RESTORATION OF SPOTTED KNAPWEED INFESTED GRASSLANDS IN GLACIER NATIONAL PARK

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Land Rehabilitation

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2003

APPROVAL

of a thesis submitted by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

I would like to thank my advisor Dr. Cathy Zabinski for her assistance, guidance, patience and support. I thank the members of my graduate committee, Drs. Bruce Maxwell and Roger Sheley, for their contributions in designing, analyzing, and reviewing this research. I also thank my fellow graduate students in the Zabinski lab for their fieldwork assistance, shared knowledge, and friendship. I am grateful to Drs. Jim Robison-Cox and Mark Taper for providing me with statistical guidance. I also thank my family for their continuous support throughout this project.

Funding for this project was provided by the Center for Invasive Plant Management and the Cooperative Ecosystem Studies Unit (CESU). I thank Joyce Lapp and the IPM and Revegetation crews at Glacier National Park for logistical support encouragement, and dedication to restoring native plant communities within Glacier National Park.

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ABSTRACT

There is an immediate and on-going need in Glacier National Park (GNP), and other public and private lands, to determine effective methods to re-establish and sustain native plant populations following control treatments of *Centaurea maculosa*. My research was developed in response to GNP concerns regarding annual herbicide treatment of *C. maculosa* invaded sites. The aim of this study was to determine if herbicide applications, site preparation and revegetation methods would increase the density and percent cover of native species, while reducing spotted knapweed at two sites in and near Glacier National Park. A priori contrast analysis was used to determine differences in treatment effects. The results of my experiment show that spot spray herbicide application reduced *C. maculosa* cover without significantly reducing existing native forbs. However, a repeat-herbicide application increased exotic graminoid cover. Tillage reduced the density of *C. maculosa* seedlings, but resulted in an increase in *C. maculosa* percent cover, and an overall decline in native forbs. Revegetation methods had limited success at increasing native species, and reducing *C. maculosa*. The only effect was at Swift Current, where the percent cover of native forbs was significantly higher with the planting treatment, and most pronounced in plots with repeat-herbicide application. Additionally, we measured the composition and density of the seed bank in *C. maculosa* dominated sites using the seedling emergence method. *C. maculosa* density was 3,900 and 6,714 seeds / m^2 at the two sites, which was 2 and 3 times higher than the sum of all other species. Seed bank composition and density needs to be considered in efforts to restore *C. maculosa* infested areas.

RESTORING WEED-INFESTED LANDS IN THE NATIONAL PARK SYSTEM

Introduction

The National Park System contains some of the United States' best habitat for protection of the nation's biodiversity. Over 400 threatened or endangered plant and animal species are managed within the parks (Mehrhoff and Dratch 2002). In spite of efforts to maintain the integrity of critical ecosystems and the species that live there, habitats continue to be lost, degraded and fragmented. Invasive species are one of the main causes of this degradation.

The National Park Service spends millions of dollars each year combating invasive nonnative plants, which infest over seven million acres of National Park System lands (USDI-NPS 1996). From the sawgrass marshes of the Everglades to the dune scrub lands of Golden Gate National Recreation Area, fire, flooding, herbicides and insects have been used to control everything from kudzu to cheatgrass. While the concept of integrated pest management underlies the National Park Service's weed control policy and strategy, many park units consider herbicides the most economical and effective means of control (D. Lafleur, Glacier National Park, personal communication, 2003).

In the western United States, weed control is primarily accomplished with herbicides (Di Tomaso 2000). However, combating exotic species with herbicides alone can have negative long-term impacts on plant community structure (Bussan and Dyer 1999). Ecological concerns, coupled with the high cost of herbicides, are leading to an integrated weed management approach that includes biological, mechanical and cultural control strategies as well as revegetation (Sheley et al. 2001).

Many weed managers and researchers recognize that treating weed-infested lands with herbicides is a symptomatic approach to a larger problem of human disturbance. Human and natural disturbances such as fire increase the invasibility of plant communities throughout the world by increasing resource availability and decreasing competition from resident species, which facilitates colonization of invasive weeds (Orians 1986, Hobbs and Huenneke 1992, D'Antonio 2000). If the conditions that favor invasive plants are not addressed, herbicides will likely provide only short-term control before weed reinvasion.

The application of herbicides to control invasive species results in major ecological disturbance to a plant community, providing space and resources for subsequent plant colonization. Exotic plant reinvasion can be reduced by reintroduction of desired vegetation (Borman et al. 1991; Lym and Tober 1997; Jacobs et al. 1998) which will preempt nutrient, water and light resources, reducing the need to re-apply herbicides (Blumenthal 2003; Sheley et al. 1996). Restoring native plant diversity can also increase forage production and wildlife habitat (see Gilbert and Anderson 1998, and Morrison 2002), increase rare and endangered plant populations (Carlsen et al. 2000), improve water quality (Schilling and Thompson 2002), and increase carbon storage (Potter et al. 1999).

Revegetation for Weed Control

Thus far, revegetation studies on weed-infested rangelands have mainly focused on the use of one or two competitive grass species, with the goal - similar to that of biological control with insects - of suppressing the plant's population by competition for nutrients, light and water. In several studies, the use of aggressive perennial grasses has reduced the biomass of *Euphorbia esula* (leafy spurge) infested range. *Agropyron cristatum* seeded into sparse stands of *E. esula* in Saskatchewan resulted in a decrease in *E. esula's* seed production and growth (Selleck et al. 1962). Farell et al. (1993) assessed the competitive potential of 11 grass species on leafy spurge after herbicide treatments, and found that 7 and 10 years after seeding, *Elymus lanceolatus* and *Agropyron cristatum* reduced the percent canopy cover of leafy spurge to about 18 and 12.5 percent respectively. In Montana, *Agropyron desertorum* and *Elytrigia intermedia* ssp. *intermedia* provided effective control of *E. esula*.

In Wyoming, seeded *Elymus janceus*, *Agropyron desertorum* (crested wheatgrass), and *Agropyron riparium* (streambank wheatgrass) are effective competitors with *Centaurea repens* (Russian knapweed) after herbicide and tillage (Bottoms and Whitson 1998). In Oregon, native perennial cool season grasses, such as *Dactylis glomerata* (Berber orchard grass) and *Festuca idahoensis* (Idaho fescue) that begin growth early in a season, are more effective than warm season grasses at competing with exotic annual grasses once they were established (Borman et al. 1991).

In a roadside prairie restoration experiment in California, a two-step revegetation process allowed for the successful establishment of both native perennial grasses and forbs. Native forbs transplanted into plots of established perennial grasses had significantly higher survivorship than plots seeded with the same forbs. Additionally, reduced weed cover was found in plots with established perennial grasses and seeded forbs together, but not in plots with only perennial grasses, indicating a possible advantage of increased diversity (Brown et al. 2001). A multi-step adaptive management approach that uses a combination of weed control methods with managed successional revegetation will likely be necessary to restore weed-infested areas.

Only recently have researchers begun testing the effects of revegetating with a broader diversity of native forbs and grasses (Blumenthal et al. 2003). Invasion ecology studies at small spatial scales have shown that more diverse systems are less prone to invasion (Hector et al. 2001, Naeem et al. 1995), perhaps because of more complete use of resources and space by a high number of species (Kennedy et al. 2002). Creating a functionally diverse plant community after weed removal may provide long-term resistance to reinvasion. However, factors such as weed life history traits, length of time since invasion, and size of invasion may influence the feasibility of restoration.

The scale of weed infestation and the degree of land degradation can impact a system even when weed control efforts have reduced the target species (D'Antonio and Meyerson 2002). Feedback loops created by invasive plants that alter physical, chemical, and biological conditions in their own favor, may make restoration more difficult after weeds have been removed. For example, in New Jersey, soils of forest understories invaded by the exotic shrub *Berberis thunbergii* (Japanese barberry), and the annual c_4 grass *Microstegium vimimeum* (siltgrass) were found to have elevated pH values, higher nitrification rates, and higher net N mineralization rates, compared to uninvaded soils. Changes in the composition and function of microbiota were also observed (Ehrenfeld et al. 2001). The degree of soil changes induced by exotics will be a function of how long systems have been invaded, and may influence the length of time these changes persist after species have been removed. Restoration efforts may be improved by remedial treatments that restore physical and chemical soil properties to pre-invasion levels.

Invasion age may also increase the propagule pressure of exotic species, and alter soil seed banks. Many invaders are known to be prolific seed producers (Rejmanek 1995) capable of creating persistent seed banks (Baskin and Baskin 1998). In Saudi Arabian rangelands, Assaeed and Al-doss (2002) measured the soil seed bank under low, mid and high density stands of *Rhazya stricta*. Total species richness and viable seed density of native plants were significantly lower in high-density patches of the noxious shrub. Exotic woody invaders have also negatively impacted the seed bank of native species in South African fynbos (Holmes 2002), and in Texas savanna (Ruiseco and Barnes 1997) due to the exclusion of native species and the transient seed bank of most native plants from those systems.

While weed control efforts such as herbicide application provide highly effective short-term weed control (Bussan and Dyer 1999), degraded grasslands may have a relatively small supply of native propagules to compete with weeds after herbicide use (Bakker et al. 1996). Additionally, the propagules of many desired grassland species may have a short-term persistence in the seed bank, and will only return by dispersal from adjacent areas (Baskin and Baskin 1998). However, in systems such as temperate grasslands, where clonal reproduction is characteristic of dominant species, plants from adjacent areas may not provide an adequate number of seeds to revegetate a site (Bakker et al. 1996). "In the final analysis, seed banks are not a panacea for restoration of native… vegetation" in highly degraded systems (Dunn and Best 1984). If we hope to create communities that are less susceptible to reinvasion after weed control, it may be imperative to artificially revegetate these areas (Whisenant 1999).

Revegetation

Successful establishment of desirable species is an essential first step towards the creation of a preferred plant community. In systems that have had large-scale disturbance, such as fire or aerial herbicide application, planting seeds is the least expensive way to revegetate (Miles 1989). However, many desired species may not be commercially available, and must be collected in the wild and increased agriculturally, making the cost prohibitively high.

Many units in the National Park System now have native plant restoration programs where seed is collected and grown in Park nurseries for various restoration projects. With this infrastructure already in place, the capacity to revegetate smaller scale weed-treated areas may be affordable, especially if restoration efforts reduce the need to reapply costly herbicides (Blumenthal et al. 2003). Park units such as Agate National Monument in Nebraska, where *Cirsium arvense* (Canada thistle) is returning after control efforts (R. Knudson, personal conversation, 2003) or in Big Horn National Recreation Area in Montana, where *Bromus tectorum* (cheatgrass) control has been largely unsuccessful, may benefit from revegetation efforts. In the Golden Gate National Recreation Area, efforts to control infestations of *Carpobrotus edulis* (ice plant) have been very successful when hand removal was followed with planting of native species (P. Brastow, personal communication, 2003).

Species choice

A goal of restoring weed-infested areas is to create a post-weed plant community that is resistant to reinvasion. Using a combination of shallow- and deep-rooted forbs and grasses that grow early and late in the year may maximize spatial and temporal niche occupation (Goodwin and Sheley 2003) and help prevent reinvasion. However, creating such a community is often the end goal of restoration efforts. A first step objective may be to introduce an aggressive species that reduces the population of the target weed, and create conditions more favorable to other desirable species.

Seedbed preparation

Seedbed preparation can increase the rate of successful germination after broadcast seeding by increasing seed safe sites and improving soil structure (Whisenant 1996). Weed infestations often occur in areas where soils have been compacted. Soil compaction is a common physical characteristic of weed-invaded areas, which creates conditions that favor stress-tolerant weeds over native species. Once weeds have been treated in compacted soils, it may be necessary to till, plow or rip the soils to increase water movement, soil aeration, and nutrient cycling. Soils are ripped by pulling a heavy shank equipped with a broad lifting tip, 30 to 50 cm deep through the soil on the contour.

This process increases soil porosity and rate of water infiltration, causes uplifting of the soil (which resists surface runoff), leaves a furrow in the center of the uplift which helps retain water, and provides a seedbed for new plant establishment. Scarification treatments such as ripping may increase the precise conditions required for the germination of artificially seeded species. By reducing remaining vegetation and litter, soil scarification treatments increase seed-soil contact and water availability (Whisenant 1999).

