Using seed rate and plant densities to enhance intermediate wheatgrass establishment in spotted knapweed dominated rangeland
by Rajendra Prasad Velagala

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Agronomy
Montana State University

Abstract:
Establishing competitive plants is essential for restoring spotted knapweed infested rangeland. Revegetation attempts typically fail because of weed competition during the initial stages of establishment. First, we hypothesized that competitive interactions can be shifted from spotted knapweed to intermediate wheatgrass by increasing wheatgrass seedling density over 1000 plants m-2. Spotted knapweed and intermediate wheatgrass were grown in addition series mixtures to assess their interference at low (0 to 1000 plants m-2) versus high (1000 to 10000 plants-2) densities. lathe spring of 1995, 7 densities (0, 100, 500, 1000, 3000, 6000, and 10000 plants m-2) of each species were seeded in a factorial arrangement (49 density combinations) in a randomized-complete-block design and replicated 3 times at 2 sites in Montana. Plants were grown in pots (2250 mm2 X 380 mm deep) for 60 days before harvesting. Regressions predicting shoot weight, root weight, total weight, leaf area, and root length were calculated using 1) low knapweed:low wheatgrass, 2) low knapweed:high wheatgrass, 3) high knapweed:low wheatgrass, and 4) high knapweed:high wheatgrass densities. Regression coefficients indicated intraspecific interference was most important in predicting intermediate wheatgrass weight at both sites. At the wet site (457 mm, annually), interspecific interference only occurred at high spotted knapweed densities. At the dry site (305 mm, annually), interspecific interference occurred at low densities. Increasing densities of intermediate wheatgrass from low to high removed the effect of spotted knapweed on intermediate wheatgrass where interspecific interference occurred.

The objective of our second study was to compare intermediate wheatgrass initial establishment at 4 seed rates in combination with tillage and/or glyphosate in spotted knapweed infested rangeland. We hypothesized that the establishment of intermediate wheatgrass seedlings would be greatest at highest densities. Treatments included glyphosate (with and without), tillage (with and without), and 4 seed rates (0, 500, 2500, 12500 m"2) of intermediate wheatgrass. Treatments were factorially applied in a randomized-complete-block design with 4 blocks at Bozeman and at Hamilton, Mont. Treatments were applied during the fall of 1995, and were harvested during the summer of 1996. Intermediate wheatgrass establishment did not occur at seed rates of 500 m-2 under any treatment or treatment combination. Plots receiving the highest seed rate had higher wheatgrass density than those receiving lower rates at Hamilton. At the highest seeding rate, tillage and tillage plus glyphosate increased intermediate wheatgrass densities over other treatments at Bozeman. Our revegetation study suggests that increasing grass seed rate will facilitate initial establishment of desirable grasses in spotted knapweed infested rangeland.

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APPROVAL

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding the 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

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CHAPTER 1

LITERATURE REVIEW

Introduction

Spotted knapweed (*Centaurea maculosa* Lam.) is a deeply taprooted perennial Eurasian weed rapidly invading rangeland throughout the northwestern United States and Canada (Watson and Renney 1974, Strang et al. 1979, Harris and Cranston 1979). Spotted knapweed was growing along Middle Creek Road south of Bozeman in 1927, and the first forest service record for the Gallatin National Forest was in 1931 (Roche' and Talbott 1986). Spotted knapweed has been spreading at about 27% per year and infests about 2.2 million hectares of grassland in Montana (Chicoine et al. 1985, Lacey et al. 1989). It also infests about 10,000 hectares in eastern Washington (Roche' 1988) and British Columbia (Cranston 1988) and can be found throughout most of the northwestern United States. This species reduces forage production (Watson and Renney 1974, Harris and Cranston 1979), plant species diversity (Tyser and Key 1988), and wildlife habitat (Bedunah and Carpenter 1989). Increases in bare-ground (Tyser and Key 1988), surface water runoff and stream sedimentation (Lacey et al. 1989), and management costs are also associated with knapweed infestations.

Life history of spotted knapweed

Spotted knapweed bolts in May after overwintering as rosettes. Immature flowers first appear in mid-June. The flower heads open approximately three weeks after maturity (Watson and Renney 1974). Flowering begins in July, and are cross-pollinated by insects.

Mature seeds are produced 18 to 26 days after fertilization (Watson and Renney 1974). It is disseminated as dry, indehiscent single seeded fruit called an achene. These achenes are referred to as cypselas in spotted knapweed because they are produced from an epigynous flower. Spotted knapweed has high seed output and longevity, which enables regeneration after herbicidal control (Watson and Renney 1974, Schirman 1981, Davis et al. 1993, Kalisz and Mcpeek 1993). Under favorable conditions spotted knapweed can produce up to 349 seeds per plant with 80% viability (Watson and Renney 1974), and up to 48,000 seeds m^{-2} (Schirman 1981). The seeds are disseminated up to 1 m by the flickering motion caused when the plants are moved abruptly (Strang et al. 1979). Motorized vehicles are partly responsible for the long distance spread of spotted knapweed in North America (Mass 1985, Watson and Renney 1974).

Nolan and Upadhyaya (1988) reported three types of germination behavior in freshly harvested spotted knapweed and diffuse knapweed (*Centaurea diffusa* Lam.) seeds (non-dormant, light-sensitive dormant, and light-insensitive dormant seeds). Knapweed seeds imbibe water and germinate within 18 hours under optimum conditions (Chicoine 1984). Maximum germination of seeds occurred at soil moisture levels of 118 to 127% of field capacity in the soil mixture used at temperatures ranging from 10 to 28^0 C. They germinate in the fall and spring when soil moisture conditions are favorable. Seedlings that germinate in fall overwinter as rosettes and flower the following June. Whereas, seedlings established in the spring usually flower the following season (Schirman 1981).

Early germination and rapid growth rates enable knapweeds (*Centaurea* spp.) to capture resources before their competitors (Sheley et al. 1993). Polymorphic germination behavior is a common phenomenon among weed species, which insures seed germination for an extended period of time (Bewley and Black 1982). Knapweeds display germination and emergence polymorphism, which allows them to avoid intraspecific competition and occupy all available safe-sites by developing a hierarchy of age classes within the population (Sheley and Larson 1996).

Economic impact

Spotted knapweed is well-adapted to a wide range of climatic and environmental conditions (Watson and Renney 1974, Chicoine et al. 1985). This weed is a strong competitor and relatively drought tolerant (Berube and Myers 1982). Chicoine et al. (1985) estimated that 18.8 million hectares could support spotted knapweed infestations in Montana. The direct impact of spotted knapweed infestations in Montana is estimated at about $ 11 million annually (Hirsch and Leitch 1996). Spotted knapweed can impact elk winter range by displacing desirable forage species (Harris and Cranston 1979, Watson and Renney 1974).

Spotted knapweed control measures

Cultural control

Plowing: Spears et al. (1980) found that spotted knapweed seeds did not emerge when the seeds were placed 5 cm below the soil surface. Spotted knapweed seeds can be depleted through attrition if seed production is prevented or significantly reduced by repeated mowing at the flowering stage (Watson and Renney 1974). Spotted knapweed infested land should be reseeded with a vigorous grass or legume species after plowing to suppress reinfestation (Harris and Cranston 1979).

Burning: Dry structures of knapweeds persist for years and they burn readily (Carpenter 1986). Strang et al. (1979) reported that spotted knapweed rarely invades burned areas. According to Zednai (1968) spotted knapweed seed germination was reduced from 68 to 3% after a burn. However, Chicoine (1984) reported that burning did not reduce the seed bank of a natural spotted knapweed population.

Grazing: Nutrient content of spotted knapweed is adequate to meet livestock needs during early summer and spring when the stems are succulent and actively growing (Kelsey and Mihalovich, 1987). However, Kelsey and Mihalovich (1987) also reported that cnicin (sesquiterpene lactone) in leaves imparts a bitter taste and may decrease palatability. Low to moderate levels of grazing of spotted knapweed by sheep, goats and cattle have been reported in Montana (Cox 1989, Robertson 1989). 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. They also found that the number of spotted knapweed seeds in the soil were reduced after three years of intensive sheep grazing.

Biological control

In Eurasia, a complex of monophagous insects feed on knapweed. As a result knapweed populations exist in small patches. A major factor contributing to the success of knapweed in North America is a lack of natural enemies. The first biological control agent to be employed against knapweeds in United States and Canada was European seed head fly, *Urophora affinis* (Harris 1980). In 1973, this Tephritidae fly was released in Montana and Oregon (Story and Anderson 1978, Maddox 1982). Story (1989) reported that if screening tests proceed satisfactorily, a total of 11 and 10 insects will be introduced against spotted and diffuse knapweed, respectively, by 1995. Seed production of spotted knapweed has been reduced by 50-75% by insects feeding on seed heads (Story et al. 1991). Harris (1980) reported up to 95% reduction in seed production in British Columbia. *Metzneria paucipunctella*, a seed head moth released in 1973 in British Columbia, has spread in Montana, Idaho, Oregon and Washington.

Harris (1980) reported that seed head flies were ineffective in reducing knapweed populations. Schirman (1981) estimated that only 0.1% of survival of seeds produced was required to maintain infestations. In a growth chamber study, Sheley and Jacobs (1996) found that 45% control of spotted knapweed did not alter the competitive relationship between spotted knapweed and bluebunch wheatgrass. Ninety percent control of spotted knapweed was necessary to shift the competitive balance in favor of bluebunch wheatgrass.

Root feeding insects reduce root storage capacity, uptake of water and nutrients, and enhance susceptibility to pathogens. *Agapeta zoegana* L., *Pelochrista medullana* Stgr., *Pterolonche inspersa* Stgr., *Cyphocleonus achates* Fahr., all root feeding insects were selected for introduction between 1979 and 1983 (Muller et al. 1988). *Agapeta zoegana* is the most promising insect introduced for control of spotted knapweed, heavy attack by the larvae of this moth can cause death to small plants (Muller et al. 1988). Harris and Cranston (1979) suggested that the establishment of at least six natural enemies would be necessary for effective biological control of spotted knapweed.

Plant pathogens have been investigated for their potential as biological control agents. Host specificity is one of the major problems limiting the use of plant pathogens like *Puccinia* spp. (Watson and Clement 1986). *Sclerotinia sclerotiorum* (Lib) de Bary, is a soil borne fungus with a wide host range (Purdy 1979). Jacobs et al. (1996) found that *Sclerotinia sclerotiorum* reduced spotted density by 68 to 80% without reducing bluebunch wheatgrass density. They also found that *Sclerotinia sclerotiorum* reduced spotted knapweed per plant weight. Long-term control of spotted knapweed using biological control agents may be effective in combination with other weed control methods (Cuda et al. 1989).

