Relationship between spotted knapweed and indigenous plant assemblages and prediction of plant community response to picloram
by Susan A Kedzie-Webb

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Land Resources and Environmental Sciences
Montana State University
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Abstract:
Spotted knapweed (Centaurea maculosa Lam.) is a perennial forb native to central Europe and east to central Russia, Caucasia and western Siberia. This weed is rapidly invading western rangelands of the United States and Canada. Non-indigenous weed invasions are suspected to degrade ecosystem function, displace indigenous species, and reduce biodiversity. The introduction and spread of spotted knapweed has often been associated with the modification of indigenous plant communities. However, few studies have quantified the relationship between indigenous species diversity and spotted knapweed. In addition, weed management decisions must be based on models that provide an understanding of the plant community as a result of weed management.

The objectives of this study were to: 1) characterize the functional relationship between plant community composition and spotted knapweed within a Festuca idahoensis-Agropyron spicatum habitat type; 2) develop models that predict the post-treatment plant community composition based on the pre-treatment plant community after a picloram treatment; 3) initiate development of a model for using easily collected field data to predict pre- and post-treatment biomass; and 4) enhance the use of predictions to improve weed management decisions.

Density, cover, and biomass of all species were collected along a gradient of spotted knapweed cover. The pre-management plant community composition was sampled in the summer of 1996, prior to a fall treatment of picloram, and again in the summer of 1998. Density,cover, and biomass were analyzed using step-down regression procedures.

This study showed that indigenous perennial grasses, indigenous species richness and indigenous species diversity were inversely related to spotted knapweed suggesting that spotted knapweed may invade areas of low diversity and grass abundance or may displace native indigenous plants. In this study, no relationship between spotted knapweed and forb was detected.

It may be feasible to use pre-management plant community data to predict postmanagement plant community response for spotted knapweed-infested rangeland using picloram. The models predicting post-management indigenous perennial grass, Idaho fescue, and indigenous species richness were based on density. The best predictive models for assessing post-management forbs and indigenous species richness were based on cover and biomass, respectively. The R2 values for these models ranged from 0.40 to 0.69.

We attempted to use easily collected pre-treatment data (i.e., spotted knapweed cover) to predict pre- and post-treatment grass biomass. Integration of these models indicated that there would be a decrease in post-treatment grass biomass at spotted knapweed cover below 35%. Above 35% spotted knapweed cover, regressions predicted greater post-treatment grass biomass than the pre-treatment biomass. Furthermore, we believe it may be possible to identify the cumulative predictive biomass gain (after treatment) by developing a biomass optimization model for each year of herbicide control. This would

provide land managers with a method to assess the economic feasibility of herbicide control prior to imposing weed management.

RELATIONSHIP BETWEEN SPOTTED KNAPWEED AND INDIGENOUS PLANT ASSEMBLAGES AND PREDICTION OF PLANT COMMUNITY RESPONSE TO PICLORAM

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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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ABSTRACT

Spotted knapweed (*Centaurea maculosa* Lam.) is a perennial forb native to central Europe and east to central Russia, Caucasia and western Siberia. This weed is rapidly invading western rangelands of the United States and Canada. Non-indigenous weed invasions are suspected to degrade ecosystem function, displace indigenous species, and reduce biodiversity. The introduction and spread of spotted knapweed has often been associated with the modification of indigenous plant communities. However, few studies have quantified the relationship between indigenous species diversity and spotted knapweed. In addition, weed management decisions must be based on models that provide an understanding of the plant community as a result of weed management.

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Density, cover, and biomass of all species were collected along a gradient of spotted knapweed cover. The pre-management plant community composition was sampled in the summer of 1996, prior to a fall treatment of picloram, and again in the summer of 1998. Density, cover, and biomass were analyzed using step-down regression procedures.

This study showed that indigenous perennial grasses, indigenous species richness and indigenous species diversity were inversely related to spotted knapweed suggesting that spotted knapweed may invade areas of low diversity and grass abundance or may displace native indigenous plants. In this study, no relationship between spotted knapweed and forb was detected.

It may be feasible to use pre-management plant community data to predict post-management plant community response for spotted knapweed-infested rangeland using picloram. The models predicting post-management indigenous perennial grass, Idaho fescue, and indigenous species richness were based on density. The best predictive models for assessing post-management forbs and indigenous species richness were based on cover and biomass, respectively. The R^2 values for these models ranged from 0.40 to 0.69.

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CHAPTER 1

LITERATURE REVIEW

Biology, Distribution, and Spread

Spotted knapweed (*Centaurea maculosa* Lam.) is a perennial forb indigenous to central Europe and east to central Russia, Caucasia and western Siberia (Rees et al. 1996). This weed is rapidly invading western rangelands of the United States and Canada (Watson and Renny 1974, Strang et al. 1979, Harris and Cranston 1979). Spotted knapweed forms dense infestations under a variety of environmental conditions, but appears to be adapted to dry, well-drained sites and disturbed areas (Roche' and Roche' 1993). In Europe, spotted knapweed is particularly aggressive on forest steppe Mollisols and mesic Aridisols, but will establish on drier sites when supplemented by summer precipitation. It does not successfully compete with vigorous grasses on moist sites. Spotted knapweed has been observed at elevations ranging from 578 to 3040 m and in annual precipitation zones ranging from 200 to 2000 mm (Lacey et al. 1995).

Spotted knapweed was first recorded in Victoria, B. C. in 1883 (Groh 1944). This weed is suspected to have been introduced through discarded ship ballast and as a contaminant in alfalfa (*Medicago sativa* L.) (Roche' and Talbot 1986). Contaminated domestic alfalfa seeds and hay apparently contributed to spotted knapweed's spread prior to its identification as a serious problem. Initial infestations of spotted knapweed were limited to the San Juan Islands, Washington, until 1920. By the 1960's, this weed had spread to 20 counties in the Pacific Northwest and to 48 counties by 1980. Its current

distribution includes 326 counties in the western United States, including every county in Washington, Idaho, Montana and Wyoming (Sheley et al. 1998). In Montana, spotted knapweed infests approximately 2.2 million hectares and is spreading at a rate of 27% per year (Chicoine et al. 1985, Lacey 1989).

Identification

Spotted knapweed is a deeply tap-rooted member of the Asteraceae family. Basal rosette leaves are borne on short pedicels and grow up to 20 cm long and 5 cm wide. Rosettes are deeply divided into lobes on both sides of the center vein. Lobes are oblong and broadest above the middle of the leaf. Flowering stems stand 2 to 12 dm tall and branch on the upper half of the stem. Stem leaves are alternate, sessile, have few lobes, or are linear and entire, and are reduced toward the apex. Flowerheads are ovate to oblong, 6 mm wide and 12 mm long, and are solitary or borne in clusters of two or three at branch ends. Flowers are purple to pink, rarely white, producing 25 to 35 flowers per head, with black bract tips and longitudinal veins (Whitson et al. 1996).

Ecological Impacts of Exotic Weeds on Indigenous Plant Communities

Non-indigenous weed invasions are suspected to degrade ecosystem function, displace indigenous species, and reduce biodiversity (Randall 1996). Invasive species may alter ecosystem function by threatening proper nutrient cycling, fire regimes, hydrologic cycles and energy flow (Vitousek 1986, Vitousek et al. 1987, Vitousek and Walker 1989, Whisenant 1990). For example, downy brome (*Bromus tectorum* L.) is a winter annual that alters ecosystem processes. Infestations occur on millions of hectares in the Great Basin where cheatgrass has increased fire frequency from once every 60 to 110 years to

once every 3 to 5 years (Whisenant 1990). Indigenous shrubs of this region, which are poorly adapted to frequent fires, have been reduced or eliminated in abundance and importance (Mack 1981). In another example, saltcedar (*Tamarix chinensis* Lour.; *T. ramossisima* Ledeb.; *T. pentandra* Pallas), which invades wetlands and riparian areas, lowers water tables and surface water required by indigenous plants and animals (Brotherson and Field 1987, Neill 1983). Changes in vegetation composition may alter the shape, carrying capacity, and flooding cycle of watercourses (Blackburn et al. 1982). Leafy spurge (*Euphorbia esula* L.) is a non-indigenous herb that invades the northern grasslands of the Great Plains and Rocky Mountains where it displaces indigenous forbs and grasses (Belcher and Wilson 1989). Yellow starthistle, a non-indigenous winter annual, has spread exponentially since the late 1950's (Maddox et al.1985, Thomsen et al. 1993). Many native plant communities have been severely altered or degraded by the introduction of yellow starthistle (Randall 1995). Displacement of indigenous species by non-indigenous weeds is generally associated with declines in biodiversity (Thompson et al. 1987, Webb and Kaunzinger 1993). However, this relationship has rarely been quantified.

The introduction and spread of spotted knapweed has often been associated with the modification of indigenous plant communities. Weed scientists and land managers repeatedly use this argument to justify their management actions. However, little information is currently available that addresses the impacts of spotted knapweed on the ecosystem or environment. Few studies have quantified the functional relationship between indigenous species diversity and spotted knapweed. Tyser and Key (1988)

showed declines in species richness and frequency in fescue grasslands as a result of spotted knapweed establishment. On sites with the highest pre-spray spotted knapweed cover, herbicide treatments of spotted knapweed tended to increase species richness (Rice and Toney 1997). Sheley and Jacobs (1997) found that bluebunch wheatgrass (*Agropyron spicatum* Pursh.) root:shoot ratio increased when spotted knapweed density was reduced by 90%. Taken together, these results suggest spotted knapweed may be capable of displacing desirable indigenous vegetation, thereby threatening plant diversity and altering ecosystem function (e.g., hydrologic cycles and energy flow). Stronger evidence is needed to confirm these suspected impacts and to contribute to our knowledge about the ecological impacts of spotted knapweed on indigenous plant communities. Without a thorough understanding of these impacts, management efforts remain largely arbitrary and lack an ecological basis from which to make wise management decisions.

When indigenous perennial grasses are displaced by non-indigenous plants, detrimental changes to soil and water resources may occur. In a single, cursory study, Lacey et al. (1989) suggest that surface run-off and sediment yield were increased on spotted knapweed-dominated sites compared to bunchgrass-dominated sites. Furthermore, on unclipped bunchgrass sites, water infiltration rates were higher and surface run-off were lower than on spotted knapweed-dominated sites (Lacey et al. 1989).

Spotted knapweed reduces wildlife forage, modifies wildlife habitat, and alters animal-plant interactions (Thompson 1996). Spotted knapweed invasions have reduced available winter forage for elk (*Cervus elaphus*) by as much as 50 to 90% in western Montana (Thompson 1996). Elk use was 98% lower on spotted knapweed infested range

than on bunchgrass dominated range (Hakim 1979).

A major economic impact associated with spotted knapweed is the loss of livestock forage. Declines in bluebunch wheatgrass biomass have been correlated with increasing spotted knapweed biomass (Watson and Renny 1974). Spotted knapweed alone currently costs the Montana livestock industry an estimated $11 million in direct costs. If spotted knapweed continues to spread to its potential range, it could cost the livestock industry over $150 million annually (Bucher 1984).

Importance of Biological Diversity

Biological diversity is an important factor in maintaining proper ecosystem function and stability (Ehrlich and Ehrlich 1981, Wilson 1992). Diverse communities are more productive than species-poor communities because they use limited and available resources more completely. In developing grassland ecosystems, plant productivity and resource use were significantly higher at sites with greater plant diversity (Tilman et al.1996). Tilman (1996) demonstrated that species-rich plots had lower proportional declines in community biomass during drought than did species-poor plots. He provided some evidence that species-rich communities may recuperate after stress or perturbation more successfully (Tilman 1996). Invasibility of native grasslands appears to be negatively associated with species diversity because maximum niche occupation preempts resource use from potential invaders (Tilman 1997).

The Shannon-Weaver diversity index was used to calculate indigenous species diversity for regression analysis. The Shannon-Weaver index is defined as:

$$H' = - \sum (p_i)(\log_2 p_i)$$

where H' is the index number, $\sum$ is a summation symbol, p_i is the proportion of all individuals in the sample which belong to species i, and $\log_2 p_i$ is the log to base 2 of that proportion (Shannon and Weaver 1949).

H' has been regarded as a measure of "uncertainty." The greater a population's diversity, the more "uncertain" we are about the identity of the species (Barbour et al. 1980).

Spotted Knapweed Control Measures

Biological control

In North America, spotted knapweed's success may be attributed to a lack of natural enemies that regulate and limit its population. Classical biological control employs pathogens, insects, and nematodes from a weed's native ecosystem to damage the host root, shoot leaf, or flower. This can result in reduced seed production or lowered competitive ability (Jacobs et al. 1996). *Urophora affinis* Frauenfeld was the first biological control agent used to reduce seed production of spotted knapweed in the United States and Canada (Harris 1980). Seed head larvae feed on phloem tissue which actively drains the plant's energy stores and may reduce seed production up to 50% (Story et al. 1989). Harris (1980) showed seed head flies have been ineffective in reducing spotted knapweed populations. Larvae of the moth *Metznèria paucipundctella* Zeller may reduce seed production by about 20% after feeding on the flowers and seeds of spotted knapweed (Story et al. 1989). Root feeding insects used to suppress knapweed include a root moth (*Agapeta zoegana* L.) and a root weevil *(Cyphocleonus achates* Frahr.) In addition to reducing root storage capacity, and nutrient and water uptake, these insects enhance susceptibility to pathogens. *Sclerotinia sclerotiorum* (Lib) de Bary is a common

soil fungus native to North America that may cause wilt and death in knapweed and shift the competitive balance to desired grass species by reducing spotted knapweed density by 68 to 80% (Ford 1989, Jacobs et al. 1996). Although biological control agents are not often directly lethal to the weed, they may increase the weed's susceptibility to secondary disease, reduce seed production, and may be combined with other weed control methods (Cuda et al. 1989).

Chemical control

Long-term control of spotted knapweed is difficult to attain. In many cases, rangeland managers use repeated applications of persistent herbicides, such as picloram (4-amino-3,5,6 trichloro-2-pyridinecarboxylic acid) to control spotted knapweed. Picloram applied at a rate of 0.28 kg/ha provides nearly 100% control of spotted knapweed for 3 to 5 years (Davis 1990). After picloram dissipates, spotted knapweed re-invades from the seedbank (Davis et al. 1993). According to Griffith and Lacey (1991), long-term chemical control is cost-effective only on highly productive rangeland with a residual grass understory. Currently, most herbicide control programs for spotted knapweed are applied with little consideration of the residual (pre-treatment) plant species or the economic feasibility of the management strategy.

