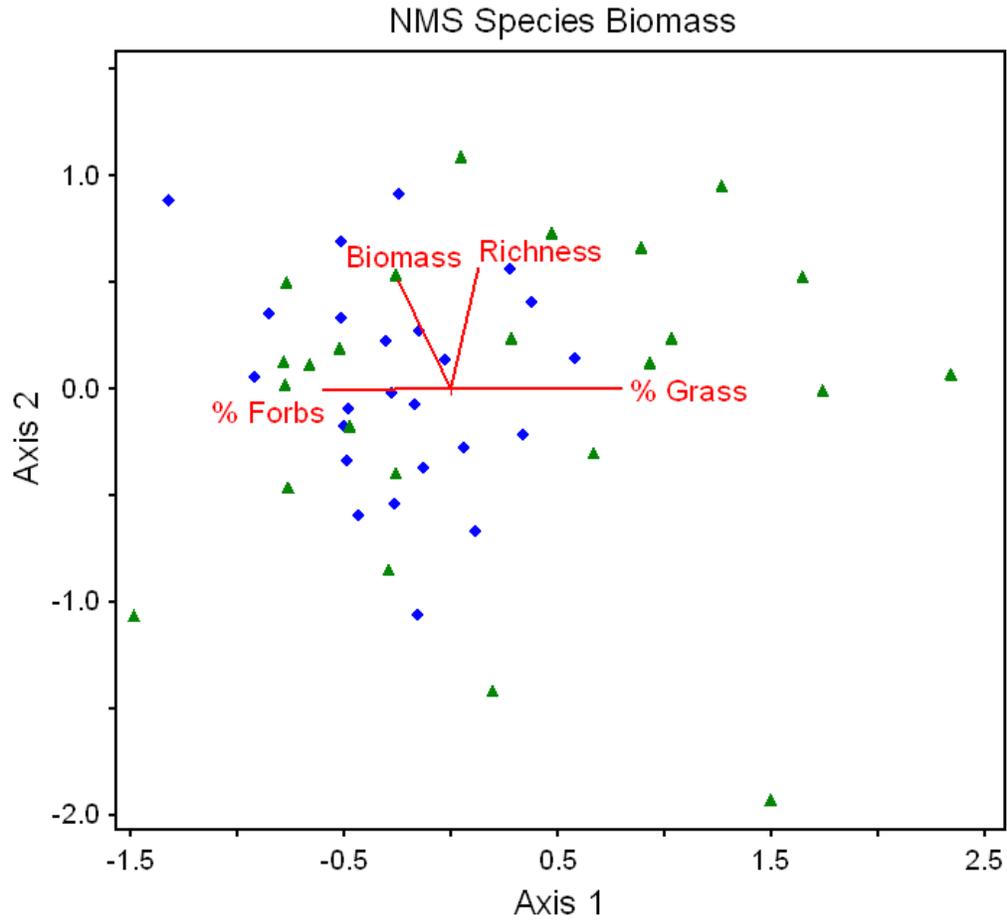
Figure 3: Non-metric multidimensional scaling graph (r² cut-off of 0.250), green points are control plots, and blue points are plots that had vegetation removed. Cut off at 0.25 as r^{2} values act as a measure of quality of fit.

Table 5: r² values (quality of fit) for species that relate to the non-metric multidimensional scaling axes for vegetation biomass. Values over 0.15 are shown in bold and indicate species that best fit the axes.

| Species	Axis 1 r^2	Axis 2 r^2
Centaurea diffusa	**.178 (-)**	.000 (-)
Sisymbrium altissimum	**.458 (-)**	.134 (+)
Lactuca serriola	.027 (+)	**.426 (-)**
Tragopogon dubious	**.539 (+)**	.082 (+)
Conyza canadensis	.002 (+)	.041 (+)
Epilobium sp.	.003 (+)	.001 (+)
Salsola kali	.049 (-)	**.193 (-)**
Polygonum sp.	.027 (+)	.005 (+)
Arenaria serpyllifolia	.000 (-)	.077 (+)
Chenopodium alba	.026 (-)	.028 (-)
Lupinus argenteus	.002 (+)	.000 (+)
Vicia sp.	.103 (+)	.002 (+)
Erodium cicutarium	.000 (+)	.025 (-)
Medicago lupulina	.007 (-)	.051 (+)
Lithospermum arvense	.011 (+)	.001 (+)
Myosotis verna	.000 (-)	**.183 (+)**
Camelina microcarpa	.002 (+)	.036 (+)
Achnatherum occidentale	.051 (+)	.101 (+)
Poa pratensis	.050 (+)	.065 (+)
Poa bulbosa	.120 (+)	.002 (+)
Bromus tectorum	.008 (+)	.078 (+)
Bromus sp.	.053 (+)	.006 (+)
Misc. grass (*Bromus*)	.035 (+)	.061 (+)
Misc. grass (*Poa*)	.141 (+)	.074 (+)
Misc. (unsorted veg.)	.000 (+)	**.220 (-)**

Of all the data included in the second matrix, the percent of grass (by mass) in the plot had the highest correlation with an axis, with percent of forbs (by mass), biomass, and richness also being important (Table 6).

Table 6: Non-species r² (quality of fit) values for variables relating to non-metric multidimensional scaling axes (matrix 2). Values over 0.15 are shown in bold as they show the greatest fit.

Other Variables	Axis 1 r^2	Axis 2 r^2
Distance from road	.002 (+)	.034 (-)
Litter	.081 (+)	.021 (-)
Biomass	.135 (-)	**.230 (+)**
% Grass	**.399 (+)**	.002 (+)
% Forb	**.295 (-)**	.006 (-)
Richness	.057 (+)	**.295 (+)**
Diversity	.000 (+)	.052 (+)
Evenness	.028 (-)	.000 (+)

The best quality of fit was found from percentage of grass, which was driven by seven vegetation control plots all having a larger percentage of grass than the remaining plots (Fig. 4).
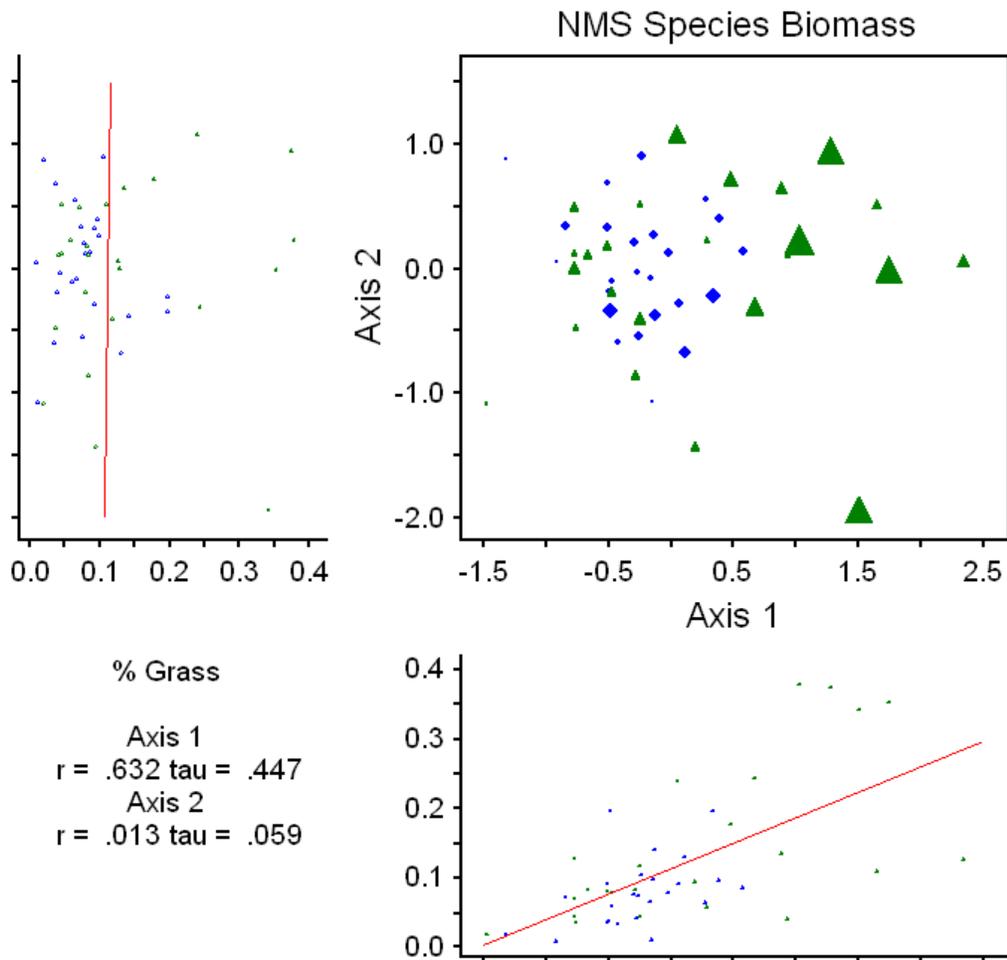
Figure 4: Non-metric multidimensional scaling (NMS) graph where size of the triangles indicates the relative amount of grass species (by mass) occurring in the plot. Green points were vegetation control plots, and blue plots had vegetation removed.

There was a significant difference between vegetation removal and no removal (p = 0.0001); however, the heterogeneity within the two groups was high (A = 0.04, with a maximum value of 1 being totally homogeneous). Sørensen's similarity index between vegetation removal treatments was 0.84 (max of 1), indicating that a large portion of species are similar between the treatments.