Scarification treatments may also increase germination of the targeted weed species from the soil seed bank, providing an opportunity to reduce a propagules source for reinvasion. While mechanical tillage of large scale infestations is prohibitively expensive, it may be economical to till small-scale areas either manually or with a Rototiller. Periodic tillage can shift weed seeds from the dormant to the active part of the soil profile, increasing weed seed germination. Seedlings can then be managed with herbicide or mechanical control methods. This practice can also have the undesired effect of promoting the spread of weeds that are less affected by herbicides, such as *Euphorbia esula* (leafy spurge). Scarification treatments such as duff removal have been shown to stimulate natural revegetation in areas where there is a persistent seed bank (Dremann and Shaw 2002).

A second seedbed preparation is land imprinting, the formation of regular depressions on the soil surface, which aid in water infiltration, soil aeration, and seed germination and survival. Seeds are broadcast in front of the imprinter and pressed firmly in contact with the soil, or broadcast behind the imprinter so that splash erosion covers seed in the depressions (Whisenant 1999). In a California field experiment that tested various seeding methods, imprinting consistently yielded significantly more plants than the other treatments (Montalvo et al. 2002).

Seeding methods

Commonly used seeding methods in restoration include broadcast, drilling, and hydroseeding (Jacobs et al. 1999, Montalvo et al. 2002). Broadcast seeding involves scattering seed mechanically or by hand, and is fast and inexpensive, but results in relatively low germination rates because of the difficulty of spreading seed evenly and at the optimal depth in the soil. With hydroseeding, seeds are mixed with water, mulch, a binding agent, and sometimes fertilizer. The mix is sprayed through a hose under high pressure, over an area with exposed soil. Hydroseeding is relatively expensive, and is usually only employed for areas that need rapid stabilization against erosion.

Drilling employs an agricultural implement which makes furrows into which seed is dropped. It was developed in dry land agricultural systems to improve germination rates, and is more effective than broadcast seeding, but more expensive (Whisenant 1999). Montalvo et al. (2002) found that small-seeded species established at higher rates with imprinted and hydroseeded treatments than with the drilled treatment, whereas large-seeded species had higher density in imprinted and drilled treatments. Differential success of seeding methods may be the result of differences in planting depth (Montalvo et al. 2002).

Knowledge of the ideal seeding depth of individual species would increase germination success rates (Call and Roundy 1991). For instance, germination of many small seeded species will not occur unless seeds are located on the seedbed surface (Mayer 1986). A revegetation strategy that includes a diversity of species may be improved if different seeding methods are employed for different seed sizes. Seeding methods that increase the precision of seed placement to optimal depth are also needed.

Seeding rate

Increasing seeding rate and enhancement of seeds may also increase germination (Taylor et al. 1998, Jacobs 1999). Velagala et al. (1997) looked at a wide range of intermediate wheatgrass (*Elytriga intermedia* (Host) Nevski) seeding rates into patches of spotted knapweed (*Centaurea maculosa* Lam), and found no intermediate wheatgrass established at the recommended seeding rate of 500 seeds/ m^2. Increasing densities of intermediate wheatgrass to more than 1000 seeds/m^2 resulted in successful establishment, as interspecific interference of spotted knapweed on intermediate wheatgrass may have been removed.

Seed enhancements that improve germination or seedling growth include: pre-sowing hydration treatments (priming), seed coating and seed conditioning (Taylor et al. 1998). In a roadside revegetation experiment in Glacier National Park, Tyser et al. (1998) found that rapid establishment of alien species prevented slower germinating native grasses from establishing. The authors concluded that rapid post-construction seeding treatments were required to produce detectable seeding effects. Increasing the rate of native seed germination for better competition with weeds will require research into seed enhancements for native seed.

Direct Planting

Many perennial species do not establish well from seed and must be transplanted (Munshower 1994). Most native grassland plants do not respond to disturbance with rapid reestablishment by seed (Bakker et al. 1996). If diversity is important to the resistance of weed reinvasion, some nursery grown plants will certainly need to be planted directly. A multi-step revegetation process in an adaptive management framework will also be necessary, as described by Brown et al. (1997). Golden Gate National Recreation has successfully restored areas infested with monocultures of *Ammophila arenaria* (European dune grass), *Hedera helix* (English ivy) and *Carpobrotus edulis* (ice plant), by mechanical control followed by direct planting of nursery grown perennial forbs, grasses and shrubs (P. Brastow, GGNRA, 2002).

Recommendations for Further Research

Weed scientists have only begun to investigate the potential of native plant restoration to control weeds. There is still much that needs to be learned about manipulating weed seed banks, improving soil properties, and improving revegetation methods. The National Park System has a unique opportunity to support such research. Within the National Parks, weed management and restoration efforts could be integrated to determine how best to revegetate weed-treated areas.

There is an immediate and on-going need in Glacier National Park (GNP), and other public and private lands, to determine effective methods to re-establish and sustain native plant populations following treatments to control or reduce populations of *Centaurea maculosa* (spotted knapweed). Over three hundred acres of GNP lands are treated annually with herbicide to control spotted knapweed. Developing revegetation methods to limit spotted knapweed re-colonization will directly address GNP concerns regarding annual herbicide treatment of the same areas.

In response to GNP concerns, I developed a research project to specifically address the density and composition of the seed bank in spotted knapweed-infested areas, and to compare the effects of site preparation methods on native plant establishment post herbicide treatment. In chapter 2 of this thesis I tested three objectives. My first objective was to determine whether "spot spray" herbicide application would effectively control spotted knapweed without negatively impacting native forbs and shrubs. My second objective was to test the effects of tillage on plant community structure, with two main questions: 1) will tillage stimulate germination of dormant spotted knapweed seeds, reducing their presence in the seed bank?, and 2) how will tillage affect desirable native species? My third objective was to determine whether seeding and planting treatments would increase the density and percent cover of desirable forbs and graminoids, and provide effective control of spotted knapweed through competition.

Restoration and revegetation research by its very nature needs to be repeated across habitat types and soil types (Montalvo et al. 2002). Documentation of the results of simple experiments that compare the efficacy of alternative methods is important for improving restoration approaches on National Park lands.

RESTORATION OF SUBALPINE MEADOWS: REVEGETATION STRATEGIES FOLLOWING SPOTTED KNAPWEED CONTROL IN GLACIER NATIONAL PARK

Introduction

Invasive species' adaptive traits give them an advantage over native species. These traits include seed dormancy (Gerlach and Rice 2003), increased flowering and fruiting time, high number of seeds produced (Rejmanek 1995, Perrins et al. 1993), high initial germinability (Grime et al. 1988) and high relative growth rates of seedlings (Marañón and Grubb 1993, Grotkopp et al. 2002). While there is no "ideal weed" that possesses all these characters (Baker 1965), identifying the particular adaptive traits that provide competitive advantage to an invasive species can be useful in developing weed control strategies (Hobbs and Humphries 1995).

The life history traits of the Eurasian forb *Centaurea maculosa* (spotted knapweed) are consistent with those of many invasive species. Organisms with high propagule pressure have a higher chance of establishing new populations and becoming invasive (Williamson and Fitter 1996; Levine 2000; McKinney 2002; Alendorf and Lundquist 2003). Spotted knapweed is a perennial that can produce from 5,000 to 40,000 seeds/ m^2 per year (Shirman 1981). Seeds germinate in the fall and early spring (Watson and Renney 1974), giving seedlings a potential competitive advantage over other species. The aggressive nature of spotted knapweed is linked to early establishment and rapid growth rates (Sheley et al. 1993). Recent evidence shows that release of the allelopathic chemical (-)-catechin inhibits native species' growth and germination (Bais et al. 2003). Spotted knapweed seeds exhibit polymorphic germination behavior, which enables germination in a range of environmental conditions (Nolan and Upadhyaya 1988). And, like many invasive species, it can form a persistent seed bank with seeds capable of surviving at least eight years (Davis et al. 1993). The legacy of such a seed bank presents a long-term management challenge (D'Antonio and Meyerson 2002).

Spotted knapweed has infested over 2.5 million hectares in the western United States and Canada (Sheley et al. 1998). This invasive weed first arrived in North America in the 1890s as a contaminant in *Medicago sativa* (alfalfa) (Maddox 1979). It was collected on Vancouver Island, British Colombia, in 1905 and San Juan Island, Washington, in 1923. By the end of the 1930s it was common in northern Idaho and Montana (Roche and Roche 1991). Spotted knapweed has been shown to reduce plant species richness and diversity (Tyser and Key 1988), and increase runoff and sediment yield (Lacey et al. 1989). Research results are inconsistent in regard to impacts of spotted knapweed on wildlife. Wright and Kelsey (1997) found no evidence that knapweed reduced the carrying capacity of *Cervus elaphus nelsoni* Bailey (elk) and *Odocileus heminonus* Raf. (mule deer), where Thompson (1996) showed that elk use increased an average of 266% after spotted knapweed was removed from a site in western Montana.

Herbicides have proven to be effective in control of spotted knapweed (Lacey et al. 1995). Long-lived broadleaf herbicides such as picloram persist in the soil for as long as seven years, providing effective control of emergent seedlings. However, such herbicides can also kill desirable native forb species, which may negatively alter community structure. Short-lived herbicides such as clopyralid, which was used in this study, become inert within hours, but provide no long-term control for seedlings emerging from the seed bank. A control strategy that uses short-lived herbicides to kill visible spotted knapweed plants will not be effective unless repeated yearly applications are made to reduce the seed bank. Efforts to prevent reinvasion must also be employed.

Restoration of desirable plant species to weed-infested lands is increasingly seen as a necessary next step in weed management (Sheley and Krueger-Mangold 2003). Establishing a functionally diverse community of native species to weed controlled areas may help prevent recolonization of target weeds by filling empty niches and preempting nutrient and water resources. Thus far, revegetation studies on weed-infested rangelands have mainly focused on the use of one or two competitive grass species (Di Tomaso 2000). Only recently have researchers tested the effects of revegetating with a broader diversity of native forbs and grasses (Blumenthal et al. 2003).

There is an immediate and on-going need in Glacier National Park (GNP), and other public and private lands, to determine effective methods to re-establish and sustain native plant populations following control treatments of spotted knapweed. Over three hundred acres of GNP lands are treated annually with herbicide to control spotted knapweed. My research was developed in response to GNP concerns regarding annual herbicide treatment of the same areas. My first objective was to determine whether “spot spray” herbicide application would effectively control spotted knapweed without negatively impacting native forbs and shrubs. My second objective was to test the effects of tillage on plant community structure, with two main questions: 1) will tillage stimulate germination of dormant spotted knapweed seeds, reducing their presence in the seed bank?, and 2) how will tillage affect desirable native species? My third objective was to determine whether seeding and planting treatments would increase the density and percent cover of desirable forbs and graminoids, and provide effective control of spotted knapweed through competition.

Materials and Methods

Sites

This study was conducted at two grassland sites in and near Glacier National Park that are of similar elevation, and with a significant cover of spotted knapweed. Mean annual precipitation at both sites is 65 cm (Finklin 1986). Site 1 is approximately eight acres, and is located in the Many Glacier area of Glacier National Park in a meadow 960 m east of the Many Glacier Entrance Station. The plant community is dominated by *Centaurea maculosa* (spotted knapweed), and other forbs including *Aster laevis*, *Balsamorhiza sagittata*, *Geranium viscosissimum* and *Potentilla gracilis*. Graminoid species include *Phleum pratense*, *Poa pratensis*, and *Pseudoroegneria spicata.* The site is bordered by stands of *Populus tremuloides* (aspen) on three sides and by Glacier Rt. 3 on the northeast. Grazing by elk, deer and other wildlife has been observed periodically. The elevation is 1463m with a southeast aspect. The soil is a gravelly loam and contains: 684 mg/kg potassium, 0.539% total Kjeldahl nitrogen, 2.6 mg/kg ammonium, 3.6 mg/kg nitrate, and 20.4 mg/kg Olsen phosphorous. Located adjacent to an old homestead, the site received periodic truck traffic between 1920-1945. Spotted knapweed infestation is uniformly distributed throughout the site.

Site 2 is approximately 100 acres, and is located 15 km east of site 1 on the Blackfeet Indian Reservation. The site is classified as short grass prairie (Kaul 1986) and is representative of the *Festuca scabrella and F. idahoensis* community types (Mueggler and Stewart 1980). At 1370m with a southeast aspect, it borders Swift Current Creek to the south. The soil is a gravelly loam and contains: 692 mg/kg potassium, 0.792% total Kjeldahl nitrogen, 5.5 mg/kg ammonium, 11.2 mg/kg nitrate, and 37.2 mg/kg Olsen phosphorous. The area was grazed by cattle through the 1980's, and is now grazed by wildlife, with heavy elk use in the winter and spring. Spotted knapweed infestation is severe along a closed and gated dirt road that bisects the site, and occurs in isolated patches throughout the site, within a matrix of native vegetation.