Cultural control

Burning: Single, low-intensity fires do not effectively control spotted knapweed because they lack the intense heat required to prevent re-sprouting from the root crown or reestablishment from the seed bank (Renny and Hughes 1969). Since knapweed increased six-fold two years after controlled burning, it is suspected that a single fire may provide

disturbance that favors spotted knapweed (S Arno, unpublished). However, Lacey et al. (1992) indicated that herbicide efficacy on spotted knapweed may increase after a prescribed burn. Where picloram had been applied to control spotted knapweed, residual grass density and cover was greater on plots that were previously burned than on unburned plots (Sheley and Roche' 1982).

Cultivation: In a study conducted by Spears et al. (1980), spotted knapweed seedlings did not emerge when seeds were planted 5 cm below the soil surface. Velagala (1996) found that a single cultivation to 20 cm increased spotted knapweed density over the uncultivated control, but reduced biomass one year following treatment. After plowing, infested areas should be reseeded with competitive grass and legume species to inhibit re-infestation (Harris and Cranston 1979).

Fertilization: Since spotted knapweed effectively captures nutrients before neighboring plants, nitrogen fertilizer treatments tend to enhance diffuse knapweed populations (Popova 1960, Story et al. 1989). Sheley and Jacobs (1997) reported that picloram plus fertilizer did not interact to affect either spotted knapweed density or grass yields on sites in western Montana.

Grazing: Nutrient content of spotted knapweed is adequate to meet livestock needs during spring and early summer when the stems are succulent and actively growing (Kelsey and Mihalovich 1987). Recently, Olson et al. (1997) found that areas repeatedly grazed by sheep had lower densities of seedlings, rosettes, and mature spotted knapweed plants than ungrazed areas. Number of spotted knapweed seeds in the seed bank was reduced after 3 years of intensive sheep grazing.

Hand-pulling: Sustained, diligent hand-pulling can control spotted knapweed populations (Lacey et al. 1995). Entire plants must be removed before seed production each year because regrowth occurs from both the crown and seedbank. Hand-pulling is best conducted under moist soil conditions when complete removal of the crown is possible. Flowering plants should be burned in a hot fire.

Mowing: Long-term effects of mowing on spotted knapweed populations are unknown. A single mowing at the bud stage reduced the number of seed-producing stems from 34 per m^2 (control) to below 8 per m^2 (Watson and Renny 1974). Watson and Renny (1974) also found that mowing at the flowering stage or both bud and flowering stage reduced seed germination. Mowing at both the bud and flower stage did not have an additive effect. In a greenhouse study by Kennet et al. (1992), some spotted knapweed plants produced flowers even after monthly clippings from June to September, suggesting the response of plants to mowing varies with environmental factors.

Revegetation: Where residual plant species are absent, herbicides (Davis et al. 1993, Griffith and Lacey 1991), biological control agents (Story et al. 1991, Cuda et al. 1989), or sheep grazing (Cox 1989) do not provide long-term, sustainable control of spotted knapweed because desirable plant species are presumably not present to re-occupy niches opened by the control method (James 1992, Sheley et al. 1996). Establishing competitive plants is critical for successful management and restoration of desirable plant communities (Sheley et al. 1996). Revegetation with aggressive species has been shown to inhibit the reinvasion of knapweeds (Hubbard 1975, Larson and McInnis 1989, Borman et al. 1991).

Revegetation usually requires late-fall disking and application of non-selective herbicides such as glyphosate (n-phosphomethyl glycine) after weeds emerge (Sheley and Larson 1996). Desirable grasses are then seeded immediately following site preparation. Germination and emergence of grass species and spotted knapweed occurs the following spring. With adequate precipitation, both spotted knapweed and grass seedlings survive. If grass seedlings survive until mid-summer, the area maybe mowed or a reduced rate of 2,4-D may be applied to weaken spotted knapweed. Seedling establishment is the most vulnerable stage of the rehabilitation process in arid and semi-arid regions (Call and Roundy 1991). The failure of desirable vegetation to thrive largely results from weed competition during initial establishment (Borman et al. 1991, James 1992). Grass seedling establishment can be enhanced by increasing seeding rates (Velagala et al. 1997).

To improve the cost-effectiveness of revegetating on rangeland, land managers need to reduce the number of entries on a management unit. Herbicide application, tillage, and seeding can be accomplished simultaneously in a single-pass system. On spotted knapweed/cheatgrass infested-rangeland, Jacobs et al. (1998) recommend applying ½ pint of picloram in conjunction with a seeding of 'Luna' pubescent wheatgrass [*Thinopyrum intermedium* (Host) Barkworth & D. R. Dewey] at 16 lbs/acre using a no-till drill. Picloram provides 3 to 5 years of spotted knapweed control while the wheatgrass aggressively competes with cheatgrass during the establishment period.

Predicting Plant Community Response

Effective rangeland weed management requires the ability to predict plant community responses to natural and imposed conditions. Predictive capabilities allow

ecological and economic assessment of various strategies based on land management objectives. Without predictive capabilities, the decision to impose a particular strategy is either based on prior experience or is arbitrary. Land management decisions must be based on models that provide an understanding of the plant community after implementation. Rangeland managers are searching for useful models on which to base their decisions (Archer 1989, Schlatterer 1989, Laycock 1991).

Keane (1987) developed a model using a successional classification system that predicts coverage of plant species based on treatment and pre-disturbance plant composition. However, successional pathway models are inappropriate for ecosystems dominated by non-indigenous species that alter succession.

Population models organize weed demographic information, identify the critical processes and mechanisms that regulate dynamics, and can be used to optimize control strategies by predicting economic threshold levels of weed infestations (Maxwell et al. 1988, Jacobs and Sheley 1998, Paterson et al. 1997). The economic injury level (EIL) is defined as the pest density at which the value of the crop loss is equal to the cost of control. The economic threshold, set below the EIL, signals the need for pest control to keep the population from reaching the EIL (Stern et al. 1959, Wagner et al. 1989). This threshold approach has been used in agroecosystems for a wide range of important crops. Knezevic et al. (1994) showed redroot pigweed (*Amaranthus retroflexus* L.) did not reduce corn production when weed emergence occurred after the corn's 7-leaf stage. Recently, Maxwell et al. (1994) developed bioeconomic models to optimize wild oat (*Avena fatua* L.) management in barley for three sites in Montana. The thresholds

concept results in improved decision-making and land management practices in cropping systems, but has not been applied in rangeland systems.

Successional management shifts the focus from simply controlling weeds to developing healthy, weed-resistant plant communities. Sheley et al. (1996) present a conceptual, ecologically-based model that applies successional theory to developing and implementing sustainable rangeland weed management. In this model, they propose using site availability, differential species availability, and differential species performance to initiate, alter, and direct succession toward a desired plant community (Pickett 1987). This management approach recognizes that the post-management plant community is influenced by both the weed management system and the pre-management plant community. To date, this model has not been widely adopted.

Few studies have focused on predicting economic thresholds for rangeland weed management. Bastin et al. (1995) determined the economic thresholds for sagebrush (*Artemisia tridentata* Nutt.) control within a narrow range of abundance levels (12-24%). Carpenter et al. (1991) investigated the economic feasibility of broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt. and Rusby)) control with picloram at three weed densities. In this study, economic losses to ranchers intensified as snakeweed densities increased and carrying capacity decreased. The economic threshold of fringed sagebrush (*Artemisia frigida* Willd.) is the density at which forage yield is reduced by about 290 kg ha $^{-1}$. Above this density, it becomes economically feasible to use 2,4-D at 1.5 kg ha^{-1} to control fringed sagebrush (Peat and Bowes 1994).

Future modeling may prove useful if it can predict the effects of management and

the psot-management plant community based on the pre-management community. The more accurate the predictions, the greater our success in developing integrated weed management systems (Schreiber 1982). Coupled with the concept of thresholds, predictions of plant communities response to regulation may enhance management by providing managers tools on which to make thoughtful decisions.

Objectives

The overall objective of this study was to determine the potential to predict the post-management plant community based on the pre-treatment community and a herbicide treatment. Specific objectives were to: 1) to characterize the functional relationship between plant community composition and spotted knapweed within an Idaho fescue-bluebunch wheatgrass (*Festuca idahoensis-Agropyron spicatum*) (Mueggler and Stewart 1980) habitat type; 2) to develop models that predict the post-treatment plant community composition based on the pre-treatment plant community after a picloram treatment; 3) initiate the development of a method for using easily collected field data to predict pre- and post-treatment biomass; and 4) enhance the use of predictions to improve weed management decisions. This study was conducted using picloram, however other management techniques (e.g., grazing, fire, etc.) could be used in a similar fashion to predict plant community response based on the initial plant community and the treatment. This research is necessary to enhance decision-making abilities and develop management strategies that result in desired plant communities.

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CHAPTER 2

RELATIONSHIPS BETWEEN SPOTTED KNAPWEED AND INDIGENOUS PLANT ASSEMBLAGES

Introduction

Ecological impacts attributed to non-indigenous weed invasions include displacement of indigenous species, degradation of ecosystem function, and declines in biodiversity (Vitousek 1986, Randall 1996). Invasive species with the potential to alter nutrient cycles, fire regimes, hydrologic cycles, and energy flow pose serious threats to ecosystem structure and function (Vitousek 1986, Vitousek et al. 1987, Vitousek and Walker 1989, Whisenant 1990). For example, cheatgrass (*Bromus tectorum* L.) is a winter annual that alters ecosystem processes. Cheatgrass dominates millions of hectares in the Great Basin and has increased fire frequency from once every 60 to 110 years to once every 3 to 5 years (Mack 1981, Whisenant 1990). Indigenous shrubs of the Great Basin, which are not adapted to frequent fires, have been reduced in abundance or eliminated. Billings (1990) suggested that cheatgrass may reduce the biotic and genetic diversity of *Artemisia*-dominated biomes by eliminating plant and animal species. This invasion has probably altered entire ecosystems. In a single, cursory study, spotted knapweed (*Centaurea maculosa* Lam.) increased erosion by 56% and sediment yield by 192% when compared to bluebunch wheatgrass-dominated rangeland under simulated rain events (Lacey et al. 1989).

Indigenous plant populations are thought to decline following invasion by non-

indigenous weeds. For example, leafy spurge (*Euphorbia esula* L.) is a perennial weed that invades northern grasslands and displaces indigenous vegetation (Belcher and Wilson 1989). Similarily, Nuzzo (1993) reported that the cover of the indigenous ephemeral, toothwort [*Cardamina concatenata* (Michx.) Sw.], declined from an average of 79 to 31% following invasion by the non-indigenous garlic mustard [*Alliaria petiolata* (Bieb) Cavara and Grande]. Studies that address displacement of indigenous by non-indigenous species often allude to subsequent declines in biodiversity (Thompson et al. 1987, Webb and Kaunzinger 1993). However, few studies have quantified the functional relationship between indigenous plant assemblages and non-indigenous weed invasions.

The objective of this study was to characterize the functional relationship between plant community composition and spotted knapweed within a *Festuca idahoensis-Agropyron spicatum* habitat type (Mueggler and Stewart 1980). I hypothesized that indigenous species, indigenous species richness, and indigenous species diversity are negatively related to spotted knapweed. This hypothesis does not imply a causal relationship. Knowledge of these relationships is essential to predict plant community changes resulting from weed invasions.

Materials and Methods

This study was conducted on two sites within a *Festuca idahoensis-Agropyron spicatum* habitat type (Mueggler and Stewart 1980). Site 1 was located in Story Hills (45° 42'N, 111° 01'W), four km northeast of Bozeman, MT. Elevation at this site is 1478 m. Average annual precipitation is 432 mm. Soil at this site is a clayey-skeletal, mixed Typic Argiborolls. Site 2 was located at Beartrap Canyon, about 45 km east of Norris, MT (45°

36' N, 111° 34' W). Elevation at this site is 788 m with an average annual precipitation of 305 mm. Soil at Site 2 is a loamy-skeletal, mixed Aridic Argiborolls.

Transects radiated from dense spotted knapweed in the center of each patch, to an area of low or no spotted knapweed occurrence on the outside of a patch. At each site, all transects radiated from the center of the same patch. Five transects, each 20 m long, were established at both sites. The plant community at each transect origin was dominated by spotted knapweed with few or no residual indigenous species in the understory. Transects ended in areas dominated by Idaho fescue with a diverse understory. Twenty permanent plots (20 x 50 cm, spacing between plots ranged from ½ to 2 m) were placed along this gradient (at each transect) of spotted knapweed cover from 0 to 100% (about every 5%). Density (juveniles plus adults) and cover of all species were sampled in each plot.

Thirty temporary plots (20 x 50 cm) were also established along the spotted knapweed gradient to sample biomass, seed bank, and soil at each site. Biomass was sampled for all species by clipping plants to ground level at peak standing crop (August 1996). Biomass and soil samples were dried at 60°C to a constant weight and weighed. The upper 65 mm of soil seed bank was sampled using a tulip bulb planter with a diameter of 80 mm. Seed bank samples were dried at 60°C to constant weights and weighed. Two-hundred cm^3 sub-samples of mixed seed bank were sieved to separate seeds from soil and debris. Seeds were counted and identified. Soil samples were collected along the transect to determine whether the spotted knapweed gradient was related to differences in soil nutrients. Soil samples were tested for available nitrogen, phosphorous, and potassium

using a standardized extraction process (Page and Klute 1982). There were no differences in available soil nutrients, therefore the data are not presented.

To test whether the spotted knapweed invasion was a function of seed availability only, the largest adult knapweed plant adjacent to each permanent plot (one plant/plot) was harvested and dissected at the root-crown and aged by counting annual growth rings (Boggs and Story 1987). This procedure was used to test the assumption that invasion by spotted knapweed was associated with the availability of seeds, rather than differences in soil and vegetation characteristics along the transects.