20

The plots could be divided into three groups based on position on the hillside (Fig 5) as the plots were placed according to the spread of knapweed. These three groups subjected to MRPP show a significant effect (p = 0.000) and with a higher level of homogeneity than in the removal treatment (A = 0.075 compared to 0.043). However, all of the plots with a very high grass biomass (Fig. 4) are within one group (group 1, yellow in Fig. 5, green triangles in Fig. 6).
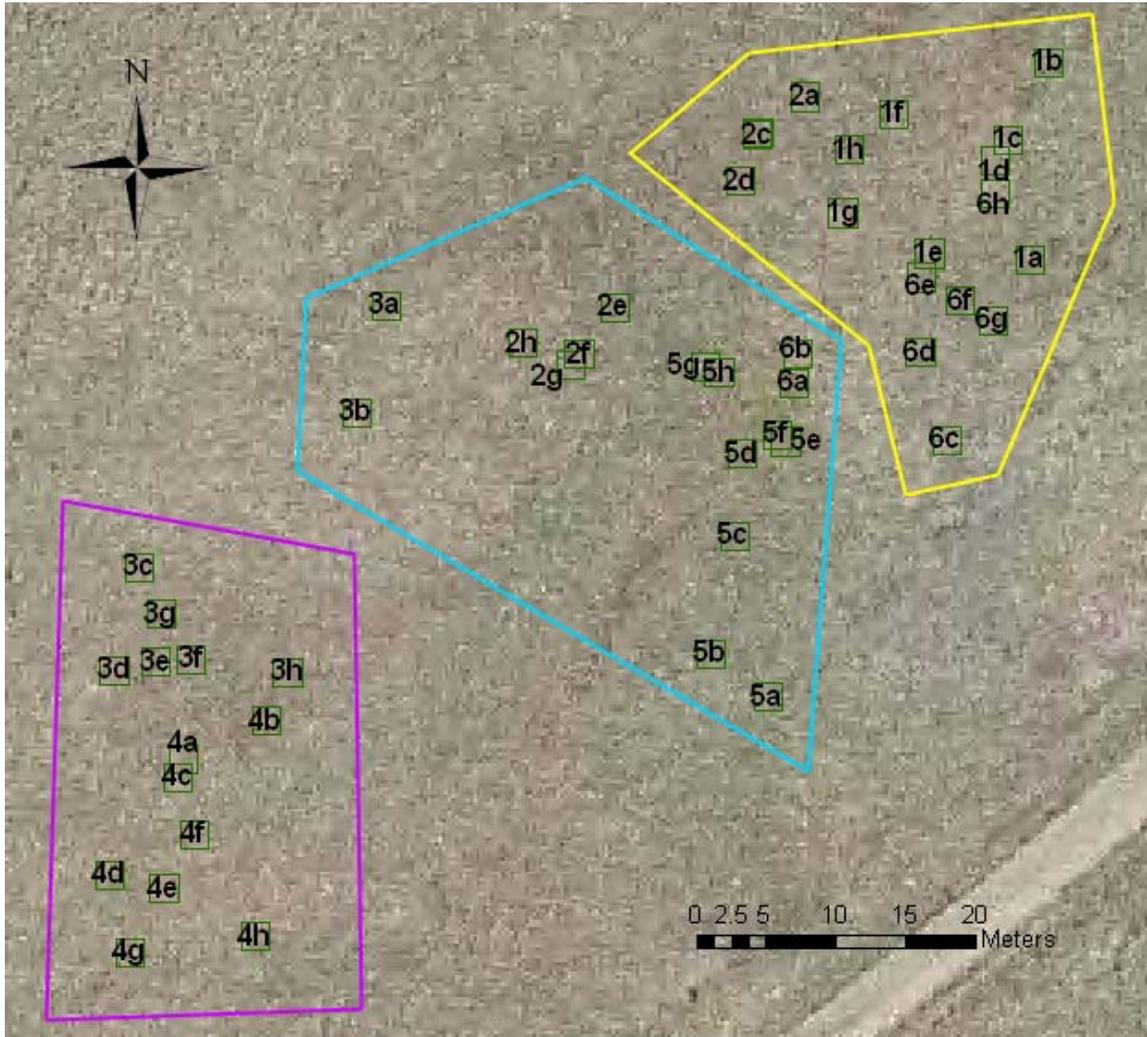
Figure 5: Approximate location of plots as grouped by position on the hillside. Group 1 is at the right outlined in yellow, group 2 is in the middle in blue, and group 3 is at the left in purple. Overlapping plots (2 x 2 m green squares) due to GPS error (approximately ±5 m accuracy).

Group 1 has many indicator species (p ≤ 0.05), including all of the grass species as well as *Lactuca serriola*, *Tragopogon dubius*, *Vicia nvisibil*, and *Myosotis verna*. Group 2 on the other hand has no indicators and group 3 only has one: *Salosi kalil*. In the field, the amount of bare ground was greater toward group 3.
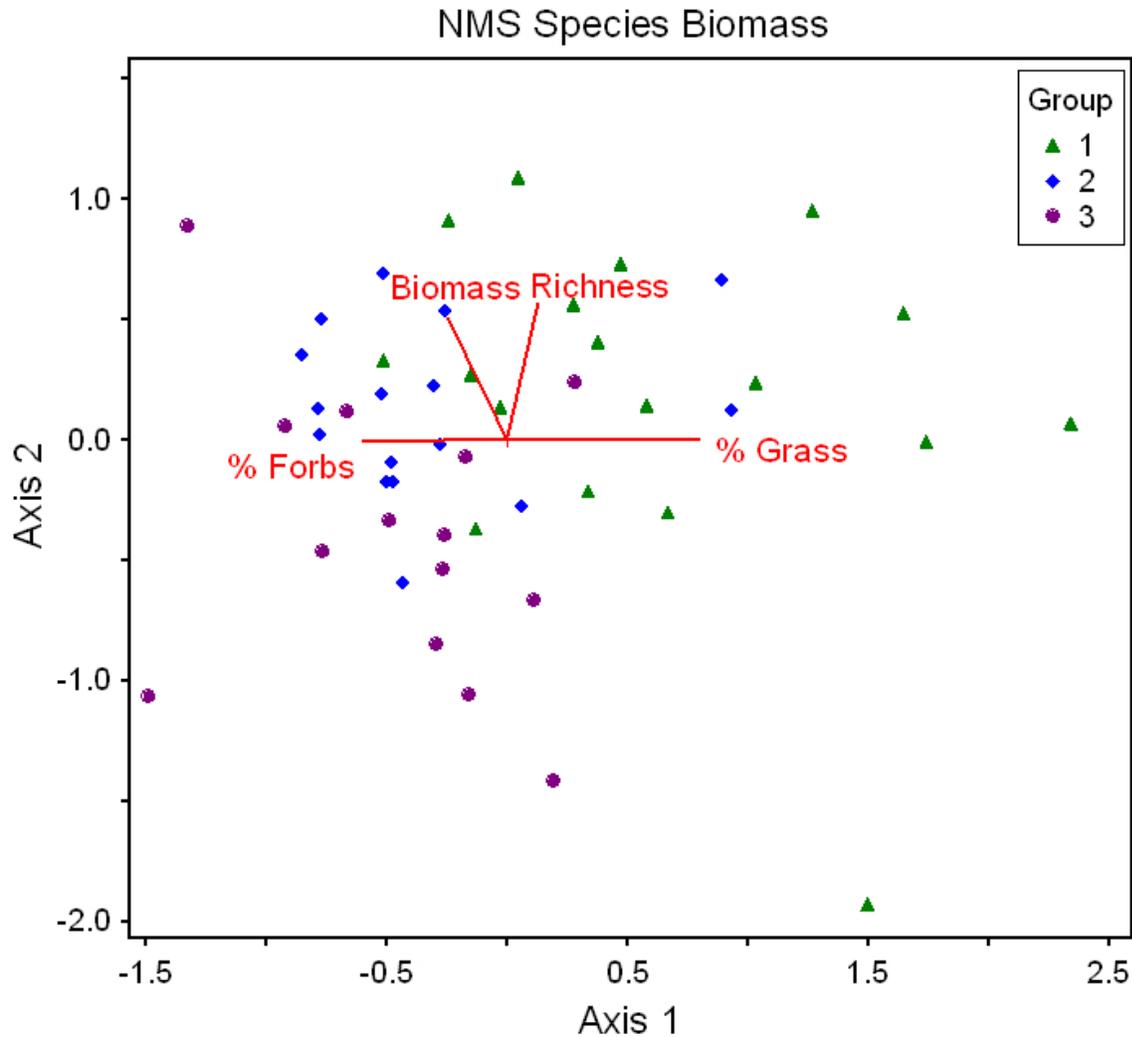
Figure 6: Non-metric multidimensional scaling graph (r² cut-off of 0.250), showing the three 'groups' of plots that can be artificially created by plot position as shown in Figure 5.

Cluster analysis resulted in two groups of one member, and four groups with multiple members. The lowest chaining (7.53 %) was achieving using Euclidian distance and Ward's measure. The groups were significant under MRPP (p = 0.00) with a good homogeneity (A = 0.24) obviously due to the groups being based on species. One group identified by *Tragopogon dubious*, one by *Centaurea diffusa* and *Sisymbrium altissimum,* and one by *Bromus* spp., *Lactuca serriola*, *Myosotis verna*, and *Polygonum* sp. (much like the location group 1, Fig. 6). The last group with multiple members was not significantly indicated by any species, though *Salosi kalil* was close to being significant (p = 0.06). The groups found by cluster analysis did not separate removal treatments or groups by location for the most part.

Plots with vegetation removed had a higher mean richness, evenness, and diversity than control plots, however, only diversity was significantly different (**p = 0.047**). Biomass was found to be the same under all treatments. Litter mass and the percentage of graminoids were greater in plots with no vegetation removal, while the percentage of forb mass was greater in plots with vegetation removal (Table 7).

Table 7: Results of Mann-Whitney U tests on biotic variables used in second matrix of the vegetation biomass non-metric multidimensional scaling analysis.

Variable	Average value in removal	Average value in control	Mann-Whitney U	p value
Total biomass	167.71 g	157.06 g	248.000	0.409
Litter mass	11.88 g	121.82 g	576.000	**0.000**
Forb biomass	90 %	81 %	180.000	**0.026**
Grass biomass	8 %	14 %	384.000	**0.048**

Control plots only had one firm indicator; the unidentifiable pieces of grass (misc. grass) that was likely *Poa* (Table 8). *Tragopogon dubious* was more abundant in plots without any vegetation removal, but was borderline significant. Removal plots were characterized (significantly) by *Arenaria serpyllifolia* and *Centaurea diffusa* (Table 8).

Table 8: Significant results from the indicator analysis test of species biomass data.

Indicator	Group	Indicator Value	P value
Arenaria serpyllifolia	Vegetation removal	49.0	0.0307
Tragopogon dubious	Control	61.5	0.0516
Misc. grass	Control	79.2	0.0005
Centaurea diffusa	Vegetation removal	81.5	<0.00001

Granivory bioassay

The NMS resulted in a 2 dimensional solution (stress = 16.919) with r^2 values indicating species correlation with the NMS axes shown in Table 9. The total r^2 was very strong at 0.913 (0.717 for axis 1 and 0.196 for axis 2) and orthogonality at 99.6.

Categorizing the data by month, showed each month had a different scatter (Fig. 7). June had the greatest predation (an average of 26.4% of seeds gone, with more plots containing less seed visualized as a larger spread) with considerably less in July (an average of 6.5% of seeds gone), and almost none in August (an average of 2.6% seeds gone).

Months were significantly different (p < 0.000) with overall heterogeneity (A) at 0.143. August had the highest homogeneity (A = 0.192), July lower (A = 0.069), and June lowest (A = 0.041).

Table 9: The r² values for bioassay seed species that relate to non-metric multidimensional scaling axes.