Experimental Treatments and Design

At each site, 35 permanent 1x2 m plots were established in July 2001. Plots were located in areas where spotted knapweed percent cover ranged between 40-60%. This consistent level of spotted knapweed infestation was chosen to better compare treatment effects. At Many Glacier, spotted knapweed was ubiquitously distributed throughout the eight-acre site, but plots were established in five severe spotted knapweed patches. Patches ranged in size from 20 to 40 m^2 and contained four to seven plots. Inter-patch distances ranged from 30 to 1000 m. At Swift Current, 11, 12, and 12 plots were located in three distinct spotted knapweed patches, each surrounded by uninvaded native vegetation. Patch size ranged from 30 to 50 m^2, and inter patch distances ranged from 100 – 1600 m. Seven treatments with five replicates were randomly assigned to the 35 plots at each site (Table 1). The seven treatments were: 1) control (no treatment); 2) herbicide only; 3) herbicide and broadcast seeding; 4) herbicide and soil tillage; 5) herbicide, broadcast seeding and soil tillage; 6) herbicide, broadcast seeding and directing planting; and 7) herbicide, broadcast seeding, soil tillage and direct planting.

Table 1. Experimental design. Treatments 1-7 show the presence (X) or absence (0) of factor levels. The seven treatments with five replicates were randomly assigned to 35 plots at each site.

Treatments	Herbicide	Tillage	Seed	Plant
1	0	0	0	0
2	X	0	0	0
3	X	0	X	0
4	X	X	0	0
5	X	0	X	X
6	X	X	X	0
7	X	X	X	X

In July 2001, prior to the application of treatments, baseline measurements were taken in all 70 experimental plots. Percent canopy cover for all species was estimated over the 1x2 m area of each plot and spotted knapweed stem density was counted. In early October 2001, the broadleaf-specific herbicide Transline (clopyralid TEA: 3,6-dichloro-2-piyridine-carboxylic acid) was applied to spotted knapweed plants in plots and in the area within two meters around plots using a pressure-regulated backpack sprayer at a rate of 0.56 kg a.i./ha. Spotted knapweed was "spot sprayed" in the fall to kill over-wintering rosettes, and fall-emerging plants. Spot spraying is a method in which individuals of the target weed are sprayed, and desirable species are avoided when possible. Two days after herbicide was sprayed, the soil tillage, broadcast seeding and direct planting treatments were applied to randomly assigned plots.

Soils in the tillage treatment were manually tilled with shovels and pulaskis to a depth of 5-8 cm. The seed mix, which consisted of eight species of native graminoids and 11 species of native forbs, was broadcast and raked into assigned plots at a density of 360 graminoid seeds/ m^2 for each species totaling 2,875 graminoid seeds/ m^2, and 53 forb seeds/ m^2 for each species totaling, 583 forb seeds/ m^2. The graminoid species were: *Bromus carinatus, Elymus trachycaulus, Koeleria macrantha, Pseudoroegneria spicata, Festuca idahoensis, Festuca scabrella, Elymus glaucus,* and *Carex hoodii*. The forb species were: *Anaphalis margaritaceae, Achillea millefolium, Aster laevis, Arnica cordifolia, Anemone multifida, Geranium viscosissimum, Lupinus sericeus, Oxytropis spendens, Penstemon confertus, Potentilla gracilis, and Solidago canadensis*. Containerized grass and forb plugs grown from locally collected seed in 10 cm square pots and 4 cm diameter cones were planted in assigned plots at a density of nine plugs per plot on 50 cm centers. Four species of grasses (*Elymus spicata, Festuca idahoensis, Festuca scabrella, Koeleria macrantha),* and five species of forbs (*Anemone multifida, Gaillardia aristata, Geranium viscosissimum, Heuchera cylindrica,*and *Potentilla gracilis)* were used in plots receiving the direct planting treatment.

In July 2002, percent cover of all species was measured again, and stem densities of spotted knapweed, non-knapweed forbs, and graminoids were estimated within the plots by counting stems in 20 randomly placed 20 x 5 cm frames. Stem counts in July

2002 revealed a high density of spotted knapweed seedlings emerging from many plots. After stem density estimates were made in July 2002, a second "spot spray" herbicide treatment (hereafter called "repeat-herbicide") was applied to half of each plot receiving treatments 2-7. Those half-plots that did not receive the repeat-herbicide treatment are hereafter called "single-herbicide". Again, spraying of native plants was avoided when possible so that only spotted knapweed plants received herbicide.

In July 2003, final measurements of percent cover for all species was conducted, and stem densities of spotted knapweed, native forbs, native graminoids, non-knapweed exotic forbs, and exotic graminoids were estimated within the half-plots by counting stems in 20 randomly placed 20 x 5 cm frames. Density data was not distinguished by these groups in 2002, as field crews were not able to identify species of emerging seedlings. All native and exotic graminoids were simply counted as "graminoids" and all native and exotic forbs were counted as "non-knapweed forbs".

Statistical Analysis

Response variables were analyzed using a mixed effects model (model III). Two-way ANOVA was performed with site and treatment as factors to test the response of spotted knapweed percent cover. All other response variables were analyzed with a two-way ANCOVA, with pre-treatment 2001 data as covariates. To test the hypotheses that herbicide, tillage, seeding and planting reduce the percent cover and density of spotted knapweed, and increase the percent cover of native graminoids and forbs, we conducted *a priori* contrast analysis of treatment level means. Contrast analysis was used to compare the effects of specific factor levels on response variables, and to avoid confounding factor levels (see Neter et al. 1996). For example, tillage effects were measured by subtracting the average of treatments 4 and 6 (tillage) from the average of treatments 2 and 3 (no tillage). Treatments 3 and 6 differ only by the presence or absence of tillage as do treatments 2 and 4. For herbicide effects, treatment 2 was contrasted with treatment 1 (control). For seeding effects, the average of treatments 2 and 4 was contrasted with the average of treatments 3 and 6, and for planting effects the average of treatments 3 and 6 was contrasted with the average of treatments 5 and 7. Paired t-tests were conducted to compare treatment means of the single-herbicide treatment with the repeat-herbicide treatment. Data were tested for normality and heterogeneity of variance and transformed as necessary. Different data transformations were attempted on percent cover and density of native shrubs, and exotic forbs; however, diagnostic analyses showed that all transformed data sets still violated ANOVA assumptions of normality and homogeneity of variance. This was likely due to the high number of zero values in these data sets. SPSS version 11.5 and R version 1.6.2 were used to perform the ANOVAS and ANCOVAS.

The rationale for categories in Table 1 is as follows: *Native forb* and *native shrub* species may augment the process of ecological restoration in disturbed communities (Bakker et al. 1996). *Native graminoids* are often the focus of grassland restoration activities, and are theoretically unaffected by broadleaf herbicides (Alexander and D'Antonio 2003; Bussan and Dyer 1999). The *exotic forb* and *exotic graminoid* species are a management concern in Glacier National, and may be an impediment to restoration efforts.

Results

Prior to the first herbicide application in 2001, mean density and mean percent cover of spotted knapweed in all plots was 107 stems/m^2 (± 6.9 SE) and 47 percent (± 3.5 SE) (Figure 1a). The mean percent cover of all other species combined was 17 per cent (± 7.8 % SE). In 2002, nine months after treatments were applied, the mean percent cover of spotted knapweed in all plots (excluding control plots) had fallen to 14 percent (± 2.0 SE), while the mean density had increased to 1,600 stems/m^2 (± 124 SE). Mean percent cover of all other species combined was 15 % (± 7.5 SE). Plant community composition is compared between sites, averaged across treatments (Figure 1 b-d).

By 2003, spotted knapweed cover was 23 % (± 5.6 SE) in control plots, 30 % in single-herbicide half-plots, and 4.4% (± 0.80 SE) in repeat-herbicide half-plots (Figure 1 c-d). Spotted knapweed density was 1270 (±196 SE) stems/m^2 in control plots, 890 (± 64 SE) stems/m^2 in single-herbicide half-plots, and 350 (± 72 SE) stems/m^2 in repeat-herbicide half-plots. In 2003, mean percent cover of all other species combined was 14 % (±1.0SE) in single-herbicide half-plots, and 18% (±0.9 SE) in repeat-herbicide half-plots.

Herbicide

In 2002 and 2003, no significant interaction effects were found between site and treatment for any of the response variables. Contrasts reveal that spotted knapweed percent cover was significantly reduced by the herbicide treatment ($p < 0.001$) at both sites (Table 3; Figure 2 a + b) in 2002. However, herbicides had no effect on spotted knapweed stem density at either site in 2002, or in 2003 single-herbicide half-plots. Repeat-herbicide half-plots had significantly fewer spotted knapweed stems/m^2 (Table 3, Figure 3). By 2003, spotted knapweed had regenerated in many half-plots that did not receive the repeat-herbicide treatment in 2002 (Figure 2 c + d), so that the initial effect of the herbicide application was lost. At Many Glacier, spotted knapweed percent cover increased in plots that received a 2001 herbicide application ($p = 0.01$; Table 3; Figure 2 c).

Only two other response variables showed a significant difference in herbicide treated plots. In 2003 at Many Glacier, the density of native forbs was lower in single-herbicide half-plots ($p = 0.02$), and the density of native graminoids was lower in repeat-herbicide half-plots ($p = 0.005$). Herbicides had no effect on the percent cover of native forbs, native graminoids, or exotic graminoids, or on the stem densities of native and exotic graminoids in 2002 or 2003 at either site (Table 3). Contrast analysis was not conducted on percent cover or density of native shrubs or exotic forbs (excluding spotted knapweed), because these data sets violated ANOVA assumptions of normality and homogeneity of variance.

Repeat Herbicide

We used paired t-tests to compare single-herbicide half-plots with repeat-herbicide half plots, and found that at Many Glacier and Swift Current, spotted knapweed percent cover and density were significantly lower in repeat-herbicide half plots in 2003 ($p<0.001$) (Figure1 b + d).

Table 2. Plant species and the number of plots (out of 35) in which they were observed at each site in 2002.

	MG	SC		MG	SC
Native Shrubs			Native forb		
Amelanchier alnifolia	4	x	*Achillea millefolium*	11	7
Arctostaphylos uva-ursi	1	x	*Agoseris glauca*	8	10
Mahonia repens	8	x	*Allium cernuum*	9	7
Pentaphylloides fruticosa	3	x	*Allium schoenoprasum*	4	1
Prunus virginiana	1	x	*Androsace septentrionalis*	x	2
Ribes viscosissimum	1	x	*Anemone multifida*	3	14
Rosa woodsii	15	10	*Anemone nuttalliana*	*x*	2
Spiraea betulifolia	1	x	*Antennaria sp.*	3	1
Symphoricarpos albus	6	3	*Arabis drumondii*	2	2
			Arabis glabra	3	x
Native Grass			*Arnica sororia*	x	4
Agropyron caninum	x	4	*Aster laevis*	27	1
Agropyron spicatum	18	14	*Balsamorhiza sagittata*	1	x
Agrostis scabra	x	1	*Campanula rotundifolia*	13	14
Bromus carinatus	2	26	*Cerastium arvense*	22	20
Carex sp.	4	26	*Collinsia parviflora*	4	1
Carex obtusata	8	9	*Collomia linearis*	9	1
Carex petasata	4	6	*Draba nemorosa*	x	x
Danthonia intermedia	x	1	*Erigeron sp.*	4	x
Elymus glaucus	x	1	*Eriogonum umbellatum*	11	x
Elymus smithii	x	8	*Fragaria virginiana*	22	3
Elymus trachycaulus	x	4	*Gaillardia aristata*	3	4
Elymus sp.	x	5	*Galium boreale*	19	27
Festuca campestris	9	9	*Geranium viscosissimum*	21	29
Festuca idahoensis	9	25	*Geum macrophyllum*	*x*	3
Koeleria montanum	x	5	*Geum triflorum*	*x*	2
Stipa nelsonii	3	10	*Heuchera cylindrica*	8	18
Stipa richardsonii	x	2	*Heuchera parviflora*	4	x
			Lithospermum ruderale	9	4
Exotic Grass			*Lomatium dissectum*	1	3
Agropyron repens	5	x	*Lomatium macrocarpum*	16	5
Phleum pratense	28	31	*Lomatium triternatum*	26	11
Poa compressa	1	2	*Lupinus sericeus*	28	15
Poa pratensis	26	29	*Microseris gracilis*	23	9
			Monarda fistulosa	1	x
Exotic Forb			*Penstemon confertus*	20	8
Capsella bursa-pastoris	1	x	*Phlox caespitosa*	x	3
Centaurea maculosa	35	35	*Plantanthera hyperborea*	1	x
Cirsium arvense	3	2	*Polygonum douglasii*	14	6
Taraxacum officinale	22	16	*Potentilla glandulosa*	23	7
Thlaspi arvense	6	3	*Potentilla gracilis*	28	11
Tragopogon dubius	x	4	*Potentilla hippiana*	1	3
			Potentilla ovina	3	x
			Selaginella sp.	5	x
			Solidago multiradiata	4	1
			Trifolium repens	x	1
			Vicia americana	x	1
			Viola nuttallii	x	3
			Zigadenus elegans	2	x

x= not present MG= Many Glacier SC= Swift Current.