Data Analysis

Data were compiled into tables showing the number of transects (maximum of 5) along the spotted knapweed gradient in which individual species were present for each site to characterize their presence and distribution . Plant density, cover, and biomass data were analyzed using a multi-step process. Covariance analysis was conducted to test for sample independence within transects. Analysis indicated independence among all plots, therefore, a step-down linear regression procedure was used to identify the best model (Neter et al. 1985). A combination of P-value, model simplicity, and R^2 values were used to identify the best model for each step-down procedure. Scatter-plots of the residuals versus the standardized predicted values were used to evaluate heterogeneity of variance for each model. Data transformations were conducted where necessary on predicted variables using square-root transformations. Inverse, quadratic, and log transformations were tested, but did not improve the models. Collinearity was evaluated using a SAS® Tolerance procedure to test for relatedness of predictors (SAS 1990). Collinearity was

not a problem in this analysis. Linear regression models were fit using density, cover, and biomass of Idaho fescue, indigenous perennial grass, indigenous forbs, indigenous species richness, and indigenous species diversity as predicted variables. The regressor variables used were density, cover, and biomass of spotted knapweed. For example, spotted knapweed density, cover, and biomass were used to predict Idaho fescue density, cover, and biomass, respectively. Based upon the design of this observational study, regressions should not be interpreted to imply causality. Diversity was estimated using Shannon-Weaver's diversity index (Shannon and Weaver 1949). Means and standard deviations were calculated for soil seed bank samples. Spotted knapweed age and density were plotted against the distance from the intact plant community.

Results

Presence and Distribution

Eleven indigenous grasses, two non-indigenous grasses, 11 indigenous forbs, and four non-indigenous forbs were present at Site 1 (Table 1). Of the indigenous grasses, bluebunch wheatgrass was found in two or more transects along the gradient. All other indigenous grasses were limited in presence after 45% spotted knapweed cover at this site. Both non-indigenous grasses, Japanese brome (*Bromus japonicus* Thunb.) and Kentucky bluegrass (*Poa pratensis* L.), were present along the gradient. The most abundant indigenous forbs included hairy goldenaster [*Chrysopsis villosa* (Pursh) Nutt.] and lupine. The non-indigenous hoary alyssum (*Alyssum alyssoides* L.) was well represented along the gradient at Site 1 (Table 2).

Eight indigenous grasses, two non-indigenous grasses, 10 indigenous forbs, and

Table 1. Number of transects in which indigenous and non-indigenous grasses are present at each sample interval at Site 1 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95
Indigenous grasses																				
Agropyron spicatum	5	5	4	5	4	4	5	5	3	4	4	5	5	4	4	5	4	4	2	3
Agropyron smithii	2	2	1	1	1	1		2		1				1						1
Aristida longiseta		1										1			1			1		
Bouteloua gracilis		1	1	1						1						1				
Danthonia unispicata	4	3	1	3	2	1	1	1		1	1		1							
Festuca idahoensis	5	5	4	4	5	5	4	3	2	1		1	1	1			1			
Koeleria macrantha		1			1				1		1									
Oryzopsis hymenoides						1														
Poa secunda	1	2	1	2	2	2		1	2		1	1								1
Stipa comata			1	1		1												1		
Stipa viridula			1		2		1								2					
Non-indigenous grasses																				
Bromus japonicus +	3	3	4	4	4	3	4	5	4	5	5	5	5	5	5	5	3	3	2	5
Poa pratensis	2	2	1	2	1	1	1	4	3	4	2	3	4	4	3	3	3	2	1	4

[1] Number of transects in which each species was present (maximum number of transects is 5).

Table 2. Number of transects in which indigenous and non-indigenous forbs are present at each sample interval at Site 1 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95
Indigenous forbs																				
Artemisia ludoviciana		2		2	1			1						2						
Aster falcatus			1		2		1	1											1	
Antennaria spp.									1											
Balsamorhiza sagittata											1				1					
Chrysopsis villosa	2	3	2	1	2	1	1	1				3	3		1	2	2	1		1
Collomia linearis						1				1										
Delphinium unispicata											1				1					
Liatris punctata		1			1			1				1		1						
Linum lewisii						1	1	1	1											
Lomatium dissectum	1	1		1	1		2	1					1		1		1			
Lupinus spp.	1	1			1	1		3	1	1		1		1	1					
Non-indigenous forbs																				
Achillea millefolium					2	1	1		1		1	1			1					
Alyssum alyssoides	5	4	5	5	4	4	4	4	3	3	4	3	3	4	5	3	3	2	1	3
Comandra umbellata	1	2	1			1														
Tragopogon dubius	2	1							1											

[1] Number of transects in which each species was present (maximum number of transects is 5).

four non-indigenous forbs were present at Site 2 (Table 3). Bluebunch wheatgrass and Idaho fescue were present along most of the gradient. All other indigenous grasses were limited in presence after 50% spotted knapweed cover at this site. Cheatgrass (*Bromus tectorum* L.) was present at all levels of spotted knapweed cover and occurred in three or more transects, except at 70 and 100% cover in which this species occurred in 2 and 1 transects, respectively. The most abundant indigenous forbs included hairy goldenaster and lupine (*Lupine* spp.) The non-indigenous hoary alyssum and *Berteroa* spp. were well represented along the gradient at Site 2 (Table 4).

Density

General linear models were generated to predict the density of indigenous species (predicted variables) using spotted knapweed density (regressor variable). For each increase in spotted knapweed density (plant m^{-2}), perennial grasses decreased linearly by about 0.07 tillers m^{-2} at both sites (Figure 1). Idaho fescue tiller density tended to decline rapidly as spotted knapweed density approached 300 spotted knapweed plants m^{-2}, and then continued to decrease, but less steeply at both sites (Table 5). Indigenous forb density was not associated with spotted knapweed density at either site.

Indigenous species richness was negatively related to spotted knapweed density (plants m^{-2}) at Site 2 (Table 5). At Site 1, indigenous species richness tended to decline until spotted knapweed densities reached about 350 plants m^{-2}. Indigenous species diversity tended to increase slightly from about 1 to 2 Shannon-Weaver's diversity index units based on spotted knapweed density, and then began to decrease after reaching approximately 400 plants m^{-2}.

Table 3. Number of transects in which indigenous and non-indigenous grasses are present at each sample interval at Site 2 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Indigenous grasses																					
Agropyron spicatum	4	4	5	4	4	3	2	4	4	1	3	3	3	3		3	2	4	4	4	
Bouteloua gracilis	1	3	2	1	1	2	2	3		1	1		1			1		1			
Calamovilfa longifolia		1	3	2	2	1		1	3		2	1				1	1	1		1	
Festuca idahoensis	5	5	5	4	4	5	3	5	3	3	3	4	1	1		3	2	4		3	
Koeleria macrantha		1	1	1	1	1	1		1			1									
Poa compressa																1					
Poa secunda																			1		
Stipa comata	1		1	1	1	2			1	1						2					
Non-indigenous grasses																					
Bromus tectorum	3	3	3	3	5	3	4	4	5	3	5	3	4	3	2	4	4	5	5	5	1
Poa pratensis							1	1					1	1	1		1	1			

[1] The number of transects in which each species was present (maximum number of transects is 5).

Table 4. Number of transects in which both indigenous and non-indigenous forbs are present at each sample interval at Site 2 [1].

Percent cover:	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Centaurea maculosa																					
Indigenous forbs																					
Arabis holboellii				1					1		1										
Artemisia frigida		1	1																		
Aster falcatus		1																			
Balsamorhiza sagittata																					
Chrysopsis villosa	3	3	3	1				2		1	2	2						2			
Coryphantha missouriensis												1									
Gallardia aristata		1																			
Liatris punctata			1	1		1												1			
Lupinus spp.	2	1	1	2		1	2	1	1		1	2	2	1				1			
Opuntia polyacantha					1			1	1		2	1		1			2	1	1		
Non-indigenous forbs																					
Achillea millefolium					2															1	
Alyssum alyssoides	2	2	1	2	2	2	1			2	3	3	1	3		1	2	3	3	1	1
Berteroa incana		1	4			2	1		3	3	2	1	3	1	1	2	1	2	2	1	
Tragopogon dubius	1	1																			

[1] The number of transects in which each species was present (maximum number of transects is 5).

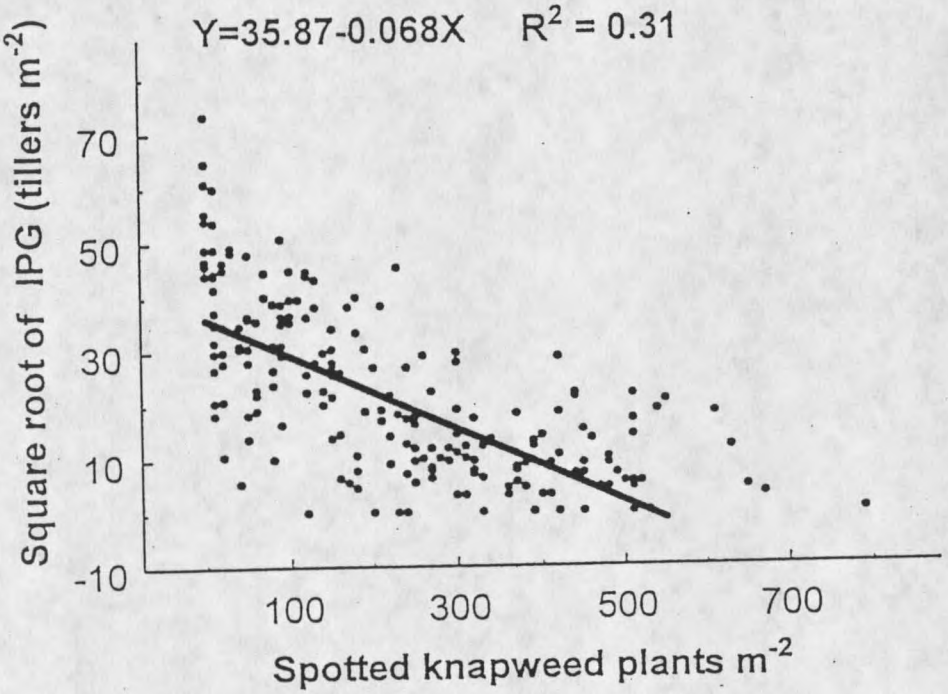

Figure 1. Relationship between indigenous perennial grass (IPG) density and spotted knapweed density. (Sites were similar; regression models represent combined data.)

Table 5. Regression models based on density with multiple significant independent variables.

Independent Variables	Dependent Variable	Equation	R^2
CEMA (X) CEMA*CEMA (X^2) CEMA*SITE (XY)	FEID⊛	$y=11.887-(0.509)X+(0.005)X^2+(0.042)XY$ (difference at Site 2 shown here)	0.55
SITE (X) CEMA (Y) CEMA*SITE (XY) CEMA*CEMA*SITE (X^2Y) TRAN(SITE) (Z)	SPECIES RICHNESS	$y=7.373-(1.020)X-(0.133)Y+(0.106)XY$ $+(0.0014)X^2-(0.0015)X^2Y-(0.1639)Z$* *tran(site) average (difference at Site 2 shown here)	0.39
CEMA (X) CEMA*CEMA (X^2) TRAN(SITE) (Y)	DIVERSITY	$y=1.432+(0.043)X-(0.0006)X^2-(0.1127)Y$* *tran(site) average	0.30

* tran(site) average

⊛ square root transformation performed on dependent variable.

Cover

General linear models indicated a negative relationship between indigenous grass cover and spotted knapweed cover at both sites. For each 1% increase in spotted knapweed cover, indigenous perennial grass cover decreased by about 2% (Figure 2). However, Idaho fescue cover declined with increasing spotted knapweed cover until about 75% spotted knapweed, after which this grass slightly increased (Figure 3). Indigenous forb cover was not associated with spotted knapweed cover.

A negative relationship between indigenous species richness and spotted knapweed cover was quantified at both sites. For each 1% increase in spotted knapweed cover, indigenous species richness decreased by about 3% (Figure 4). At both sites, the prediction of plant diversity resulted in a quadratic model with a spotted knapweed quadratic component (Figure 5). However, the quadratic component was so small that plant indigenous species diversity decreased nearly linearly based on spotted knapweed cover.

Biomass

Indigenous perennial grass biomass was negatively related to spotted knapweed biomass at both sites (Figure 6). Indigenous perennial grass biomass tended to decline quickly from 0 to 800 g m^{-2} of spotted knapweed, after which no further decrease in grass occurred. Idaho fescue biomass followed a trend similar to indigenous perennial grasses (Figure 7). Indigenous forb biomass was not associated with spotted knapweed biomass. The regression predicting indigenous species richness based on spotted knapweed biomass was y=4.619-(0.015)X-(1.434)Y, R^2=0.38 (X=spotted knapweed biomass, Y=average of

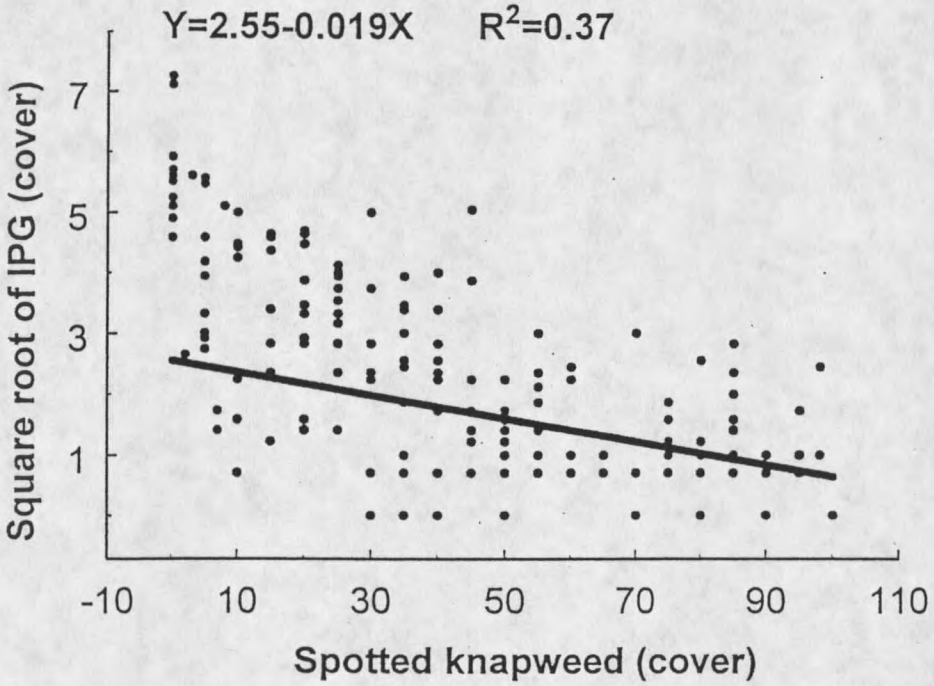

Figure 2. Relationship between indigenous perennial grass (IPG) cover and spotted knapweed cover. (Sites were similar; regression models represent combined data.)

