Restoring Russian knapweed-infested riparian areas

by Stephen Michael Laufenberg

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

Abstract:
Non-native plants are degrading the ecological integrity of native plant communities throughout North America. The goals of this research were: 1) to determine the potential for restoring Russian knapweed-infested plant communities using herbicides alone, and 2) to identify a revegetation technique that would maximize the establishment of a native species seed mixture in a plant community dominated by Russian knapweed. We investigated the influence of 3 herbicides, 3 application rates, and 3 application timings on Russian knapweed and associated plants. We hypothesized that clopyralid plus 2,4-D (3,6-dichloropicolinic acid + 2,4-dichlorophenoxyacetic acid), applied at 0.18 plus 0.92 kg a.i. ha^-1 in August, would provide the lowest density and biomass of Russian knapweed and forbs/shrubs, and the highest density and biomass of grasses. We also hypothesized that clopyralid plus 2,4-D or fosamine [ethyl hydrogen (aminocarbonyl) phosphonate] treatments would provide greater species richness and diversity than those of glyphosate [N-(phosphonomethyl) glycine], Clopyralid plus 2,4-D provided the best control of Russian knapweed two years after treatment and increased the density and biomass of grasses, but not desirable forbs or shrubs. These results suggest that herbicides alone cannot increase the long-term productivity of this plant community because Russian knapweed will most likely recover from herbicide suppression without competition from an adequate diversity of associated plant species. Glyphosate caused the greatest increase in total species richness and diversity two years after treatments. Although the majority of these species were non-native, glyphosate may be appropriate for enhancing ecosystem function and possibly niche occupation to preempt re-invasion by Russian knapweed. We also investigated the influence of four seeding methods and two herbicides on the establishment of a native species seed mixture. We hypothesized that the combination of clopyralid plus 2,4-D and till and drill seeding would provide the greatest establishment. Glyphosate or till and drill seeding produced the highest establishment one year after treatment. We believe that the combination of glyphosate and till and drill seeding may suppress Russian knapweed enough to allow established seedlings to persist. The short-term success of our revegetation technique increases the potential for restoration of riparian native plant communities infested with Russian knapweed.

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Stephen Michael Laufenberg

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

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ABSTRACT

Non-native plants are degrading the ecological integrity of native plant communities throughout North America. The goals of this research were: 1) to determine the potential for restoring Russian knapweed-infested plant communities using herbicides alone, and 2) to identify a revegetation technique that would maximize the establishment of a native species seed mixture in a plant community dominated by Russian knapweed. We investigated the influence of 3 herbicides, 3 application rates, and 3 application timings on Russian knapweed and associated plants. We hypothesized that clopyralid plus 2,4-D (3,6-dichloropicolinic acid + 2,4-dichlorophenoxyacetic acid), applied at 0.18 plus 0.92 kg a.i. ha^{-1} in August, would provide the lowest density and biomass of Russian knapweed and forbs/shrubs, and the highest density and biomass of grasses. We also hypothesized that clopyralid plus 2,4-D or fosamine [ethyl hydrogen (aminocarbonyl) phosphonate] treatments would provide greater species richness and diversity than those of glyphosate [N- (phosphonomethyl) glycine]. Clopyralid plus 2,4-D provided the best control of Russian knapweed two years after treatment and increased the density and biomass of grasses, but not desirable forbs or shrubs. These results suggest that herbicides alone cannot increase the long-term productivity of this plant community because Russian knapweed will most likely recover from herbicide suppression without competition from an adequate diversity of associated plant species. Glyphosate caused the greatest increase in total species richness and diversity two years after treatments. Although the majority of these species were non-native, glyphosate may be appropriate for enhancing ecosystem function and possibly niche occupation to preempt re-invasion by Russian knapweed. We also investigated the influence of four seeding methods and two herbicides on the establishment of a native species seed mixture. We hypothesized that the combination of clopyralid plus 2,4-D and till and drill seeding would provide the greatest establishment. Glyphosate or till and drill seeding produced the highest establishment one year after treatment. We believe that the combination of glyphosate and till and drill seeding may suppress Russian knapweed enough to allow established seedlings to persist. The short-term success of our revegetation technique increases the potential for restoration of riparian native plant communities infested with Russian knapweed.