Chemical control

Long-term, sustained control of spotted knapweed is difficult to achieve. Two,4-D (2,4-diclorophenoxy acetic acid) applied from bolt to early flowering stage provides adequate control of spotted knapweed (Lacey et al. 1986). Reapplication of 2,4-D is necessary to control regrowth of older established plants (Lacey 1985). Ester formulations of 2,4-D are more effective than amines (Belles et al. 1978). Dicamba (3,6-dicloro-o-anisic acid) gives 2 to 3 years control of spotted knapweed (Fay et al. 1989).

Currently, some rangeland managers rely on repeated application of persistent herbicides like picloram (4-amino-3,5,6 trichloro-2-pyridinecarboxylic acid) to control spotted knapweed. It is the most effective herbicide for long term control of spotted knapweed (Lacey 1985). The efficacy of picloram depends on soil conditions, especially the presence of organic matter, moisture and temperature (Goring and Haymaker 1971). The time between application of picloram and occurance of precipitation greatly influence's loss of picloram (Hall et al. 1968). Davis (1990) found that picloram applied at 0.07, 0.11, 0.14, 0.22, 0.25, and 0.28 kg a.i./ha provided 4 and 7 years of control with 200 and 700% increase in grass yield, respectively, at two study sites in Montana. However, after picloram dissipates, spotted knapweed invades from its seed bank (Davis et al. 1993). Sheley and Jacobs (1997) found that picloram increased grass yield by an average of 1500 kg ha^{-1} and reduced spotted knapweed density to zero. Clopyralid is more selective than picloram and has a shorter soil residual period, it provided 100% control of spotted knapweed 1 year following application without affecting native forbs (Lacey et al. 1989).

Long-term chemical control is cost effective only on highly productive rangeland with a residual grass understory (Griffith and Lacey 1991). However, reseeding of spotted knapweed infested areas following herbicide treatment increases forage production by suppressing knapweed seedling establishment (Hubbard 1975).

Revegetation of spotted knapweed infested rangeland

In areas where residual plant species are absent, herbicides (Davis et al. 1993, Griffith and Lacey 1991), natural enemies (Story et al. 1991, Cuda et al. 1989), or sheep grazing (Cox 1989) do not provide long-term control of spotted knapweed because desirable species are not available to occupy niches opened by the control procedure (James 1992, Sheley et al. 1996). In these areas, establishing competitive plants is essential for successional management of spotted knapweed and the restoration of desirable plant communities (Sheley et al. 1996). Revegetation with aggressive species has been shown to inhibit the reinvasion of knapweeds (Borman et al. 1991, Hubbard 1975, Larson and McInnis 1989).

Typically, revegetation of spotted knapweed infested rangeland involves late-fall discing and application of a non-selective herbicide, such as glyphosate (n-phosphomethyl glycine) (Sheley and Larson 1994), after weeds emerge. Then, desirable grasses are immediately seeded. Grass and knapweed germination and emergence occur the following spring. As long as there is adequate spring precipitation, both grass and knapweed seedlings survive. If grass seedlings survive until mid-summer, a reduced rate of 2,4-D or mowing is usually applied to weaken spotted knapweed. Seedling establishment is the most vulnerable stage in the rehabilitation of plant communities in arid and semiarid regions (Call and Roundy 1991). Rehabilitation with desirable vegetation typically fails because of weed competition during these initial stages of establishment (Borman et al. 1991, James 1992).

Density dependent interference

Crop density may influence weed competition. Increasing seed rate has been shown to decrease weed growth and weed-caused crop loss (Godel 1935, IRRI 1993, Thurston 1962, Pfeiffer and Holmes 1961). Rangeland weeds are more competitive than perennial grass seedlings (Harris 1967, Prather and Callihan 1991). For example, Prather and Callihan (1991) found that yellow starthistle (*Centaurea solstitialis* L.) was more competitive than pubescent wheatgrass (*Thinopyrum intermedium* spp. *barbulatum* (Schur) Barkw. and D. R. Dewey) at densities up to 390 plants m^{-2}. However, they also found the aggressiveness of pubescent wheatgrass increased with increasing wheatgrass densities. In a growth chamber, Jacobs et al. (1996) found that bluebunch wheatgrass (*Agropyron spicatum* (Pursh.) Scribn. and Smith.) was 4 times more competitive than spotted knapweed seedlings at densities considered high for seedings (1000-5000 plants m^{-2}). Although crop-weed interactions at agronomic planting densities have been widely studied, very little is known about interference at extremely high densities (Zimdall 1980).

Objectives of study

The overall objective of this study was to determine the potential to use plant density as a tool to facilitate the establishment of desirable grasses in spotted knapweed infested rangeland. Specific objectives were to 1) quantify the interference between intermediate wheatgrass (*Elytriga intermedia* (Host) Nevski) and spotted knapweed, 2) compare the change in interference between these species at low versus high densities, and 3) compare intermediate wheatgrass density and biomass at four seeding rates in combination with tillage and/or glyphosate application. We hypothesized that competitive interactions can be shifted from spotted knapweed to intermediate wheatgrass by increasing wheatgrass seedling density to over 1000 plants m^{-2}. In the revegetation study, we expected intermediate wheatgrass seedling density to be highest and spotted knapweed biomass to be lowest at the highest densities of wheatgrass.

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CHAPTER 2

INTERFERENCE BETWEEN SPOTTED KNAPWEED AND INTERMEDIATE WHEATGRASS AT LOW VERSUS HIGH DENSITIES

Introduction

Spotted knapweed (*Centaurea maculosa* Lam.) is a deep taprooted perennial Eurasian weed rapidly invading rangeland throughout the northwestern United States and Canada (Watson and Renney 1974, Strang et al. 1979, Harris and Cranston 1979). Spotted knapweed has been spreading at about 27% per year and infests about 2.2 million hectares of grassland in Montana alone (Chicoine et al. 1985, Lacey et al. 1989). This species reduces forage production (Watson and Renney 1974, Harris and Cranston 1979), plant species diversity (Tyser and Key 1988) and wildlife habitat (Bedunah and Carpenter 1989). Increases in bare-ground (Tyser and Key 1988), surface water runoff (Lacey et al. 1989), and management costs are also associated with knapweed infestations.

Spotted knapweed is adapted to a wide range of climatic and environmental conditions (Watson and Renney 1974, Chicoine et al. 1985). This weed is a strong competitor and relatively drought tolerant (Berube and Myers 1982). It has high seed output and longevity, which enables regeneration after herbicidal control (Watson and Renney 1974, Schirman 1981, Davis et al. 1993, Kalisz and McPeek 1993). Early germination and rapid growth rates enable knapweeds (*Centaurea spp.*) to capture resources before their competitors (Sheley et al. 1993). Knapweeds display germination and emergence polymorphism, which allows them to avoid intraspecific competition and occupy all available safe-sites by developing a hierarchy of age classes within the population (Sheley and Larson 1996).

In areas where residual plant species are absent, herbicides (Davis et al. 1993, Griffith and Lacey 1991), natural enemies (Story et al. 1991, Cuda et al, 1989), or sheep grazing (Cox 1989) do not provide long-term control of spotted knapweed because desirable species are not available to occupy niches opened by the control procedure. In these areas, establishing competitive plants is essential for successional management of spotted knapweed and the restoration of desirable plant communities (Sheley et al. 1996). Revegetation with aggressive species has been shown to inhibit the re-invasion of knapweeds (Hubbard 1975, Larson and McInnis 1989).

Typically, revegetation of spotted knapweed infested rangeland involves late-fall discing and application of a non-selective herbicide, such as glyphosate (n-phosphomethyl glycine) (Sheley and Larson 1994), after weeds emerge. Desirable grasses are immediately seeded. Grass and knapweed germination and emergence occurs the following spring. As long as there is adequate spring precipitation, both grass and knapweed seedlings survive. If grass seedlings survive until mid-summer, a reduced rate of 2,4-D (2,4-diclorophenoxy acetic acid) or mowing is usually applied to weaken spotted knapweed. Rehabilitation with desirable vegetation typically fails because of weed competition during these initial stages of establishment (Borman et al. 1991).

Rangeland weeds are more competitive than perennial grass seedlings (Harris 1967, Prather and Callihan 1991). For example, Prather and Callihan (1991) found that yellow starthistle (*Centaurea solstitialis* L.) was more competitive than pubescent wheatgrass (*Thinopyrum intermedium* spp. *barbulatum* (Schur) Barkw. & D. R. Dewey) at densities up to 390 plants m^{-2}. However, they also found the aggressiveness of pubescent wheatgrass increased with increasing wheatgrass densities. In a growth chamber, Jacobs et al. (1996) found that bluebunch wheatgrass was 4 times more competitive than spotted knapweed seedlings at densities considered high for seedlings (1000-5000 plants m^{-2}). Although crop-weed interactions at agronomic planting densities have been widely studied, little is known about interference at extremely high densities (Zimdall 1980).

The overall objective of this study was to determine the potential to use plant density as a tool to facilitate the establishment of desirable grasses in spotted knapweed infested rangeland. Specific objectives were to 1) quantify the interference between intermediate wheatgrass and spotted knapweed, and 2) compare the change in interference between these species at low versus high densities. We hypothesized that competitive interactions can be shifted from spotted knapweed to intermediate wheatgrass by increasing wheatgrass seedling density over 1000 plants m^{-2}.

Materials and Methods

Study sites

The study was conducted at two Montana State University research sites. Both sites lie on a Idaho fescue (*Festuca idahoensis* Elmer)-bluebunch wheatgrass habitat type (Mueggler and Stewart 1980). One site was at the Red Bluff Research Ranch (45^0 34' N, 111^0 40' W) located 8 km east of Norris, Mont. Elevation at the site is 1500 m. Average annual precipitation is 305 mm. Site 2 was at the Arthur H. Post Research Farm (45^0 41' N, 111^0 9' W). This farm is located 6.5 km west of Bozeman, Mont. Elevation at this site is 1463 m with an average annual precipitation of 457 mm. Precipitation and temperature were monitored within 6.5 km of each site during the study period (Table 1).

Interference

Monocultures and mixtures of spotted knapweed and intermediate wheatgrass were grown to assess their interference using addition series methodology. Density series were 0:0, 0:100, 0:500, 0:1000, 0:3000, 0:6000, 0:10000, 100:0, 100:100, 100:500, 100:1000, 100:3000, 100:6000, 100:10000, 500:0, 500:100, 500:500, 500:1000, 500:3000, 500:6000, 500:10000, 1000:0, 1000:100, 1000:500, 1000:1000, 1000:3000, 1000:6000, 1000:10000, 3000:0, 3000:100, 3000:500, 3000:1000, 3000:3000, 3000:6000, 3000:10,000, 6000:0, 6000:100, 6000:500, 6000:1000, 6000:3000, 6000:6000, 6000:10000, 10000:0, 10000:100, 10,000:500, 10,000:1000, 10000:3000, 10000:6000, 10000:10000 plants m^{-2} for spotted knapweed and intermediate wheatgrass, respectively. Density matrices were arranged in a randomized-complete-block design with 3 blocks (replications) at each site.