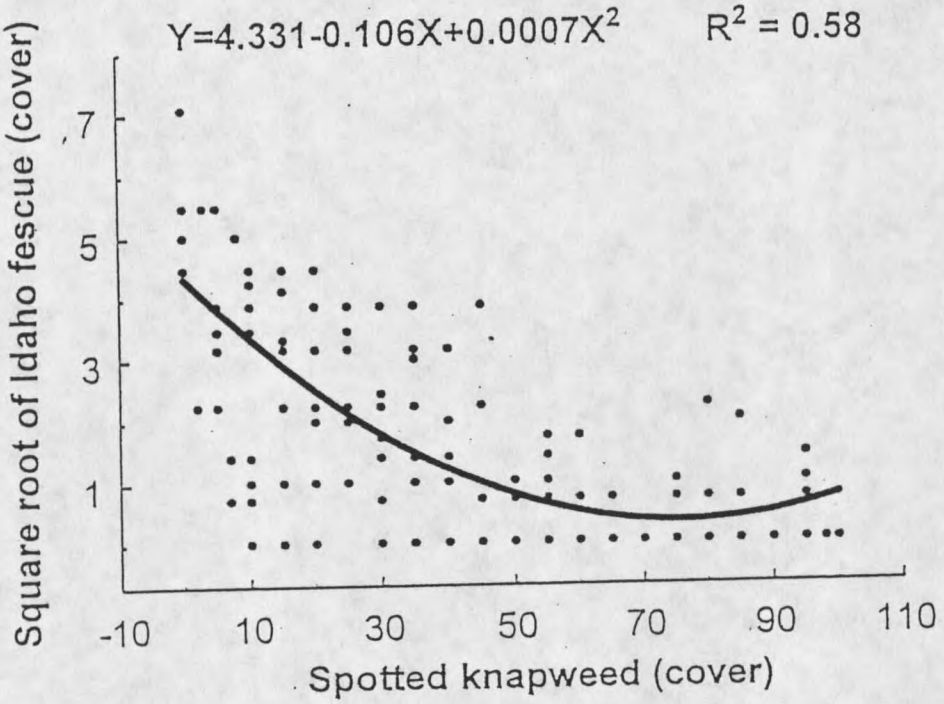

Figure 3. Relationship among Idaho fescue, spotted knapweed and a spotted knapweed quadratic component based on cover.

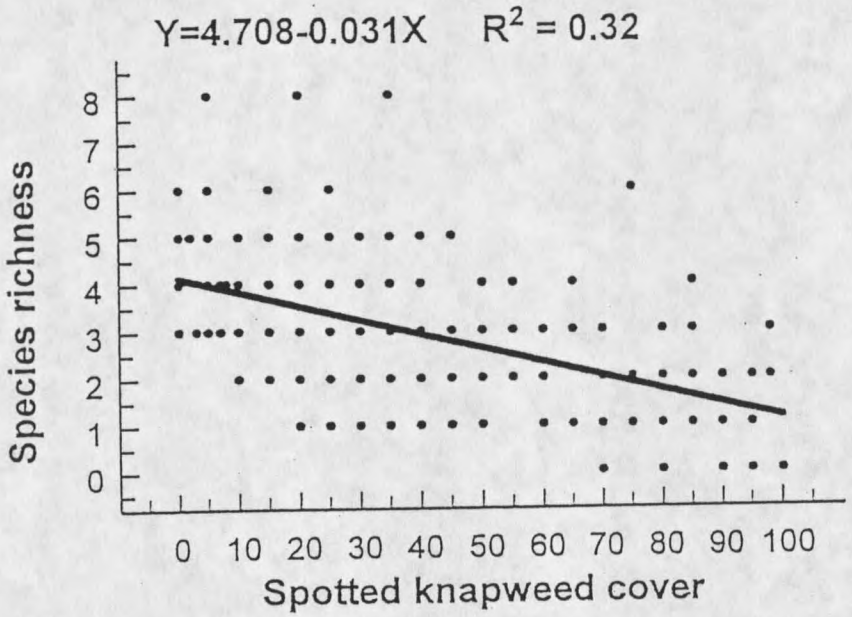

Figure 4. Relationship between species richness and spotted knapweed based on cover.

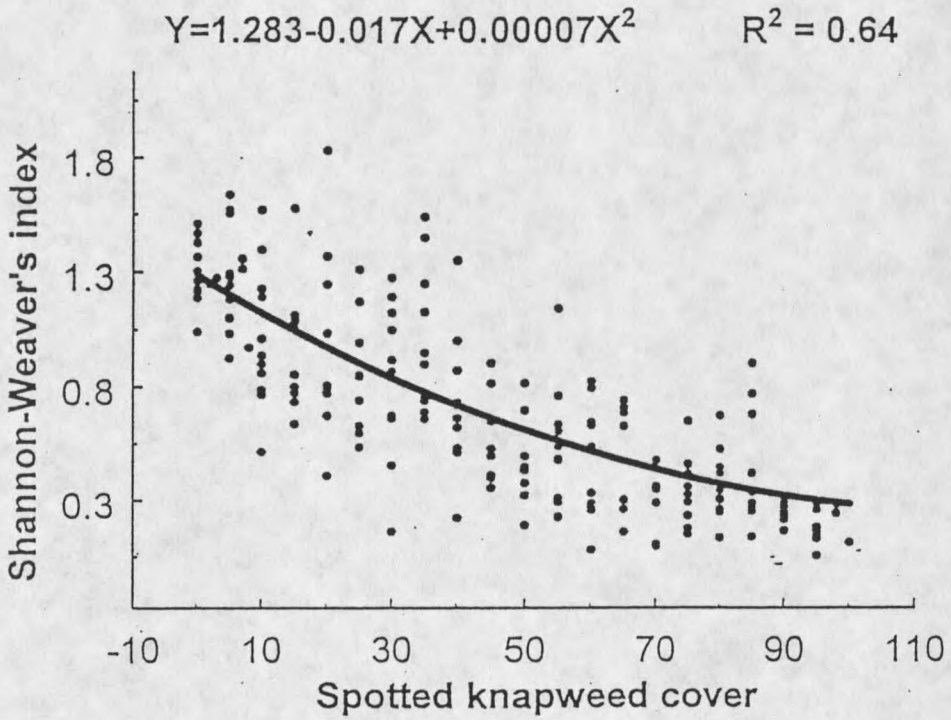

Figure 5. Relationship between Shannon-Weaver's diversity index and spotted knapweed based on cover.

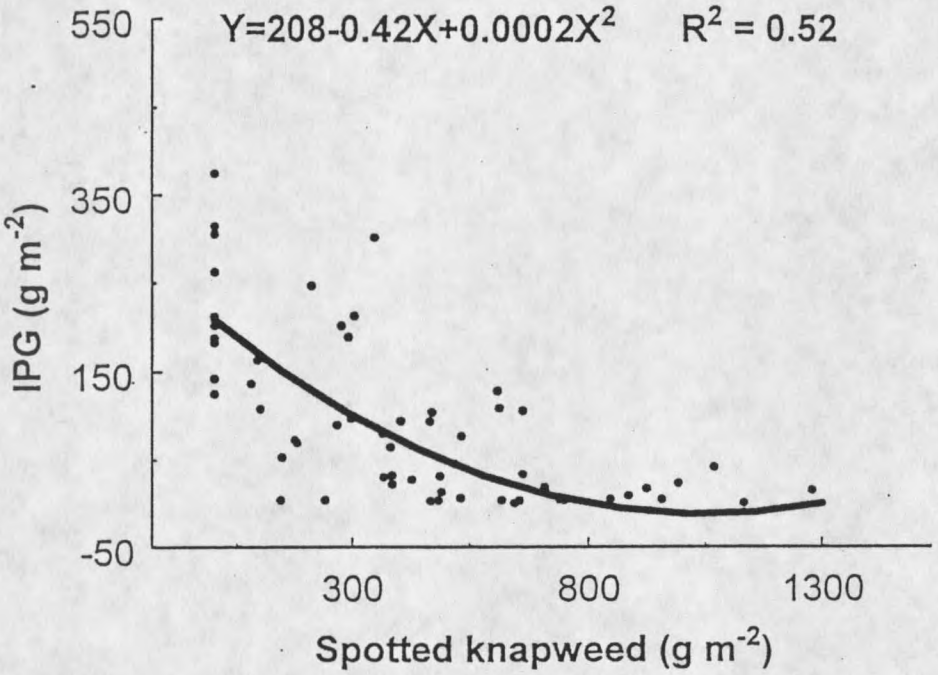

Figure 6. Relationship among indigenous perennial grass (IPG), spotted knapweed, and a spotted knapweed quadratic component based on biomass.

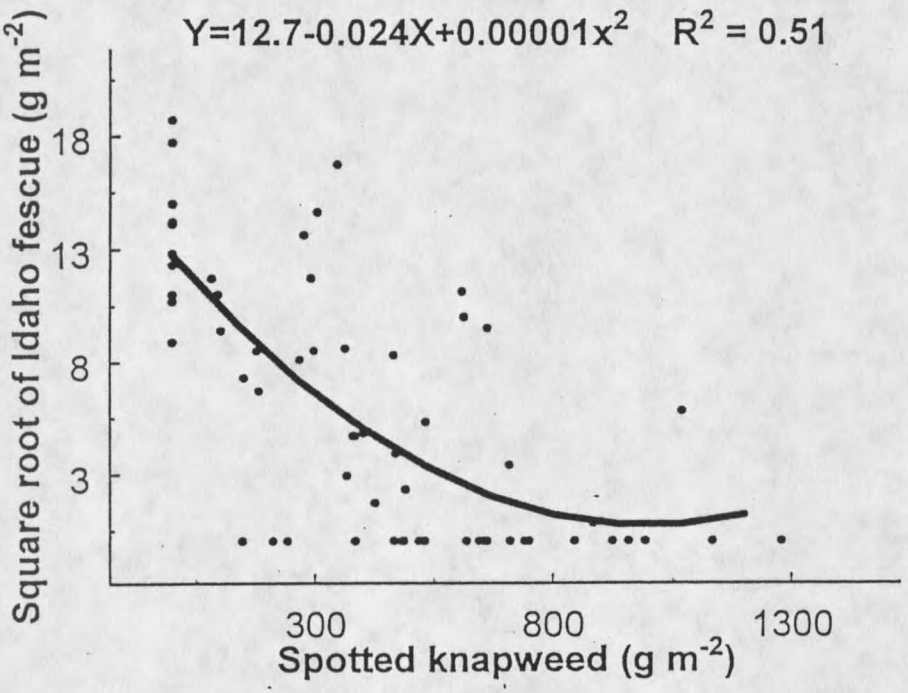

Figure 7. Relationship among Idaho fescue, spotted knapweed, and a spotted knapweed quadratic component based on biomass.

transect within site). Differences among transects within site occurred at both sites. For each increase in spotted knapweed biomass, the Shannon-Weaver indices decreased by 0.007 (Figure 8).

Soil Seed Bank

There were no statistical differences among species found in the seed bank at either site. Spotted knapweed and Japanese brome were prevalent species in the seed bank at Site 1 (Figure 9). Cheatgrass was the prevalent species in the seed bank at Site 2. Seeds of perennial grasses were either not present or were present at very low densities. Few indigenous forb seeds were present (Figure 10).

Growth Ring Results

Adult knapweed ranged in age from 1 to 7 years, but age and distance along transect did not appear to be related at either site (Figures 11 and 12).

Discussion

The invasion of semiarid rangeland by non-indigenous species is often associated with changes in plant community composition through the displacement of indigenous species (Randall 1996). My study showed that the occurrence of spotted knapweed and indigenous perennial grasses are inversely related. Spotted knapweed's invasive success is attributed to rapid growth rate, prolific seed production, and high biomass (Watson and Renney 1974, Sheley et al.1998). Watson and Renney (1974) also reported that declines in bluebunch wheatgrass biomass were associated with increases in spotted knapweed biomass. Bluebunch wheatgrass/rough fescue (*Festuca scabrella* Torr.) production was reduced by 88% following diffuse knapweed (*Centaurea diffusa* Lam.) invasion (Watson

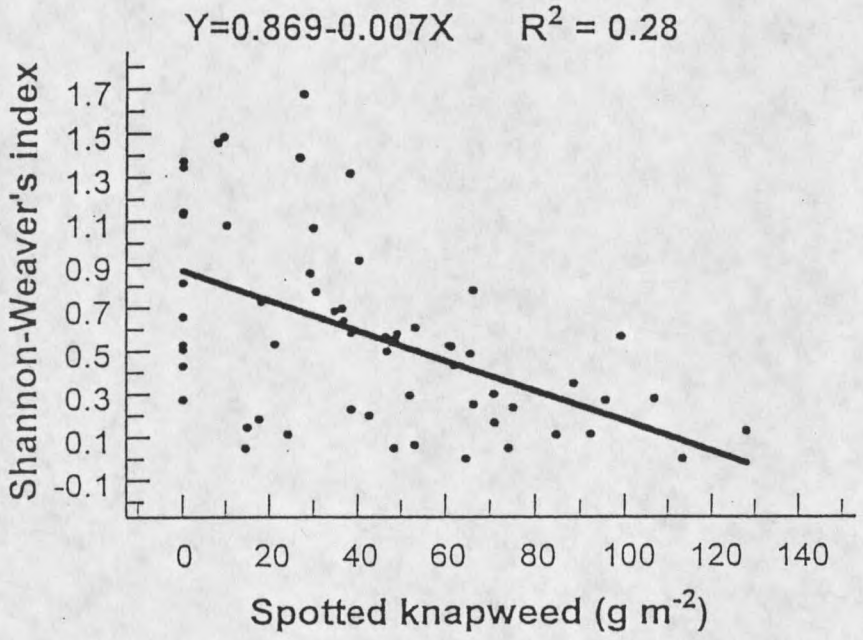

Figure 8. Relationship between Shannon-Weaver's diversity index and spotted knapweed based on biomass.