	Axis 1	Axis 2
Species	r^2	r^2
Achnatherum occidentale	0.163 (+)	0.356 (+)
Hesperostipa comata	0.127(-)	0.592 (+)
Koeleria macrantha	0.173 (-)	0.368 (+)
Pseudoroegneria spicata	0.002 (-)	0.225 (+)
Gaillardia aristata	0.226 (-)	0.404(+)
Monarda fistulosa	0.425 (+)	0.211 (+)
Geum triflorum	0.019 (-)	0.423 (+)
Heuchera cylindrica	0.044 (+)	0.055 (+)
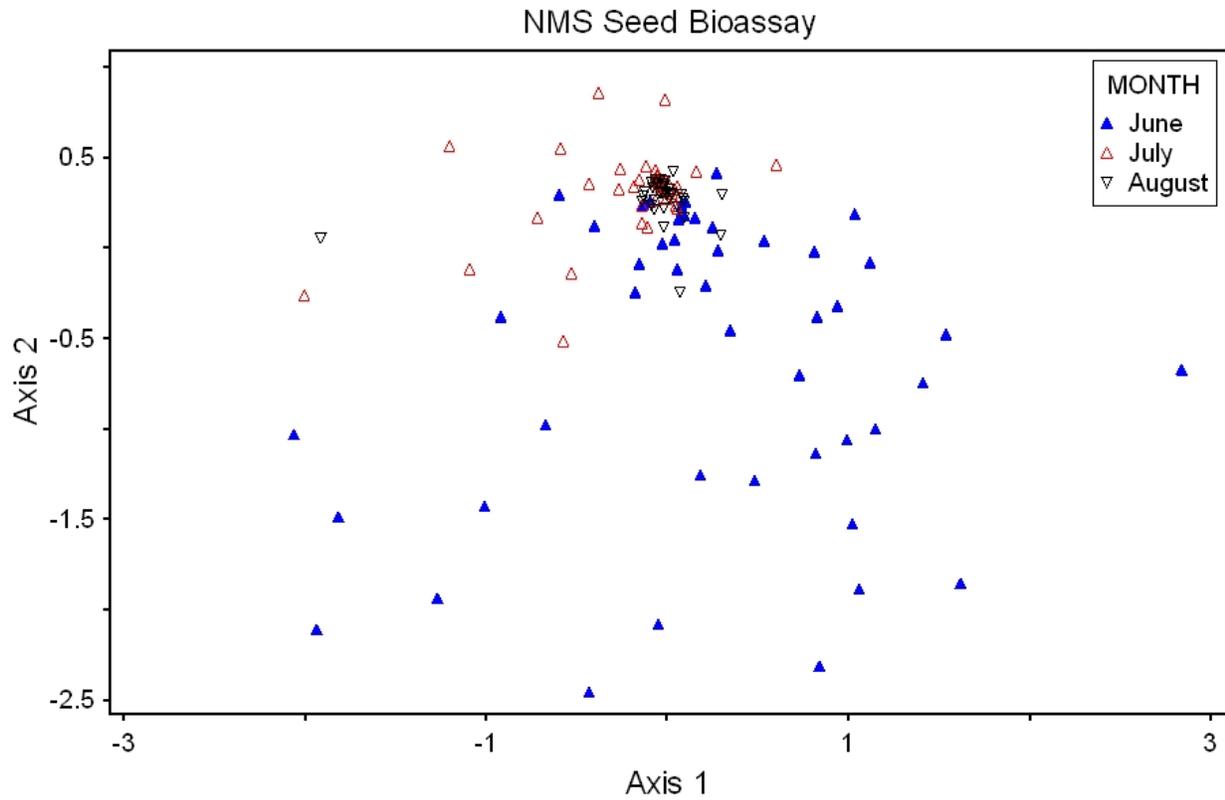
Figure 7: Non-metric multidimensional scaling showing variation amoung Petri dish contents (number of seeds of each species remaining) for June, July and August.

The average number of seeds remaining over all the trials monthly and overall is shown in Figure 8. *Galardia aristata* was the least chosen seed species. *Monarda fistulosa, Koeleria macrantha,* and *Heuchera nvisibilit* were the species with the least seeds remaining (Table 10). These are the two smallest-seeded forb species and the smallest-seeded grass species. Table 10 shows pair-wise comparisons of all eight species seeds, establishing significant differences in preference.
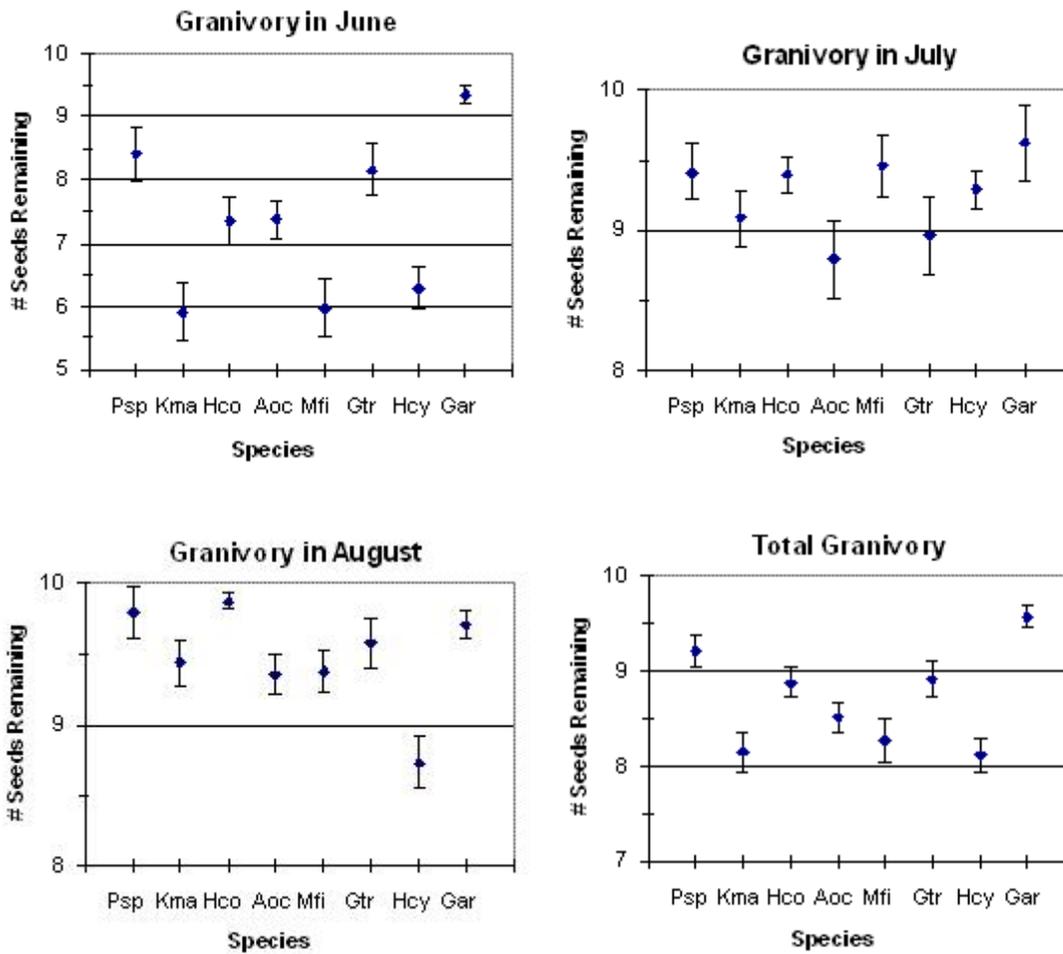
Figure 8: Granivory from Petri dishes. The average number of seeds remaining of each species used in the bioassay each month measured and the average over all three months. Bars are +/- standard error. Species codes: Psp = *Psuedoroegneria spicata*; Gar = *Gallardia aristata*; Kma = *Koeleria macrantha*; Mfi = *Monarda fistulosa*; Hco = *Hesperostipa comata*; Aoc = *Achnatherum occidentale*; Hcy = *Heuchera   nvisibilit*; Gtr = *Geum trifolium*.

Table 10: P values from Mann-Whitney U test comparing overall consumption of seeds. Significant values in bold. Species codes as in Fig. 8

SPECIES	Psp	Kma	Hco	Aoc	Mfi	Gtr	Hcy
Kma	**0.000**	-	-	-	-	-	-
Hco	**0.000**	**0.009**	-	-	-	-	-
Aoc	**0.000**	0.786	**0.012**	-	-	-	-
Mfi	**0.000**	0.351	0.116	0.465	-	-	-
Gtr	**0.015**	**0.000**	0.233	**0.000**	**0.008**	-	-
Hcy	**0.000**	0.107	**0.000**	**0.040**	**0.011**	**0.000**	-
Gar	0.614	**0.000**	**0.001**	**0.000**	**0.000**	**0.040**	**0.000**

Three species had all ten seeds removed from a number of the Petri dishes in June; *Monarda fistulosa* (completely removed from 10% of the Petri dishes), *Pseudoroegneria spicata* and *Koeleria macrantha* (both completely removed from 6% of the Petri dishes). Though *M. fistulosa* and *K. macrantha* were statistically preferred, *P. spicata* was one of the least preferred seeds overall (Fig. 8). In July *Achnatherum occidentale, Geum triflorum,* and *Monarda fistulosa* were completely removed from 2% of Petri dishes. As with June, only two of these species (*G. triflorum* and *A. occidentale*) were identified as preferred, while *M. fistulosa* was one of the least preferred over all the dishes (Fig. 8). August was the only month when there were no species that had all seeds removed from any of the Petri dishes.

DISCUSSION

Although each experiment is discussed separately, management implications are discussed as well. These take into account the fact that soil differences and vegetation cover together may need to be considered together to succeed in even partial restoration.

Soil samples

I found evidence to suggest that invasive species can alter soil nutrient concentrations in the southern interior of British Columbia, Canada. A dominant plant species in a community can influence ecosystem attributes (Denslow and Hughes 2004), therefore, determining the effect of potentially dominant invasive species on nutrient cycling is important for ecosystem restoration. LeJune *et al*. (2006) concluded that diffuse knapweed had no effect on nutrient cycling because they detected no response when the species was removed. However, as in my studies, Meiman *et al*. (2006) reported that nitrogen was lower in communities dominated by diffuse knapweed compared to a native-dominated site, but their sample size was inadequate for statistical analysis. Little is known about the effect that sulphur cinquefoil has upon soils.

There was greater soil N within the bunchgrass-dominated communities compared to the knapweed-dominated communities, but the reasons could be varied. Hook *et al*. (2004) found that the effect of spotted knapweed was not consistent on soil carbon and nitrogen, but that generally these nutrient pools were reduced under spotted knapweed. Bunchgrass-dominated communities have cryptogamic crusts (also called biological soil crusts), which increase both soil moisture and nitrogen (Belnap *et al*. 2003; Marsh et al. 2006) and may partly explain this difference where disturbance severely reduced the crust in knapweed-dominated communities. Cryptogamic crusts also affect the alkalinity of the soil surface, with a pH of up to 10 (Belnap *et*

al. 2003). While such high pH levels are not likely to penetrate deeply into the soil, it was surprising to find that the bunchgrass community with more cryptogamic crust had more acidic soils than the knapweed community as it seemed likely abundant crust would lead to a more alkaline pH. In addition to the cryptogamic crusts, bunchgrass-dominated communities also contained silky lupine (*Lupinus sericeus*), which is a nitrogen-fixing legume that adds nitrogen to the soil. Available nitrate did not change between years or communities, which indicates it was limiting to all communities.