CHAPTER 1

INTRODUCTION

Non-native plant species are degrading the ecological integrity of native plant communities throughout North America (Olson 1999). Infestations of these species are increasing annually, and now dominate millions of hectares of grasslands in the West (Sheley and Petroff 1999). Research has indicated that non-native species can increase soil erosion and stream sedimentation (Lacey et al. 1989), alter native plant regeneration (Tyser and Key 1988), and reduce wildlife habitat and livestock forage (Lym and Messersmith 1987, Trammel and Butler 1995).

One invasive species causing detrimental impacts to native flora and fauna is Russian knapweed [*Acroptilon repens* (L.) DC.]. Native to Eurasia, this rhizomatous perennial forb was introduced to North America in the early 1900's and has invaded about 630,344 hectares in the western U.S. and adjacent Canada (Watson 1980, Duncan 2001). Russian knapweed can establish and persist as a monoculture in a variety of habitat types and plant communities (Zouhar 2001). Infestations are common in areas with shallow water tables or excess moisture, such as irrigation ditches, floodplains, and river corridors (Whitson 1999). These riparian areas are some of the most productive ecosystems in the West, possessing a greater diversity of plant and wildlife species than adjoining uplands (Sheley et al. 1995). Vegetation along waterways reduces streambank erosion, mediates water temperature for fish, and provides habitat for terrestrial wildlife.

Due to the severe ecological consequences associated with Russian knapweed infestations, controlling this exotic weed must be a priority among land managers.

Previous attempts to control Russian knapweed have typically included a herbicide component. In areas with a substantial composition of desirable species, herbicides alone can remove the target weed and possibly shift the competitive balance in favor of the desirable plant community (Sheley et al. 2001). While specific herbicide treatments can provide effective suppression of Russian knapweed, some herbicides such as picloram have high soil mobility and persistence (Tu et al. 2001), which makes them inappropriate for use in areas near water. Benz et al. (1999) found that a July application of clopyralid plus 2,4-D, a herbicide with low environmental impacts, reduced Russian knapweed cover 92% two years after treatment. Previous research involving herbicide suppression has focused primarily on controlling the target weed, with limited regard to community level effects (but see Rice et al. 1997). While single herbicide applications can provide short-term control of Russian knapweed, no studies have investigated the potential restoration of native plant communities using this weed management method.

Testing herbicide effects on desired species density and biomass could provide insight to plant community structure and productivity. These data can be valuable for determining the success of land management goals such as wildlife habitat enhancement. Furthermore, plant richness (number of species) and diversity (relative abundance of species) have been recognized as valuable indicators of ecosystem function (McNaughton 1993). Ecosystem processes such as plant productivity, nutrient cycling, and energy and material flow are directly influenced by the structure and organization of those systems. Research has implied that greater species richness/diversity may improve the efficiency of ecosystem function (Tilman et al. 1996) and the resilience/resistance of native plant communities (Naeem and Li 1997). For example, in a comparison of eight grasslands in Yellowstone National Park, Frank and McNaughton (1991) found that grasslands with greater plant diversity had community compositions shift less in response to drought than those with lower diversity. In another study, Carpinelli (2000) found as species richness increased and niche occupation by desired species increased, invasion by spotted knapweed (*Centaurea maculosa* Lam.) decreased. In fact, including three desired species in the plant community, all differing in niche, nearly prevented establishment of this invasive weed.

Competition from seeded plant species can also provide effective control of Russian knapweed (Dall'Armellina and Zimdahl 1988). Previous studies involving revegetation of Russian knapweed-infested plant communities have focused on controlling the weed, or establishment and/or performance of seeded species (Sulima 1968, Benz et al. 1999). These strategies, as well as revegetation techniques promoting monoculture establishment, fail to address structural diversity of the plant community and functioning of the system. It has been suggested that sustainable management of ecosystems infested by weedy species must focus on establishing desirable species with plant traits that maximize niche occupation (Larson et al. 1994). The establishment of desirable species with diverse above- and belowground life forms may minimize interspecific competition, maximize spatial and temporal structure, and enhance their resource capture (Pyke and Archer 1991, Tilman 1996).