Table 3. Summary of treatment effects' t* values derived from contrast analyses. Positive and negative values indicate a respective increase or decrease in the response variables.

		2002		2003 S		2003 R	
		MG	SC	MG	SC	MG	SC
Spotted Knapweed percent Cover	Till	1.59	2.36 *	0.84	3.37**	-2.08	-0.81
	Seed	-0.49	1.00	-1.68	-0.84	0.27	-0.74
	Plant	0.41	1.56	0.04	0.60	0.29	-0.79
	Herbicide	-3.41 **	-6.47 **	2.78 *	-1.33	-2.34 *	-2.97**
Spotted knapweed stems / m^2	Till	-1.98 *	0.90	-1.67	0.26	-3.38 **	-1.20
	Seed	-0.41	0.09	-0.43	0.35	1.04	1.48
	Plant	1.25	-0.17	1.68	0.67	-0.79	-0.78
	Herbicide	-0.84	-0.98	-1.05	-0.79	-2.62*	-3.16**
Native Forbs percent Cover	Till	-2.83 *	1.35	-2.22 *	0.12	-0.79	1.62
	Seed	-0.04	-0.04	-0.65	-0.05	-1.71	-1.32
	Plant	-0.17	2.60 *	0.78	1.07	1.81	3.14 **
	Herbicide	1.18	-1.45	-0.85	-1.26	1.16	-1.74
Native Forbs stems / m^2	Till	N/A	N/A	-3.11 **	-0.98	-4.38 **	-0.65
	Seed	N/A	N/A	-0.70	0.04	1.10	-0.45
	Plant	N/A	N/A	1.39	0.50	1.69	0.42
	Herbicide	N/A	N/A	-2.47*	-0.13	-1.84	0.59
Exotic Graminoids percent Cover	Till	-0.88	-2.52 *	-0.58	-2.34 *	1.04	-1.39
	Seed	0.76	-0.46	0.15	0.31	-0.42	-1.46
	Plant	-0.93	-0.13	-0.85	1.38	-1.28	0.24
	Herbicide	0.94	-0.40	0.92	0.45	0.33	0.81
Exotic Graminoids stems / m^2	Till	N/A	N/A	-2.97 **	-0.63	-2.82 *	-0.87
	Seed	N/A	N/A	-0.03	-0.10	-0.87	-0.56
	Plant	N/A	N/A	-0.72	0.01	-0.81	-0.60
	Herbicide	N/A	N/A	-0.13	0.10	-0.53	0.80
Native Graminoids percent Cover	Till	-1.41	0.12	0.52	-0.59	-2.09	0.29
	Seed	1.08	-0.79	1.69	0.27	0.78	0.44
	Plant	-0.75	1.08	-1.99 *	-0.31	-1.66	-0.10
	Herbicide	1.51	0.40	-1.76	1.02	1.50	-1.80
Native Graminoids stems / m^2	Till	N/A	N/A	-1.21	-0.85	0.05	-0.77
	Seed	N/A	N/A	1.62	-0.32	2.42 *	-0.58
	Plant	N/A	N/A	-2.60 *	0.27	-1.29	0.10
	Herbicide	N/A	N/A	1.08	0.14	-2.96 **	-0.69

MG = Many Glacier; * = significance ($p < 0.05$); S = single-herbicide; N/A = no data
SC = Swift Current; **= significance ($p < 0.005$); R = repeat-herbicide

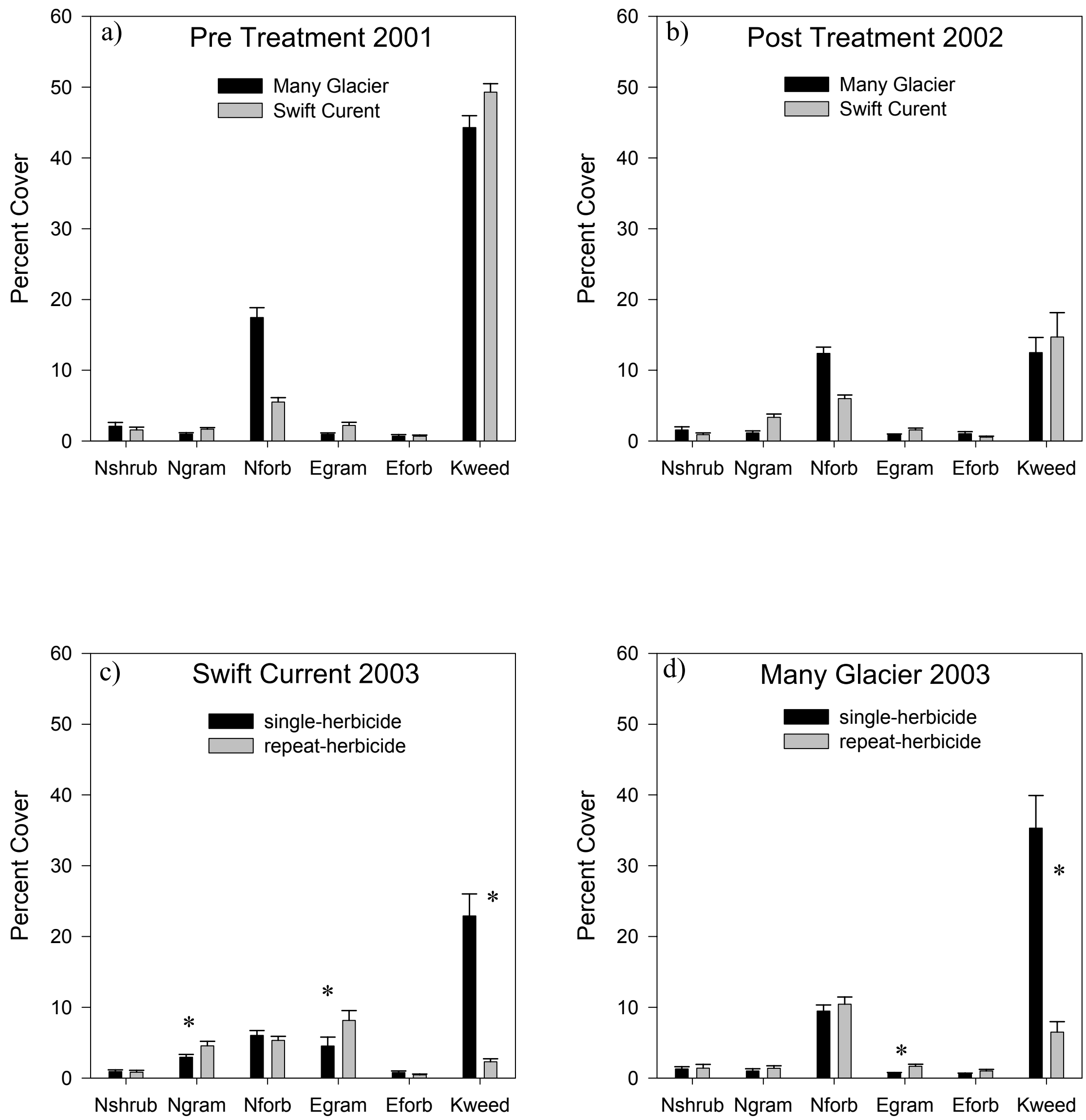

Figure 1. Post treatment data is the mean of all plots, excluding control plots. Mean spotted knapweed cover was reduced by 36 % and 40 % at Many Glacier and Swift Current sites by 2002. All other plant groups did not significantly change between 2001 and 2002. Values are means (± SE) for all 2-m^2. 2003 significance values * are based on paired t-tests between single-herbicide and repeat-herbicide treatments for each site.

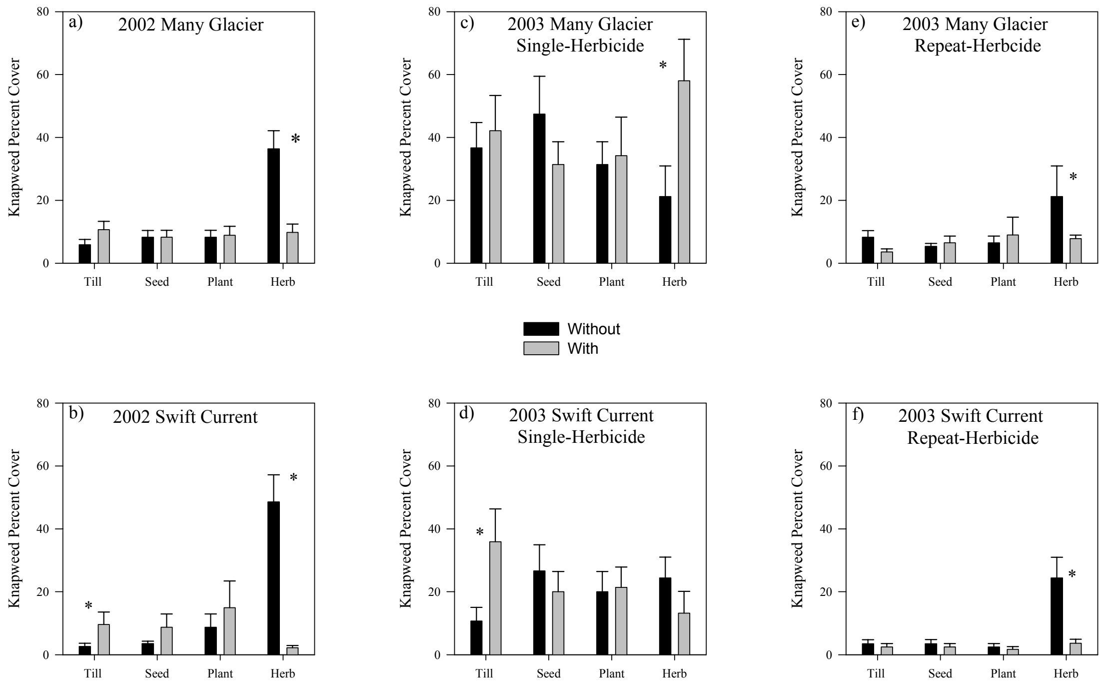

Figure 2. The effect of treatments on spotted knapweed percent cover for each year. A significant difference is indicated by *. Values are means (± SE) derived from contrast analysis.

Exotic graminoid cover was higher in repeat-herbicide half-plots at both sites ($p<0.001$) (Figure 1 b + d). At Swift Current, native graminoid percent cover was also higher in repeat-herbicide half-plots ($p=0.007$), but no difference was found at Many Glacier ($p=0.70$) (Figure 1 a + b). No differences were found between single-herbicide half-plots and repeat-herbicide half-plots for native forbs percent cover (MG: $p=0.20$; SC: $p=0.40$; figure 1 b + d) and density (MG: $p=0.98$; SC: $p=0.60$). Paired t-tests were not conducted on percent cover or density of native shrubs, or exotic forbs (excluding spotted knapweed), because we were unable to normalize these data.

Tillage

Spotted knapweed cover was higher in tilled versus untilled plots at the Swift Current site in 2002 (p=0.02; Table 3; Figure 2 b). This effect persisted in 2003 single-herbicide half-plots (p = 0.002; Table 3; Figure 2 d). No tillage effects on spotted knapweed cover were found at Many Glacier for either year (2002: p = 0.10; 2003: p = 0.40; Table 3; Figure 2 a + c + e). In 2002, spotted knapweed stem densities were lower in tillage plots than in no tillage plots at Many Glacier (p = 0.05; Table 3; Figure 3 a), but not at Swift Current (p = 0.40; Table 3; Figure 3 b). This effect persisted in 2003 in repeat-herbicide half-plots (p = 0.001), but not in single-herbicide half-plots (p = 0.1).