Seeds of spotted knapweed were collected from Deer Lodge County, Mont. in August 1989. 'Oahe' intermediate wheatgrass seeds were purchased from Circle S Seeds Inc., Three Forks, Mont. in March 1994. Seeds of intermediate wheatgrass and spotted knapweed were sown in plastic pots, each with 2250 mm^2 soil surface area and 380 mm deep. Pots provided minimal rooting restriction to knapweed plants grown for a similar duration (Sheley and Larson 1994). Pots were filled with pasteurized soil mixture consisting of 2/3 Farland silt loam (fine silty, mixed Typic Agriboroll), and 1/3 sand. The soil was saturated with water and allowed to equilibrate to column capacity in the greenhouse and then transferred to each site.

Pots were placed underground with the soil surface in pots level to that of the surrounding area. Seeds were broadcast on the soil surface of each pot during June 10 through June 14, 1995 at Red Bluff and June 16 through 20, 1995 at the Post Farm. Based on a preliminary emergence test, seeding densities were 2 times that of the desired plant densities. Seeds were manually arranged until a uniform distribution was achieved. Less than 2 mm depth of dry soil was used to cover seeds. Initially, pots were lightly watered and covered with clear plastic to ensure uniform seedling emergence. There was no additional watering. Plants were allowed to grow for 60 days.

Initial densities of spotted knapweed and intermediate wheatgrass were counted 1 week after emergence. Final harvesting involved manually shaking the dry soil from the roots, separating the species, and counting the number of plants of each species in each pot. Roots were cut from shoots, measured for total length (m) using a root length scanner (Comair Corp., Melbourne, Australia), dried to constant weight (48 hours, 60^0 C) and weighed (mg). Shoots and leaf material were scanned for surface area (cm^2) (Licor-3100 with conveyor belt, LI-COR, Inc. Lincoln, Neb.) and then dried to a constant weight and weighed (mg).

Addition series data were divided into low (0-1000 plants m^{-2}) and high (1000-10000 plants m^{-2}) density matrices for each species. Data were transformed to their inverse and incorporated into multiple linear regression models (Spitters 1983). Coefficients of determination, sums of squares, and residuals were evaluated to determine the most suitable model. Regressions were calculated using 1) low knapweed:low wheatgrass, 2) low knapweed:high wheatgrass, 3) high knapweed:low wheatgrass, and 4) high knapweed:high wheatgrass densities.

Regressions predicted shoot weight, root weight, total weight, leaf area and root length using harvest densities of spotted knapweed and intermediate wheatgrass as independent variables. Models were of the form:

$$w_s^{-1} = \beta_{0s} + \beta_{ss}N_s + \beta_{si}N_i,$$

$$w_i^{-1} = \beta_{0i} + \beta_{ii}N_i + \beta_{is}N_s,$$

where w_s and w_i were the average per plant growth response for spotted knapweed and intermediate wheatgrass, respectively, and N_s and N_I were their density. Regression coefficients β_{0s} and β_{0i} represent the inverse of the maximum response of each variable for an isolated individual for spotted knapweed and intermediate wheatgrass, respectively. Regression coefficients β_{ss} and β_{ii} and β_{si} and β_{is} represent intraspecific and interspecific competitive coefficient for spotted knapweed and intermediate wheatgrass, respectively.

The extra sums of squares procedure was used to compare slopes generated using each density matrix (Snedecor and Cochran 1980). For example, slopes generated from low spotted knapweed and intermediate wheatgrass densities were compared to slopes from low spotted knapweed and high wheatgrass densities. Coefficient of determination (R^2) values were calculated to indicate the proportion of the variability associated with the dependent variables that were accounted for by plant density.

Growth analysis

Isolated plants of spotted knapweed and intermediate wheatgrass were grown by broadcasting 15 seeds on the soil surface of each individual pot. Seeds were sown, similar to that described above, on June 15 (Red Bluff) and June 20, 1995 (Post Farm). Plants were lightly watered and covered with plastic to facilitate seedling emergence and then thinned to a single individual 10 days after emergence. Pots were replicated to provide 5 harvest dates and 3 blocks in a randomized-block design (2 species, 5 harvest dates, 3 blocks). Harvest dates occurred on 12-day intervals beginning 16 days after planting. Final harvests occurred on August 30 (Red Bluff) and September 3 (Post Farm), 1995. Sampling procedures followed those of the interference experiments. Data were analyzed using simple linear regression using time as the independent variable.

Emergence and survivorship

Initial densities were fitted into simple linear regression models using seeding density as the independent variable. Similarly, harvest densities were fitted into linear regression models using initial density as the independent variable.

Results

Interference

Intermediate wheatgrass: Intraspecific interference was most important in predicting intermediate wheatgrass weight at all densities at the Post Farm (Tables 2 and 3). Based on plant weight, regressions indicate that no interspecific interference occurred between spotted knapweed and intermediate wheatgrass at low spotted knapweed densities at this site. At high spotted knapweed and low wheatgrass densities, spotted knapweed reduced intermediate wheatgrass total and shoot weight. Effects of spotted knapweed were removed at high wheatgrass densities. At the Post Farm, regressions predicting intermediate wheatgrass leaf area and root length followed a similar pattern as that of weight (Tables 3 and 4).

Only models at low spotted knapweed densities were significant in predicting intermediate wheatgrass weight at Red Bluff (Tables 2 and 3). Intraspecific interference was most important at all densities, similar to that at the Post Farm. At low densities of both species, increasing spotted knapweed density reduced intermediate wheatgrass total and shoot weight. At high wheatgrass densities, the effects of spotted knapweed were removed on this site.

At low densities of both species, only intraspecific interference was associated with intermediate wheatgrass leaf area and root length at Red Bluff (Tables 3 and 4). At low spotted knapweed and high intermediate wheatgrass densities, spotted knapweed was most important in predicting intermediate wheatgrass leaf area. Density was not associated with root length at these densities at this site.

Spotted Knapweed: At low spotted knapweed densities, models predicting spotted knapweed weight, leaf area, or root length were either non-significant or had a poor fit at the Post Farm (Tables 5, 6, and 7). At high spotted knapweed and low wheatgrass densities, only intraspecific interference was associated with spotted knapweed total and shoot weight. Intraspecific and interspecific interference was associated with spotted knapweed leaf area at these densities. At high densities of both species, wheatgrass density was most important in predicting spotted knapweed weight and leaf area at this site.

Regression models indicated that at low spotted knapweed densities and high wheatgrass densities, spotted knapweed increased its own weight at Red Bluff (Table 5 and 6). At these same densities, only wheatgrass density was associated with spotted knapweed leaf area (Table 6 and 7). All other regressions were either non-significant or poor fitting models.

Growth Analysis

Regressions predicting total plant weight over time indicate that intermediate wheatgrass grew 4 and 14 times faster than spotted knapweed at the Post Farm and Red

Bluff, respectively (Table 8). Intermediate wheatgrass and spotted knapweed grew 2 and 7 times faster at the Post Farm than at Red Bluff. Other parameters followed a similar pattern to total weight.

Emergence and Survivorship

Regressions predicting initial density based on seeding rate indicated that 29 and 18% of the seeds emerged for spotted knapweed and intermediate wheatgrass at the Post Farm. Conversely, 19 and 36% of knapweed and wheatgrass emerged at Red Bluff.

Regression models predicting harvest densities using initial densities as the independent variable showed that 83% of spotted knapweed plants and 86% of the wheatgrass plants survived to the end of the experiment at the Post Farm. Only 13% of the initial spotted knapweed seedlings survived to the end of the experiment at Red Bluff, whereas 91% of the wheatgrass seedlings survived.

Discussion

Our study indicates that density-independent and density-dependent factors interact to determine seedling survival and competitiveness of spotted knapweed and to a lesser extent, intermediate wheatgrass. Weldon and Slauson (1986) proposed that R^2 values from addition series regressions indicate the degree to which interference is important to the success of the target species. R^2 for spotted knapweed at all density ranges, except high densities of both species, were below 0.29 at the Post Farm. In this case, we believe that competition was minimized by high precipitation (Table 1). At high densities, competition became more important.

At the drier site, Red Bluff, R^2 values ranged from 0.46 to 0.64 at low densities of spotted knapweed and high densities of intermediate wheatgrass. All other models had lower R^2. This suggests that enough soil moisture was available at lower densities to minimize interference. At higher densities of spotted knapweed, survivorship lines (Figure 1) and R^2 values show that seedling mortality was high. Furthermore, growth rates of isolated spotted knapweed individuals were lower on this site than on at the Post Farm.

Survivorship lines and R^2 values indicate that, in most situations, interference was important in determining the success of intermediate wheatgrass. In those cases, intraspecific competition accounted for most of the variation in the model. However, at high densities of both species under the dry conditions at Red Bluff, intermediate wheatgrass was influenced by other factors than density. A majority of those individuals emerging survived to the end of the study, suggesting mortality was not a major factor.

Interference between species depends on their density, proportion, and spatial arrangement (Radosevich 1987). In a growth chamber study, Jacobs et al. (1996) found bluebunch wheatgrass was more competitive than spotted knapweed at densities ranging from 1000 to 5000 plants m^{-2}. In our study, increasing intermediate wheatgrass density removed the competitive influence of spotted knapweed under those conditions where interspecific interference was significant. Our study indicates that the competitive balance between spotted knapweed and intermediate wheatgrass can be shifted from spotted knapweed by establishing high densities (>1000 plants m^{-2}) of wheatgrass under those conditions where interspecific interference occurs.

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CHAPTER 3

USING SEED RATE TO ENHANCE INTERMEDIATE WHEATGRASS ESTABLISHMENT IN SPOTTED KNAPWEED INFESTED RANGELAND

Introduction

Spotted knapweed (*Centaurea maculosa* Lam.), a deep-taprooted perennial weed of Eurasian origin, has been invading rangeland throughout the northwestern United States and Canada since the late 1800s (Roche and Talbott 1986, Watson and Renney 1974, Strang et al. 1979, Harris and Cranston 1979). This invasive weed has been spreading at about 27% per year and infests about 2.2 million hectares of grassland in Montana (Chicoine et al. 1985, Lacey et al. 1989). It also infests about 10,000 hectares in eastern Washington (Roche' 1988) and in British Columbia (Cranston 1988), and it can be found throughout most of the northwestern United States. Spotted knapweed reduces forage production (Watson and Renney 1974, Harris and Cranston 1979), plant species diversity (Tyser and Key 1988), and wildlife habitat (Bedunah and Carpenter 1989). Increases in bare-ground (Tyser and Key 1988), surface water runoff and stream sedimentation (Lacey et al. 1989), and management costs are also associated with knapweed (*Centaurea* spp.) infestations.