Seedling establishment is the most critical phase of revegetation (James 1992). Revegetation efforts in Russian knapweed-infested plant communities have been successful with both native and non-native perennial grasses (Whitson et al. 1993, Bottoms and Whitson 1998). While seeding desirable non-native species may satisfy weed management objectives such as forage production or rehabilitation (partial restoration), this approach is inadequate in areas where management goals include the restoration of native plant communities. To increase the probability of restoring native systems, revegetation must include a diverse assemblage of native species that promote the enhancement of ecological functioning and resistance to invasion by exotic species.

The overall goals of this research are to investigate the potential of restoring Russian knapweed-infested plant communities using herbicides by focusing on community-level effects, and to determine if a seeding method, herbicide, or a seeding method/herbicide combination will facilitate native species establishment in a Russian knapweed-infested plant community. This study has three specific objectives:

I. To determine the influence of clopyralid plus 2,4-D, glyphosate, and fosamine, at different application rates and timings, on Russian knapweed and associated existing plant groups, based on species density and biomass.

II. To determine the influence of clopyralid plus 2,4-D, glyphosate, and fosamine, at different application rates and timings, on richness and diversity of total species, total native species, and total non-native species within a Russian knapweed-infested plant community.

III. To determine the influence of four seeding methods, two herbicides, and a non-treated control on the density, cover, biomass, richness, and diversity of ten native species seeded simultaneously into a Russian knapweed-infested plant community.

These specific objectives, and associated hypotheses, are addressed separately in Chapters 2, 3, and 4. A summary of results is presented in Chapter 5.

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CHAPTER 2

HERBICIDE EFFECTS ON DENSITY AND BIOMASS OF RUSSIAN KNAPWEED AND ASSOCIATED PLANT COMMUNITY SPECIES

Introduction

Non-native invasive plants can reduce wildlife habitat and livestock forage (Hakim 1979, Lym and Messersmith 1987, Trammel and Butler 1995, Thompson 1996), increase soil erosion and stream sedimentation (Lacey et al. 1989), and decrease plant species diversity (Tyser and Key 1988). One such invasive species of concern is Russian knapweed [*Acroptilon repens* (L.) DC.], a rhizomatous perennial forb that is difficult to control and considered to be the most persistent of the knapweeds (Lacey 1989).

Russian knapweed is native to Eurasia and was introduced to North America in the early 1900's as a contaminant of Turkestan alfalfa (Watson 1980). This invasive weed is widespread throughout the western U.S. and adjacent Canada, with severe infestations occurring in California, Idaho, Montana, Oregon, and Washington (Carpenter and Murray 1999). In Montana alone, Russian knapweed has infested approximately 26,085 hectares (Duncan 2001), and is common on Missouri River bottomlands in the north-central part of the state (Zouhar 2001).

Infestations of Russian knapweed can displace desirable vegetation through a combination of competition and allelopathy (Maddox et al. 1985, Whitson 1999). As a result, reductions in forage production for wildlife and livestock can occur. Kurz et al. (1995) found that Russian knapweed caused a large shift in species composition for both small mammal and plant communities, constituting a loss of forage, habitat, and overall rangeland biodiversity. Due to its bitter taste, Russian knapweed is generally avoided by grazing animals (Watson 1980). Fresh and dried plants are poisonous to horses, and can cause a fatal neurological disorder called nigropallidal encephalomalacia (Panter 1991, Robles et al. 1997). Previous research indicates that Russian knapweed has decreased feed and market values of hay (Rogers 1928, Watson 1980). Additionally, Russian knapweed has reduced grain yields 28-75% and fresh weight of corn yields 64-88% (Watson 1980), and caused cropland to be abandoned (Renny and Dent 1958, Maddox et al. 1985).