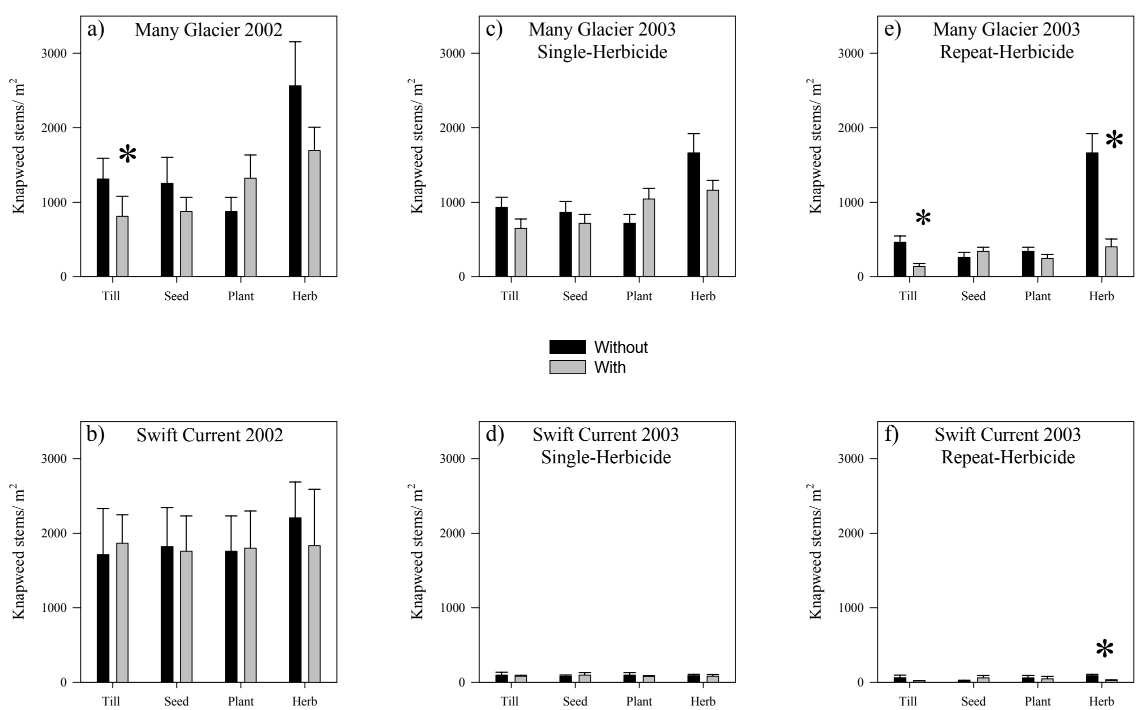

Figure 3. The effect of treatments on spotted knapweed stems/m^2. A significant difference is indicated by $*$. Values are means (± SE) derived from contrast analysis.

There were no significant effects of tillage on percent cover (2002: $p = 0.20$; 2003: $p = 0.90$; Table 3) or stem density (2003: $p = 0.50$; Table 3) of native forbs at Swift Current. At Many Glacier, tillage had a negative effect on the percent cover of native forbs (2002: $p = 0.008$; 2003: $p = 0.03$; Table 3), and a negative effect on stem density (2003: $p = 0.003$; Table 3).

The percent cover of exotic graminoids was negatively affected by tillage at Swift Current (2002: $p = 0.02$; 2003: $p = 0.02$; Table 3), with no effect at Many Glacier (2002: $p = 0.40$; 2003: $p = 0.60$; Table 3). The stem density of exotic graminoids was negatively affected at Many Glacier (2003: $p = 0.005$; Table 3), with no effect at Swift Current (2003: $p = 0.5$; Table 3). No significant effects on native grass percent cover (MG 2002: $p = 0.2$; MG 2003: $p = 0.7$; SC 2002: $p= 0.9$; SC 2003: $p= 0.6$; Table 3), and density (MG 2003: $p = 0.2$; SC 2003: $p= 1.0$; Table 3) were observed.

Seeding

Native grass stem density was higher in seeded plots than in unseeded plots at Many Glacier in 2003 in repeat-herbicide half-plots (p=0.01; Table 3), and nearly significant in repeat-herbicide half-plots (p =0.06; Table 3). No other seeding effects were observed for any other response variables (Table 3).

Planting

Positive increases with planting were observed in the percent cover of native forbs at Swift Current in 2002 ($p = 0.01$; Table 3). This effect persisted in 2003 in repeat-herbicide half-plots ($p = 0.003$; Table 3), but not in single-herbicide half-plots ($p = 0.30$;

Table 3). Percent cover ($p = 0.05$; Table 3) and stem density ($p = 0.01$; Table 3) of native graminoids were also higher at Many Glacier in 2003 in single-herbicide half-plots. No other planting effects were observed for any other response variables (Table 3).

Discussion

Using broadleaf-specific herbicides to control exotic forbs can have the undesired effect of reducing native forb and shrub cover when applied indiscriminately. The results of my experiment show that spot spray herbicide application reduced spotted knapweed cover without significantly reducing existing native forbs in 2002 or 2003.

However, by 2003, single-herbicide half-plots at both sites saw an overall increase in mean spotted knapweed percent cover between 2002 and 2003, while control plots had an overall decline in spotted knapweed percent cover. At Many Glacier, spotted knapweed cover actually exceeded 2001 pre-treatment levels by 23%.

This increase in spotted knapweed cover in herbicide treated plots between 2002 and 2003 may be the result of treatment timing. The first herbicide treatment was applied in October of 2001, after spotted knapweed had set seed. The reduction in overall spotted knapweed cover likely promoted germination of seed dropped the previous year, as more light, nutrients, and water were available for emergent seedlings. Spotted knapweed density was higher at both sites in 2002 compared to 2001 and 2003 (Figure 4). Density dependent competition in 2002 likely resulted in fewer more vigorous spotted knapweed individuals that benefited from the initial herbicide effect of reducing intraspecific competition. This may explain the higher percent cover in 2003 single-herbicide half-plots.

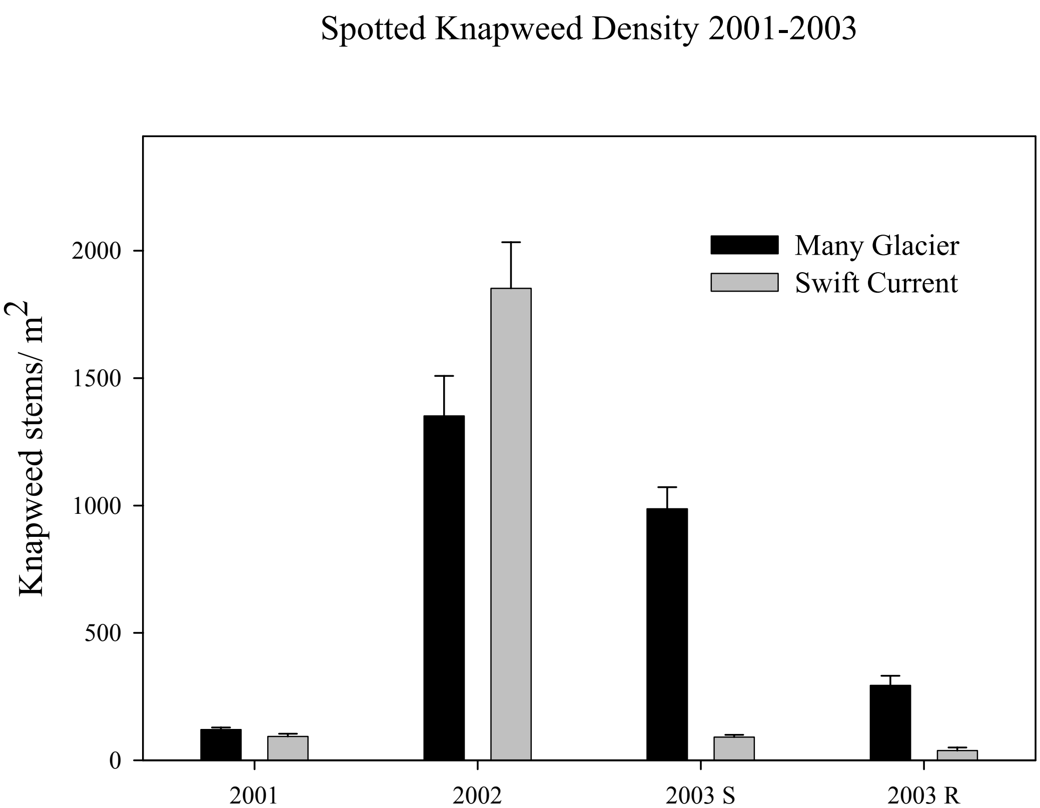

Figure 4. Spotted knapweed mean density (± SE). S= single-herbicide, R= repeat-herbicide.

Using short-lived herbicides as part of a strategy to restore spotted knapweed-infested grasslands will require repeated herbicide applications to reduce the spotted knapweed seedbank and prevent reinfestation. In a separate investigation of seed bank densities within my plots, we found that spotted knapweed seeds were 10 times more abundant than all other species combined (Chapter 3). This data supports my observation that while the fall 2001 application of clopyralid was highly effective at reducing spotted knapweed cover, spotted knapweed seedlings germinated early and in high densities at both sites in June 2002. By 2003, spotted knapweed percent cover had rebounded in half-plots that did not receive the repeat-herbicide treatment.

The time required to deplete the seed bank will vary by site. For instance, at Many Glacier in 2003, spotted knapweed cover averaged only 6.5 % in repeat-herbicide half-plots. However, the average stem density in the same repeat-herbicide half-plots was 300 stems/m^2 (± 40 SE). While this is a significant improvement compared to single-herbicide half-plots (percent cover = 35 % (± 5 SE); density = 990 stems/m^2 (± 85 SE)), stem densities may be high enough to allow spotted knapweed to become dominant again. In repeat-herbicide half-plots at Swift Current in 2003, both spotted knapweed percent cover (2.3% (± 0.5 SE)) and stem-density (37 stems/m^2 (± 12 SE)) were reduced to a level that may improve efforts to reestablish desired native species, and reduce the frequency of follow-up herbicide applications on spotted knapweed.

While repeated herbicide treatments may provide effective control over spotted knapweed, they may also shift plant community structure in an undesirable direction. My results show that exotic graminoid cover benefited from a second herbicide application. At Swift Current, exotic graminoid percent cover was 8 % (± 1.3 SE) in repeat-herbicide half-plots, and 4% (± 1.2 SE) in single-herbicide half plots; while overall exotic graminoid cover was much lower at Many Glacier, it was significantly higher in repeat-herbicide half-plots. These results are consistent with Rice et al. (1997), who found that grasses responded positively after spotted knapweed is treated with herbicides. While native graminoids also benefited from repeat herbicides at Swift Current, increases in the highly competitive invasive exotic grasses *Phleum pratense* (Timothy) and *Poa pratensis* (Kentucky bluegrass) creates a further impediment to restoration of desirable species.

One of my objectives was to determine if tillage would stimulate germination of spotted knapweed thereby reducing its presence from the seed bank. When combined with herbicide application, tillage may reduce the density of spotted knapweed seed stored in the soil. Nolan and Upadhyaya (1988) determined that a portion of the spotted knapweed seed population requires exposure to red light to germinate. By bringing buried spotted knapweed seed to the soil surface we expected to see increased germination, resulting in higher seedling densities and higher percent cover.

In 2002, spotted knapweed seedling densities were not significantly higher in tilled versus untilled plots at either site. In 2003, tilled repeat-herbicide half-plots at Many Glacier had an average of 324 (± 46 SE) fewer stems/m^2 than no till plots in 2003. Many seeds were likely buried by tillage which may delay and or prevent a certain percentage of seeds from germinating. Spotted knapweed seeds rarely germinate below a depth of 5 cm (Spears et al. 1980).

Increased spotted knapweed cover at Swift Current in tilled plots for 2002 and 2003 single-herbicide half-plots appears to have no relation to higher germination rates and is likely due to decreased interspecific competition from exotic graminoids impacted by tillage and increased plant available nitrogen due to soil disturbance (Tardiff and Stanford 1998). Spotted knapweed is more competitive than perennial grasses and forbs in high nutrient environments (Heron et al. 2001, Velagala et al. 1997). Soil tillage causes increased mineralization rates (Grant 2001), and can result in a short-term pulse of plant available nitrogen , which may provide spotted knapweed with further competitive advantage over perennial forbs and grasses. My results show that the combination of tillage and herbicide application does not provide more effective control of spotted knapweed than the use of herbicides alone.