In areas where residual plant species are absent, spotted knapweed control is short-term because desirable species are not available to occupy niches opened by the control procedure (James 1992, Sheley et al. 1996). In these areas, establishing competitive plants is essential for successful management of spotted knapweed and the restoration of desirable plant communities. Once established, competitive species inhibit the reinvasion of knapweeds (Hubbard 1975, Larson and McInnis 1989, Borman et al. 1991).

Typically, revegetation of spotted knapweed infested rangeland involves late-fall discing and application of a non-selective herbicide, such as glyphosate (n-phosphomethyl glycine) (Sheley and Larson 1994). Desirable grasses are immediately seeded. Grass and knapweed germination and emergence occur the following spring. With adequate spring precipitation, both grass and knapweed seedlings survive. If grass seedlings survive until mid-summer, a reduced rate of 2,4-D (2,4-diclorophenoxy acetic acid) or mowing is usually applied to weaken spotted knapweed. However, land managers are reluctant to revegetate spotted knapweed infested rangeland because of the difficulty in seedling establishment.

Seedling establishment is the most vulnerable stage in the rehabilitation of plant communities in arid and semiarid regions (Call and Roundy 1991). Rehabilitating knapweed infested rangeland with desirable grasses typically fails because of weed competition during the initial stages of establishment (Borman et al. 1991, James 1992).

Plant density may influence weed competition during the initial stages of establishment. In a growth chamber, Jacobs et al. (1996) found that bluebunch wheatgrass (*Agropyron spicatum* (Pursh.) Scribn. and Smith.) was 4 times more competitive than spotted knapweed seedlings at densities considered high for seedings (1000-5000 plants m^{-2}). Similarly, Velagala et al. (1997) found that increasing intermediate wheatgrass (*Elytriga intermedia* (Host) Nevski) from low (< 1000 plants m^{-2}) to high (>1000 plants m^{-2}) densities removed the effect of spotted knapweed on intermediate wheatgrass where interspecific interference occurred.

The overall objective of this study was to determine the potential to use plant density as a tool to facilitate the initial establishment of desirable grasses in spotted knapweed infested rangeland. The specific objective was to compare intermediate wheatgrass density and biomass at four seed rates in combination with tillage and/or glyphosate application. We hypothesized that the establishment of intermediate wheatgrass seedlings would be greatest at their highest densities. We also expected spotted knapweed biomass would be lowest at the highest densities of wheatgrass.

Materials and Methods

Study sites

The study was conducted during 1995 and 1996 at two sites in Montana. Site 1 was located 11 km east-northeast of Hamilton, Mont. (46^0 17' N, 114^0 1' W) at an elevation of 1341 m. Site 2 was located 15 km southwest of Bozeman, Mont. (45° 36' N, 111^0 11' W) at an elevation of 1524 m. The Hamilton site lies on a *Festuca scabrella/ Agropyron spicatum* habitat type and the Bozeman site lies on a *Festuca idahoensis/ Agropyron spicatum* habitat type (Mueggler and Stewart 1980). Hamilton soils were Stecum stony loamy coarse sand, moderately steep (mixed typic Cryorthents). Bozeman soils were loamy-skeletal over sandy or sandy skeletal (mixed typic Argiboroll). Annual precipitation at both sites ranges from 406 to 457 mm. The mean annual temperature at the Hamilton site is 6.6 ° C. and 6.1 ° C. at Bozeman. Precipitation and temperature were monitored within 6.5 km of each site during the study period (Table 9).

Procedures

Glyphosate (with and without), tillage (with and without), and 4 seed rates (0, 500, 2500, 12500 m^{-2}) of intermediate wheatgrass seeds were factorially applied in a randomized-complete-block design with 4 blocks (replications) at each site. Glyphosate was applied at

1.16 l ha^{-1} using a CO_2 pressurized backpack sprayer calibrated to deliver 410 l ha^{-1}. Tillage was accomplished using a tractor mounted rototiller which mixed the soil to a depth of about 200 mm. Seeds of 'Oahe' intermediate wheatgrass were broadcast on the soil surface of each plot (1.82 m^{-2}) immediately after application and were covered with a small amount of soil (< 2 mm). Intermediate wheatgrass seeds were purchased from Circle S Seeds Inc., Three Forks, Mont. in October 1995. Ninety-four percent of the seeds germinated in a standard test. Treatments were applied during November 4 through November 8, 1995 at Bozeman, and November 11 through November 14, 1995 at Hamilton.

Sampling

Density of intermediate wheatgrass, spotted knapweed, cheatgrass (*Bromus tectorum* L.), Idaho fescue (*Festuca idahoensis* Elmer), and other forbs were determined by counting the number of plants in a 0.44 m^{-2} circular hoop in each plot. Biomass was determined by clipping plants to ground level. Plants were separated by species, dried to a constant weight and weighed. Sampling occurred on July 11 and July 12, 1996 at Hamilton, and July 22 through July 30, 1996 at Bozeman.

Analysis

Analysis of variance was used to determine the effects of glyphosate, tillage, and intermediate wheatgrass seed rate on density and biomass of intermediate wheatgrass, spotted knapweed, cheatgrass, Idaho fescue, and other forbs. Glyphosate, tillage, seed rate, glyphosate*seed rate, glyphosate*tillage, tillage*seed rate, and glyphosate*tillage*seed rate were included in the model. Means were separated using Fisher's protected L.S.D. comparisons. Error bars represent $\pm$ 2 S.E.

Results

Intermediate wheatgrass

Analysis of variance indicated glyphosate*tillage*seed rate interacted to affect intermediate wheatgrass density at the Hamilton and Bozeman sites (Table 10). Unseeded plots and those seeded at rates of 500 m^{-2} yielded similar wheatgrass density, regardless of any additional treatment at both sites (Figures 2a and b). Plots receiving the highest seed rate had higher wheatgrass density than those receiving lower rates at Hamilton. At 2500 seeds m^{-2}, tillage increased wheatgrass density over all other treatments. Plots tilled and seeded at 12500 m^{-2} had the highest wheatgrass density (312 plants m^{-2}) at this site.

At the highest seeding rate, tillage and tillage plus glyphosate increased intermediate wheatgrass densities over all other treatments at Bozeman (Figure 2b). Tillage in combination with glyphosate at the highest seed rate had the highest wheatgrass densities (572 plants m^{-2}). All other treatments yielded similar wheatgrass densities at this site.

Glyphosate combined with the highest seed rate yielded the highest wheatgrass biomass at Hamilton (Figure 3a). At this seed rate, tillage increased intermediate wheatgrass biomass nearly 7 times that of all other treatments at Bozeman (Figure 3b). Analysis of variance of weight per plant indicates intraspecific competition did not affect individual wheatgrass weight (Hamilton: Mean = 0.019 g $plant^{-1}$, $P = 0.693$; Bozeman: Mean = 0.022 g $plant^{-1}$, $P = 0.804$).

Spotted knapweed

Spotted knapweed density was not affected by any treatments at Hamilton (Table 10). However, tillage*glyphosate*seed rate interacted to affect spotted knapweed density at

Bozeman (Figure 4). Among unseeded plots, those without either tillage or glyphosate yielded the highest knapweed density. Tillage and tillage plus glyphosate yielded similar knapweed densities in unseeded plots. Seeding (all rates), glyphosate or glyphosate plus tillage at the highest seed rate reduced knapweed to the lowest density. At 2500 seeds m^{-2}, plots treated with glyphosate and tilled had the highest density. At the highest seed rate tilled plots had the highest knapweed density.

Tillage and glyphosate reduced spotted knapweed biomass from 108 to 73 g m^{-2} ($P = 0.0015$) and 103 to 78 g m^{-2} ($P = 0.0192$), respectively at Hamilton. Increasing the wheatgrass seed rate reduced knapweed biomass at Bozeman (Figure 5). The highest seed rate alone yielded greater knapweed biomass than those treatments including tillage and/or glyphosate. The only exception was that unseeded plots, sprayed with glyphosate, yielded similar knapweed biomass as those seeded at the highest rate alone.

Cheatgrass

Cheatgrass density was not affected by any of the treatments at Hamilton (Table 10). Glyphosate combined with tillage increased cheatgrass biomass over all other treatments at this site. Glyphosate increased cheatgrass density (54 to 126 plants m^{-2}, $P = 0.008$) and biomass (2.2 to 8.43 g m^{-2}, $P = 0.0002$) over those treatments without the herbicide at Bozeman.

Idaho fescue

Idaho fescue was absent at Hamilton. Glyphosate and tillage reduced Idaho fescue density from 177 to 84 plants m^{-2} ($P = 0.0184$) and 220 to 41 plants m^{-2} ($P = 0.0001$), respectively, at Bozeman. Idaho fescue biomass was also reduced by glyphosate (10.6 to 4.4

g m^{-2}, $P = 0.0816$) and tillage (13 to 2 g m^{-2}, $P = 0.0027$) at this site.

Discussion

Most revegetation studies of weed infested rangeland have examined methods using agronomic seed rates that are designed to optimize crop yield. The recommended seed rate of intermediate wheatgrass ranges from 170 (Granite Seed Co. Lehi, UT) to 430 seeds m^{-2} (Sheley and Larson 1994). In our study, initial wheatgrass establishment did not occur at 500 seeds m^{-2} under any treatment or treatment combinations. Since wheatgrass seeds remain in the seedbank, seedlings may become established under more favorable conditions.

Our revegetation study suggests that increasing grass seed rate will facilitate initial establishment of desirable grasses in spotted knapweed infested rangeland and in some cases can reduce knapweed density and biomass. We believe increasing the number of available seeds increased their probability of reaching safe sites (Harper et al. 1965). In addition, weed competition may have been reduced at high wheatgrass densities (Jacobs et al. 1996, Velagala et al. 1997). The fact that spotted knapweed density and biomass was reduced at high seeding rates at Bozeman supports this hypothesis.

Tillage tended to enhance initial establishment of intermediate wheatgrass, especially at the highest seed rate. Tillage may have created safe sites (Kocher and Stubbendieck 1986), while high seed rate may have provided enough seeds to fill a majority of those safe sites (Young 1988, Call and Roundy 1991). In addition, improved soil conditions may have enhanced growth (Donahue et al. 1977).

Glyphosate, when applied with tillage and high seed rate, decreased spotted knapweed density at Bozeman, which resulted in an increase in wheatgrass density. We speculate that a decrease in knapweed density increased the availability of safe sites for intermediate wheatgrass seedlings. At Hamilton, this combination of treatments reduced knapweed biomass, but had no effect on its density. Knapweed biomass reduction resulted in a corresponding increase in intermediate wheatgrass biomass. In this case, we believe safe sites remained occupied and intermediate wheatgrass could only respond in the form of biomass.

We believe plant density can be used as a tool to facilitate the initial establishment of desirable grasses in spotted knapweed infested rangeland. Strategies which maximize the advantage of high seed rate, while reducing the blanket distribution of seeds are needed in order for this tool to become economically feasible.