It has become clear that controlling Russian knapweed is paramount to recovering and maintaining the plant communities that it infests. Previous attempts to control Russian knapweed have typically included a herbicide component. Herbicides alone can effectively suppress Russian knapweed infestations, but single applications are usually limited to short-term control (Bottoms and Whitson 1998). Fall applications of various herbicides provided 91-100% control of Russian knapweed one year following treatments (Whitson et al. 1992). On Colorado rangeland, Sebastian and Beck (1993) applied numerous formulations of picloram, dicamba, chlorsulfuron, and metsulfuron, at different rates and timings to Russian knapweed. Picloram applied at 1.12 kg a.i. ha^{-1} in the spring reduced Russian knapweed by 91% two years following treatment; picloram applied at the same rate in the fall provided 86% control of Russian knapweed three years after treatment. Duncan (1994) also found picloram to be the most effective herbicide for controlling Russian knapweed, regardless of application timing. However, picloram is highly mobile and can persist in soils for several years (Tu et al. 2001). Therefore, its use may be inappropriate in areas of ecological-sensitivity or where water contamination is a concern. Herbicides with low environmental impact have also been tested for efficacy on Russian knapweed suppression. Benz et al. (1999) found that a July application of clopyralid plus 2,4-D reduced Russian knapweed cover 92% two years after treatment.

Research suggests that integrating grass competition with herbicides can be more effective for providing long-term control of Russian knapweed than herbicides used alone (Bottoms and Whitson 1998). Whitson (1999) reported that five years following initial treatments, the lowest amount of Russian knapweed (13.1%) and the highest percent live canopy of grasses (24.2%) were found in areas treated with clopyralid plus 2,4-D and seeded to streambank wheatgrass [*Elymus lanceolatus* (Scribn. & Smith) Gould]. However, clopyralid plus 2,4-D was reapplied 2 years after initial treatments. In a different study, various grass species seeded after a clopyralid plus 2,4-D application produced 66 to 93% less Russian knapweed biomass than when no grass was sown (Benz et al. 1999).

Although seeding competitive grasses can be an important component for controlling Russian knapweed, revegetation is expensive and has a high risk of failure (Sheley et al. 2001). In areas with a substantial composition of desirable species, herbicides alone can remove the target weed and possibly shift the competitive balance in favor of the desirable plant community. However, previous research involving herbicide suppression of Russian knapweed has focused primarily on controlling the weed, with limited regard to the effects on the existing plant community. The effects of herbicide applications on native plant communities are poorly understood (except see Rice et al.

1997). To achieve land use objectives such as wildlife production, invasive weed management strategies must address the effects on desirable vegetation.

The overall objectives of this study were: 1) to determine if herbicides have the ability to increase density and biomass of existing desirable species, while controlling Russian knapweed, and 2) to quantify the response of those residual species to determine if herbicides alone would enhance wildlife habitat. Our specific objective was to determine the influence of clopyralid plus 2,4-D, glyphosate, and fosamine, at different application rates and timings, on Russian knapweed and associated existing plant groups, based on species density and biomass. We hypothesized that clopyralid plus 2,4-D, applied at the highest rate in August, would provide the lowest density and biomass of Russian knapweed and forbs/shrubs, and the highest density and biomass of grasses. Our rationale for this hypothesis was based on expectations that: 1) Russian knapweed would be most vulnerable to the highest rate of a broadleaf-selective herbicide at its flowering stage, 2) forbs and shrubs would be susceptible to this selective herbicide, 3) grasses would not be adversely affected by this herbicide, and 4) grasses would utilize excess water and nutrients made available from broadleaf species suppression. Although this study focused on the rehabilitation of a Russian knapweed-infested plant community, results of herbicide effects on existing plant species groups can be useful for determining appropriate management strategies in areas dominated by other rhizomatous, broadleaved invasive species.

Materials and Methods

Study Sites

This study was conducted in north-central Montana on the Charles M. Russell (CMR) National Wildlife Refuge, about 105 kilometers north (22°29'N, 23°29'E) of Lewistown, Montana. Two study sites were located on a floodplain known as Knox Bottom along the Missouri River, near the western boundary of the refuge. Sites were on a north aspect of 0-2% slopes at 670 m elevation with an annual average precipitation of 30 cm and an annual average temperature of 7° C. Soils at both sites were Kobar silty clay loams (fine, montmorillonitic Borollic Camborthids). These soils were formed in alluvium material and have slow permeability (USDA 1978).