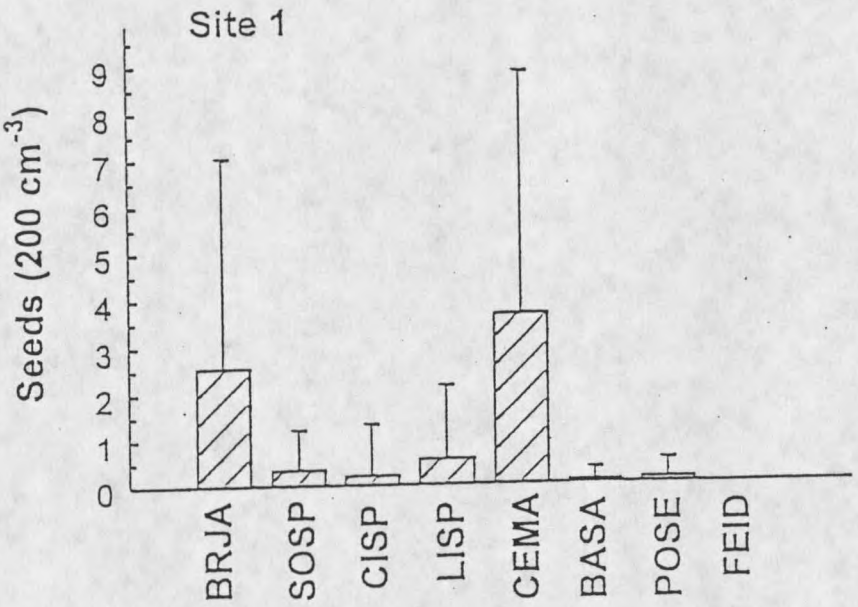

Figure 9. Seed bank present in a 200-cm^{-3} soil sample at Site 1.

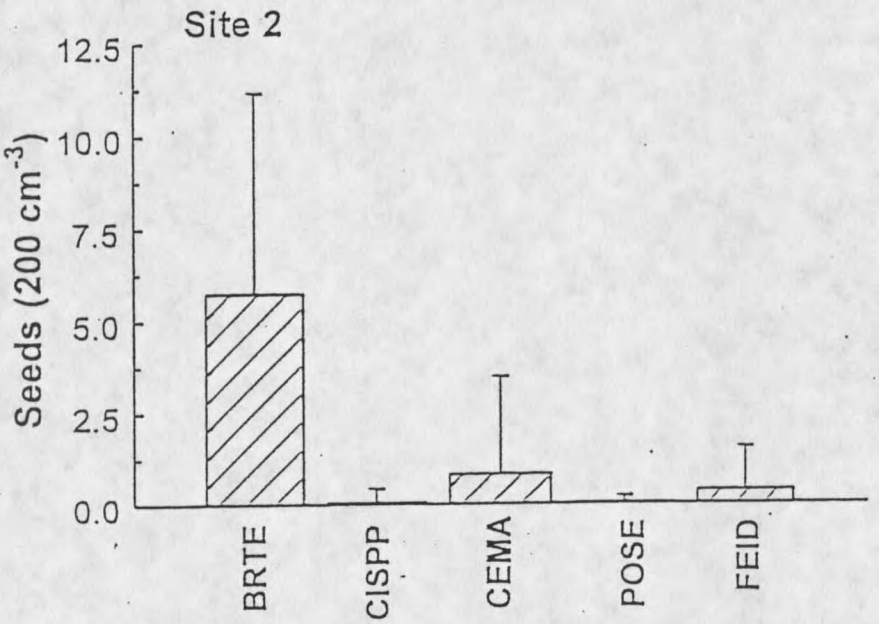

Figure 10. Seed bank present in a 200-cm^{-3} soil sample at Site 2.

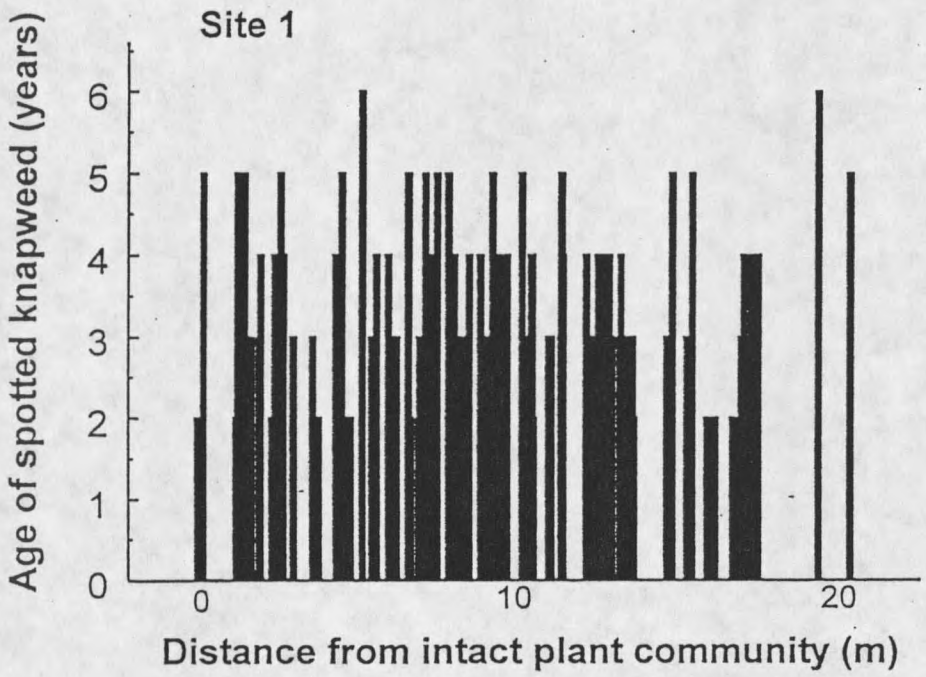

Figure 11. Age (years) of spotted knapweed in relation to distance from the intact plant community at Site 1.

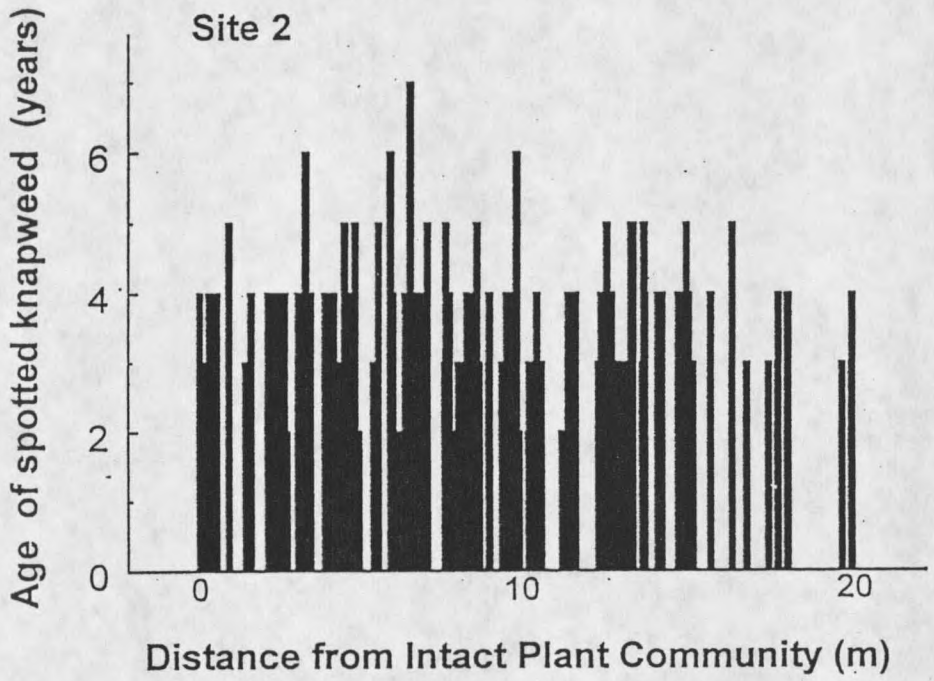

Figure 12. Age (years) of spotted knapweed in relation to distance from the intact plant community at Site 2.

and Renny 1974). In a seedling study, spotted knapweed was over 4 times more competitive than bluebunch wheatgrass when predicting bluebunch wheatgrass weight (Sheley and Jacobs 1997). Velagala et al. (1997) showed that at high spotted knapweed and low intermediate wheatgrass (*Elytriga intermedia* Host.) seedling densities, spotted knapweed reduced wheatgrass total (root and shoot) and shoot weight. Increasing intermediate wheatgrass density (>1,000 seeds/m^2) removed the competitive effects of spotted knapweed on intermediate wheatgrass. These studies indicate that spotted knapweed's competitive ability may allow it to dominate and, as a result, displace indigenous perennial grass in some situations.

In contrast, spotted knapweed establishment and the apparent decline in indigenous perennial grasses may occur in areas of low grass abundance (recruitment and dispersal) where open niches exist. Tilman (1997) demonstrated that native undisturbed grasslands contain many available niches which invasive species may exploit and occupy. The lack of indigenous species found in the seed bank supports the hypothesis that spotted knapweed may occupy available niches left unfilled by indigenous species.

Models predicting Idaho fescue density, cover, and biomass based on spotted knapweed density, cover, and biomass, respectively, demonstrated a sharp decline in fescue followed by its low-level persistence at higher levels of spotted knapweed (> 350 plants m^{-2}, > 55% cover, and > 550 g m^{-2}). One objective of land managers in treating spotted knapweed infestations with herbicides includes returning rangeland to pre-invasion levels of desirable grass species. It is recommended that land managers consider the understory of residual grass species that is available to respond to management before

weed management decisions are made (Sheley and Jacobs 1997). This knowledge could potentially help land managers predict the levels of perennial grasses necessary to return a spotted knapweed-infested area to a desired perennial grass-dominated community.

Based on the temporal and spatial similarities among forbs, some cursory evidence suggests that spotted knapweed directly competes with indigenous forbs (Jacobs and Sheley 1999). In our study, no relationship between spotted knapweed density, cover, or biomass, and forb density, cover, or biomass was detected, respectively. In a study to assess herbicide impacts on non-target species, Rice and Toney (1998) reported that forb [e.g., (*Arabis holboelli* Hornem., *Balsamorhiza sagittata* Nutt., *Chrysopsis villosa* (Nutt.) Ell.] cover in control plots remained constant over time for three out of four important species in areas of early to intermediate stages of spotted knapweed invasion. Some indigenous rangeland forbs may not occupy the same niche as spotted knapweed. This is surprising because Sheley and Larson (1996) indicated that knapweed can occupy all available niches by developing a hierarchy of age classes. These results may not apply to spring ephemeral forbs, which this study did not consider.

This study showed indigenous species richness and diversity were inversely related to spotted knapweed. Invasibility of grassland dominated by indigenous species appear to be negatively related to species diversity (Tilman 1997). Tyser and Key (1988) suggest that spotted knapweed is capable of modifying plant community composition by changing species frequency. It has been hypothesized that areas of poor species diversity result in incomplete use of limiting resources, thereby increasing invasibility by aggressive species (McNaughton 1993, Robinson et al.1995). Tilman (1997) observed that community

invasibility was greater in species-poor plant communities. Therefore, two hypotheses are plausible: spotted knapweed may displace indigenous species, or it may invade areas of low diversity and low indigenous species richness.

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CHAPTER 3

PREDICTING PLANT COMMUNITY AND BIOMASS RESPONSE TO PICLORAM

Introduction

Over the past century, loss of indigenous rangeland communities in North America has been related to the invasion of aggressive non-indigenous species. Ecological impacts attributed to non-indigenous invasions include the displacement of indigenous plant species, declines in biodiversity, and degradation of ecosystem function (Vitousek 1986, Randall 1996). In the western United States, saltcedar (*Tamarix* spp.) (Brotherson and Field 1987), leafy spurge (*Euphorbia esula* L.) (Belcher and Wilson 1989), downy brome (*Bromus tectorum* L.) (Mack 1981, Whisenant 1990), spotted knapweed (*Centaurea maculosa* Lam.), and others have been documented to alter ecosystem function (Tyser and Key 1988). Ecosystem processes threatened by invasive species include changes in primary and secondary productivity, decomposition, nutrient cycles (accumulation or loss), soil development and fertility, and hydrologic cycles (Vitousek and Hooper 1993). In a single, cursory study, Lacey et al. (1989) suggested that surface run-off and sediment yield were increased on spotted knapweed-dominated sites under simulated rain events. Spotted knapweed negatively impacts wildlife through forage production loss, habitat modification, or by altering animal-plant interactions (Thompson 1996). Invasion by spotted knapweed into western Montana has reduced winter forage for elk resulting in an estimated loss of 220 elk annually (Spoon et al. 1983). A major economic impact of

spotted knapweed invasion is the loss of livestock forage production. Spotted knapweed infestations currently cost an estimated $11 million to livestock producers of Montana, annually and could potentially cost up to $150 million each year (Bucher 1984).

Historically, the decision to manage noxious weeds has been legislatively mandated. In accordance with these laws, managers have attempted to control weeds that are detected. This strategy is primarily focused on the use of herbicides and has been effective for small infestations when there location is known. For large infestations, weed control requires periodic, repeated herbicide applications for many years, which is rarely cost-effective (Griffith and Lacey 1991). Effective large-scale weed management must focus on establishing and maintaining desired plant communities rather than controlling undesirable weeds, because weeds often rapidly re-occupy niches opened by the control procedure (Sheley et al.1996). The decision to manage weeds requires an economic and ecological assessment of the cost and benefits based on an understanding of the plant community's response to the management procedures. In areas where desired understory species do not respond to control procedures, revegetation or restoration of desired species may be required.

Land managers must be able to predict the outcome of their weed management strategies in order to optimize economic and ecological benefits. Predictive capabilities allow ecological and economic assessment of various strategies based on land management objectives. Without predictive capabilities, the decision to impose a particular strategy is either based on prior experience or is arbitrary. Effective rangeland weed management requires the ability to predict plant community responses to imposed

regulations.

Rangeland managers are searching for useful models on which to base their decisions (Archer 1989, Laycock 1991, Schlatterer 1989). Future modeling may prove useful if it can predict the effects of management and the post-management plant community based on the pre-management plant community. The more accurate the predictions, the greater success in developing integrated weed management systems (Schreiber 1982). Coupled with the concept of thresholds, predicting plant community response to regulation may enhance management by providing managers with the information necessary to make thoughtful decisions (Griffith and Lacey 1991).