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APPENDIX A

TABLES 1-10

Table 1. Precipitation and temperature at study sites.

Site	Period (1995)	Total precipitation	Mean temperature Min	Max
		(mm)	-------- (°C) --------	
Red Bluff	15 Jun. to 1 Jul.	13	12.5	14.2
	2 Jul. to 13 Jul.	23	16.1	18.0
	14 Jul. to 25 Jul.	6	16.2	18.5
	26 Jul. to 6 Aug.	13	18.7	20.9
	7 Aug. to 18 Aug.	27	14.6	16.5
	19 Aug. to 30 Aug.	25	16.6	18.8
Post Farm	20 Jun. to 5 Jul.	23	14.2	22.1
	6 Jul. to 17 Jul.	21	9.7	26.5
	18 Jul. to 29 Jul.	20	9.9	28.6
	30 Jul. to 10 Aug.	65	8.5	26.4
	11 Aug. to 22 Aug.	3	6.6	26.4
	23 Aug. to 3 Sep.	12	7.8	28.5

Environmental conditions were monitored daily. Twelve day values are presented during the study to correspond with harvest dates. Precipitation amounts are 12 day cumulative values. Maximum and minimum temperatures are means for the designated time period.

Table 2. Regression coefficients predicting intermediate wheatgrass weight (mg) using harvest densities[1].

Density	Dependent	Post Farm				Red Bluff			
matrices	variable (W)	β_{0i}	β_{ii}	β_{is}	R_i^2	β_{0i}	β_{ii}	β_{is}	R_i^2
$Low_s\ Low_i$	Total weight	0	60.0	0	0.78	308.5	60.8	10.7	0.81
		(NS)	(6.8)	(NS)		(74.7)	(4.8)	(4.3)	
	Shoot weight	0	91.6	0	0.71	412.8	98.5	19.9	0.73
		(NS)	(12.6)	(NS)		(150.7)	(9.8)	(8.7)	
	Root weight	0	190.0	0	0.49	1262.0	162.2	0	0.53
		(NS)	(39.2)	(NS)		(378.4)	(24.7)	(NS)	
$Low_s\ High_i$	Total weight	0	49.8	0	0.75	0	63.9	0	0.98
		(NS)	(7.8)	(NS)		(NS)	(3.7)	(NS)	
	Shoot weight	0	74.2	0	0.76	0	109.5	0	0.93
		(NS)	(12.0)	(NS)		(NS)	(10.7)	(NS)	
	Root weight	0	149.0	0	0.52	0	151.3	0	0.93
		(NS)	(33.1)	(NS)		(NS)	(14.5)	(NS)	
$High_s\ Low_i$	Total weight	427.1	50.7	3.4	0.67	0	0	0	0.87
		(139.5)	(9.7)	(0.9)		(NS)	(NS)	(NS)	
	Shoot weight	0	83.0	7.3	0.69	0	0	0	0.85
		(NS)	(15.6)	(1.5)		(NS)	(NS)	(NS)	
	Root weight	2710.0	108.0	0	0.24	0	0	0	0.89
		(640.0)	(44.5)	(NS)		(NS)	(NS)	(NS)	
$High_s\ High_i$	Total weight	0	74.4	0	0.93	0	0	0	
		(NS)	(7.0)	(NS)		(NS)	(NS)	(NS)	NS
	Shoot weight	0	102.7	0	0.78	0	0	0	
		(NS)	(16.4)	(NS)		(NS)	(NS)	(NS)	NS
	Root weight	0	253.9	0	0.82	0	0	0	
		(NS)	(43.9)	(NS)		(NS)	(NS)	(NS)	NS

[1]The model used was: $w_i^{-1} = \beta_{0i} + \beta_{ii}N_i + \beta_{is}N_s$. Where w_i is the average per plant growth response for intermediate wheatgrass, and N_i is its density. Regression coefficients β_{0i}, β_{ii} and β_{is} represent the inverse of the maximum response of each variable for an isolated individual, intraspecific competitive coefficient and the interspecific competition coefficient for intermediate wheatgrass, respectively.

Table 3. Extra sums of squares[1] comparing intermediate wheatgrass regression slopes generated for each density range.

Intermediate wheatgrass	Dependent variable	$Low_s\ Low_i$ vs $Low_s\ High_i$		$Low_s\ Low_i$ vs $High_s\ Low_i$		$Low_s\ Low_i$ vs $High_s\ High_i$		$Low_s\ High_i$ vs $High_s\ Low_i$		$Low_s\ High_i$ vs $High_s\ High_i$		$High_s\ Low_i$ vs $High_s\ High_i$	
		F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat
Post Farm	Total weight	42.7	4.08	1.49	3.21	1.84	1.78	4.13	1.74	0.39	3.01	11.04	2.95
	Shoot weight	42.6	4.08	1.34	3.21	2.19	1.77	3.65	1.73	0.26	3.01	12.8	2.93
	Root weight	42.1	4.08	-1.36	3.21	1.32	1.78	5.38	1.74	0.21	3.01	10.7	2.95
	Leaf area	32.5	4.08	11.5	3.21	2.74	1.77	2.31	1.73	-0.02	3.01	11.8	2.93
	Root length	43.4	4.08	2.75	3.21	3.07	1.78	2.38	1.74	-0.24	3.01	10.39	2.95
Red Bluff	Total weight	25.4	3.21	-0.03	3.23	NS	NS	0.29	2.65	NS	NS	NS	NS
	Shoot weight	21.3	3.21	-0.10	3.23	NS	NS	0.24	2.65	NS	NS	NS	NS
	Root weight	34.42	3.21	-0.80	3.23	NS	NS	0.39	2.65	NS	NS	NS	NS
	Leaf area	30.06	3.21	0.92	3.23	NS	NS	0.35	2.65	NS	NS	NS	NS
	Root length	390	2.21	-1.77	3.23	NS	NS	5.62	2.65	NS	NS	NS	NS

[1]Slopes were compared at $P = 0.05$

Table 4. Regression coefficients predicting intermediate wheatgrass leaf area (mm^2) and root length (cm) using harvest densities[1].

Density matrices	Dependent variable (V)	Post Farm				Red Bluff			
		β_{0i}	β_{ii}	β_{is}	R_i^2	β_{0i}	β_{ii}	β_{is}	R_i^2
Low_s	Leaf area	0	0.01	0	0.73	0.97	0.13	0	0.54
Low_i		(NS)	(0.001)	(NS)		(0.31)	(0.02)	(NS)	
	Root length	0	0.38	0	0.69	2.64	0.33	0	0.31
		(NS)	(0.05)	(NS)		(1.25)	(0.08)	(NS)	
Low_s	Leaf area	0	0.13	0	0.65	2.23	0.09	0.14	0.97
$High_i$		(NS)	(0.02)	(NS)		(0.73)	(0.005)	(0.05)	
	Root length	0	0.31	0	0.37	28.55	0	0	0.07
		(NS)	(0.11)	(NS)		(9.07)	(NS)	(NS)	
$High_s$	Leaf area	0	0.01	0.01	0.64	0	0	0	0.53
Low_i		(NS)	(0.02)	(0.002)		(NS)	(NS)	(NS)	
	Root length	0	0.66	0	0.34	0	0	0	0.25
		(NS)	(0.24)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Leaf area	0	0.12	0	0.52	0	0	0	NS
$High_i$		(NS)	(0.04)	(NS)		(NS)	(NS)	(NS)	
	Root length	0	0	0	0.33	0	0	0	NS
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	

[1]The model used was: $V_i^{-1} = \beta_{0i} + \beta_{ii}N_i + \beta_{is}N_s$; where V_i is the average per plant growth response for intermediate wheatgrass, and N_i is its density. Regression coefficients β_{0i}, β_{ii} and β_{is} represent the inverse of the maximum response of each variable for an isolated individual, intraspecific competitive coefficient and the interspecific competition coefficient for intermediate wheatgrass, respectively.

Table 5. Regression coefficients predicting spotted knapweed weight (mg) using harvest densities[1].

Density matrices	Dependent variable (W)	Post Farm β_{0s}	Post Farm β_{ss}	Post Farm β_{si}	Post Farm R_s^2	Red Bluff β_{0s}	Red Bluff β_{ss}	Red Bluff β_{si}	Red Bluff R_s^2
Low_s	Total weight	29130.0	0	0	0.11	139740.0	0	0	0.07
Low_i		(15630.0)	(NS)	(NS)		(40370.0)	(NS)	(NS)	
	Shoot weight	0	0	0	0.11	147240.0	0	0	0.09
		(NS)	(NS)	(NS)		(47990.0)	(NS)	(NS)	
	Root weight	0	0	0	0.07	591510.0	0	0	0.04
		(NS)	(NS)	(NS)		(17994.0)	(NS)	(NS)	
Low_s	Total weight	0	0	0	0.07	204850.0	-4013.0	0	0.64
$High_i$		(NS)	(NS)	(NS)		(27990.0)	(1223.0)	(NS)	
	Shoot weight	0	0	0	0.05	238140.0	-6130.0	0	0.59
		(NS)	(NS)	(NS)		(36360.0)	(2080.0)	(NS)	
	Root weight	0	0	0	0.12	0	0	0	0.46
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Total weight	0	51.9	0	0.27	0	0	0	0.04
Low_i		(NS)	(23.4)	(NS)		(NS)	(NS)	(NS)	
	Shoot weight	0	67.2	0	0.29	0	0	0	0.02
		(NS)	(27.1)	(NS)		(NS)	(NS)	(NS)	
	Root weight	0	0	0	0.08	0	0	0	0.31
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Total weight	0	0	703.8	0.67	0	0	0	NS
$High_i$		(NS)	(NS)	(183.9)		(NS)	(NS)	(NS)	
	Shoot weight	0	0	805.1	0.68	0	0	0	NS
		(NS)	(NS)	(205.0)		(NS)	(NS)	(NS)	
	Root weight	0	0	5624.0	0.64	0	0	0	NS
		(NS)	(NS)	(1695.0)		(NS)	(NS)	(NS)	

[a]The model used was: $w_s^{-1} = \beta_{0s} + \beta_{ss}N_s + \beta_{si}N_I$; where w_s is the average per plant growth response for spotted knapweed, and Ns is its density. Regression coefficients β_{0s} ,β_{ss} and β_{si} represent the inverse of the maximum response of each variable for an isolated individual , intraspecific competitive coefficient and the interspecific competition coefficient for spotted knapweed, respectively.

Table 6. Extra sums of squares[1] comparing spotted knapweed regression slopes generated for each density range.