Study sites were located within the silver sage/western wheatgrass (*Artemisia cana/Agropyron smithii*) habitat type (Hansen et al. 1995). Similar habitat types have been described for the northern Great Plains by Hanson and Whitman (1938), Mackie (1970), and Jorgensen (1979). This habitat type, common in central and eastern Montana, represents one of the driest extremes of the riparian zone. Plant communities at both sites consist of native and non-native species. The non-native invader Russian knapweed was abundant at the study area and had displaced desirable plant species. Study sites were chosen based on similarities of habitat type as well as obvious differences in predominant graminoid species. Grass species at site 1 were dominated by quackgrass [*Elytrigia repens* (L.) Desv. ex Nevski], a non-native grass, while the native western wheatgrass (*Pascopyrum smithii* P.A. Love) was the dominant grass species at site 2.

The silver sage/western wheatgrass habitat type typically occurs as a result of disturbance, where site potential has changed, possibly due to prolonged heavy grazing (Hansen et al. 1995). Land use at these sites over the past century (approximately 1920's - 1980's) has included crop production and cattle grazing. Throughout that period, cattle were moved from upland summer pastures to the river bottoms for winter grazing. In addition, flooding from the Missouri River occurs with varying frequency and intensity. Because of its location within the CMR National Wildlife Refuge, Knox Bottom provides critical wildlife habitat and continues to be managed for wildlife production.

Experimental Design

In a randomized complete block design at both sites, 28 treatments (3 herbicides x 3 herbicide rates x 3 herbicide application timings, and a control) were applied from June through August 2000 to 4.3 m x 4.6 m plots. Treatments were replicated four times at both sites for a total of 224 plots. Clopyralid plus 2,4-D (3,6-dichloropicolinic acid + 2,4-dichlorophenoxyacetic acid), glyphosate [N- (phosphonomethyl) glycine], and fosamine [ethyl hydrogen (aminocarbonyl) phosphonate] were applied in June (spring rosette stage of Russian knapweed), July (bud to bloom stage of Russian knapweed), and August (flowering stage of Russian knapweed) in accordance with CMR National Wildlife Refuge and U.S. Fish and Wildlife Service restrictions. Low, medium, and high rates [clopyralid plus 2,4-D at 0.08 (clopyralid) + 0.42 (2,4-D), 0.13 + 0.67, and 0.18 + 0.92 kg a.i. ha^{-1}; glyphosate at 0.6, 1.2, and 1.8 kg a.i. ha^{-1}; fosamine at 3.6, 7.2, and 10.8 kg a.i. ha^{-1}] were applied based on label rates for Russian knapweed. These herbicides were chosen because of their low environmental risk in areas near water and wildlife

(Table 2.1). Herbicides were applied using a 4-nozzle backpack sprayer delivering 130 liters ha^{-1} of spray solution.

Table 2.1. Properties, soil and water behavior, and fish toxicity of herbicides (Tu et al. 2001).

Herbicide	Mode of Action	Average Soil Half-Life	Soil Sorption (Koc)	Soil Mobility	Water Solubility	LC-50 (bluegill sunfish)
Clopyralid	Auxin mimic	40 days	avg. 6 mL/g	Moderate-High	1,000 mg/L (acid)	125 mL/g (moderate)
2,4-D	Auxin mimic	10 days	20 mL/g (acid)	Moderate-High	900 mg/L (acid)	263 mL/g (moderate)
Glyphosate	Inhibits the shikimac acid pathway depleting aromatic amino acids	47 days	24,000 mL/g	Low	900,000 mg/L (IPA salt)	120 mL/g (moderate)
Fosamine	Mitotic inhibitor	8 days	150 mL/g	Moderate	1,790,000 mg/L	670 mL/g (low)

Sampling

Density was recorded for all existing plant species and Russian knapweed during June and August of 2001 and 2002. A Daubenmire frame (0.10 m^2) was randomly placed three times within each plot. Grasses were identified using Cronquist et al. (1977), while forbs and shrubs were classified according to Dorn (1984). Biomass of all species and Russian knapweed was collected in August 2001 and 2002 using a 0.44 m^2 hoop randomly placed once within each plot. Plants were harvested at ground level and separated by species in the field. Plant material was then dried to a constant weight and biomass was recorded.