Revegetating desirable species to spotted knapweed-infested lands after herbicide application may preempt nutrient, water and light resources against future exotic invasion, which reduces the need to perpetually re-apply herbicide (Jacobs et al. 1998). The percent cover and density of native graminoids and native forbs were not higher as a result of the seeding treatment in July 2002 or 2003 with one exception. Stem density of native graminoids was higher at Many Glacier in 2nd herbicide treated half-plots, but this increase did not correspond with a reduction in spotted knapweed density or percent cover. Native species seeded in the fall should have had the necessary cold temperature and snow moisture needed to overcome dormancy. Given the method of seeding –broadcast application- seeds may not have had adequate seed-soil contact and or soil moisture to meet germination requirements.

It is also possible that the native species seeding rate used for this study as recommend by the USGS (1991) was not high enough to overcome interspecific interference with spotted knapweed. Spotted knapweed seedlings are highly competitive and known to emerge early with minimal mortality during normal years (Sheley et al 1999). In a study that assessed the effect of seeding rate on establishment, Sheley et al. (1999) found that no *Elytriga intermedia* (intermediate wheat grass) established at the recommended maximum seeding rate of 430 seeds m^{-2}. In my study, the seed of eight native graminoid species was combined and seeded at the recommended rate of 500 seeds m^{-2}. Recent evidence also shows the release of the chemical racemic (-)-catechin by spotted knapweed inhibits germination of native species (Bais et al. 2003).

While the planting treatment was effective at increasing native forb percent cover at the Swift Current site, this treatment had no effect on spotted knapweed percent cover or density in 2002 or 2003. The nine individuals planted per plot accounted for approximately ten percent cover of the plots at the time they were planted in October 2001. Some planted grasses were found dead on the soil surface the following spring likely due to frost heave or grazing.

Restoration of native grasslands invaded by spotted knapweed may not be feasible until spotted knapweed is effectively reduced in aboveground biomass and belowground seed bank, by mechanical, cultural or chemical control. While revegetation studies have shown that the use of one or several aggressive perennial grass species can be effective at reducing invasive weeds by competition (Bottoms and Whitson 1998, Ferrell et al. 1993, Sheley et al. 2001), restoration of a functionally diverse plant community is a much harder goal. Species rich communities may be more resistant to invasion (Tilman 1997, for alternate view see D'Antonio and Meyerson 2002), but reestablishing diversity in areas infested with weeds will require long-term management to allow desirable species to proliferate and to prevent the target weed from becoming dominant again.

In Glacier National Park, spotted knapweed is primarily found along roadsides and in small patches in native sub-alpine meadows (Tyser and Key 1988). In these areas, where spotted knapweed grows amongst native plants, National Park Service employees use backpack sprayers to manually “spot spray” broadleaf herbicides directly to spotted knapweed individuals. My study, which employed the same application method, shows that spotted knapweed can be reduced without significant detriment to surrounding native species. Revegetation of desirable species may not be an effective means of controlling spotted knapweed until knapweed seed density is sufficiently reduced from the seed bank. A better strategy may be to wait until spotted knapweed seed has been effectively minimized through repeated applications of short-lived herbicides such as clopyralid, and then to use a combination of seeding and planting techniques that will effectively establish a diversity of species.

SEED BANK DYNAMICS IN SPOTTED KNAPWEED INFESTED GRASSLANDS: EFFECTS OF HERBICIDE ON CONTROL AND RESTORATION

Introduction

The prevalence of invasive species in natural areas is becoming a larger management issue in parks, reserves and federal lands (D'Antonio and Meyerson 2002, National Invasive Species Council 2001). Once naturalized, invasive species can change plant community structure, and alter successional trajectories (Di Tomasso 2000). Efforts to manage established weed populations are enhanced by an understanding of individual adaptive traits that give those species a competitive advantage (Sheley and Krueger-Mangold 2003). Many invasive weeds are capable of producing a large number of dormant seeds resulting in a large persistent seed bank (Holmes 1989) that contributes to weed reestablishment after weed management (D'Antonio and Meyerson 2002; Alexander and D'Antonio 2003).

In the western United States, *Centaurea maculosa* (spotted knapweed) has invaded millions of hectares (Sheley et al. 1998). Like other invasive plant species, it produces many seeds that can persist in the seed bank for at least eight years (Davis et al. 1993). Spotted knapweed forms dense stands in disturbed areas, and is capable of spreading into native habitats, displacing resident species (Tyser and Key 1988). Once knapweed is established, the seed rain of excluded species will theoretically diminish as species disappear. Subsequent declines in seed bank density will follow, as seeds age and become unviable (D'Antonio and Meyerson 2002). Other invasive plants reduce seed bank density of native species throughout the world (Ruiseco and Barnes 1997; Assaeed and Al-doss 2002; Collier et al. 2002; Holmes 2002; Alexander and D'Antonio 2003).

Restoration of weed infested areas will require that weeds first be removed, and that propagule pressure be diminished. Desired species lost from the persistent soil seed bank will have to be transported to the site by some vector, i.e., wind, water, animals, or humans. However, natural dispersal may not occur in a time frame that allows for the formation of a diverse weed-resistant community. Bakker et al. (1996) reported that several European grassland restoration studies had few native species recolonize after years and decades. Seed rain measurements showed low species richness and diversity, as well as the absence of species growing in close proximity to the sites (Bakker et al. 1996).

The objectives of this study were 1) to estimate the species richness and abundance of the seed bank in my experimental plots, and 2) to use aboveground estimates of species' stem densities and percent cover to predict seed bank longevity of spotted knapweed.

Materials and Methods

Sites

This study was conducted at two grassland sites in and near Glacier National Park that are of similar elevation, and with a significant cover of spotted knapweed. Mean annual precipitation at both sites is 65 cm (Finklin 1986). Site 1 is approximately eight acres, in the Many Glacier area of Glacier National Park, in a meadow 960 m east of the

Many Glacier Entrance Station. The plant community is dominated by spotted knapweed, and other forbs including *Aster laevis*, *Balsamorhiza sagittata*, *Geranium viscosissimum* and *Potentilla gracilis*. Graminoid species include *Phleum pratense*, *Poa pratensis*, and *Pseudoroegneria spicata.* The site is bordered by stands of *Populus tremuloides* (aspen) on three sides and by Glacier Rt. 3 on the northeast. Grazing by elk, deer and other wildlife has been observed periodically. The elevation is 1463m with a southeast aspect. The soil is a gravelly loam and contains: 684 mg/kg potassium, 0.539% total Kjeldahl nitrogen, 2.6 mg/kg ammonium, 3.6 mg/kg nitrate, and 20.4 mg/kg Olsen phosphorous. Located adjacent to an old homestead, the site received periodic truck traffic between 1920-1945. Knapweed is uniformly distributed throughout the site.

Site 2 is approximately 100 acres, and is located 15 km east of site 1 on the Blackfeet Indian Reservation. The site is classified as short grass prairie (Kaul 1986) and is representative of the *Festuca scabrella and F. idahoensis* community types (Mueggler and Stewart 1980). At 1,370m with a southeast aspect, it borders Swift Current Creek to the south. The soil is a gravelly loam and contains: 692 mg/kg potassium, 0.792% total Kjeldahl nitrogen, 5.5 mg/kg ammonium, 11.2 mg/kg nitrate, and 37.2 mg/kg Olsen phosphorous. The area was grazed by cattle through the 1980's, and is now grazed only by wildlife, with heavy elk use in the winter and spring. Knapweed infestation is severe along a closed and gated dirt road that bisects the site, and occurs in isolated patches throughout the site, within a matrix of native vegetation.

Experimental Treatments and Design

Field sampling

At each site, 35 permanent 1x2 m plots were established in July 2001. Plots were located in areas where knapweed percent cover ranged between 40-60%. In July 2001, baseline measurements were taken in all 70 experimental plots. Percent canopy cover for all species was estimated over the 1x2 m area of each plot and spotted knapweed stem density was counted. In early October 2001, the broadleaf-specific herbicide Transline (clopyralid TEA: 3,6-dichloro-2-piyridine-carboxylic acid) was applied to knapweed individuals in plots and in the area within two meters around plots using a pressure-regulated backpack sprayer at a rate of 0.56 kg a.i./ ha. Knapweed was "spot sprayed" in the fall to kill over-wintering rosettes, and fall-emerging plants. Spot spraying is a method in which individuals of the target weed are sprayed, and desirable species are avoided when possible.

In July 2002, percent cover of all species was measured again, and stem densities of spotted knapweed, non-knapweed forbs, and graminoids were estimated within the plots by counting stems in 20 randomly placed 20 x 5 cm frames. Stem counts in July 2002 revealed a high density of spotted knapweed seedlings emerging from many plots. After stem density estimates were made in July 2002, a second "spot spray" herbicide treatment (hereafter called "repeat-herbicide") was applied to half of each plot. Those half-plots that did not receive the repeat-herbicide treatment are hereafter called "single-herbicide". Again, spraying of native plants was avoided when possible so that only knapweed plants received herbicide.

In July 2003, final measurements of percent cover for all species was made, and stem densities of spotted knapweed, native forbs, native graminoids, non-knapweed exotic forbs, and exotic graminoids were estimated within the half-plots by counting stems in 20 randomly placed 20 x 5 cm frames. Density data was not distinguished by these groups in 2002, as field crews were not able to identify species of emerging seedlings. All native and exotic graminoids were simply counted as "graminoids" and all native and exotic forbs were counted as "non-knapweed forbs".

Seed bank

In autumn 2001 the seed bank was sampled in 15 permanent $2m^2$ plots at each site. Twelve randomly located soil cores (6 cm diameter by 10 cm depth) were extracted per plot. Organic matter, stolon and rhizome fragments were left in cores to account for all possible propagules.

Soil cores were wetted to field capacity and placed in cold storage (4 ºC) for 90 days to mimic a cold stratification period, and to maximize subsequent germination (Gross 1990). Seed bank species composition and seed density were determined from germination in a greenhouse. Samples were spread thinly (<0.5 cm) over potting soil in circular 16 cm diameter x 18 cm depth pots and placed in a greenhouse at the Plant Growth Center at Montana State University on February 3, 2002.

Thirteen control pots containing only potting soil were included to eliminate the possibility that the potting soil contained seeds. Pots were randomly located on greenhouse benches and moved bimonthly to account for heterogeneity in greenhouse conditions. Greenhouse temperatures varied between 10 °C and 24 °C during the night and 18 °C and 27 °C during the day. Photoperiod was supplemented to 14 hours using 1000 watt metal halide lamps. Pots were watered daily, and fertilized with liquid 20-10-20 (20N-4.4P-16.6K) Peters Peteliteliquid fertilizer (W.R. Grace Inc, Fogelsville, PA.) at the rate of 2.2 g per liter two times over nine months. Seedlings of all species were counted weekly, until they were identified to species, counted and removed. A final count was conducted on October 15, 2002. All the species that emerged were summed by species and plot.

The rationale for categories in Table 1 is as follows: *Native annual forb* species are small and ephemeral and thus provide little long-term competition against spotted knapweed. *Native perennial forbs* may augment the process of ecological restoration in disturbed communities (Bakker et al. 1996). Native graminoids are often the focus of grassland restoration activities, and are theoretically unaffected by broadleaf herbicides (Alexander and D'Antonio 2003; Bussan and Dyer 1999). The *exotic forb* and *exotic graminoid* species are a management concern in Glacier National, and may be an impediment to restoration efforts.

Results

Seed Bank

Soil cores collected at Many Glacier and Swift Current had 5,592 and 9,013 seedlings/m^2 emerge from pots comprised of 27 and 34 species respectively (Table 1). No seedlings emerged from any of the 13 control pots. Spotted knapweed propagules were found in 100 % of the sampled plots at both sites (Table 1). Spotted knapweed seeds accounted for 70 % of the total seed bank at Many Glacier, and 75% of the total at Swift Current (Figure 1). The seed bank contained 3,900 seeds/m^2 at Many Glacier, and 6,715 knapweed seeds/m^2 at Swift Current (Table 1; Figure 2).