Another common invasive in the diffuse knapweed and yellow cinquefoil communities was cheatgrass (*Bromus tectorum*), which might have affected soil nutrients. Compared to native grasses, cheatgrass increases litter on the soil surface. Cheatgrass litter has a high C:N; typically higher than native grasses (Evans *et al*. 2001). In my study the C:N varied too widely to be significantly different in any community, but the differences in total nitrogen might be due to cheatgrass presence as cheatgrass can drastically lower nitrogen pools (Sperry *et al*. 2006). Cheatgrass reduces total soil nitrogen by up to 50% within two years of invasion (Evans *et al*. 2001, Sperry *et al*. 2006, Rimer and Evans 2006), and uptakes more nitrate than forb neighbours (Leonard *et al*. 2008). In my study the difference between bunchgrass and the two invasive forb-dominated communities could be due in part to the presence of cheatgrass in these invaded communities.

The potential of cheatgrass to lower soil nitrogen may facilitate dominance by diffuse knapweed, as *C. diffusa* has been found to be highly competitive under low nitrogen conditions and able to utilize phosphorous to its competitive advantage (Suding *et al*. 2004, LeJeune *et al*. 2006). Phosphorous increases in the presence of spotted knapweed (Zabinski *et al*. 2002, Thorpe *et al*. 2006). Thorpe *et al*. (2006) found the soluble phosphorous in the rhizosphere of spotted

knapweed was greater on two of three sites, which they suggested may be caused by catechin chelating metals that bind phosphorous. Diffuse knapweed does not have catechin, but it secretes 8-hydroxyquinoline, which also acts as a chelating agent (Ferrero and De la Torre 1986). This chelation activity could be very important in alkaline environments (Tharayil *et al*. 2009), such as were discovered in areas dominated by knapweed. A chelating agent can bind minerals that immobilize phosphorous and this could give diffuse knapweed an advantage over competing plants by increasing the concentration of phosphorous over what could otherwise be found in the soil. Since phosphorous is immobilized at lower pH, chelation ability may be a factor in the success and dominance of diffuse knapweed on my site because it was found on sites with lower pH than areas dominated by other species. Levels of calcium, potassium, and magnesium may be more influenced by the pH rather than the plant community, but because little research has been done on plant effects on these nutrients it is difficult to speculate.

Any abundant invasive plant species will likely change the input of litter as well as nutrient uptake, which could alter nutrients in the soil, changing the C:N. The sulphur cinquefoil- and the bunchgrass-dominated communities are both dominated by smaller perennial species, while diffuse knapweed-dominated communities are covered by the knapweed and annual species that grow to a larger size than the perennial species, and so depletion of soil nutrients may be due to a change in nutrient uptake and litter decomposition time. Nitrogen retention through microbial mineralization relies on moisture and carbon input from plants (Hooper and Vitousek 1997), and a higher moisture and carbon content may be why total nitrogen is higher in the bunchgrass dominated community.

My results also showed that there was a lower soil organic matter and carbon content compared to the bunchgrass-dominated communities, which may be a consequence of an altered

litter regime or nutrient uptake. In Spain, Albaladejo *et al*. (1998) removed all vegetation as a pulse experiment and soil carbon decreased by 35% over the following 55 months. Considering the 40% difference in soil carbon between bunchgrass and knapweed-dominated communities in my study, this suggests that invasion may have a large effect on carbon cycling. LeJeune *et al*. (2006) concluded that diffuse knapweed does not affect soil nitrogen; however, their one year removal experiment may not have been long enough for carbon content in the soil to change and allow the microbial community to affect nitrogen. If the study by LeJeune *et al*. (2006) was too short, diffuse knapweed may have more of an effect on soils than previously believed. Invasive species may also indirectly affect nutrient cycling through soil microbial communities (Kourtev *et al*. 2002), and diffuse knapweed has been reported to exude an anti-microbial chemical (Vivanco *et al*. 2004, Watkins *et al*. 2009), though production may be limited or transient (Tharayil *et al*. 2009). Both reduced carbon levels and lack of microbes could have combined to result in reduced nitrogen levels in the soil of communities dominated by diffuse knapweed.

Tilman and Downing (1994) determined that communities with increased species numbers had increased moisture retention. My results showed that areas with knapweed and various other non-native species had less moisture than areas with a near monoculture of cinquefoil. However, this may be due to the physiology of the plants in the communities; tap rooted invasive species such as knapweed have been shown to reduce soil moisture to a greater degree than fibrous-rooted species such as cinquefoil (Allen and Knight 1984). In other words, the functional role of particular plant species may be more relevant than species richness *per se* in the determination of certain ecosystem functions (Huston 1999). Spotted knapweed invasion also increases soil surface run off (Lacey *et al*. 1989). If diffuse knapweed acts in the same

manner as spotted knapweed, this impact and the lack of soil crusts may be further explanation for the low level of soil moisture in knapweed-dominated communities.

As well as the difference between communities, soil properties were significantly different between years, which may be in part due to increased moisture in 2007 from 2006. This is typical for dry ecosystems, where nutrients are available in pulses (Austin *et al.* 2004). Soil moisture strongly affects the availability of both carbon and nutrient ions needed by plants (Ehrenfeld 2003), allowing greater mobility of soil nutrients. The lower soil moisture found in the knapweed community may explain why available calcium did not change between years in this community, the species present pulling the moisture to such a low level as to make the ion less available.

Diverse environments are often supported by heterogeneity in soil nutrients (Davies *et al.* 2005), and it is interesting to note that the soils of the knapweed-dominated communities had a high level of homogeneity for ecological communities (A value, see McCune and Mefford 1999) compared to the others. If diffuse knapweed does not affect soil nutrients as stated by LeJeune *et al.* (2006), then on my site it seems to only dominate communities under certain conditions. This means that knapweed could be reacting to, rather than causing, soils being more alkaline and lower in moisture and nutrients. Sulphur cinquefoil formed near monocultures in all areas tested, and the heterogeneity in soil characteristics may mean that this plant has little impact on the soils and that it can successfully dominate the community in a greater variety of areas than diffuse knapweed.

I have linked each result, *a priori*, to current literature to show that experiments to determine causation have been carried out, and which case is most likely to explain my own

results. Increasing the number of samples taken and analyzing soils before and after invasion

would lead to a clearer picture.

Main field experiment: seed addition and invasive removal

The seeding treatment did not result in any seedling establishment. Seed addition was predicted to be important in restoration of the target area because seed limitation of native plants has been found in grasslands (Turnbull *et al.* 2000, Seabloom *et al.* 2003, Sanderson and Elwinger 2004, Bush *et al.* 2007). Turnbull *et al.* (2000) reviewed several studies that added seeds of a species not already present, and found that although many seeds germinated, considerably fewer survived to form adult populations. In my study, there was no evidence of any germination. It is most likely that several factors together were responsible for this result and possible explanations include; freezing temperatures, moisture restriction in combination with the seeding method, poor germination rates, microsite limitation, alternative stable states, and granivory. In addition, the area is exposed to strong winds that may have blown many of the seeds away.

Removing vegetation can open up microsites (Aguilera and Lauenroth 1995), reduce competition from adult plants (Reader 1993), reduce litter (Bosy and Reader 1995), and expose the surface of the seed bank to a quality of light that seeds may need to germinate (Semenza *et al.* 1978). Though removal will eliminate competition from adults, it will not eliminate seedling competition. In fact, vegetation removal may increase seedling competition as seeds germinate from the seed bank, or alternatively create unfavourable abiotic conditions by increased evaporation and wind. Species that respond positively to vegetation removal (diffuse knapweed and thyme-leaved sandwort) are probably less sensitive to seedling competition than that from adult plants, with competition for light being important to their early growth.

Vegetation removal

Diffuse knapweed biomass increased when vegetation was removed, likely due to increased light, while the amount of annual grass decreased, perhaps because of removal of much of the

grass seed the previous summer. Though knapweed had dominated prior to 2006, *Sisymbrium altissimum* (tall tumble-mustard) was the dominant in all plots in 2006 and 2007, and was therefore expected to have a strong effect on the community (Huston 1997, Grime 1998). The dominant invasive forbs in the community (diffuse knapweed, tumble mustard, prickly lettuce, and Russian thistle) mostly take a tumbleweed form that is very effective in dispersal, and all have tap roots to reach deeper water sources than many of the native forbs that can lead to drought-like conditions for shallower rooted species and seedlings (Allen and Knight 1984). Removal of these plants reduced resource use and increased light levels at the soil surface. Though removal of these plants may have meant less water was used, it also exposed the soil surface to increased sun and wind, which would have a drying effect, but this did not seem to adversely affect most of the annual invasive species as biomass was equal under all treatments at harvest. Water and light levels were not measured so it is not known how vegetation removal affected these characteristics.

My findings on the effect of vegetation removal on diffuse knapweed support the findings of other experiments. Myers and Berube (1983) found that grazing increased *C. diffusa*, and Lejune *et al.* (2006) found that *C. diffusa* increased by up to eighty percent in a removal experiment. These results show that for diffuse knapweed, removal of competition outweighs other possible disadvantages of removal, such as increased desiccation. As removal of neighbours is known to increase the abundance of diffuse knapweed, it seems likely that the important factor is light, because the rosette form of knapweed is at a disadvantage if heavily shaded, especially in early stages of growth (Sheley and Carpinelli 2005). In addition, because the most effective biological control agent (*Larinus minutus* Gyllenhal) winters under adult plants (Seastedt *et al.* 2005); the complete elimination of knapweed the previous year suggested

a sharp reduction in agents in the area to damage the young plants. This could mean that the many young seedlings of diffuse knapweed had less competition from other species, and that their complete removal by biological control led to greater success as the agents had to 'discover' the area again.

As with diffuse knapweed, *A. serpyllifolia* has been observed to grow in disturbed areas and is light-dependant (King 1975) and this is likely the reason it also increased in abundance. Other species may also react favourably to the elimination of adult plants, especially annual species like tumble mustard. Though clipping decreased the biomass of annual grasses, no species of *Bromus* was found to be significantly different between treatments. Thus the positive effect on knapweed is more important for restoration purposes, especially because the other annual grasses are not known to have a large impact on soils.