Data Analysis

Analysis of variance (ANOVA) was used to determine the effects of site, year (following treatments), herbicide, application rate, and application timing on Russian knapweed and desirable plant species density and biomass. Treatment main effects and all interactions were included in the model. Five-way, 4-way, and non-significant ($P > 0.05$) 3-way interactions were pooled and included in the error term to improve the sensitivity of the analysis to detect important effects. Non-native forb density data (+ 0.10) were transformed to the log10 scale to meet homogeneity of variance and normality assumptions of ANOVA. Biomass data of non-native forbs were square root-transformed to meet ANOVA assumptions. When a significant P-value ($P < 0.05$) was observed, mean separations for main effects and interactions were achieved based on standard errors (SE). Each SE was calculated by determining the square root of the quotient MSE/N, where MSE is the model mean square error, and N is the number of experimental units associated with a main effect or interaction. Detecting mean differences with this SE calculation was appropriate because the number of experimental units (N) differed among treatments and controls, and it was necessary to incorporate varying sample sizes in the formula. For transformed data, untransformed means are presented with P-values referring to transformed mean comparisons.

Due to the infrequent occurrence of native forbs and native shrubs, no ANOVA models were appropriate for statistical analysis of these plant groups. Additionally, low abundance of the species representing these plant groups prevented the identification of any substantial trends caused by treatment main effects. Therefore, data related to native forbs and native shrubs will be excluded.

Results

Russian Knapweed Density and Biomass

The effect of herbicide on Russian knapweed density was dependent upon the year after treatment ($P = 0.02$). For each herbicide, Russian knapweed density (9 to 21 plants m^{-2}) was lower than that of the control (34 plants m^{-2}) in June 2001 (Figure 2.1). By August 2001, the effect of fosamine on Russian knapweed density disappeared. In June 2002, glyphosate and fosamine provided similar suppression of Russian knapweed (34 to 36 plants m^{-2}) as the untreated control (55 plants m^{-2}). For clopyralid plus 2,4-D, the fewest Russian knapweed plants (15 plants m^{-2}) were present at this sampling date. By August 2002, there was no significant difference between the control and the effects of glyphosate and fosamine. However, for clopyralid plus 2,4-D, Russian knapweed density was less than half (13 plants m^{-2}) as that of the control (35 plants m^{-2}).

Russian knapweed density was also affected by the herbicide*rate*timing of application interaction ($P = 0.003$). Most rates of the three herbicides applied in June provided control of Russian knapweed density, ranging from 10 to 23 plants m^{-2}, relative to the control (40 plants m^{-2}; Figure 2.2). The one exception was the low rate of fosamine, which did not affect Russian knapweed density. For July applications, all herbicide and rate combinations reduced Russian knapweed density relative to the control. The medium and high rates of clopyralid plus 2,4-D provided substantial control by reducing Russian knapweed to about 8 plants m^{-2}. All three rates of clopyralid plus

2,4-D applied in August yielded the lowest Russian knapweed density (4 to 11 plants m^{-2}) compared to all other treatments.