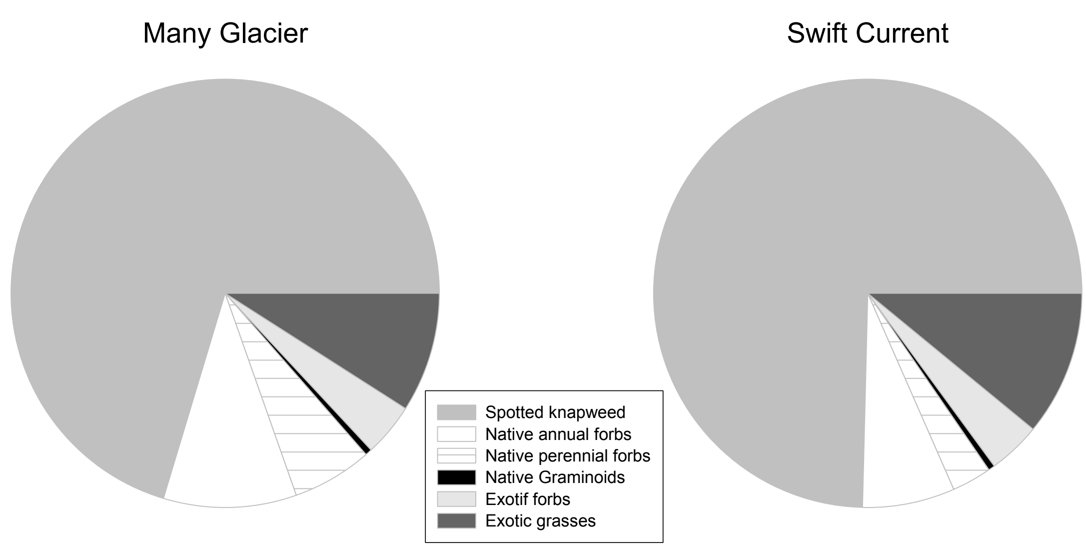

Figure 5. Percentage of the total seed bank per plant group.

Table 4. Summary of species seed/m2 derived from soil cores.

Species	Annual v. Perennial	Many Glacier	MG % Presence	Swift Current	SC % Presence
Centaurea maculosa	p	3900	100	6714	100
Native Annual Forb		533		655	
Androcase septentrionalis	a	185	60	533	100
Collinsia parviflora	a	104	67	20	40
Decurainia sophia	a	0	0	8	13
Draba nemorosa	a	244	0	89	47
Epilobium brachycarpum	a	0	0	6	13
Native Perennial Forb		352		226	
Achillea millefolium	p	75	87	20	47
Agoseris glauca	p	0	0	10	27
Antennaria sp.	p	0	0	14	20
Aster leavis	p	33	47	2	7
Campanula rotundfolia	p	106	53	53	60
Cerastium arvense	p	41	47	39	33
Epilobium glaberrium	p	2	7	0	0
Fragaria Virginiana	p	28	0	0	0
Galium boreal	p	0	0	4	13
Geum macrophyllum	p	8	27	8	20
Geum rriflorum	p	0	0	2	7
Heuchera cylindrica	p	0	0	12	20
Lupinus sericeus	p	4	73	2	7
Pensteman confurtus	p	2	7	2	7
Polygonum douglasii	p	0	0	2	7
Potentilla fruticosa	p	10	27	0	0
Potentilla grandulosa	p	2	7	12	20
Potentilla gracilis	p	41	53	28	47
Potentilla hippiana	p	0	0	14	27
Symphoriocarpus albus	p	0	0	4	13
Native Graminoid		18		43	
Bromus carinatus	p	0	0	12	27
Carex sp.	p	6	13	0	0
Elymus trachycaulus	p	0	0	18	33
Festuca idahoensis	p	2	7	0	27
Koeleria cristata	p	0	0	2	7
Stipa nelsonia	p	10	27	12	27
Exotic Forb		262		346	
Capsella bursa-pastoris	a	51	40	26	20
Medicago Lupulina	p	8	20	6	13
Rumex crispus	p	2	7	6	13
Taraxacum officianal	p	116	87	110	80
Thlaspi arvense	a	59	87	199	20
Cirsium sp.	p	26	7	0	0
Exotic Graminoid		527		1029	
Poa pratensis	p	277	93	576	100
Phleum pratense	p	250	100	452	100

At Swift Current, the sum of all other species was 2,299 propagules/m^2, which accounted for 25 % of the seed bank; at Many Glacier, all other species summed to 1,692 propagules/m^2, which was 30 % of the total seed bank (Table 1, Figures 1 & 2). After spotted knapweed, the second largest component of the seed bank at Swift Current was exotic graminoids (of which there were two grass species, *Phleum pratense* and *Poa pratensis*) which accounted for eleven percent of the seed bank. These grasses were found in 100 % of the sampled plots at both sites (Table 1). At Many Glacier, the second largest component of the seed back was annual native forbs, which accounted for 10 % of the seed bank.

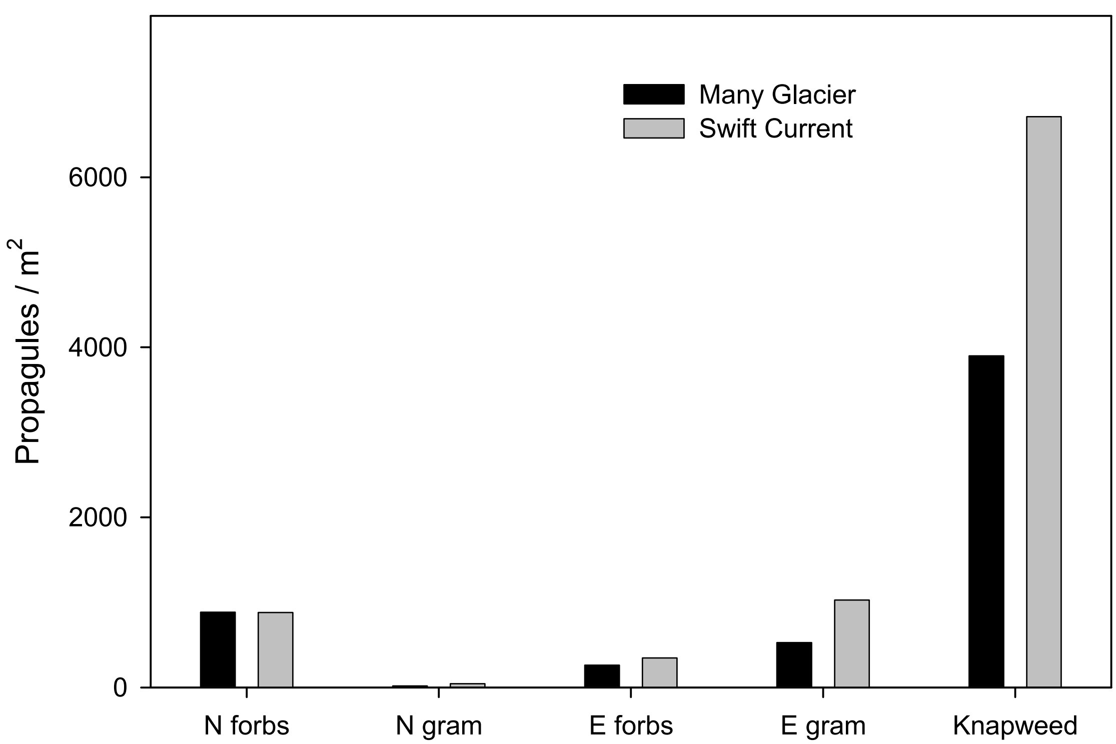

Figure 6. Number of viable propagules per m^2 at each site. N = native, E = exotic, and gram = graminoids.

Field Plots

In 2001, spotted knapweed stem density was 94 stems/m^2 at Many Glacier, and 120 stems/m^2 at Swift Current (Figure 3a+c). In 2002, nine months after treatments were applied, there were 1,351 stems/m^2 at Many Glacier, and 1,852 stems/m^2 at Swift Current (Figure 3a+c). In single-herbicide half-plots in 2003, knapweed stem densities were 987 stems/m^2 at Many Glacier, and 91 stems/m^2 at Swift Current (Figure 3a+c). Repeat-herbicide half-plots had 294 stems/m^2 at Many Glacier, and 38 stems/m^2 at Swift Current in 2003 (Figure 3a+c). At Many Glacier, there was a 78 % decrease in knapweed stems/ m^2 between 2002 and 2003 repeat-herbicide half-plots versus a 27 % decrease in single-herbicide half-plots. At Swift Current the decrease was 98 % in repeat-herbicide half-plots and 95 % in single-herbicide half-plots.

In 2001, spotted knapweed percent cover was 44 % (±1.7 SE) at Many Glacier, and 49 % (±1.2 SE) at Swift Current (Figure 3b+d). In 2002, knapweed percent cover was 13 % (±2.1 SE) at Many Glacier, and 15 % (±3.4 SE) at Swift Current (Figure 3b+d). In single-herbicide half-plots in 2003, knapweed percent cover was 35 % (± 4.6 SE) at Many Glacier, and 23 % (±3.1 SE) at Swift Current, and in repeat herbicide half-plots it was 6.5 % (±1.5 SE) at Many Glacier, and 2.3 % (±0.4 SE) at Swift Current (Figure 3b+d).

In 2001, exotic graminoid percent cover was 1.0 % (±0.19 SE) at Many Glacier, and 2.2 % (±0.46 SE) at Swift Current (Figure 4). In 2002, exotic graminoid percent cover was 0.9 % (±0.12 SE) at Many Glacier, and 2.2 % (±0.27 SE) at Swift Current (Figure 4). In single-herbicide half-plots in 2003,exotic graminoid percent cover was

0.7% (± 0.11 SE) at Many Glacier, and 4.5 % (±1.30 SE) at Swift Current, and in repeat herbicide half-plots it was 1.7 % (±0.30 SE) at Many Glacier, and 8.2 % (±1.40 SE) at Swift Current (Figure 4).

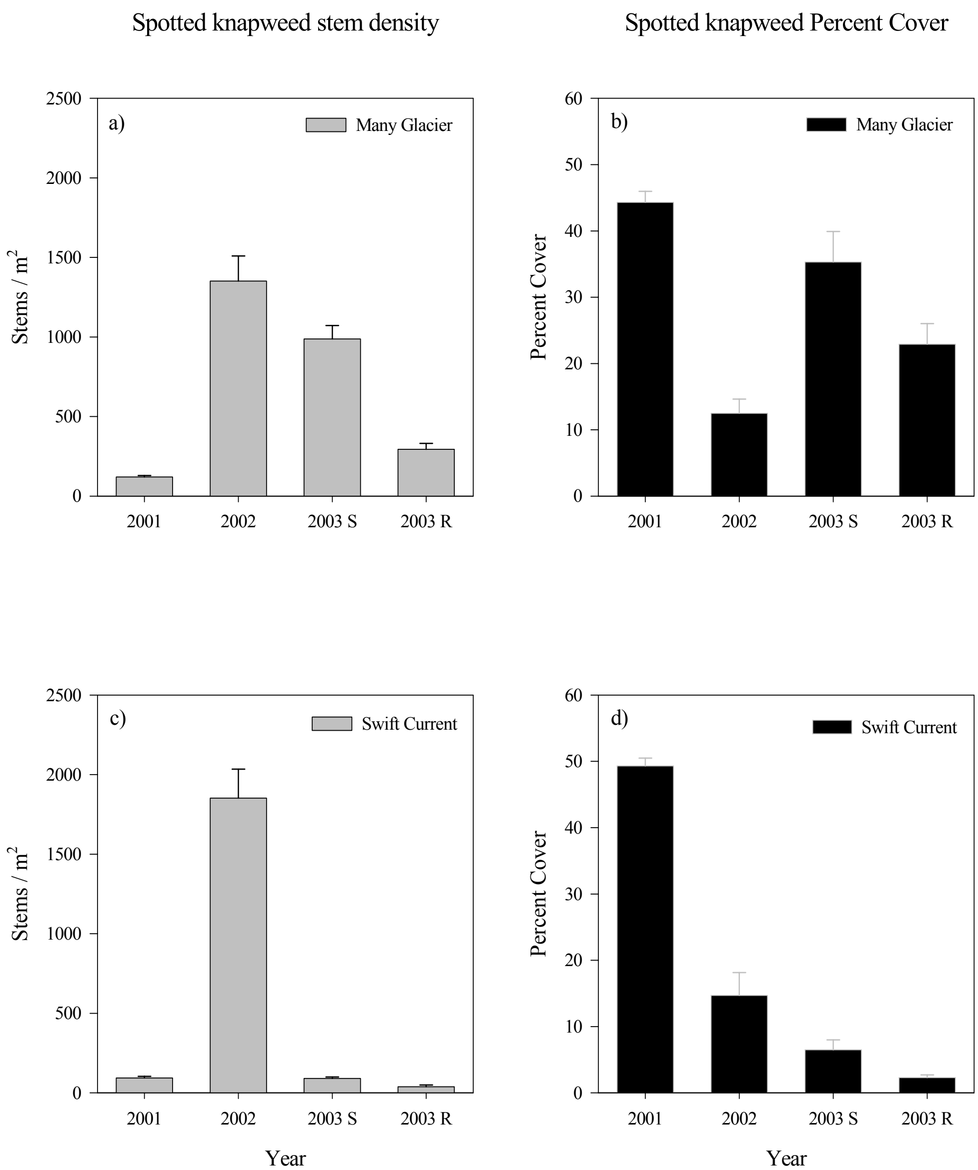

Figure 7. Mean spotted knapweed stem density and percent cover in field plots per year (± SE). S = single-herbicide, R = repeat-herbicide.