Biomass was approximately equal between treatments, due to an abundance of late season annual forbs germinating from the seed bank after the final removal treatment. Biomass removal did have an impact on the percentage of forb to grass biomass, however, as well as increasing diversity. Increased diversity can be explained by the hump-backed model (Grime 1973), as vegetation removal means that dominant species no longer suppress subordinate species, leading to increased species diversity. Vegetation was removed once in the first summer and then again the following spring. This allowed the seedlings a better opportunity to establish, but the disturbance was not great enough to eliminate any species from the plots. The removal treatment may have initially altered the evenness of the vegetation, but by the time of harvest this effect was not apparent. Grime (1973) also predicted that diversity and biomass increase together (to a point where competition becomes more important and diversity declines), which was not supported by my results. It is possible that the range of biomass (productivity) between

my experimental plots was not great enough to adequately test Grime's hypothesis (see Moore and Keddy 1989).

The pattern seen in the non-metric multidimensional scaling (Fig. 3) is an indication that plots that had vegetation removed were more homogenous in species composition than plots that had no removals. Though groups of species based on position on the hillside were also significant, closer inspection suggests that the plots were only different because one of the groups contained a greater amount of grass biomass than the others. Spotted knapweeds do vary proportionally with bunchgrasses in several studies, however, this relates to their mycorrhizae and phosphate absorption and may not apply to diffuse knapweed or invasive species of grass (Zabinski *et al*. 2002, Marler *et al*. 1999). It is more likely that the clipping treatment negatively affected the grass (Maron and Jefferies 2001) than a negative relationship between diffuse knapweed and annual grass biomass. Bush *et al*. (2007) found that when the density of diffuse knapweed was decreased by biological control, some other invasive grasses significantly increased due to propagule pressure. The native species did not exploit the space opened by the decreasing knapweed, suggesting that seed addition or some other treatment may be needed (Bush *et al*. 2007). In my case, only one native species (*Hesperostipa comata*) was found to be common in the area. It is possible that *H. comata* may become more abundant in the area because it was also found in the seed bank study. Propagule pressure is known to be an important aspect in both invasion and resistance of invasion (Levine and D'Antonio 1999, Sakai *et al*. 2001), and the annual grasses on my site demonstrate the principle by being the most numerically abundant and producing large quantities of propagules.

For purposes of invasive plant management, the increase of knapweed with vegetation removal may be more important than any associated decrease of annual grasses. However, if

biological control agents were able to reduce the abundance of knapweed to a consistently low level, vegetation removal may be an important step in replacing annual grasses with perennial ones. It is highly improbable that either diffuse knapweed or annual grasses like *Bromus tectorum* will ever be eliminated, but with restoration efforts and effective biological control, their dominance and impacts on ecosystems may be reduced.

Seed addition

Of the 4000 seeds added to the plots with the seeding treatment, not a single plant established in the experimental plots. The pre-sowing treatment of the seeds likely led to the death of the few seeds that had developed radicles before sowing because of the lack of moisture, the cold, and lack of penetration into the soil. Lack of precipitation may have been another factor preventing germination and establishment of the introduced seeds. Yearly variation in the outcome of restoration can be expected as germination of seeds in semi-arid grasslands is commonly limited by water availability (Nelson *et al*. 1970, Winkel *et al*. 1991, Chambers 2000, Ambrose and Wilson 2003, Bakker *et al*. 2003). Though the seeds were watered after sowing, the entire month only had 3.5 mm of rain whereas the average rainfall for April is 27.2 mm, making this an abnormally dry month (Environment Canada, 2008). The amount of water needed is highly species-dependent as evidenced by the results of my germination trials (Appendix B). Of all the species, *Gaillardia aristata* and *Psuedoroegneria spicata* had the best chance of still being able to germinate despite the unusual and unfavourable conditions because they required less water and germinated faster than other species that were planted.

Freezing temperatures in the early stages of germination may have killed many of the sown seeds, especially those with exposed radicles. In greenhouse germination trials, seeds continued to germinate after 'sowing' so even if a percentage of the seeds (that had already

begun germination) were damaged by the freeze, there should have still been viable seeds that would not be vulnerable until after the last freezing night. *Heterostipa comata* and *Achnatherum occidentale*, in particular, evidenced a delay in germination after sowing. On the other hand, *Gaillardia aristata* germinated almost completely within five days in the lab and if this pattern was the same in the field, all seedlings of this species would have been exposed to below zero night temperatures during their period of growth.

The aspect of poor germination relates to the two grass species collected on site. Both *H. comata* and *A. occidentale* had low germination rates. In fact, *H. comata* should probably have not been used at all and *A. occidentale* should have been used in higher numbers to make up for poor germination rates. All other species had at least a 50% germination rate, except *Heuchera nvisibilit* in dry conditions, and so *H. nvisibilit* would most likely have a low germination rate in the field.

As an alternative to environmental conditions causing seeding failure, pressures from the plant community can also be considered. Ecosystems are often seed limited or microsite limited (Turnbull *et al*. 2000, Martin and Wilsey 2006). Different types of substrates are favoured by different species, but the best germination is dependent upon contact with soil moisture and humidity in microsites (Chambers 2000, Nelson *et al*. 1970, Winkel *et al*. 1991). The microsite hypothesis states that recruitment is limited as recruits of a dominant and competitively superior species are plentiful enough to fill available microsites (Coulson *et al.* 2001, Seabloom *et al.* 2003, Martin and Wilsey 2006, Renne and Tracy, 2007). When seedlings are expected and no seedlings are found, it is tempting to conclude that microsite limitation prevented germination, establishment and growth. In this case, I can postulate that lack of light early in the process was most likely not the cause because vegetation was clipped in half of the study plots prior to

sowing. Another reason to suggest that the area was not microsite limited was that under lower nutrient conditions bluebunch wheatgrass was competitively superior to both diffuse and spotted knapweed (Larson and Kiemnec 2003, Herron *et al.* 2001), and knapweed seedlings emerged from the seed bank, while sown bluebunch wheatgrass seed did not survive.

A final factor that could have an adverse affect on seed addition is granivory (see next section). In British Columbia, deer mice (*Peromyscus maniculatus*) and voles (Microtus spp.) are the major herbivores that can lead to restoration failure (Sullivan and Sullivan 1984). The feed used as decoy did not respond well to rain as it was crushed and formed as pellets, which became swollen with water. The decoy may also have not been a preferred food at the time of year the plots were seeded. There has been some work on seed preferences (Hulme 1994, Hoffmann *et al.* 1995, Longland and Bateman 1998), but little carried out using any part of the species pool that is found in the southern interior of British Columbia, Canada. Rather than seed decoys, predator cues (such as coyote urine scent) may be used to reduce foraging in experimental plots (Brinkerhoff *et al.* 2005). Research would need to be done to determine what item should be used as a decoy in this area.

A combination of factors likely resulted in the failure of the seeding treatment to show any effect. Trials to demine if seeding works best in spring or fall could be carried out, hopefully in concert with granivory work. Experiments to tease apart these possible effects would be beneficial, but Seasteadt (2003) found that seeding worked differently in different areas and years mostly due to changes in precipitation. Another example would be the rise and fall of granivore abundances in cycles (Espeland *et al.* 2005), which would affect yearly rates of granivory and that effect upon seed addition. A short term experiment may only apply to the

year under consideration, and I believe that seeding may result in germination under conditions other than those in 2007.

Granivory bioassay

Granivory was expected to reduce the number of seeds placed in the plots because many rodent holes and tunnels were visible in the hillside and deer mice are known to eat large quantities of seed (Sullivan and Sullivan 2004). In fact, granivores can decrease seed by up to 80% in annual grasslands, or up to 45% per day in an old field (Archer and Pike, 1991). Unfortunately, the bioassay was not started until after the seeding treatment had been determined to have failed, and so the result is not a good predictor of granivory rate at the time of sowing.

In the bioassay, two different types of granivory seemed to occur; one resulted in seeds vanishing from the Petri dishes and the other resulted in the remains of seed being found in the dishes, often with distinctive rodent bite marks. Even if the seeds that were missing were consumed, the dishes may not have been left in place long enough for the majority of the seeds to be found by rodents. An assumption that all granivores had an equal chance of finding the dishes had to be made; however, this is plainly not a realistic assumption. The ability of a herbivore to locate food will vary with species, and this means that the results may not accurately represent actual preference. On the other hand, the lack of dish discovery means that an assumption of full choice upon discovery is likely valid. Rodents prefer larger (or clumped) seeds and birds seem to like smaller-sized grass seeds (Everett *et al*. 1978, Goebel and Berry 1976, Hulme 1994, Hoffmann *et al*. 1995), so there is no seed size in particular that could be predicted to be least preferred by granivores in general. Birds can eat large amounts of seeds,

disrupting experiments (Goebel and Berry 1976). However, the impact of birds on seed addition is much less researched than that of rodents and it is impossible to conclude causation for the recorded preferences. In the few dishes that were obviously found by rodents, *P. spicata* seemed to be highly preferred, and there were bite marks in the large-seeded forb species as well (*G. aristata* and *G. trifolium*), none of which are on the list of preferred species.

Assuming that species with spiny or other deterrent structures on their seeds may be less palatable to granivorous species explains why *G. aristata* was least chosen in the preference test. Considering that this species germinated quickest in all trials (including when dried out for part of the time, Appendix B) and is not preferred by granivores, there must be another explanation for the lack of seedlings discovered, at least for this one species. It is possible that some seeds did germinate, but were consumed by herbivores. In the greenhouse germination trial, this species often evidenced heavy herbivory while other flats of seedlings remained untouched (Appendix B).

Seed predators may be attracted to disturbances (Thorpe *et al.* 2006), but I found no effect of treatment on either granivore discovery or preference of the species of seed eaten. The species with the least seeds remaining were the two smallest-seeded forb species and the smallest seed grass species. For *H. nvisibilit*, it is possible that the seeds were lost because they are so small they could be overlooked and often clung to the Petri dish. Wind also might have an effect on these seeds because they are light and could be blown away. Another possibility is that rodents are not the only granivores impacting seed addition. Smaller-sized seeds of perennial grasses were the preferred food of bird species in semi-arid bunchgrass rangeland in Washington (Goebel and Berry 1976). However, it does not seem plausible that these birds would only eat the very smallest seeds without touching the larger ones. Ants are not considered major

granivores in North America (Archer and Pike, 1991), but several species were noted in the study area and may have been responsible for removing smaller seeds.

A better test of the impact of granivores would be a preference trial between native and invasive species over an entire year as a preference for invasive species would mean that their effect on seed additions in grasslands may not be as strong. If this were not the case, it would still provide information on the patterns of granivory and activity throughout the year that would be valuable in restoration efforts. It has already been established that in terms of general seed size and density preferences, rodents as a group are similar worldwide (Hoffmann *et al*. 1995, Hulme 1994). It is also possible to carry out the trials in such a manner that granivory by birds, ants, and rodents can be adequately separated. To determine how granivory changes, and how it can be expected to affect seeding, more experiments need to be done. A weekly or even monthly bioassay over the growing season or perhaps the whole year would provide valuable information on granivore activity and the impact it has on supplied seeds.