The overall objective of this study was to determine the potential to predict the post-treatment plant community after a herbicide treatment of spotted knapweed based on the pre-treatment plant community. Specific objectives were to: 1) develop models that predict the post-management plant community composition based on the pre-treatment plant community after a picloram treatment; 2) initiate development of a method for using easily collected field data to predict pre- and post-management biomass; and 3) introduce a method to use predictions to enhance weed management decisions. Since cover data is one of the easiest parameters to collect, using cover to predict biomass may be the most practical and efficient model for decision-making. Although this study was conducted using an herbicide, this method could be used in a similar fashion to predict post-treatment plant community response based on the pre-treatment plant community and the treatment for other management techniques (e.g., grazing, fire, biocontrol, etc.). This research is necessary to improve decision-making abilities and management strategies.

Materials and Methods

This study was conducted on two sites from 1996 through 1998 within a Idaho fescue-bluebunch wheatgrass (*Festuca idahoensis-Agropyron spicatum*) habitat type (Mueggler and Stewart 1980). Site 1 was located in Story Hills (45° 42' N, 111° 01' W), four km northeast of Bozeman, Mont. Elevation at this site is 1478 m. Average annual precipitation is 432 mm. Soil at this site is a clayey-skeletal, mixed Typic Argiborolls. Site 2 was located at Beartrap Canyon, about 45 km east of Norris, Mont. (45° 36' N, 111° 34' W). Elevation at this site is 788 m with an average annual precipitation of 305 mm. Soil at Site 2 is classified as a loamy-skeletal, mixed Aridic Argiborolls.

Transects radiated from dense spotted knapweed in the center of each patch to an area of low or no spotted knapweed occurrence on the outside of the patch. At each site, all transects radiated from the center of the same patch. Five transects, each 20 m long, were established at both sites. The plant community at each transect origin was dominated by spotted knapweed with few or no residual indigenous species in the understory. Transects ended in areas dominated by Idaho fescue with a diverse understory. Twenty permanent plots (20 x 50 cm, spacing along the transect ranged from ½ to 2 m) were placed along this gradient of spotted knapweed cover from 0 to 100% (about every 5%). Pre-treatment density (juveniles plus adults) and cover of all species were sampled in each plot. Picloram (4-amino-3,5,6-trichloropicolinic acid) was applied along each transect at a rate of 0.28 kg a.i.ha^{-1} in the fall (October) of 1996 to each plot. Density (juveniles plus adults) and cover of all species were re-sampled in August 1998.

Thirty temporary plots (20 x 50 cm) were also established along the spotted

knapweed gradient to sample biomass and soil at each site. Biomass was sampled for all species by clipping plants to ground level at peak standing crop in August 1996 and 1998. Samples were dried at 60°C to a constant weight and weighed. Soil samples were collected along the transect to determine whether the spotted knapweed gradient was related to differences in soil nutrients. Soil samples were tested for available nitrogen, phosphorous, and potassium using a standardized extraction process (Page and Klute. 1982). There were no differences in available soil nutrients, therefore the data are not present.

Data Analysis

Data were compiled into tables showing the number of transects in which individual species were present both before and after the picloram treatment (maximum of five). Plant density, cover, and biomass data were analyzed using a multi-step process. Covariance analysis was conducted to test for sample independence within transects. Analysis indicated independence among all plots, therefore, a step-down linear regression procedure was used to identify the best model (Neter et al. 1985). A combination of *P*-value, model simplicity, and R^2 values was used to identify the best model for each step-down procedure. Scatter-plots of the residuals versus the standardized predicted values were used to evaluate heterogeneity of variance for each model. Data transformations were conducted where necessary on predicted and/or regressor variables using square-root transformations. Inverse, quadratic, and log transformations were tested, but did not improve the models. Collinearity was evaluated using a SAS® Tolerance procedure to test for relatedness of predictors (SAS 1990). Collinearity was not a problem in this analysis.

Regression models were fit using density, cover, and biomass after treatment (1998) as predicted variables which include perennial grasses, Idaho fescue, forbs, indigenous species richness, and indigenous species diversity. All predicted variables were indigenous species. Regressor variables used were site, transect, and density, cover, and biomass of spotted knapweed, a spotted knapweed quadratic component, indigenous perennial grasses, Idaho fescue, indigenous forbs, indigenous species richness, and indigenous species diversity sampled in the first year (1996), prior to treatment.

Regression models were also fit using density, cover, and biomass of brome species post-treatment as predicted variables. In these models, regressor variables were density, cover, and biomass of pre-treatment brome species, a brome quadratic component, spotted knapweed, and a spotted knapweed quadratic component.

Additionally, regression models were fit to predict production from cover. The predicted variables include: post-treatment indigenous perennial grass, Idaho fescue, forbs, and brome species biomass. Regressor variables used were pre-treatment indigenous perennial grass, Idaho fescue, indigenous forbs, brome species cover, and their respective quadratic components .

All models presented were significant at $P \leq 0.05$. The effects of transects were averaged across sites when significant. Coefficient means and standard deviations for transects are presented. Predictive models presented in this chapter do not imply causality. Diversity measurements were estimated using Shannon-Weaver's diversity index (Shannon and Weaver 1949).

Results

Presence and Distribution

Nine indigenous grasses, two non-indigenous grasses, nine indigenous forbs, and three non-indigenous forbs were present at Site 1 (Tables 6 and 7). Of the indigenous grasses, bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. & Smith] was found in three or more transects, and western wheatgrass (*Agropyron smithii* Rydb.) was present in at least one transect along the gradient. Idaho fescue was present in all transects except at 85 and 90% pre-treatment spotted knapweed. All other indigenous grasses were limited in presence after 50% pre-treatment spotted knapweed. Japanese brome (*Bromus japonicus* Thunb.) was present along the entire transect. Kentucky bluegrass (*Poa pratensis* L.) was limited in presence below 30% pre-treatment spotted knapweed. The most abundant indigenous forbs included hairy goldenaster [*Chrysopsis villosa* (Pursh) Nutt.], blazing-star (*Liatris punctata* Hook.) and sagewort cudweed (*Artemisia ludoviciana*). Post-treatment bastard toadflax [*Comandra umbellata* (L). Nutt.] was the most abundant non-indigenous forb present at Site 1.

Seven indigenous grasses, three non-indigenous grasses, five indigenous forbs and two non-indigenous forbs were present at Site 2 (Tables 8 and 9). Blue grama [*Bouteloua gracilis* (H. B. K.) Lag.] was present along the entire gradient. Idaho fescue was found at all pre-treatment spotted knapweed levels except 70 and 100%. Prairie sandreed (*Calamovilfa longifolia* Hook.) and needle-and-thread grass (*Stipa comata* Trin. & Rupr.) were well represented along the transect except above 60% spotted knapweed. The most abundant forb based on presence in number of transects was the non-indigenous *Berteroa*

Table 6. Number of transects in which both indigenous and non-indigenous grasses are present at each sample interval at Site 1 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95
Indigenous grasses																				
Agropyron spicatum	(5) [2] 3	(5) 4	(4) 5	(5) 5	(4) 5	(4) 5	(5) 5	(5) 5	(3) 4	(4) 3	(4) 4	(5) 5	(5) 4	(4) 3	(4) 4	(5) 3	(4) 5	(4) 4	(2) 3	(3) 3
Agropyron smithii	(2) 2	(2) 2	(1) 2	(1) 3	(1) 5	(1) 5	1	(2) 3	2	(1) 5	3	3	2	(1) 3	3	2	4	3	1	(1) 3
Aristida longiseta	1	(1) 1				3			1			(1) 2		1	(1)	1		(1) 1		
Bouteloua gracilis		(1)	(1)	(1)						(1)						(1)				
Danthonia unispicata	(4) 4	(3) 3	(1) 3	(3) 3	(2)	(1) 1	(1) 2	(1) 2	1	(1) 1	(1) 1		(1) 1	1		1	1			1
Festuca idahoensis	(5) 5	(5) 5	(4) 5	(4) 5	(5) 5	(5) 5	(4) 3	(3) 3	(2) 4	(1) 1	1	(1) 1	(1) 1	(1) 1	1	2	(1) 1			1
Koeleria macrantha		(1) 2		1	(1) 1	1	1	1	(1) 2	1	(1) 1									3
Oryzopsis hymenoides						(1)														
Poa secunda	(1)	(2) 1	(1)	(2)	(2)	(2) 1		(1)	(2)	1	(1)	(1)								(1)
Stipa comata	1	2	(1) 1	(1) 2	4	(1) 2	1		2	1	1	1				1		(1) 1		
Stipa viridula			(1) 1	2	(2) 1	2	(1) 1		1						(2)					
Non-indigenous grasses																				
Bromus japonicus	(3) 1	(3) 2	(4) 3	(4) 3	(4) 3	(3) 2	(4) 3	(5) 3	(4) 3	(5) 4	(5) 4	(5) 3	(5) 5	(5) 5	(5) 4	(5) 2	(3) 4	(3) 2	(2) 3	(5) 1
Poa pratensis	(2)	(2) 1	(1) 2	(2)	(1) 2	(1)	(1) 2	(4) 3	(3) 2	(4) 3	(2) 5	(3) 5	(4) 4	(4) 3	(3) 5	(3) 4	(3) 4	(2) 3	(1) 2	(4) 5

[1] Maximum number of transects per sample unit equals 5.

[2] The top number represents pre-treatment data and the bottom number represents post-treatment data.

Table 7. Number of transects in which both indigenous and non-indigenous forbs are present at each sample interval at Site 1 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Indigenous forbs																					
Artemisia ludoviciana	1	(2)[2] 2	1	(2) 1	(1) 2	1		(1)	1				1	(2) 1	1						
Aster falcatus	1		(1) 2		(2)	1	(1) 1	(1) 1									1		(1) 1	1	
Antennaria spp.									(1)												
Balsamorhiza sagittata			1		1			1	1	1	(1)				(1)	1	1				
Chrysopsis villosa	(2)	(3) 1	(2)	(1)	(2) 2	(1) 2	(1) 1	(1) 1	3			(3) 1	(3)		(1) 1	(2)	(2)	(1) 2		(1)	
Collomia linearis						(1)				(1)											
Delphinium unispicata	1										(1)	1			(1) 1	1			1		
Liatris punctata	1	(1) 2		1	(1) 1		1	(1)	1	1	1	(1) 1		(1) 2			1				
Linum lewisii			1			(1) 1	(1)	(1) 1	(1) 1												
Lomatium dissectum	(1)	(1)		(1)	(1) 1	1	(2) 1	(1)	1				(1)		(1)	1	(1) 1				
Lupinus spp.	(1)	(1)			(1)	(1) 1		(3) 1	(1)	(1)		(1)		(1) 1	(1) 1		1	1			
Non-indigenous forbs																					
Achillea millefolium					(2)	(1) 1	(1) 1		(1) 1		(1) 1	(1) 1	1		(1) 2	1					
Alyssum alyssoides	(5)	(4)	(5)	(5)	(4)	(4)	(4)	(4)	(3)	(3)	(4)	(3)	(3)	(4)	(5)	(3)	(3)	(2)	(1)	(3)	
Comandra umbellata	(1) 1	(2) 2	(1) 1		1	(1) 2	1	1	2	1		1									
Tragopogon dubius	(2) 2	(1)	1				1		(1) 1		1		1	2				1			

[1] Maximum number of transects per sample unit equals 5.

[2] The top number represent pre-treament data and the bottom number represents post-treatment data.

Table 8. Number of transects in which both indigenous and non-indigenous grasses are present at each sample interval at Site 2 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Indigenous grasses																					
Agropyron spicatum	(4)[2] 3	(4) 5	(5) 5	(4) 4	(4) 4	(3) 3	(2) 4	(4) 4	(4) 3	(1) 1	(3) 2	(3) 5	(3) 4	(3) 1		(3) 2	(2) 4	(4) 3	(4) 3	(4) 5	
Bouteloua gracilis	(1)2	(3) 4	(2) 4	(1) 2	(1) 3	(2) 2	(2) 2	(3) 3	1	(1) 4	(1) 2	4	(1) 4	2	1	(1) 2	3	(1) 2	1	1	1
Calamovilfa longifolia		(1) 1	(3) 2	(2)	(2) 1	(1) 1	2	(1) 2	(3) 3	1	(2) 1	(1) 1	2		1	(1)	(1)	(1)		(1) 1	
Festuca idahoensis	(5)5	(5) 5	(5) 5	(4) 5	(4) 4	(5) 5	(3) 4	(5) 5	(3) 3	(3) 3	(3) 5	(4) 4	(1) 3	(1) 1		(3) 4	(2) 5	(4) 1	1	(3) 3	
Koeleria macrantha		(1) 1	(1) 1	(1)	(1) 1	(1) 1	(1) 1		(1)	1	1	(1)			1			1	2		
Poa compressa																(1) 1					
Poa secunda																			(1)		
Stipa comata	(1)2	4	(1) 2	(1) 1	(1) 2	(2) 3	1	1	(1) 3	(1) 1	2	3	2	1		(2) 3		3	1		
Non-indigenous grasses																					
Bromus tectorum +	(3)1	(3) 3	(3) 3	(3) 2	(5) 2	(3) 2	(4) 2	(4) 3	(5)	(3)	(5) 3	(3) 2	(4) 5	(3)	(2)	(4) 1	(4) 2	(5) 2	(5) 1	(5)	(1)
Poa pratensis	2	1	1			1	(1)	(1)					(1)	(1)	(1)		(1)	1			
Carex spp.	2	2	1				1		1	1		1									

[1] Maximum number of transects per sample unit equals 5.

[2] The top number represents pre-treatment data and the bottom number represents post-treatment data.

Table 9. Number of transects in which both indigenous and non-indigenous forbs are present at each sample interval at Site 2 [1].