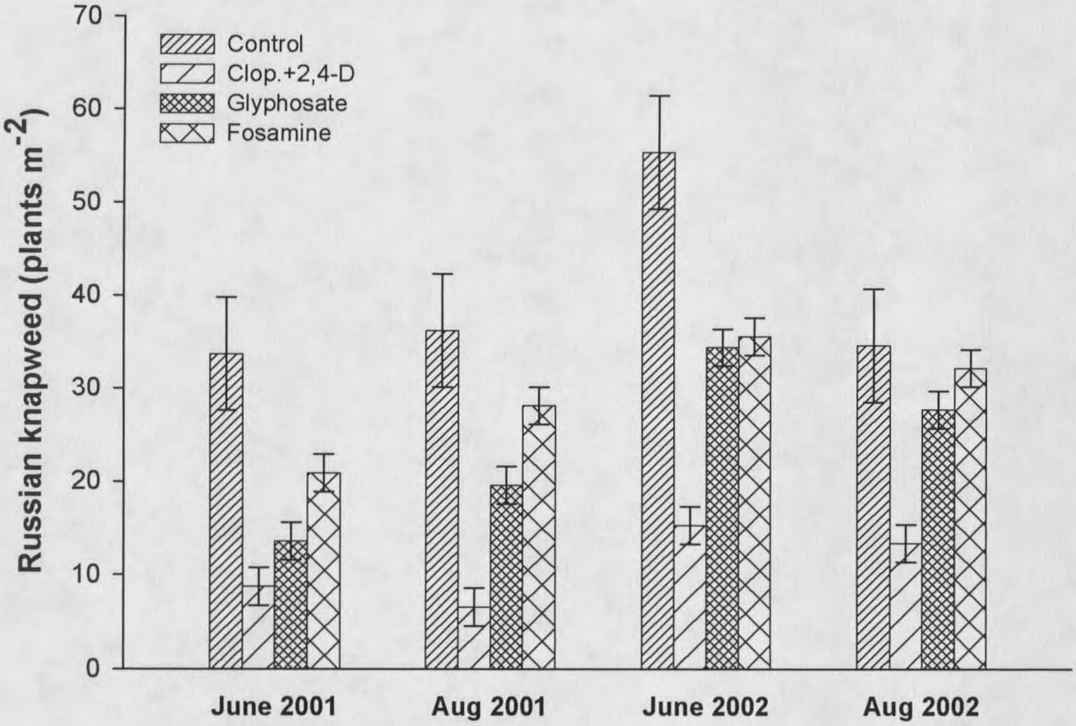

Figure 2.1. The effect of herbicide on Russian knapweed density at four sampling dates. Error bars represent a SE of 6.1 (controls) and 2.0 (treatments).

Analysis indicated that a site*herbicide*rate interaction (P = 0.001) affected Russian knapweed density. For all herbicide and rate combinations at site 1, Russian knapweed density was less than that of the control (Figure 2.3). The clopyralid plus 2,4-D herbicide provided the best control of density, averaging 16 knapweed plants m^{-2} for the three rates, compared to 48 plants m^{-2} in the control. Furthermore, for the medium and high rates of clopyralid plus 2,4-D, there were about half as many Russian