Management Implications

Diffuse knapweed is undesirable because it is not preferred by cattle and, in the case of the Vernon military site, causes rashes on the exposed skin of people using the training area. Control of diffuse knapweed is regulated by provincial law, while cheatgrass is not (*Weed Control Act* 1996). From a military standpoint grasses are less likely to irritate skin, but an invasion of annual grasses may make off-road driving dangerous as the heat of exhaust systems sometimes start fires. Both species may form monocultures in some areas, however, the literature suggests that dominance by annual grasses seems to have a greater ecological impact (D'Antonio and Vitousek 1992). Annual grasses may have more of an effect on nutrient cycling

than diffuse knapweed (Rimer and Evans 2006, LeJeune *et al*. 2006), and increase the chances of fire (Link *et al*. 2006). A treatment that decreases the abundance of annual grasses may be seen as advantageous for reasons beyond preventing fires or preserving nutrient cycles. These grasses die early in the year providing little nutrients to cattle, and unlike perennial grasses they do not serve to prevent erosion, pulling easily from the soil when they die.

Vegetation management is easier than soil management. My results suggest that soils must be taken into consideration, if only for the effect of water content on germination ability. Near monocultures of sulphur cinquefoil seem to have soils that are quite similar to knapweed dominated communities, and it is possible that this will give them an advantage over members of a native community, leading to the problem of one invasive plant replacing another as has previously been observed (Bush *et al*. 2007, Seastedt *et al*. 2008). Though seed addition was not successful in this case, seeding may be viable in a year with sufficient rain in the spring. Seed addition has the best chance of success in heavily invaded communities if the species chosen can germinate and survive under drier conditions. Success may also be increased for species that germinate in the fall. There was heavy seed rain and little granivory in August, thus an early fall addition of seeds might be more successful than addition in the spring, even though rodent populations are generally lower in the early spring. Without more information on timing of seed addition and techniques to distract or discourage rodents, management recommendations cannot be made.

Native species generally do not have the seed production capability of the successful invasive species, and without competition, invasive species will maintain their populations. Diffuse knapweed is negatively influenced by competition (LeJeune *et al*. 2006), therefore, the best effort towards control would be establishing other vegetation. When vegetation was not

disturbed, annual grasses were highly successful in the spring. When these species senesce, later season species (particularly annuals such as *Sisymbrium altissimum*) are able to inhabit the 'empty' space. The 'lawn' of annual grasses in the spring seems to require either species that grow later in the season, or species that begin growth in the fall or very early spring to be competitive.

Management of the invasive species through seed addition would require appropriate weather conditions as well as careful choice of competitive species. If seed addition is used, applying seeds in both spring and fall over several years will increase the chances of success (Bakker *et al.* 2003, Pywell *et al.* 2003). Species that can tolerate low soil moisture and nutrients during establishment phases are likely the only ones that can be added successfully as seed. It may also be important that species that do not compete with the spring growth of *Bromus tectorum*, as the other successful non-native species show.

CONCLUSION

Evidence suggests that invasive plants affect soil properties. The soil nutrient concentrations I measured in the three different vegetation communities cannot be determined to be caused by that community, however, vegetation plays a large part in the cycling of nutrients and it is possible that observed differences were due to the plants. Invasive species that result in lower soil carbon levels from native systems may even be a concern in terms of an area's ability to sequester carbon.

Propagule addition may not change community structure without added nutrients or soil protection (Hobbs 1999), which may be the case in my system. It seems likely that removal of one invasive species would lead to dominance by another without interference through seed addition (Seastedt *et al.* 2008), especially as there was only one native species common enough to show up in the seed bank. When vegetation was removed annual grasses were reduced while diffuse knapweed increased, the knapweed taking the space of the annual grass and supporting the idea that invasive species may simply replace each other rather than native species recovering.

Removal of grazing may allow a slow re-invasion of an area by native species that were adversely affected by overgrazing (Huffaker 1951, Zimmermann *et al.* 2001). Elimination of invasive species is not likely to occur, however, it may be possible to obtain a community that contains native species in a richness approximating uninvaded grassland as succession proceeds (Wilson and Partel 2003), particularly if biological control agents continue to have large impacts on diffuse knapweed.

REFERENCES

Aguilera, M.O., and Lauenroth, W.K. 1995. Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. J. Ecol. **83**(1): 87-97.

Albaladejo, J., Martinez-Mena, M., Roldan, A., and Castillo, V. 1998. Soil degradation and desertification induced by vegetation removal in a semiarid environment. Soil Use and Management. **14**(1): 1-5.

Allen, E.B., and Knight, D.H. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. The Southwestern Naturalist. **29**(4): 407-421.

Ambrose, L.G., and Wilson, S.D. 2003. Emergence of the introduced grass *Agropyron cristatum* and the native grass *Bouteloua gracilis* in a mixed-grass prairie restoration. Restor. Ecol. **11**(1): 110-115.

Archer, S., and Pyke, D.A. 1991. Plant-animal interactions affecting plant establishment and persistence on revegetated rangeland. J. Range Manage. **44**: 558-565.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A. and Schaeffer, S.M. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia. **141**(2): 221-235.

Bais, H.P., Vepachedu, R., Gilroy, S., Callaway, R.M. and Vivanco, J.M. 2003. Allelopathy and exotic plant invasion: From molecules and genes to species interactions. Science. **301**(5638): 1377-1380.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G. and Waddington, J. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecol. Appl. **13**(1): 137-153.

Belnap, J., Hawkes, C.V. and Firestone, M.K. 2003. Boundaries in miniature: Two examples

from soil. Bioscience. **53**(8): 739-749.

Belnap, J., and Phillips, S.L. 2001. Soil biota in an ungrazed grassland: Response to annual grass

(*Bromus tectorum*) invasion. Ecol. Appl. **11**(5): 1261-1275.

Bosy, J.L., and Reader, R.J. 1995. Mechanisms underlying the suppression of forb seedling

emergence by grass (*Poa pratensis*) litter. Funct. Ecol. **9**(4): 635-639.

Brinkerhoff, R. J., Haddad, N. M., and Orrock, J. L. 2005. Corridors and olfactory predator cues

affect small mammal   nvisibil. Journal of Mammalogy **86**: 662-669

Bush, R.T., Seastedt, T.R., and Buckner, D. 2007. Plant community response to the decline of

Diffuse Knapweed in a Colorado grassland. Ecol. Res. **25**(3): 169-174.

Chambers, J.C. 2000. Seed movements and seedling fates in   nvisibil sagebrush steppe

ecosystems: Implications for restoration. Ecol. Appl. **10**(5): 1400-1413.

Choi, Y.D. 2004. Theories for ecological restoration in changing environment: Toward

'futuristic' restoration. Ecol. Res. **19**:75-81

Conservation Data Centre. 2006. BC Species and Ecosystems Explorer. Available from

http://srmapps.gov.bc.ca/apps/eswp/ [Cited Jan.28, 2007]. B.C. Ministry of Environment

Victoria, British Columbia.

Coulson, S.J., Bullock, J.M., Stevenson, M.J. and Pywell, R.F. 2001. Colonization of grassland

by sown species: Dispersal versus microsite limitation in responses to management. J. App.

Ecol. **38**(1): 204-216.

D'Antonio, C.M., Dudley, T.L., and Mack, M. 1999. Disturbance and biological invasions:

Direct effects and feedbacks. *In* Ecosystems of Disturbed Ground. *Edited by* L. Walker.

Amsterdam, Elsevier. Pp. 143–452.

D'Antonio, C.M., and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the Grass/Fire cycle, and global change. Ann. Rev. Ecol. Syst. **23**: 63-87.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. and Rice, K.J. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology. **86**(6): 1602-1610.

Denslow, J.S., and Hughes, R.F. 2004. Exotic plants as ecosystem dominants. Weed Technol. **18**: 1283-1287.

Dwire, K.A., Parks, C.G., McInnis, M.L. and Naylor, B.J. 2006. Seed production and dispersal of nvisib cinquefoil in northeast Oregon. Rangeland Ecology & Management. **59**(1): 63-72.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems. **6**(6): 503-523.

Elton, C.S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Environment Canada. 2008. National Climate Data and Information Archive. Available from http://www.climate.weatheroffice.ec.gc.ca [Cited Jan.28, 2008].

Espeland, E.K., Carlsen, T.M. and Macqueen, D. 2005. Fire and dynamics of granivory on a nvisibili grassland forb. Biodivers. Conserv. **14**(2): 267-280.

Evans, R.D., Rimer, R., Sperry, L. and Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecol. Appl. **11**(5): 1301-1310.

Everett, R.L., Meeuwig, R.O. and Stevens, R. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. J. Range Manage. **31**(1) : 70-73.

Ferrero, M.L. and De la Torre, C. 1986. Cell Proliferation in *Allium cepa* L. Meristems Under 8-Hydroxyquinoline, a Chelating Agent That Affects DNA and RNA Polymerases. J. Cell Sci. **80**: 171-180.

Goebel, C.J., and Berry, G. 1976. Selectivity of range grass seeds by local birds. J. Range Manage. **29**(5): 393-395.

Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: Lessons from Florida. Ecol. Appl. **8**(4): 975-989.

Grassland Conservation Council. 2004. BC grasslands mapping project: A conservation risk assessment. Available from http://www.bcgrasslands.org/SiteCM/U/D/D51D823AC0A09A05.pdf [Cited Jan.8, 2007]. Kamloops, BC. Grassland Conservation Council of British Columbia.

Grime, J.P. 1973. Competitive exclusion in nvisibili vegetation. Nature. **242**: 344-347.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. The Journal of Ecology. **86**(6): 902-910.

Herron, G.J., Sheley, R.L., Maxwell, B.D. and Jacobsen, J.S. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. Restor. Ecol. **9**(3): 326-331.

Hobbs, R. J. 1999. Restoration of disturbed ecosystems. *In* Ecosystems of Disturbed Ground. Ecosystems of the World. *Edited by* L. Walker. Amsterdam, Elsevier. Pp. 673–687.

Hofmann, M., and Isselstein, J. 2005. Species enrichment in an agriculturally improved grassland and its effects on botanical composition, yield and forage quality. Grass Forage Sci. **60**(2): 136-145.

Hoffmann, L.A., Redente, E.F. and McEwen, L.C. 1995. Effects of selective seed predation by rodents on shortgrass establishment. Ecol. Appl. **5**(1): 200-208.

Hook, P.B., Olson, B.E. and Jon M. Wraith. 2004. Effects of the invasive forb *Centaurea maculosa* on grassland carbon and nitrogen pools in Montana, USA. Ecosystems. **7**(6): 686-694.