Percent cover: *Centaurea maculosa*	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100
Indigenous forbs																					
Arabis holboellii				(1)					(1)		(1)										
Artemisia frigida		(1)	(1)			1															
Aster falcatus		(1)																			
Balsamorhiza sagittata																					
Chrysopsis villosa	(3)	(3)	(3)	(1)				(2)		(1)	(2)	(2)						(2)			
Coryphantha missouriensis												(1) 1									
Gallardia aristata		(1) 1																			
Liatris punctata			(1)	(1)		(1)	1	1								1		(1)	3		
Lupinus spp.	(2) 1	(1)	(1)	(2)		(1)	(2)	(1)	(1)		(1)	(2)	(2)	(1)				(1)			
Opuntia polyacantha			1	1	(1)	1		(1)	(1)		(2)	(1) 1	1	(1)	1		(2)	(1) 1	(1)	1	
Non-indigenous forbs																					
Achillea millefolium					(2)															(1)	
Alyssum alyssoides	(2)	(2)	(1)	(2)	(2)	(2) 1	(1)			(2)	(3)	(3)	(1)	(3)		(1)	(2)	(3)	(3)	(1)	(1)
Berteroa incana		(1) 1	(4) 1	1	1	(2) 1	(1) 1		(3) 1	(3)	(2)	(1)	(3) 1	(1)	(1)	(2) 1	(1) 2	(2) 1	(2) 3	(1)	
Tragopogon dubius	(1)	(1)																			

[1] Maximum number of transects per sample units equals 5.
[2] The top number represents pre-treatment data and the bottom number represents post-treatment data.

spp.

Density

Regression models were generated to predict the plant density two years after picloram treatment (predicted variables) based on the density of plants sampled prior to treatment (regressor variables) (Table 10). Site was significant when predicting Idaho fescue and forb density, as well as indigenous species richness based on density. Estimated effects of site were -8.8, -5.0, and 19.7 for indigenous species richness, forbs, and Idaho fescue density, respectively.

For each one unit increase in pre-treatment indigenous perennial grass density, predicted post-treatment indigenous perennial grass density increased by about 9.2 tillers m^{-2} (Table 10). For each one unit increase in spotted knapweed density, predicted indigenous perennial grass density decreased by 0.1 tillers m^{-2} at Site 1. At Site 2, for each one unit increase in spotted knapweed density, predicted indigenous perennial grass density increased by 0.4 tillers m^{-2}. Effect of transect was positively associated with indigenous perennial grass density.

In the model predicting Idaho fescue density, post-treatment Idaho fescue density was positively associated with pre-treatment Idaho fescue density and indigenous species diversity (Table 10). Specifically, each one unit increase in pre-treatment Idaho fescue density was associated with a 9.5 tillers m^{-2} increase in post-treatment Idaho fescue density. For each one unit increase in indigenous species diversity, Idaho fescue density increased by 14.1 tillers m^{-2}. In general, predicted post-treatment indigenous forb density was negatively related to pre-treatment indigenous perennial grass density and positively

Table 10. Regression models predicting post-treatment indigenous species based on pre-treatment density (plants m^{-2}) of regressor variables. Empty cells represent non-significant regressor variables.

		Regressor variables										
Site	Predicted variables	Intercept	Site	Transect (1)[1]	Perennial grass (0 to 7,280)	Idaho fescue (0 to 3,970)	Forbs (0 to 550)	Species richness (0 to 8)	Species diversity (0 to 2.26)	Spotted knapweed (0 to 1,170)	Spotted knapweed[2] (0 to 313,290)	R^2
1	Perennial grass[2]	19.2		5.5[3] (6.8)	9.2					-0.1		0.51
2	Perennial grass	19.2		5.5 (6.8)	9.2					0.4		0.51
1	Idaho fescue	-17.4	0.00			9.5			14.1			0.69
2	Idaho fescue	-17.4	19.7			9.5			14.1			0.69
1	Forbs	7.2	0.00	-2.8 (2.8)	-0.68			2.3				0.34
2	Forbs	7.2	-5.0	-2.8 (2.8)	-0.68			2.3				0.34
1	Species richness	17.8	0.00		1.5			4.4			0.002	0.46
2	Species richness	17.8	-8.8		1.5			4.4			-0.004	0.46
1	Diversity	3.3		-1.0 (1.1)	0.8				1.7			0.30
2	Diversity	3.3		-1.0 (1.1)	0.8				1.7			0.30

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting post-treatment IPG density based on pre-treatment density of IPG and CEMA treatment includes:
Site1; $y = 19.2(B_0) + 5.5(B_1) + 9.2(B_2) - 0.10(B_3)$,
where B_0 is the intercept, B_1 is the average of transect, B_2 is the density of indigenous perennial grass prior to treatment, and B_3 is the density of CEMA at Site 1;
Site 2; $y = 19.2(B_0) + 5.5(B_1) + 9.2(B_2) + 0.40(B_3)$,
where B_0 is the intercept, B_1 is the average of transect, B_2 is the density of IPG prior to treatment, and B_3 is the density of CEMA at Site 2.

[3] Means represent the average of ten transects across site with standard deviations are provided below means in table.

related to indigenous species richness (Table 10). For each one unit increase in indigenous perennial grass density, forb density decreased by 0.68 plants m^{-2}. Each one unit increase in indigenous species richness was associated with a predicted 2.3 plants m^{-2} increase in forb density. Effect of transect was negatively associated with forb density.

For each one unit increase in indigenous perennial grass density, predicted indigenous species richness increased by about 1.5 plants m^{-2} at both sites (Table 10). For each one unit increase in pre-treatment indigenous species richness, predicted post-treatment species richness increased by 4.4 plants m^{-2} at both sites. The spotted knapweed quadratic component was associated with an increase in indigenous species richness by about 0.002 indigenous species m^{-2} at Site 1 and a decrease of 0.004 indigenous species m^{-2} at Site 2.

Predicted post-treatment indigenous species diversity was positively related to both pre-treatment indigenous perennial grass density and indigenous species diversity (Table 10). Each one unit increase in indigenous perennial grass density was associated with an increase in indigenous species diversity by 0.8 Shannon-Weaver's diversity index units. For each one unit increase in pre-treatment indigenous species richness, post-treatment indigenous species diversity increased by 1.7 Shannon-Weaver's diversity index units. Effect of transect was negatively associated with indigenous species diversity at both sites.

Cover

Site was significant when predicting forb cover and indigenous species richness based on cover. The estimated effects of site were -.94 and -.69 for forbs and indigenous

species richness, respectively (Table 11).

Predicted post-treatment indigenous perennial grass cover was positively related to indigenous perennial grass and indigenous species richness, but negatively related to forb cover at both sites (Table 11). Each 1% increase in pre-treatment indigenous perennial grass cover was associated with a 52% increase in post-treatment indigenous perennial grass cover. For each 1% increase in forb cover, indigenous perennial grass cover decreased by 19%. Each 1% increase in indigenous species richness based on cover was associated with a predicted increase in indigenous perennial grass cover by 16%. For each 1% increase in spotted knapweed cover, indigenous perennial grass cover decreased by 0.9 % at Site 1 and increased by 2.8% at Site 2. Each 1% increase in the spotted knapweed quadratic component was associated with a decrease in indigenous perennial grass cover by 0.005 and 0.04% for Sites 1 and 2, respectively.

In general, predicted post-treatment Idaho fescue cover was positively related to pre-treatment Idaho fescue cover (Table 11). Each 1% increase in pre-treatment Idaho fescue cover was associated with an increase in post-treatment Idaho fescue cover by 63%. Each 1% increase in spotted knapweed cover was associated with a predicted decrease in Idaho fescue cover by about 1.8 and 0.8% at Sites 1 and 2, respectively.

Predicted post-treatment indigenous forb cover was positively related to pre-treatment indigenous forb cover (Table11). For each 1% increase in forb cover prior to treatment, forb cover after treatment increased by 53% at both sites. At Site 2, the effect of transect was negatively associated with forb cover.

In the model predicting indigenous species richness, post-treatment indigenous

Table 11. Regression models predicting post-treatment indigenous species based on pre-treatment cover of regressor variables. Empty cells represent non-significant regressor variables.

		Regressor variables										
Site	Predicted variables	Intercept	Site	Transect (1)[1]	Perennial grass (0 to 76)	Idaho fescue (0 to 50)	Forbs (0 to 50)	Species richness (0 to 8)	Species diversity (0 to 2.26)	Spotted knapweed (0 to 100)	Spotted knapweed[2] (0 to 10,000)	R^2
1	Perennial grass[2]	2.12			0.52		-0.19	0.16		-0.009	-0.00005	0.44
2	Perennial grass	2.12			0.52		-0.19	0.16		0.028	-0.0004	0.44
1	Idaho fescue	1.55				0.63				-0.018		0.63
2	Idaho fescue	1.55				0.63				-0.008		0.63
1	Forbs	1.33	0.00	-0.58[3] (4.3)			0.53					0.46
2	Forbs	1.33	-0.94	-0.58 (4.3)			0.53					0.46
1	Species richness	1.61	0.00					0.58				0.40
2	Species richness	1.61	-0.69					0.58				0.40
1	Diversity	0.37					-0.041	0.13		0.007	-0.00008	0.22
2	Diversity	0.37					-0.041	0.13		0.007	-0.00008	0.22

[1] Possible range of values for each parameter on m^{-2} basis.

[2] A model predicting IPG cover (after treatment) based on cover of IPG, Forbs, Species Richness, CEMA, and CEMA^2 prior to treatment includes:
Site1; $y = 2.17(B_0) + 0.52(B_1) - 0.19(B_2) + 0.16(B_3) - 0.009(B_4) - 0.00005(B_5)$, where B_0 is the intercept, B_1 is the cover of IPG prior to treatment, B_2 is the of cover of forbs, B_3 is the species richness, B_4 the cover of CEMA, and B_5 is the cover of CEMA^2 at Site 1;
Site 2; $y = 2.17(B_0) + 0.52(B_1) - 0.19(B_2) + 0.16(B_3) + 0.028(B_4) - 0.0004(B_5)$, where B_0 is the intercept, B_1 is the cover of IPG prior to treatment, B_2 is the of cover of forbs, B_3 is the species richness, B_4 the cover of CEMA, and B_5 is the cover of CEMA^2 at Site 2.

[3] Means represent the average of ten transects across site with standard deviations provided below means in table.

species richness was positively associated with pre-treatment indigenous species richness (Table 11). Specifically, for each 1% increase in indigenous species richness, indigenous species richness increased by about 58% two years after treatment.

Predicted indigenous species diversity was negatively associated with forb cover and the spotted knapweed quadratic component, but positively related to species richness and spotted knapweed cover alone (Table 11). Specifically, each 1% increase in pre-treatment forb cover was associated with a decrease in indigenous species diversity by 0.041 Shannon-Weaver's diversity index units. For 1% unit increase in indigenous species richness, indigenous species diversity increased by 0.13 Shannon-Weaver's diversity index units. For each 1% increase in adult spotted knapweed cover, diversity increased by 0.007 Shannon-Weaver's diversity index units. For each 1% increase in the spotted knapweed quadratic component, diversity decreased by 0.00008 diversity index units.

Biomass

Indigenous perennial grass biomass prior to treatment was positively related to post-treatment forb cover and both positively and negatively related to spotted knapweed (Table 12). For each one unit increase in forb biomass, indigenous perennial grass biomass increased by 2.7 g m^{-2}. Each one unit increase in spotted knapweed biomass was associated with a predicted 0.07 g m^{-2} decrease in indigenous perennial grass biomass at Site 1. At Site 2, for each one unit increase in spotted knapweed biomass, indigenous perennial grass biomass increased by 0.40 g m^{-2}. Each one unit increase in the spotted knapweed quadratic component was associated with a predicted 0.0007 g m^{-2} increase in

Table 12. Regression models predicting post-treatment indigenous species based on pre-treatment biomass (g m^{-2}) of regressor variables. Empty cells represent non-significant regressor variables.

		Regressor variables										
Site	Predicted variables	Intercept	Site	Transect (1)[1]	Perennial grass (0 to 380)	Idaho fescue (0 to 360)	Forbs (0 to 150)	Species richness (0 to 5)	Species diversity (0 to 2.26)	Spotted knapweed (0 to 1,280)	Spotted knapweed[2] (0 to 163,840)	R^2
1	Perennial grass[2]	14.7					2.7			-0.07	0.0007	0.32
2	Perennial grass	14.7					2.7			0.40	-0.004	0.32
1	Idaho fescue	-1.2			5.4							0.39
2	Idaho fescue	-1.2			5.4							0.39
1	Forbs	3.2		-2.5[3] (7.5)			-5.0	4.0		-0.18		0.38
2	Forbs	3.2		-2.5 (7.5)			-5.0	4.0		0.02		0.38
1	Species richness	32.8								-0.26		0.29
2	Species richness	32.8								-0.12		0.29
1	Diversity	3.1		-3.6 (3.9)	2.2					0.11	-0.0015	0.52
2	Diversity	3.1		-3.6 (3.9)	2.2					0.24	-0.0015	0.52

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting pre-treatment IPG biomass based on biomass of Forbs, CEMA, and CEMA^2 prior to treatment includes:
Site1; $y = 14.7(B_0) + 2.7(B_1) - 0.07(B_2) + 0.0007(B_3)$,
where B_0 is the intercept, B_1 is the biomass of Forbs prior to treatment, B_2 is the biomass of CEMA, B_3 is the biomass of CEMA^2 at Site 1;
Site 2; $y = 14.7(B_0) + 2.7(B_1) + 0.38(B_2) - 00004(B_3)$,
where B_0 is the intercept, B_1 is the biomass of Forbs prior to treatment, B_2 is the biomass of CEMA, B_3 is the biomass of CEMA^2 at Site 2.

[3] Means represent the average of ten transects across site with standard deviations are provided below means in table.

indigenous perennial grass biomass at Site 1 and a 0.004 g m^{-2} decrease at Site 2.

Predicted Idaho fescue biomass was positively related to indigenous perennial grass biomass from year one (Table 12). For each one unit increase in indigenous perennial grass biomass, Idaho fescue biomass increased by 5.4 g m^{-2}.

Each one unit increase in pre-treatment forb biomass was associated with a predicted 5.0 g m^{-2} decrease in post-treatment forb biomass (Table 12). Each one unit increase in indigenous species richness based on biomass was associated with an increase in forb biomass by 4.0 g m^{-2} at both sites. Forb biomass was negatively related to spotted knapweed biomass (-0.18 g m^{-2}) at Site 1 and positively related to spotted knapweed biomass (0.02 g m^{-2}) at Site 2. Effect of transect was negatively associated with forb biomass.

Predicted indigenous species richness based on biomass was negatively related to spotted knapweed biomass (Table 12). Specifically, each one unit increase in spotted knapweed biomass was associated with a decrease in indigenous species richness by 0.26 g m^{-2} and 0.12 g m^{-2} at Sites 1 and 2, respectively.

