



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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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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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. ramossissima* 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 *Metzneria paucipunctella* 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 m² (control) to below 8 per m² (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 post-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). Similarly, 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 cm³ 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