Hooper, D.U., and Vitousek, P.M. 1997. The effects of plant composition and diversity on ecosystem processes. Science. **277**(5330; 5330): 1302.

Hope, G.D., Mitchell, W.R., Lloyd, D.A., Erickson, W.R., Harper, W.L., and Wikeem, B.M. 1991. Interior Douglas Fir Zone. *In* Special Report Series 6: Ecosystems of British Columbia. *Edited by* D. Meidinger and J. Pojar, BC Ministry of Forests. Victoria, Crown Publications. Pp.153-166

Huffaker, C.B. 1951. The return of native perennial bunchgrass following the removal of Klamath weed (*Hypericum perforatum* L.) by imported beetles. Ecology. **32**(3): 443-458.

Hulme, P.E. 1994. Post-dispersal seed predation in grassland: Its magnitude and sources of variation. J. Ecol. **82**(3): 645-652.

Huston, M.A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. Oecologia. **110**(4): 449-460.

Ives, A.R., and Carpenter, S.R. 2007. Stability and diversity of ecosystems. Science. **317**(5834): 58-62.

Kelrick, M.I., MacMahon, J.A., Parmenter, R.R., and Sisson, D.V. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. Oecologia (Berlin). **68**:327-337.

King, T.J. 1975. Inhibition of seed germination under leaf canopies in *Arenaria serpyllifolia*, *Veronica arvensis* and *Cerastium holosteoides*. New Phytol. **75**(1): 87-90.

Knopp, D and Larkin, L. 2000. Biophysical Survey of Vernon Military Camp. Prepared by BC's
    Wild Heritage Environmental Consultants for the Department of National Defence, CFB
    Chilliwack.

Kourtev, P.S., Ehrenfeld, J.G. and Haggblom, M. 2002. Exotic plant species alter the microbial
    community structure and function in the soil. Ecology. **83**(11): 3152-3166.

Lacey, J.R., Clayton B. Marlow and Lane, J.R. 1989. Influence of spotted knapweed (*Centaurea
    maculosa*) on surface runoff and sediment yield. Weed Technol. **3**(4): 627-631.

Larson, L., and Kiemnec, G. 2003. Seedling growth and interference of diffuse knapweed
    (*Centaurea diffusa*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). Weed Technol.
    17(1): 79-83.

LeJeune, K.D., Suding, K.N. and Seastedt, T.R. 2006. Nutrient availability does not explain
    invasion and dominance of a mixed grass prairie by the exotic forb *Centaurea diffusa* lam.
    Appl. Soil Ecol. **32**(1): 98-110.

Leonard, E.D., Monaco, T.A., Stark, J.M. and Ryel, R.J. 2008. Invasive forb, annual grass, and
    exotic shrub competition with three sagebrush-steppe growth forms: Acquisition of a spring
    [15]N tracer. Invasive Plant Science and Management. **1**(2): 168-177.

Levine, J.M., and D'Antonio, C.M. 1999. Elton revisited: A review of evidence linking diversity
    and   nvisibility. Oikos. **87**(1): 15-26.

Link, S.O., Keeler, C.W., Hill, R.W. and Hagen, E. 2006. *Bromus tectorum* cover mapping and
    fire risk. Int. J. Wildland Fire. **15**(1): 113-119.

Longland, W.S., and Bateman, S.L. 1998. Implications of desert rodent seed preferences for
    range remediation. J. Range Manage. **51**(6): 679-684.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecol. Appl. **10**(3): 689-710.

Malmstrom, C.M., McCullough, A.J., Johnson, H.A., Newton, L.A. and Borer, E.T. 2005. Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. Oecologia. **145**(1): 153-164.

Marler, M.J., Zabinski, C.A. and Callaway, R.M. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology. **80**(4): 1180-1186.

Maron, J.L., and Jefferies, R.L. 2001. Restoring enriched grasslands: Effects of mowing on species richness, productivity, and nitrogen retention. Ecol. Appl. **11**(4): 1088-1100.

Marsh, J., Nouvet, S., Sanborn, P. and Coxson, D. 2006. Composition and function of biological soil crust communities along topographic gradients in grasslands of central interior British Columbia (Chilcotin) and southwestern Yukon (Kluane). Can. J. Bot. **84**: 717-736.

Martin, L.M., and Wilsey, B.J. 2006. Assessing grassland restoration success: Relative roles of seed additions and native ungulate activities. J. Appl. Ecol. **43**(6): 1098-1109.

Masters, R.A., and Sheley, R.L. 2001. Principles and practices for managing rangeland invasive plants. J. Range Manage. **54**(5): 502-517.

McCune, B. and Grace, J.B. 2002. Analysis of Ecological Communities. MjM Press, Gleneden Beach, Oregon.

McCune, B. and Mefford, M. J. 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.34. MjM Software, Gleneden Beach, Oregon, U.S.A.

Meiman, P.J., Redente, E.F. and Paschke, M.W. 2006. The role of the native soil community in

the invasion ecology of spotted (*Centaurea maculosa* auct. Non lam.) and diffuse (*Centaurea*

diffusa lam.) knapweed. Applied Soil Ecology. **32**(1): 77-88.

Moore, D.R.J. and Keddy, P.A. 1989. The relationship between species richness and standing

crop in wetlands: the importance of scale. Vegetation **79**: 99-106.

Myers, J.H., and Berube, D.E. 1983. Diffuse knapweed invasion into rangeland in the dry

interior of British Columbia. Can. J. Plant Sci. **63**: 981-987.

Nelson, J.R., Wilson, A.M. and Goebel, C.J. 1970. Factors influencing broadcast seeding in

bunchgrass range. J. Range Manage. **23**(3): 163-170.

Olson, B.E., Wallander, R.T. and Lacey, J.R. 1997. Effects of sheep grazing on a spotted

knapweed-infested Idaho fescue community. J. Range Manage. **50**: 386-390.

Piper, J.K., Schmidt, E.S., and Janzen, A.J. 2007. Effects of species richness on resident and

target species components in a prairie restoration. Restor. Ecol. **15**(2): 189-198.

Pywell, R.F., Bullock, J.M. and Roy, D.B. 2003. Plant traits as predictors of performance in

ecological restoration. The Journal of Applied Ecology. **40**(1): 65-77.

Reader, R.J. 1993. Control of seedling emergence by ground cover and seed predation in relation

to seed size for some old-field species. J. Ecol. **81**(1): 169-175.

Renne, I.J., and Tracy, B.F. 2007. Disturbance persistence in managed grasslands: Shifts in

aboveground community structure and the weed seed bank. Plant Ecol. **190**(1): 71-80.

Rimer, R.L., and Evans, R.D. 2006. Invasion of downy brome (*Bromus tectorum* L.) causes rapid changes in the nitrogen cycle. Am. Midl. Nat. **156**(2): 252-258.

Rubec, C. D. A., and Lee, G.O. 1997. Conserving vitality and diversity: Proceedings of the world conservation congress workshop on alien invasive species. Montreal, Canada, 1996. Environment Canada, Canadian Wildlife Service, Ottawa.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N. and Weller, S.G. 2001. The population biology of invasive species. Annual Review of Ecology & Systematics. **32**: 305.

Sanderson, M.A., and Elwinger, G.F. 2004. Emergence and seedling structure of temperate grasses at different planting depths. Agron. J. **96**(3): 685-691.

Seabloom, E.W., Borer, E.T., Boucher, V.L., Burton, R.S., Cottingham, K.L., Goldwasser, L., Gram, W.K., Kendall, B.E. and Micheli, F. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecol. Appl. **13**(3): 575-592.

Seastedt, T.R., Gregory, N. and Buckner, D. 2003. Effect of biocontrol insects on diffuse knapweed (*Centaurea diffusa*) in a Colorado grassland. Weed Sci. **51**(2): 237-245.

Seastedt, T.R., Suding, K.N., and LeJeune, K.D. 2005. Understanding invasions: The rise and fall of diffuse knapweed (*Centaurea diffusa*) in North America. *In* Invasive plants: Ecological and agricultural aspects. *Edited by* S. Inderjit. Basel, Switzerland: Birkhäuser Verlag. Pp. 129–139 .

Seastedt, T.R., Hobbs, R.J. and Suding, K.N. 2008. Management of novel ecosystems: are novel approaches required? Front. Ecol. Environ. **6**(10): 547-553.

Semenza, R.J., Young, J.A. and Evans, R.A. 1978. Influence of light and temperature on the germination and seedbed ecology of common mullein (*Verbascum thapsus*). Weed Sci. **26**(6): 577-581.

Society for Ecological Restoration International (SERI) Science & Policy Working Group. 2004. The SER International Primer on Ecological Restoration. Tucson, Society for Ecological Restoration International.

Sheley, R.L., and Carpinelli, M.F. 2005. Creating weed-resistant plant communities using niche-differentiated non-native species. Rangeland Ecology & Management. **58**(5): 480-488.

Sheley, R.L., and Half, M.L. 2006. Enhancing native forb establishment and persistence using a rich seed mixture. Restor. Ecol. **14**(4): 627-635.

Sheley, R.L., Jacobs, J.S. and Velagala, R.P. 1999. Enhancing intermediate wheatgrass establishment in spotted knapweed infested rangeland. J. Range Manage. **52**(1): 68-74.

Sheley, R.L., Jacobs, J.S. and Lucas, D.E. 2001. Revegetating spotted knapweed infested rangeland in a single entry. J. Range Manage. **54**(2): 144-151.

Sperry, L.J., Belnap, J. and Evans, R.D. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology. **87**(3): 603-615.

Strang, R.M., Lindsay, K.M. and Price, R.S. 1979. Knapweeds: British Columbia's undesirable aliens. Rangelands. **1**(4): 141-143.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. and Pace, M.L. 2006. Understanding the long-term effects of species invasions. Trends Ecol. Evol. **21**(11): 645-651.

Stein, C., Auge, H., Fischer, M., Weisser, W.W., and Prati, D. 2008. Dispersal and seed limitation affect diversity and productivity of montane grasslands. Oikos. **117**(10): 1469-1478.

Suding, K.N., LeJeune, K.D. and Seastedt, T.R. 2004. Competitive impacts and responses of an invasive weed: Dependencies on nitrogen and phosphorus availability. Oecologia. **141**(3): 526-535.

Sullivan, T.P., and Sullivan, D.S. 1984. Influence of range seeding on rodent populations in the interior of British Columbia. J. Range Manage. **37**: 163-165.

Sullivan, T.P., and Sullivan, D.S. 2004. Influence of a granivorous diversionary food on population dynamics of montane voles (*Microtus montanus*), deer mice (*Peromyscus maniculatus*), and western harvest mice (*Reithrodontomys megalotis*). Crop Protection. **23**(3): 191-200.

Tharayil, N., Bhowmik, P., Alpert, P., Walker, E., Amarasiriwardena, D. and Xing, B. 2009. Dual purpose secondary compounds: Phytotoxin of *Centaurea diffusa* also facilitates nutrient uptake. New Phytol. **181**(2): 424-434.