Spotted knapweed	Dependent variable	$Low_s\,Low_i$ vs $Low_s\,High_i$		$Low_s\,Low_i$ vs $High_s\,Low_i$		$Low_s\,Low_i$ vs $High_s\,High_i$		$Low_s\,High_i$ vs $High_s\,Low_i$		$Low_s\,High_i$ vs $High_s\,High_i$		$High_s\,Low_i$ vs $High_s\,High_i$	
		F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat
Post Farm	Total weight	167.06	4.08	-12.27	3.21	0.95	1.77	15.8	1.73	0.55	3.01	8.1	2.93
	Shoot weight	40.8	4.08	-11.8	3.21	1.55	1.77	1.45	1.73	-1.64	3.01	8.02	2.93
	Root weight	45.9	4.08	-21.2	3.21	1.09	1.77	0.87	1.73	-1.66	3.01	7.60	2.93
	Leaf area	165.9	4.08	-4.6	3.21	0.82	1.77	7.79	1.73	-0.14	3.01	6.09	2.93
	Root length	60.5	4.09	-8.57	3.21	1.53	1.78	1.90	1.74	0.96	3.03	5.32	2.93
Red Bluff	Total weight	-2.49	3.23	39.5	3.26	NS	NS	2.06	3.04	NS	NS	NS	NS
	Shoot weight	9.74	3.21	36.4	3.23	NS	NS	1.62	2.65	NS	NS	NS	NS
	Root weight	-3.45	2.87	-8.47	3.29	NS	NS	.006	3.35	NS	NS	NS	NS
	Leaf area	5.46	3.21	45.1	3.23	NS	NS	.09	2.65	NS	NS	NS	NS
	Root length	-16.65	3.23	3.08	3.26	NS	NS	0.21	3.04	NS	NS	NS	NS

[1]Slopes were compared at $P = 0.05$

Table 7. Regression coefficients predicting spotted knapweed leaf area (mm^2) and root length (cm) using harvest densities[1].

Density matrices	Dependent variable (V)	Post Farm β_{0s}	Post Farm β_{ss}	Post Farm β_{si}	Post Farm R_s^2	Red Bluff β_{0s}	Red Bluff β_{ss}	Red Bluff β_{si}	Red Bluff R_s^2
Low_s	Leaf area	0	0	0	0.06	94.73	0	0	0.02
Low_i		(NS)	(NS)	(NS)		(32.16)	(NS)	(NS)	
	Root length	356.6	0	0	0.07	2640.0	0	0	0.05
		(120.5)	(NS)	(NS)		(1240.0)	(NS)	(NS)	
Low_s	Leaf area	0	0	0	0.09	84.96	0	0.41	0.51
$High_i$		(NS)	(NS)	(NS)		(24.50)	(NS)	(0.17)	
	Root length	0	0	0	0.11	0	0	0	0.36
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Leaf area	0	0.07	0.68	0.52	0	0	0	0.02
Low_i		(NS)	(0.02)	(0.24)		(NS)	(NS)	(NS)	
	Root length	0	0	0	0.19	0	0	0	0.06
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Leaf area	0	0	0.62	0.48	0	0	0	NS
$High_i$		(NS)	(NS)	(0.24)		(NS)	(NS)	(NS)	
	Root length	441.2	0	0	0.36	0	0	0	NS
		(174.5)	(NS)	(NS)		(NS)	(NS)	(NS)	

[1]The model used was: $V_s^{-1} = \beta_{0s} + \beta_{ss}N_s + \beta_{si}N_i$; where V_s is the average per plant growth response for spotted knapweed, and Ns is its density. Regression coefficients β_{0s} ,β_{ss} and β_{si} represent the inverse of the maximum response of each variable for an isolated individual , intraspecific competitive coefficient and the interspecific competition coefficient for spotted knapweed, respectively.

Table 8. Mean total weight, leaf area, shoot weight, root length, root weight per day for spotted knapweed and intermediate wheatgrass at Post Farm and Red Bluff.

	Post Farm		Red Bluff	
Growth parameter	Knapweed	Wheatgrass	Knapweed	Wheatgrass
Plant weight (mg d^{-1})	40.5	162.5	5.8	81.6
	(11.66)	(22.33)	(2.08)	(11.66)
Leaf area (cm^2 d^{-1})	2.73	7.68	0.44	4.37
	(0.53)	(0.98)	(0.17)	(0.53)
Shoot weight (mg d^{-1})	34.1	130.7	4.1	58.3
	(10.66)	(17.50)	(1.66)	(10.25)
Root length (m d^{-1})	0.27	2.29	0.06	2.01
	(0.09)	(0.45)	(0.02)	(0.55)
Root weight (mg d^{-1})	6.0	31.6	1.6	22.5
	(1.66)	(6.66)	(0.75)	(5.33)

Table 9. Precipitation and temperature at study sites.

Site	Period	Total precipitation	Mean temperature Max	Min
		(mm)	(°C)	
Hamilton	Nov. '95	44	8.8	-1.2
	Dec. '95	40	1.6	-5.7
	Jan. '96	38	1.2	-8.0
	Feb. '96	16	3.5	-8.0
	Mar. '96	9	8.6	-4.3
	Apr. '96	64	15.5	2.0
	May '96	40	16.1	3.4
	Jun. '96	37	24.9	6.9
	Jul. '96	13	30.7	10.0
Bozeman	Nov. '95	31	8.9	-3.5
	Dec. '95	15	3.6	-9.0
	Jan. '96	13	-0.6	-12.9
	Feb. '96	25	3.8	-9.6
	Mar. '96	12	4.8	-7.9
	Apr. '96	31	14.6	0.3
	May '96	115	14.7	2.2
	Jun. '96	21	25.2	6.8
	Jul. '96	2	29.3	13.9

Environmental conditions were monitored daily. Precipitation amounts are monthly cumulative values. Maximum and minimum temperatures are means for the designated period.

Table 10. Pr ≤ F values generated from ANOVA.

Site	Treatment	df	Intermediate wheatgrass		Spotted knapweed		Cheatgrass		Idaho fescue	
			Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
			(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})
Hamilton	Block	3	0.7890	0.6442	0.0131	0.1309	0.0054	0.4680	-	-
	Tillage	1	0.0029	0.0765	0.7596	0.0015	0.6237	0.1179	-	-
	Glyphosate	1	0.2953	0.6429	0.6230	0.0192	0.1127	0.2286	-	-
	Seed rate	3	0.0001	0.0001	0.5350	0.1474	0.4761	0.3469	-	-
	Tillage* Glyphosate	1	0.0540	0.1113	0.8959	0.3545	0.2310	0.4711	-	-
	Tillage* Seed rate	3	0.0369	0.5341	0.7699	0.3940	0.3023	0.5109	-	-
	Glyphosate* Seed rate	3	0.4719	0.1058	0.8227	0.6703	0.5258	0.4501	-	-
	Tillage* Glyphosate* Seed rate	3	0.1063	0.2236	0.1239	0.8237	0.3844	0.0903	-	-
Bozeman	Block	3	0.1123	0.1218	0.6414	0.7699	0.0226	0.0181	0.0436	0.0843
	Tillage	1	0.0001	0.0024	0.0008	0.0001	0.5843	0.1781	0.0001	0.0027
	Glyphosate	1	0.0453	0.2780	0.3215	0.0001	0.0080	0.0002	0.0184	0.0816

Site	Treatment	df	Intermediate wheatgrass		Spotted knapweed		Cheatgrass		Idaho fescue	
			Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
	Seed rate	3	0.0001	0.0001	0.0162	0.0007	0.9209	0.3551	0.3706	0.5858
	Tillage* Glyphosate	1	0.1039	0.7033	0.2538	0.0001	0.0874	0.7273	0.2140	0.3204
	Tillage* Seed rate	3	0.0001	0.0005	0.1747	0.0023	0.9346	0.8309	0.1883	0.5154
	Glyphosate* Seed rate	3	0.0187	0.5923	0.2370	0.1353	0.9496	0.5409	0.8858	0.6061
	Tillage* Glyphosate* Seed rate	3	0.0533	0.9232	0.1084	0.0403	0.8392	0.8022	0.8347	0.5984

APPENDIX B

FIGURES 1-5

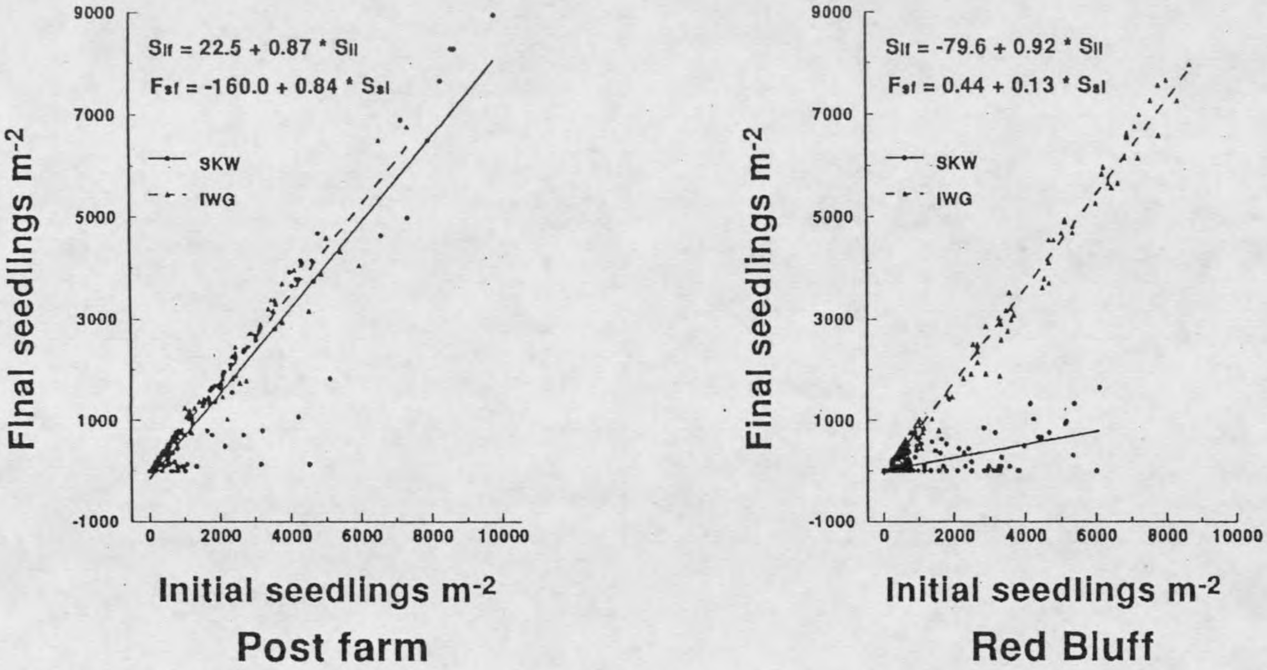

Figure 1. Regression predicting spotted knapweed (SKW) and intermediate wheatgrass (IWG) survivorship.