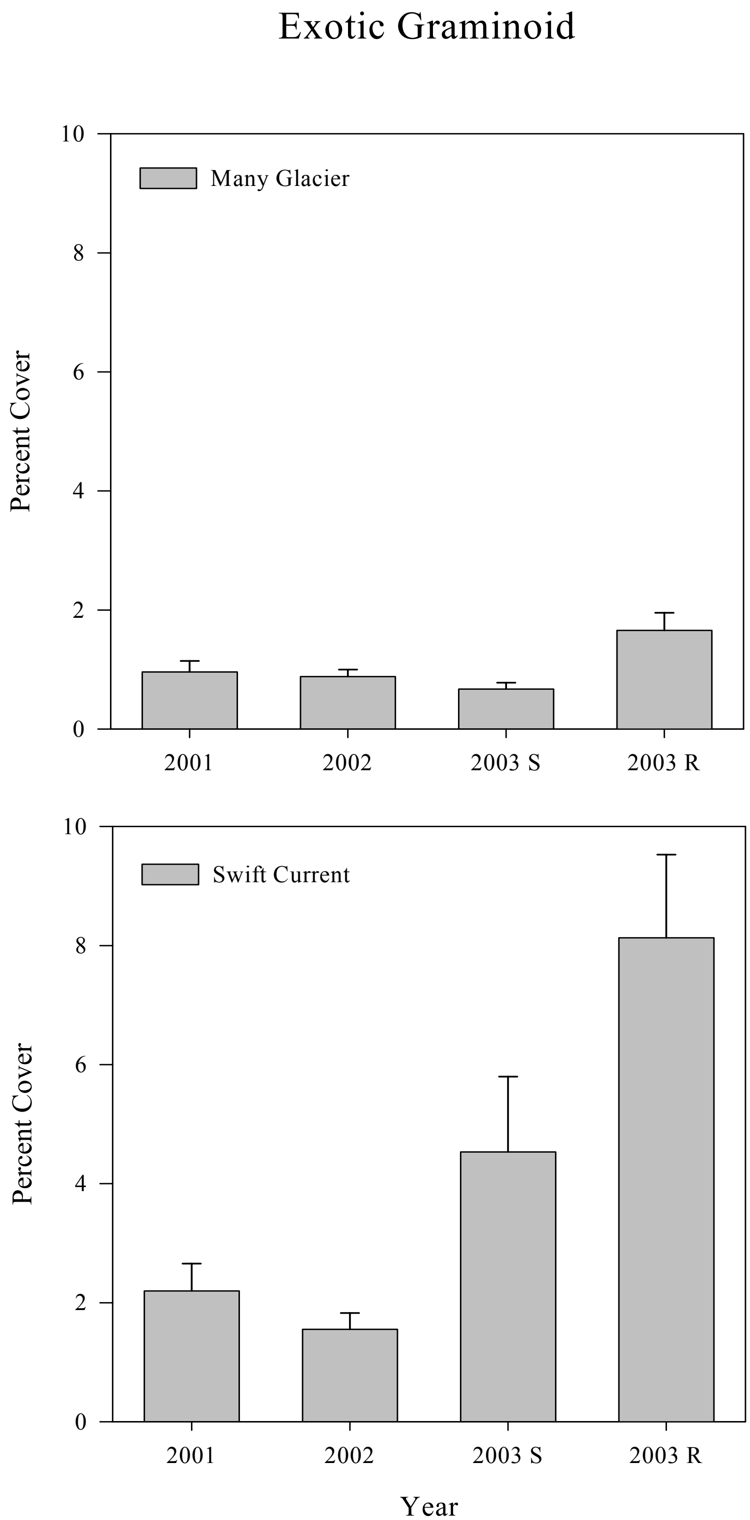

Figure 8. Mean percent cover of exotic graminoids in field plots (± SE). S = single-herbicide, R = repeat-herbicide.

Discussion

In 2001, spotted knapweed seed bank density was 34 and 43 % higher than the sum of all other species at Many Glacier and Swift Current, with 3900 and 6714 seeds/m^2 respectively. This finding is in the range observed by Jacobs and Sheley (1998) who found between 34 and 8,466 viable spotted knapweed seeds/m^2 in knapweed dominated mixed-grass prairies in Montana.

While we did not measure the seed bank in 2002 or 2003, field estimates of percent cover and stem density were used as a proxy for seed bank populations in those years. The rationale for this assessment distinguishes between several mechanisms that could have driven observed population dynamics. The possibilities are that post-herbicide density counts included knapweed individuals that: 1) were either missed or were not affected by herbicide applications, 2) germinated from seed dispersed into the site post-herbicide, and 3) germinated from seed stored in the seed bank. The population structure of spotted knapweed shifted between 2001 and 2002, from fewer larger individuals to many smaller seedlings, which makes the likely proportion of individuals missed by herbicide low. The number of seeds that dispersed into plots was probably low as well, as the pappus-bearing seed of spotted knapweed is not an effective long distance wind dispersal mechanism (Roché 1992). Ninety-two percent of the seeds of *Centaurea solstitialis* (Yellow star-thistle)–which has a similar seed weight and morphology to spotted knapweed–was found to be within 60 cm of the parent plant, with a maximum dispersal distance of 4.9 m over bare ground at gusts of 40km/ hr (Roché 1992). Spotted knapweed seedlings emerging from the seed bank provides the most likely explanation for observed stem densities in 2002 and 2003.

In 2002, stem densities increased at both sites from the previous year, corresponding with large decreases in overall knapweed cover. The reduced post-herbicide knapweed canopy allowed more light to reach the soil surface, and resulted in an increase in seed germination caused by increased light. A portion of spotted knapweed seeds are photodormant, and will not germinate in light with a low red to far-red ratio (Nolan and Upadhyaya 1988).

By 2003, decreased knapweed stem densities indicate a possible decline in knapweed seeds stored in the seed bank; however self-thinning between 2002 and 2003 may explain some of this decrease as knapweed stem densities were between 1350 (± 158 SE) stems/m2 at Many Glacier and 1850 (± 181 SE) at Swift Current in 2002. A trend toward a slow decline in knapweed stem densities was observed at Many Glacier in single-herbicide half-plots, with a potentially significant reduction in repeat-herbicide half-plots. At Swift Current, the decrease in stem densities was more substantial in both single and repeat-herbicide half-plots. These results indicate that within two-years, repeat-herbicide applications may effectively reduce the ability of knapweed to regenerate from the seed bank and compete with desirable species. This estimate is supported by Davis et al. (1993) who found that after terminating seed production, the number of viable spotted knapweed seeds in the soil declined exponentially over time, so that 75-90 % of the total knapweed seed bank was gone after two years.

However, the presence of desirable species in the seed bank was small. The population of native forbs in the seed bank was much larger than native graminoids at both sites, but most of those propagules were from small ephemeral annual species that would likely not create a community resistant to knapweed reinvasion. Native graminoids accounted for less than one percent of the total seed bank at both sites with 18 and 43 propagules/m^2 at Many Glacier and Swift Current respectively. Studies of seed bank grass densities in grassland communities of western North America range from 377 grasses/m^2 in a short-grass prairie in Kansas (Lippert and Hopkins 1950), to 2,697 and 4,743 grass seeds/m^2 in fescue and mixed-grass prairies of Alberta (Major and Pyott 1966). Thus, natural regeneration of graminoids from the seed bank may be limited at both sites.

The large presence of the exotic grasses *Phleum pretense* (timothy) and *Poa pratensis* (Kentucky bluegrass) in the seed bank creates a further challenge to restoring desirable species, as these exotics are strong competitors that displace native species (Tyser and Worley 1992). Propagule density of these grasses was especially high at Swift Current with more than twice as many propagules/m^2 than Many Glacier. Both grasses appeared to benefit from the repeat-herbicide application. While we did not measure exotic graminoid stem density in 2001 or 2002, we did see an increase in the percent cover of exotic graminoids in repeat-herbicide half-plots, especially at Swift Current, where the mean percent cover was almost double that of single-herbicide half-plots. Exotic grasses released from spotted knapweed competition may have a further advantage over native species by being resistant to the allopathic compound (-)-catechin (see Bais et al. 2003), which may remain in the soil after knapweed has been removed.

When broadleaf herbicides are used to control spotted knapweed, we may end up with an undesirable community dominated by exotic graminoids. In many rangeland systems this result would be favorable as species such as timothy are of much greater forage value than spotted knapweed. However, in nature preserves, where protection of biodiversity is the goal, replacing one invasive species with another (albeit less damaging) may be an unacceptable end result. Other treatments that effectively reduce these species may be needed to ensure that restoration can proceed on a desired course.

CONCLUSIONS

The first of my research objective was to determine whether “spot spray” herbicide application would effectively control spotted knapweed without negatively impacting native forbs. My second objective was to test the effects of tillage on plant community structure, with two main questions: 1) will tillage stimulate germination of dormant spotted knapweed seeds, reducing their presence in the seed bank? and 2) how will tillage affect desirable native species? My third objective was to determine whether seeding and planting treatments would increase the density and percent cover of desirable forbs and graminoids, and provide effective control of spotted knapweed through competition.

Additionally, I measured the seed bank of knapweed-invaded plots so that I could 1) estimate the species richness and abundance of the seed bank in my experimental plots, and 2) use aboveground estimates of species’ stem densities and percent cover to predict seed bank longevity of spotted knapweed.

The results of my first experiment show that spot spray herbicide application reduced spotted knapweed cover without significantly reducing existing native forbs in 2002 or 2003. Between 2001 and 2002, spot spray herbicide application reduced spotted knapweed percent cover by 79 and 96 % at Many Glacier and Swift Current respectively. However, reductions in knapweed cover were not sustained with a single-herbicide application at Many Glacier. By 2003, spotted knapweed percent cover was 23 % higher than pre-treatment levels, which was likely due to increased resources available to knapweed seedlings germinating from the seed bank.

Repeat-herbicide applications are needed to control spotted knapweed regeneration from the seed bank. However, I found that the time required to reduce these seeds varied by site. While percent cover and stem density were significantly reduced by repeat-herbicide application at both sites, Many Glacier still had relatively high seedling densities (300 stems/m^2 (± 40 SE)), where Swift Current did not (37 stems/ m^2 (± 12 SE)).

Establishment of desirable species by artificial seeding may be more successful with a greater reduction in the density of spotted knapweed individuals. However, my research shows that when aggressive exotic grasses such as *Phleum pratense* (Timothy) and *Poa pratensis* (Kentucky bluegrass) are present, they benefit from repeat-herbicide applications. Restoration efforts will likely be impeded by the proliferation of these species.

One of my objectives was to determine if tillage would stimulate germination of spotted knapweed thereby reducing its presence from the seed bank. The results of my first experiment show that tillage, when combined with herbicide application, does not provide more effective control of spotted knapweed than the use of herbicides alone. In fact, tillage plots had a higher percent cover of spotted knapweed versus no tillage plots in 2002 and 2003 single-herbicide half-plots, and a significantly lower percent cover of spotted knapweed and density of native forbs.

The seeding and planting treatments had marginal success overall. The only observed effects were an increase in the percent cover of native forbs at Swift Current, and higher densities of native graminoids in repeat-herbicide seeded plots at Many Glacier. These increases were not substantial enough to provide any reduction in spotted knapweed.

Given the method of seeding–broadcast application–seeds may not have had adequate seed-soil contact and or soil moisture to meet germination requirements. The seeding rate used for this study as recommend by the USGS (1991) was likely not high enough to overcome interspecific interference from the high number of emerging knapweed seedlings. Restoration of native grasslands invaded by spotted knapweed may not be feasible until knapweed is effectively reduced in aboveground biomass and belowground seed bank, by mechanical, cultural or chemical control.

The seed banks of Many Glacier and Swift Current contained 5,592 and 9,013 seedlings/m^2 comprised of 27 and 34 species respectively. Spotted knapweed seed bank density was 34 and 43 % higher than the sum of all other species at Many Glacier and Swift Current, with 3900 and 6714 seeds/m^2 respectively. Downward trends in knapweed stems/m^2 indicate that within two-years, repeat-herbicide applications may effectively reduce the ability of knapweed to regenerate from the seed bank and compete with desirable species. However, the high seed bank density of exotic grasses appeared to benefit from the repeat-herbicide application which creates a further challenge to restoring desirable species.

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