Thomsen, M.A., D'Antonio, C.M., Suttle, K.B. and Sousa, W.P. 2006. Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. Ecol. Lett. **9**(2): 160-170.

Thorpe, A.S., Archer, V. and DeLuca, T.H. 2006. The invasive forb, *Centaurea maculosa*, increases phosphorus availability in Montana grasslands. Applied Soil Ecology. **32**(1): 118-122.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.

Tilman, D., and Downing, J.A. 1994. Biodiversity and stability in grasslands. Nature. **367**(6461): 363-365.

Turnbull, L.A., Crawley, M.J. and Rees, M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos. **88**(2): 225-238.

Van Riper, L.C., and Larson, D.L. 2008. Role of invasive *Melilotus officinalis* in two native
plant communities. Plant Ecol. **200**(1): 129-139.

Vivanco, J.M., Bais, H.P., Stermitz, F.R., Thelen, G.C. and Callaway, R.M. 2004.
Biogeographical variation in community response to root allelochemistry: Novel weapons
and exotic invasion. Ecol. Lett. **7**(4): 285-292.

Warren, J., Christal, A. and Wilson, F. 2002. Effects of sowing and management on vegetation
succession during grassland habitat restoration. Agriculture Ecosystems & Environment.
93(1-3): 393-402.

Watkins, A.J., Nicol, G.W. and Shaw, L.J. 2009. Use of an artificial root to examine the
influence of 8-hydroxyquinoline on soil microbial activity and bacterial community structure.
Soil Biology and Biochemistry. **41**(3): 580-585.

Weed Control Act. RSBC 1996. Chapter 487.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. and Losos, E. 1998. Quantifying threats to
imperilled species in the United States. Bioscience. **48**(8): 607.

Wilson, S.D., and Partel, M. 2003. Extirpation or coexistence? Management of a persistent
introduced grass in a prairie restoration. Restor. Ecol. **11**(4): 410-416.

Winkel, V.K., Roundy, B.A. and Cox, J.R. 1991. Influence of seedbed microsite characteristics
on grass seedling emergence. J. Range Manage. **44**: 210-214.

Zabinski, C.A., Quinn, L. and Callaway, R.M. 2002. Phosphorus uptake, not carbon transfer,
explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of
native grassland species. Funct. Ecol. **16**(6): 758-765.

Zimmermann, H.G., Moran, V.C. and Hoffmann, J.H. 2001. The renowned cactus moth,
Cactoblastis cactorum (Lepidoptera: Pyralidae): Its natural history and threat to native

opuntia floras in Mexico and the United States of America. The Florida Entomologist. **84**(4): 543-551.

APPENDICES

The information in the following appendices acts as supplementary data to this thesis, but is not vital to understanding.

Appendix A: treatment by plot

Note that the letter the plots were given was *defined* by removal treatment (Table A.1), and that on the ground there may be multiple plots side by side that have all been weeded due to the lay out (Fig. 5). Choice of treatment was randomized the first time each treatment was applied.

Table A.1: Plot numbers and the treatment applied to each plot.

Plot	Vegetation Removal*	# Species	Plot	Vegetation Removal*	# Species
1A	no	4	4A	no	4
1B	yes	0	4B	yes	2
1C	no	8	4C	no	0
1D	yes	8	4D	yes	2
1E	no	8	4E	no	2
1F	yes	4	4F	yes	0
1G	no	4	4G	no	0
1H	yes	4	4H	yes	0
2A	no	0	5A	no	2
2B	yes	4	5B	yes	8
2C	no	0	5C	no	4
2D	yes	0	5D	yes	4
2E	no	2	5E	no	0
2F	yes	8	5F	yes	0
2G	no	2	5G	no	8
2H	yes	2	5H	yes	4
3A	no	8	6A	no	8
3B	yes	8	6B	yes	4
3C	no	8	6C	no	0
3D	yes	8	6D	yes	0
3E	no	2	6E	no	4
3F	yes	2	6F	yes	2
3G	no	2	6G	no	4
3H	yes	8	6H	yes	2

Appendix B: germination trials

Germination trials were carried out in order to determine what kind of germination could be expected from in species in the field under several conditions. This data is important in that it reveals several species have low germination rates and that some are more sensitive to lack of water than others.

METHODS

Because the last species seed used in the field (*Pseudoroegneria spicata*) was only acquired a week before the seeds were planted in the field, germination trials were not begun until after planting had been completed, so that the germination of all species could be tested at one time and there would be no effects of time/light cycle differences. The seeds of both *Koeleria macrantha* and *P. spicata* were purchased (seed sources from Alberta and Oregon respectively) and the others collected on site in 2006.

Germination was tested in soil and in Petri dishes. In order to determine percent germination for each species used in the plots, exactly 1000 seeds of each species were counted out (in sets of 100), treated to the same cold-moist scarification procedure as the seeds placed into the plots, and then planted into flats of potting soil in a greenhouse or plated onto a wet filter in a Petri dish. Germination on Petri dishes was defined as radicle emergence and germination in soil was defined by cotyledon emergence as seeing radicles is not possible, and no individual that grew a radical on the Petri dishes did not later also have cotyledons emerge. This means that the timing of germination in soil cannot be compared to that in the Petri dishes as the measurement was different. The seeds that showed signs of germination (radical emergence) were counted after scarification and before planting.

The potting soil had a very low incidence of seed present, and was used because too much drying out was noticed in the sand mixture. In addition, any seedlings of different species were easily determined and discarded. As with the seed bank work, many of the young plants were subject to herbivory when germination was tested in soil in the greenhouse. As soon as *Gaillardia aristata* seedling emerged, many of the cotyledons and first leaves were consumed. The flats were separated into five sections and 100 seeds were planted into each section and watered to ensure replication. Petri dishes held 50 seeds per dish. The seedlings that germinated were counted.

RESULTS

Best germination for all species was achieved in a Petri dish with ample watering (Table B.1). It was noted that all *Gaillardia aristata* that germinated did so within five days of removal from stratification and 'planting' in Petri dishes. The majority of the other species germinated rather quickly as well under all conditions though the percent germination was lower if the seeds were allowed to dry out. Few *Heuchera cylindrica* would germinate under dry conditions, needing constant moisture for seven to ten days before germinating. The germination for *Hesperostipa comata* found in the lab was extremely low at three percent and the germination of *Achnatherum occidentale* was not very good either with a maximum of twenty-seven percent (Table B.1).

Table B.1: Results of germination trails for three conditions.

SPECIES	Percent germination – Continuously wet Petri	Percent germination – Petri dried occasionally	Percent germination – Soil (watered)
Achnatherum occidentale	27	18	14.7
Hesperostipa comata	3	1	2
Koeleria macrantha	64	50	47.7
Pseudoroegneria spicata	81	62	65.9
Gaillardia aristata	52	52	24.3
Monarda fistulosa	89	62	48.9
Geum triflorum	86	72	31.1
Heuchera cylindrica	75	10	5.1

In most species, maximum germination on Petri dish was reached by 10 days with mould reducing survivorship after this point. *Achnatherum occidentale*, however, was one species that continued to germinate after the 10 day mark despite the presence of mould. Mould began to grow almost immediately on some species (*H. comata* in particular); however, most species developed mould on many of the seeds after the 10 day mark (Fig. B.1).

Figure B.1: Mould growing on the seeds in Petri dishes, showing four different species to illustrate that the mould grew in most dishes.

Hesperostipa comata and *A. occidentale* evidenced a delay in germination after planting in soil; however, this was particularly noticeable in *H. comata* as no seeds at all germinated for almost one month.

Of the grass species *P. spicata* was the germinated best, and of the forb species *Monardia fistulosa* and *Geum triflorum* had the greatest success (all over 80% germination under favourable conditions, Table B.1).

DISCUSSION

The results of the germination trials indicated that *Hesperostipa comata* should not have been used as the viability was extremely low. All other seeds had germination rates of over 50% under various conditions except for *Achnatherum occidentale*, which was also collected in the field. No real predictions were made for germination trials, though there was the possibility that the *Achnatherum* was not frozen for a long enough period of time.

Different germination rates were achieved using different methods, with continuously wetted Petri dishes being the highest and soil being the lowest. *G. aristata* germinated faster than other species, and this is likely the reason they were not affected by lack of moisture in the dishes. The reason *H. cylindrica* did not do well in the soil was likely because watering pushed the small seeds too deep. It is possible that germination was slower in the soil than in the Petri dish, due to lower temperatures, unfortunately I was not able to continue monitoring the germination of seeds in the soil to see if the percentage increased, though it is likely it did. The seeds were left on the soil surface to approximate the conditions in the field and so the germination in the soil may have been sporadic due to lack of contact with soil to access moisture, as the flats were watered often enough to prevent drying.

In soil, seedlings of *G. aristata* were often eaten by herbivores (probably slugs) as it may be extremely palatable; it was favoured (up to 20% consumed compared to very minor [<5%] grazing on other species). An attempt was made to count the remains of seedlings that did germinate and were then eaten. It is likely that some of the difference between germination counts in soil and Petri dishes was caused by this herbivory.

The depth watering pushed seeds into the soil may have had an adverse effect on soil germination. Many native species are known to only germinate and survive well when planted near the surface (Hull 1964), though most of this work has been done on grass species (Hull 1964, Fulbright *et al*. 1985, Newman and Moser 1988, Ries and Hofmann 1995, Sanderson and Elwinger 2004). In this case, many species had worse germination rates in soil, but only the seeds of *H. cylindrica* and *M. fistulosa* were small enough to be pushed deeply into the soil when watered.

Despite all of this, it seems likely that the lower soil germination rates are more accurate for the field than those gained by standard methods. Germination in a consistently moist Petri dish may give maximum rates, but these germination rates are unlikely to be achieved in the field. Over all *P. spicata*, *M. fistulosa,* and *G. triflorum* had the greatest success and would be expected to have the greatest success in the field.

REFERENCES FOR APPENDIX

Hull, A.C.J. 1964. Emergence of cheatgrass and three wheatgrasses from four seeding depths. J. Range Manage. **17**(1): 32-35.

Fulbright, T.E., Wilson, A.M. and Redente, E.F. 1985. Green needlegrass seedling morphology in relation to planting depth. J. Range Manage. **38**: 266-270.

Newman, P.R., and Moser, L.E. 1988. Grass seedling emergence, morphology, and establishment as affected by planting depth. Agron. J. **80**: 383-387.

Ries, R.E., and Hofmann, L. 1995. Grass seedling morphology when planted at different depths. J. Range Manage. **48**: 218-223.

Sanderson, M.A., and Elwinger, G.F. 2004. Emergence and seedling structure of temperate grasses at different planting depths. Agron. J. **96**(3): 685-691.