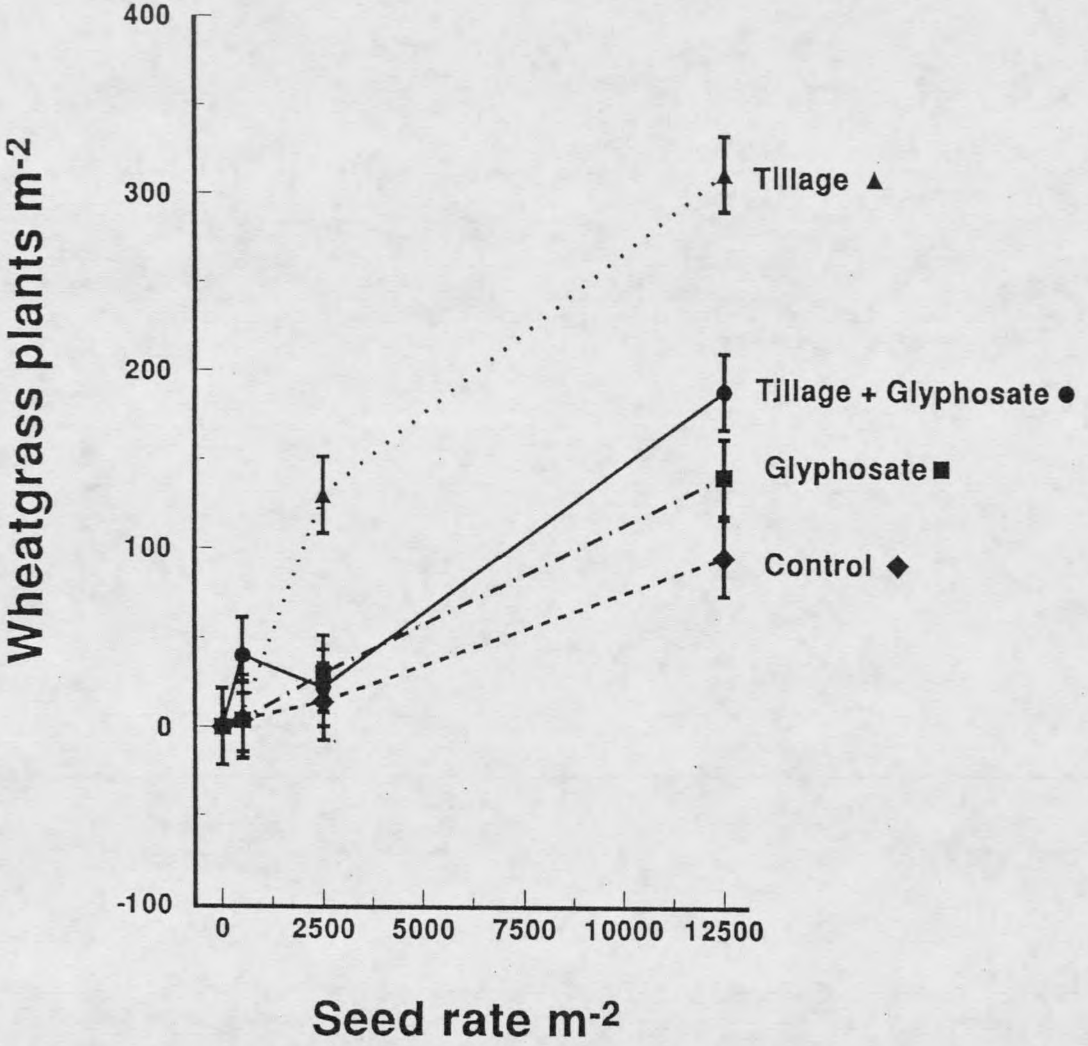

Figure 2a. Effects of glyphosate*tillage*seed rate on intermediate wheatgrass density at Hamilton (P = 0.1063).

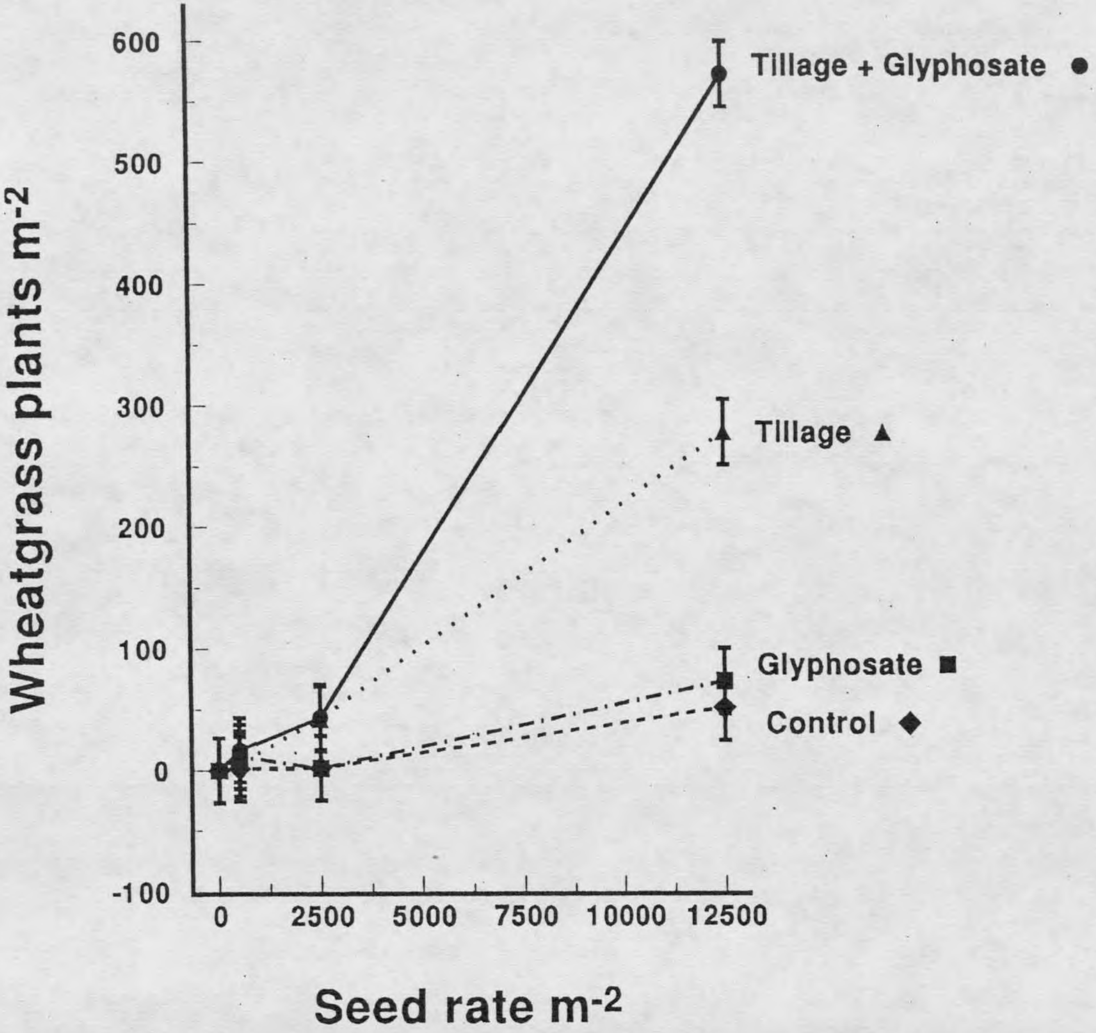

Figure 2b. The effects of glyphosate*tillage*seed rate on intermediate wheatgrass density at Bozeman.

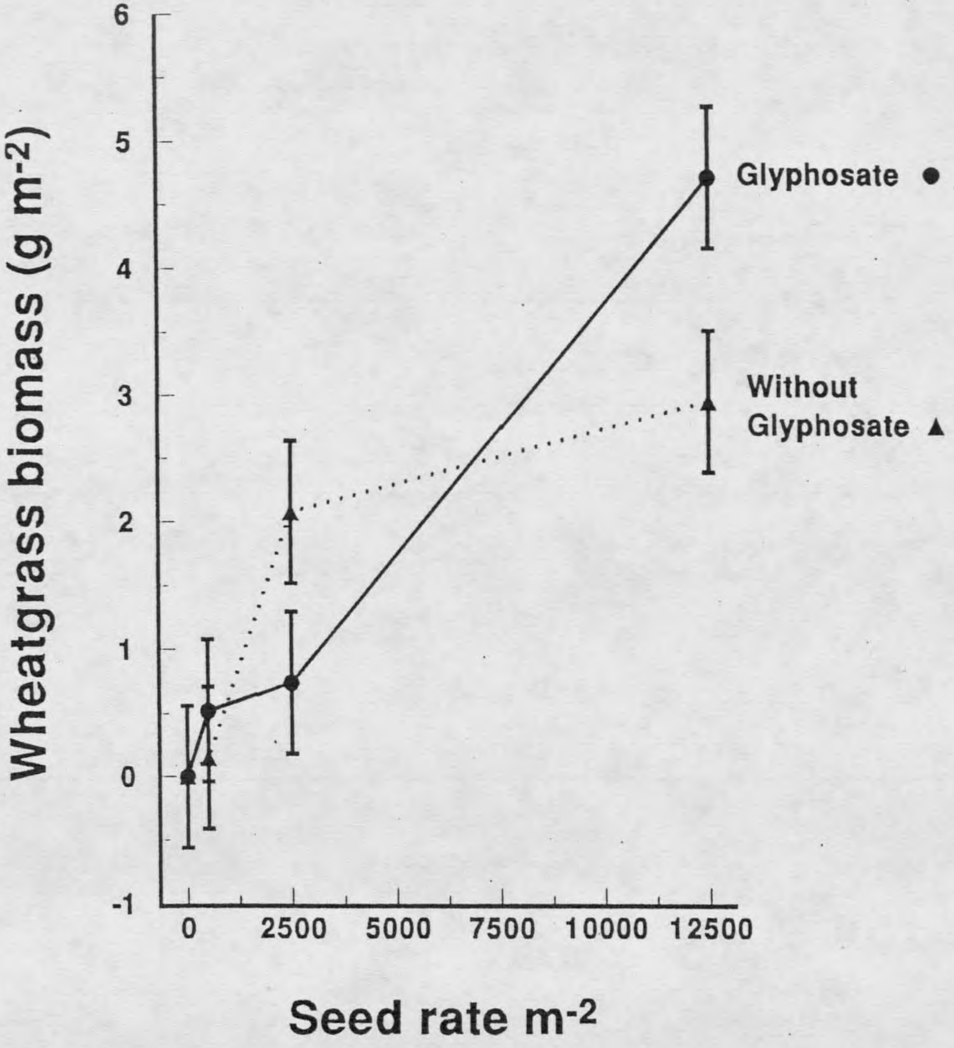

Figure 3a. Effects of glyphosate*seed rate on intermediate wheatgrass biomass at Hamilton.