Post-treatment indigenous species diversity was positively associated with perennial grass biomass and the spotted knapweed biomass alone, but negatively related to the spotted knapweed quadratic component (Table 12). Each one unit increase in indigenous perennial grass biomass was associated with an increase in indigenous species diversity by 2.2 Shannon-Weaver's diversity index units. For each one unit increase in spotted knapweed biomass, indigenous species diversity increased by 0.11 and 0.24 Shannon-Weaver's diversity index units at Sites 1 and 2, respectively. The spotted

knapweed quadratic component was related to a decrease of 0.0015 Shannon-Weaver's diversity index units. Indigenous species diversity was negatively related to transect.

Brome species

Density. Regression models were generated to predict density of post-treatment brome species based on pre-treatment brome species (Table 13). For each one unit increase in pre-treatment brome density, post-treatment brome increased by 10.6 tillers m^{-2} at Site 1. At Site 2, each one unit increase in pre-treatment brome was associated with a 1.1 tillers m^{-2} increase in post-treatment brome. For each one unit increase in the brome quadratic component, post-treatment brome decreased by 0.006 tillers m^{-2} at Site 1. Each one unit increase in spotted knapweed was associated with a predicted 3.9 tillers m^{-2} increase in brome at Site 1. At Site 2, each one unit increase in spotted knapweed was associated with a 1.4 tillers m^{-2} increase in brome.

Cover. For each 1% increase in pre-treatment brome cover, predicted post-treatment brome cover increased by 141% at Site 1 (Table 13). For each 1% increase in the brome quadratic component, post-treatment brome decreased by 11% at Site 1. At Site 2, each 1% increase in spotted knapweed cover was associated with a 0.8% increase in brome.

Biomass. For each one unit increase in pre-treatment brome biomass, post-treatment brome biomass increased by 0.05 g m^{-2} at Site 1 (Table 13). At Site 2, for each one unit increase in spotted knapweed, post-treatment brome decreased by 2.0 g m^{-2}. Each one unit increase in the spotted knapweed quadratic component was associated with a 2.5 x 10^{-5} g m^{-2} increase in brome.

Table 13. Regression models predicting post-treatment non-indigenous species based on density (plants m^{-2}), cover, and biomass (g m^{-2}) of regressor variables. Empty cells represent non-significant regressor variables.

		Regressor variables					
Site	Predicted variables (Brome spp.)	Intercept	Brome[1] (0 to 1,950)[2] (0 to 12) (0 to 78)	Brome[2] (0 to 38,025) (0 to 100) (0 to 608)	Spotted knapweed (0 to 1,170) (1 to 100) (0 to 1,280)	Spotted knapweed[2] (0 to 313,290) (0 to 10,00) (0 to 163,840)	R^2
1	Density[3]	-633	10.6	-0.006	3.9		0.30
2	Density	-220	1.1	0.00	1.4		0.31
1	Cover	-0.40	1.41	-0.11	0.00		0.13
2	Cover	-0.11	0.00	0.00	0.008		0.10
1	Biomass	43.0	0.05		0.00		0.15
2	Biomass	181	0.00		-2.0	2.5×10^{-5}	0.62

[1] Represents a pre-treatment parameter based on density, cover, and biomass to predict post-treatment Brome density, cover, and biomass, respectively.

[2] Possible range of values for each parameter based on density, cover, and biomass on a m^{-2} basis, respectively.

[3] A model predicting pre-treatment brome density based on density of Brome, Brome², and CEMA, prior to treatment includes:

Site1; $y = -633(B_0) + 10.6(B_1) - 0.006(B_2) + 3.9(B_3)$,

where B_0 is the intercept, B_1 is the biomass of pre-treatment Brome, B_2 is the biomass of pre-treatment Brome², and B_3 is the biomass of CEMA at Site 1;

Site 2; $y = -220(B_0) + 1.1(B_1) + 1.4(B_2)$,

where B_0 is the intercept, B_1 is the biomass of pre-treatment Brome, and B_2 is the biomass of CEMA at Site 2.

Predicting Biomass Using Cover

Post-treatment perennial grass biomass was positively associated to pre-treatment indigenous perennial grass cover alone, but negatively associated to the indigenous perennial grass quadratic component (Table 14). For each one unit increase in pre-treatment indigenous perennial grass cover, predicted post-treatment perennial grass biomass increased by 57.2 g m^{-2} at both sites. For each one unit increase in the pre-treatment perennial grass quadratic component based on cover, post-treatment perennial grass biomass decreased by 0.86 g m^{-2} at both sites.

Predicted post-treatment Idaho fescue biomass was positively associated to pre-treatment Idaho fescue cover alone, but negatively associated to the Idaho fescue quadratic component (Table 14). At both sites, each one unit increase in pre-treatment Idaho fescue cover was associated with a 53.2 g m^{-2} increase in post-treatment Idaho fescue biomass. For each one unit increase in the Idaho fescue quadratic component based on cover, post-treatment Idaho fescue biomass decreased by 0.63 g m^{-2}.

Forb biomass after treatment was positively related to forb cover prior to treatment (Table 14). Each one unit increase in pre-treatment forb cover was associated with a 24.1 g m^{-2} increase in post-treatment forb biomass at both sites.

For each one unit increase in pre-treatment brome cover, post-treatment brome biomass increased by 40.5 g m^{-2} at Site1 (Table 14). For each one unit increase in the pre-treatment brome quadratic component based on cover, post-treatment brome biomass decreased by 6.5 g m^{-2}. Regression analysis showed lack of fit when predicting brome production from brome cover at Site 2.

Table 14. Regression models predicting post-treatment biomass (g m^{-2}) indigenous species based on pre-treatment cover of regressor variables. Empty cells represent non-significant regressor variables.

		Regressor variables											
Site	Predicted variable	Intercept	Perennial grass (0 to 76)[1]	Perennial grass^2 (0 to 5,776)	Idaho fescue (0 to 50)	Idaho fescue^2 (0 to 2500)	Forb (0 to 50)	Forb^2 (0to2500)	Brome (0 to 12)	Brome^2 (0 to 144)	Spotted knapweed (0 to 100)	Spotted knapweed^2 (0 to 10,000)	R^2
1	Perennial grass[2]	571.1	57.2	-0.86									0.35
2	Perennial grass	571.1	57.2	-0.86									0.35
1	Idaho fescue	69.0			53.2	-0.63							0.71
2	Idaho fescue	69.0			53.2	-0.63							0.71
1	Forbs	24.4					24.1						0.13
2	Forbs	24.4					24.1						0.13
1	Brome	-4.74							40.5	-6.5			0.31
2	Brome			Lack	of	Fit							0.00

[1] Possible range of values for each parameter on a m^{-2} basis.

[2] A model predicting pre-treatment brome density based on density of IPG, and IPG^2 prior to treatment includes:

Sites 1 and 2 $y = -571(B_0) + 57.2(B_1) - 0.86(B_2)$,

where B_0 is the intercept, B_1 is the biomass of pre-treatment IPG, and B_2 is the biomass of pre-treatment IPG^2 at Site 1;

Biomass Optimization Model

Pre-treatment spotted knapweed cover was used as the regressor variable to predict pre- and post- treatment indigenous perennial grass biomass (Figure 13). At zero spotted knapweed cover, predicted pre-treatment grass biomass was about 2250 kg ha^{-1} and post-treatment grass biomass was about 1400 kg ha^{-1}. Pre-treatment grass biomass decreased most rapidly as pre-treatment spotted knapweed cover increased to about 50%. At that point, predicted grass biomass was about 800 kg ha^{-1}. After that point, predicted grass biomass declined more slowly as spotted knapweed cover increased. The regression model predicted that areas with 95% pre-treatment spotted knapweed cover would produce 200 kg ha^{-1} indigenous perennial grass prior to treatment. Post-treatment grass biomass decreased linearly. Predicted post-treatment grass biomass was about 500 kg ha^{-1} at maximum spotted knapweed cover (95%).

Discussion

Predicting Indigenous Species

Weed managers are searching for useful models on which to base their management decisions (Archer 1989, Laycock 1991, Schlatterer 1989). In agroecosystems, predictive models have been used to assess economic thresholds to better manage a wide range of important crops. For example, Maxwell et al. (1994) developed bioeconomic models to optimize control strategies of wild oats (*Avena fatua* L.) in barley production. Knezevic et al. (1994) determined redroot pigweed (*Amaranthus retroflexus* L.) did not reduce corn production when weed emergence occurred after the corn's 7-leaf stage. However, the use of predictive models to optimize rangeland weed management has

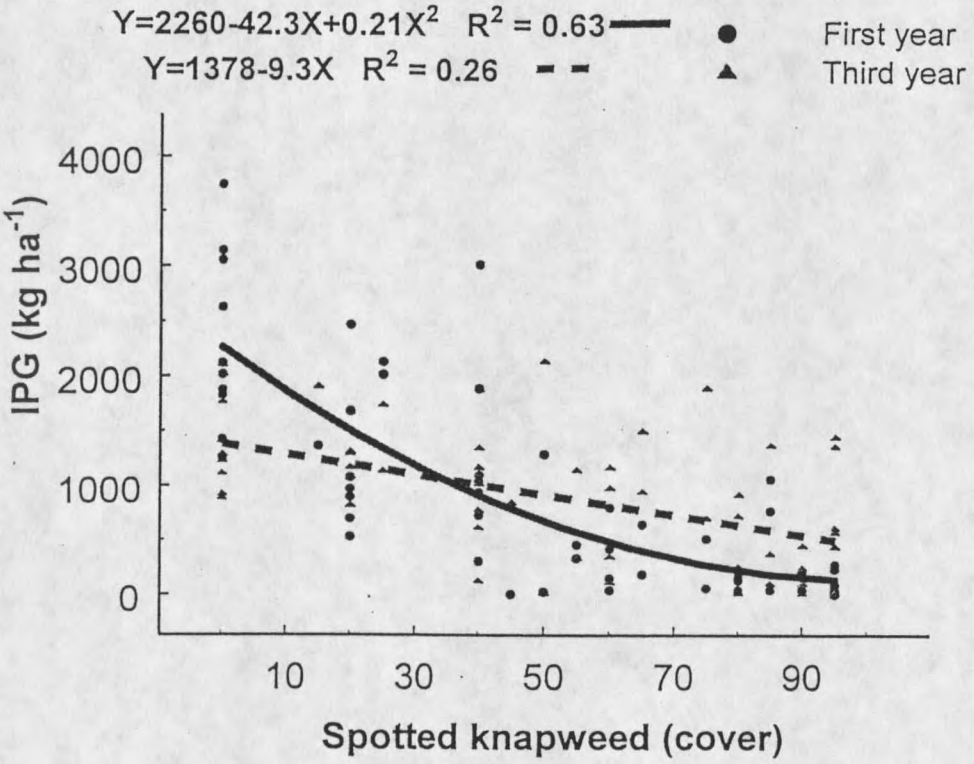

Figure 13. Biomass model comparing differences between pre-treatment grass biomass and post-treatment grass biomass.

been limited. Peat and Bowes (1994) predicted that at biomass above 290 kg ha^{-1} of fringed sagebrush (*Artemisia frigida* Willd.), it becomes economically viable to control this plant using picloram. Keane (1987) developed successional pathway models to predict plant coverage based on treatment and pre-disturbance plant composition.

This study indicated that it may be feasible to use pre-management plant community data to predict post-management plant community response for spotted knapweed-infested rangeland using picloram. The best predictive models for assessing post-management indigenous perennial grass, Idaho fescue, and indigenous species richness were based on density. The best models predicting post-management forbs and indigenous species diversity were based on cover and biomass, respectively. In four out of the five models, for a given post-management parameter, an important predictor in the model was its pre-management regressor variable. For example, pre-management indigenous grass density was the best predictor of post-management grass density. Additionally, pre-management spotted knapweed was a relatively unimportant predictor in most models. Incorporating environmental factors other than plant community composition into models may enhance their predictive abilities. Although this study was conducted using picloram to control spotted knapweed, other management strategies and/or other weeds could be tested in a similar fashion to predict post-management plant community response.

Indigenous Species Richness and Indigenous Species Diversity

The model predicting indigenous species diversity based on density predicted an increase in indigenous species diversity two years after management. However, the

species presence data along transect indicated a decrease in 14 out 30 post-management indigenous forb and grass species (Tables 6, 7, 8, and 9). Five out of 30 species (16%) were no longer present following the picloram treatment. Four of these species were indigenous forbs. Rice et al. (1997) detected transitory declines in both species richness and diversity in response to picloram. However, this relationship may be an artifact of using Shannon-Weaver's diversity index which sums the proportion of individuals present and provides an "average diversity" (Pielou 1966). Presumably an increase in post-management grass presence (e.g., western wheatgrass, Idaho fescue, needle-and-thread, etc.) may account for this simultaneous gain in indigenous species diversity and loss of indigenous species richness (number of species), post-management. It is also important to note that different measurements of diversity would likely yield different predictive models.

Biomass Optimization Model

Many land management programs are aimed at maximizing grass production. These weed management programs must use our understanding of the change in grass biomass as a response to management. We attempted to use easily collected pre-treatment data (i.e., spotted knapweed cover) to predict pre- and post-treatment grass biomass. To identify the relative difference in biomass production between years, we compared difference between the predicted pre-treatment and post-treatment biomass. The integration of these models indicated that there would be a decrease in post-treatment grass biomass at spotted knapweed cover below 35%. We suspect that at low spotted knapweed cover, interference between spotted knapweed and indigenous grass was low

(Velagala 1996). Therefore, spotted knapweed removal did not result in an increase in grass biomass. We speculate that the decrease in grass biomass was associated with other environmental factors, such as weather. However, since the study was conducted without a control (no herbicide), it is impossible to determine whether this response is a result of year-to-year variations in the plant community or a response due to treatment.

Above 35% spotted knapweed cover, regressions predicted greater post-treatment grass biomass than the pre-treatment biomass. In this case, spotted knapweed may have influenced grass production, and its removal may have favored grasses. In either case, including other environmental factors in the models should improve our ability to predict post-management outcomes based on pre-management conditions. Furthermore, we believe it may be possible to identify the cumulative predictive biomass gain (after treatment) by developing a biomass optimization model for each year of herbicide control. Once the change in biomass is predicted and the predictions verified, economic analysis based on the value of the biomass change may be possible using this method prior to imposing weed management.

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