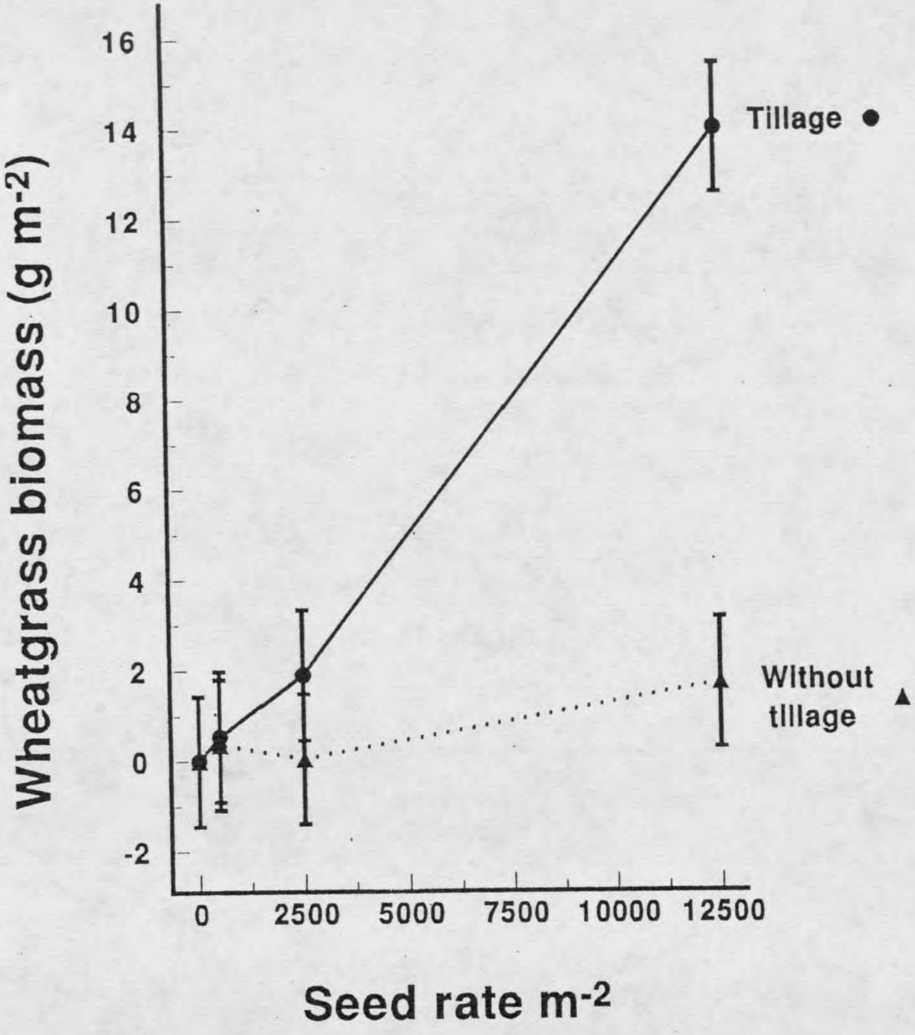

Figure 3b. Effects of tillage*seed rate on intermediate wheatgrass biomass at Bozeman.

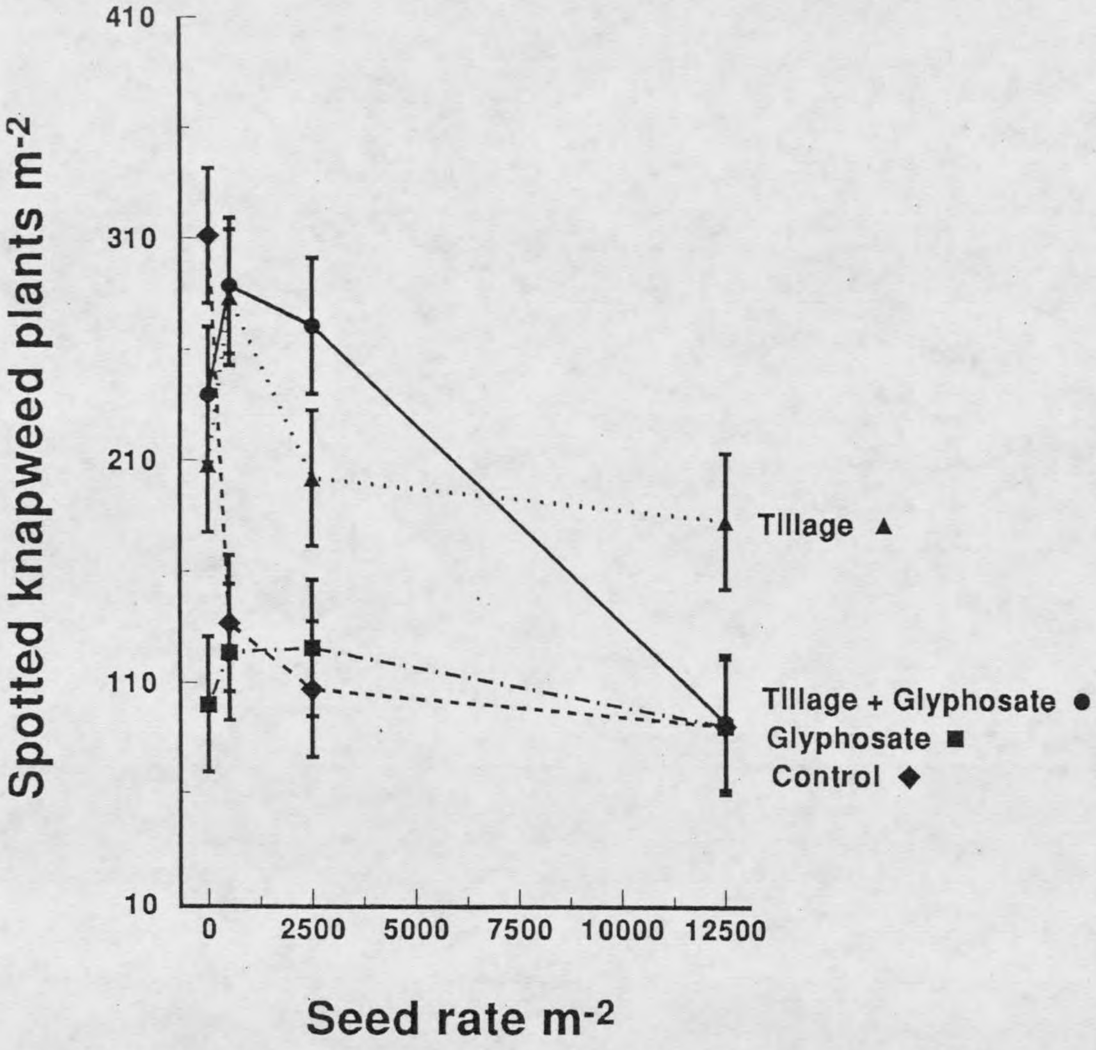

Figure 4. Effects of glyphosate*tillage*seed rate on spotted knapweed density at Bozeman.

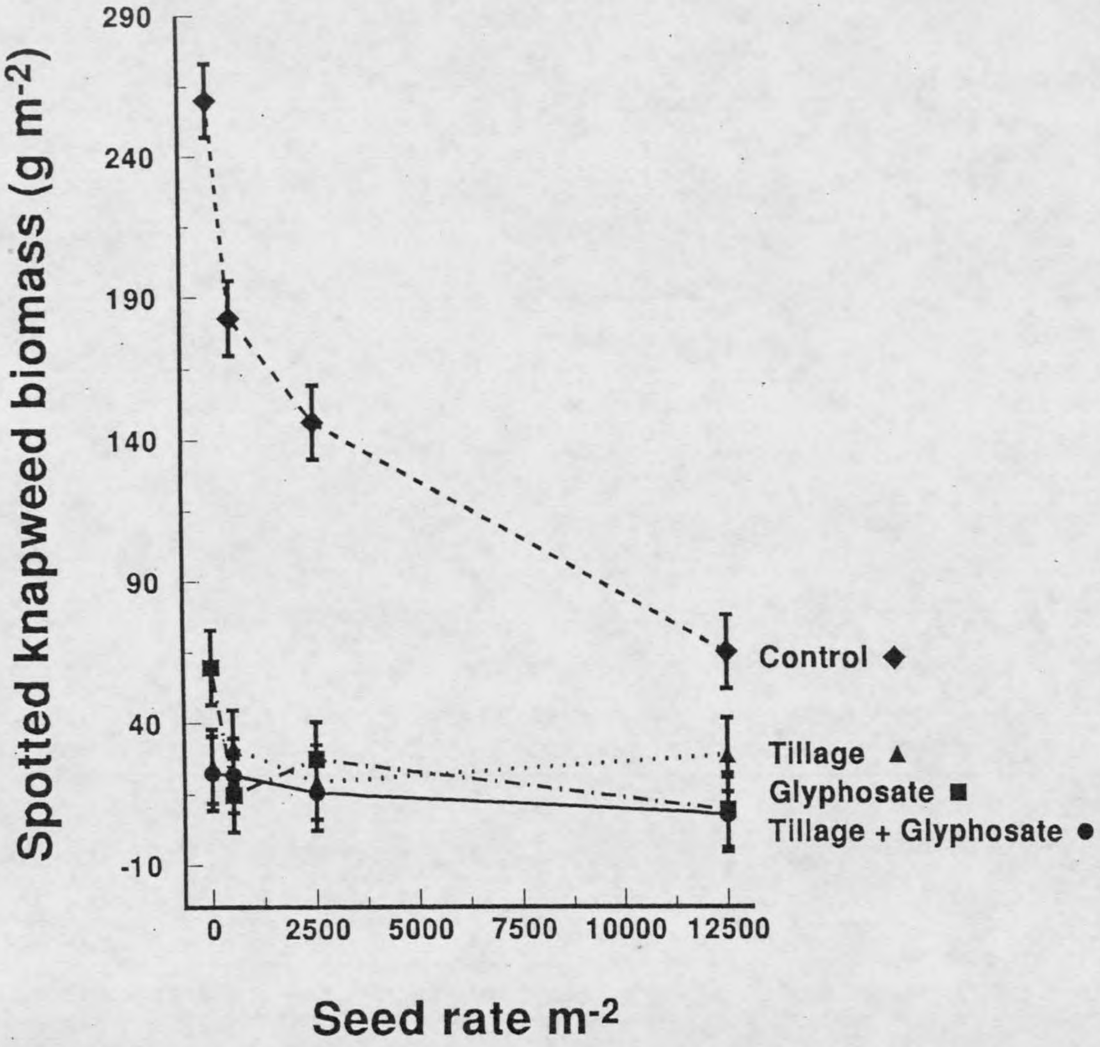

Figure 5. Effects of glyphosate*tillage*seed rate on spotted knapweed biomass at Bozeman.