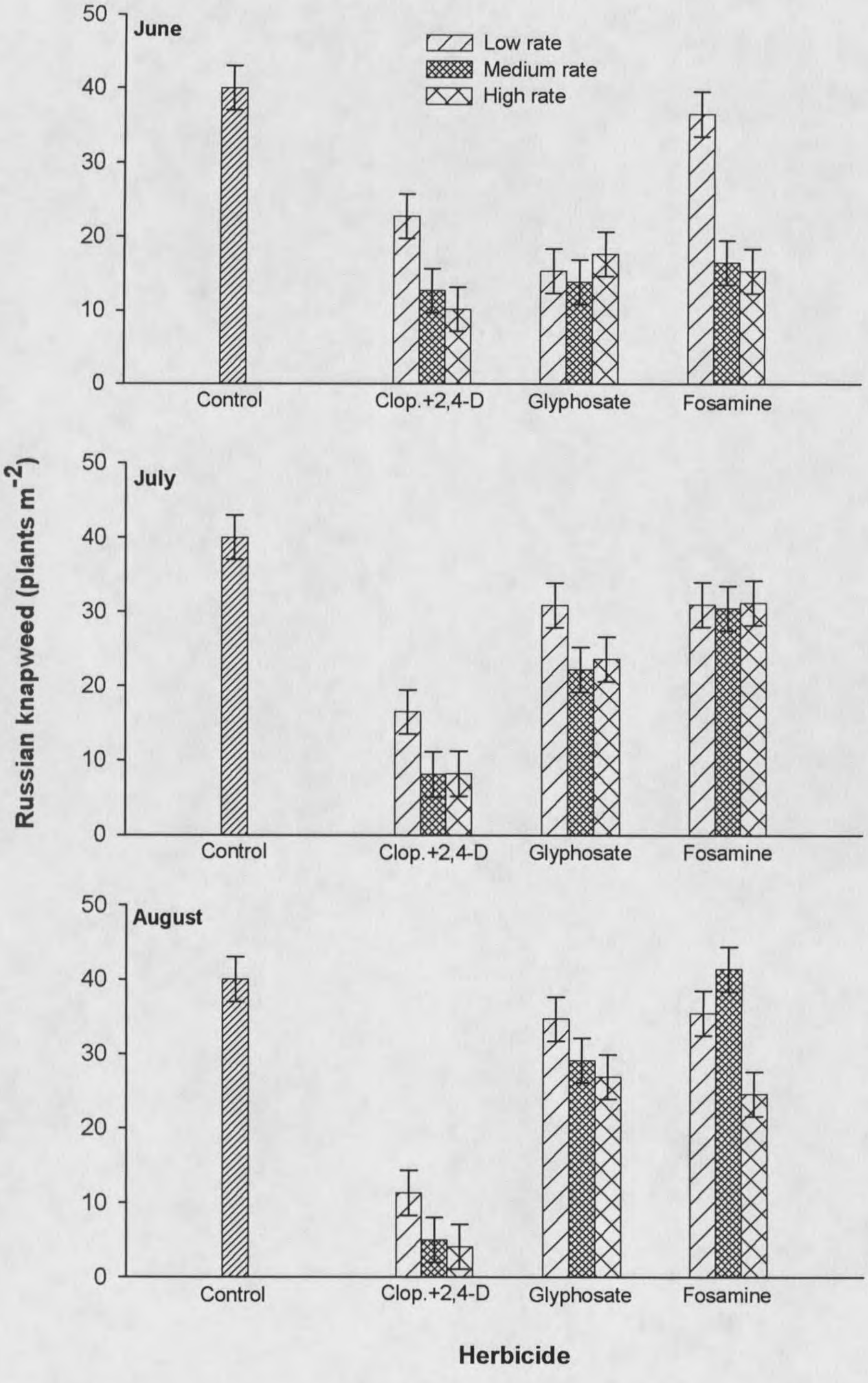

Figure 2.2. The effect of herbicide by application rate and timing on Russian knapweed density. Error bars for the controls and all treatments represent a SE of 3.0.

knapweed plants compared to the low rate. Densities at site 2 indicated a similar trend to that at site 1, except that the low rate of fosamine did not significantly affect Russian knapweed density. All other herbicides and rates significantly decreased knapweed plants below the control. Again, the three rates of clopyralid plus 2,4-D yielded the lowest Russian knapweed density, averaging 6 plants m^{-2}, relative to the control (32 plants m^{-2}). Unlike site 1 however, there was no difference in Russian knapweed density among the three rates of clopyralid plus 2,4-D.

The effect of site on Russian knapweed density was also influenced by herbicide and application timing ($P = 0.004$). At site 1, the three application timings of clopyralid plus 2,4-D and the June application of glyphosate yielded the lowest Russian knapweed densities relative to the control (Figure 2.4). Among the clopyralid plus 2,4-D timings, the reduction in knapweed density was greater for the July and August applications (15 and 11 plants m^{-2}, respectively) than for the June application (23 plants m^{-2}), relative to the 48 plants m^{-2} of the untreated control. At site 2, the best suppression of Russian knapweed density was again associated with the three application timings of clopyralid plus 2,4-D, and no significant differences were detected among them. Additionally, June and July applications of glyphosate, and the June application of fosamine, all reduced knapweed density below 17 plants m^{-2}.

The effect of application timing on Russian knapweed biomass was herbicide dependent ($P = 0.001$). All applications of the three herbicides reduced biomass below that of the control (Figure 2.5a). The three application times of clopyralid plus 2,4-D provided similar control of Russian knapweed biomass, reducing biomass to an average of 26 g m^{-2}. June and July applications of glyphosate resulted in lower knapweed

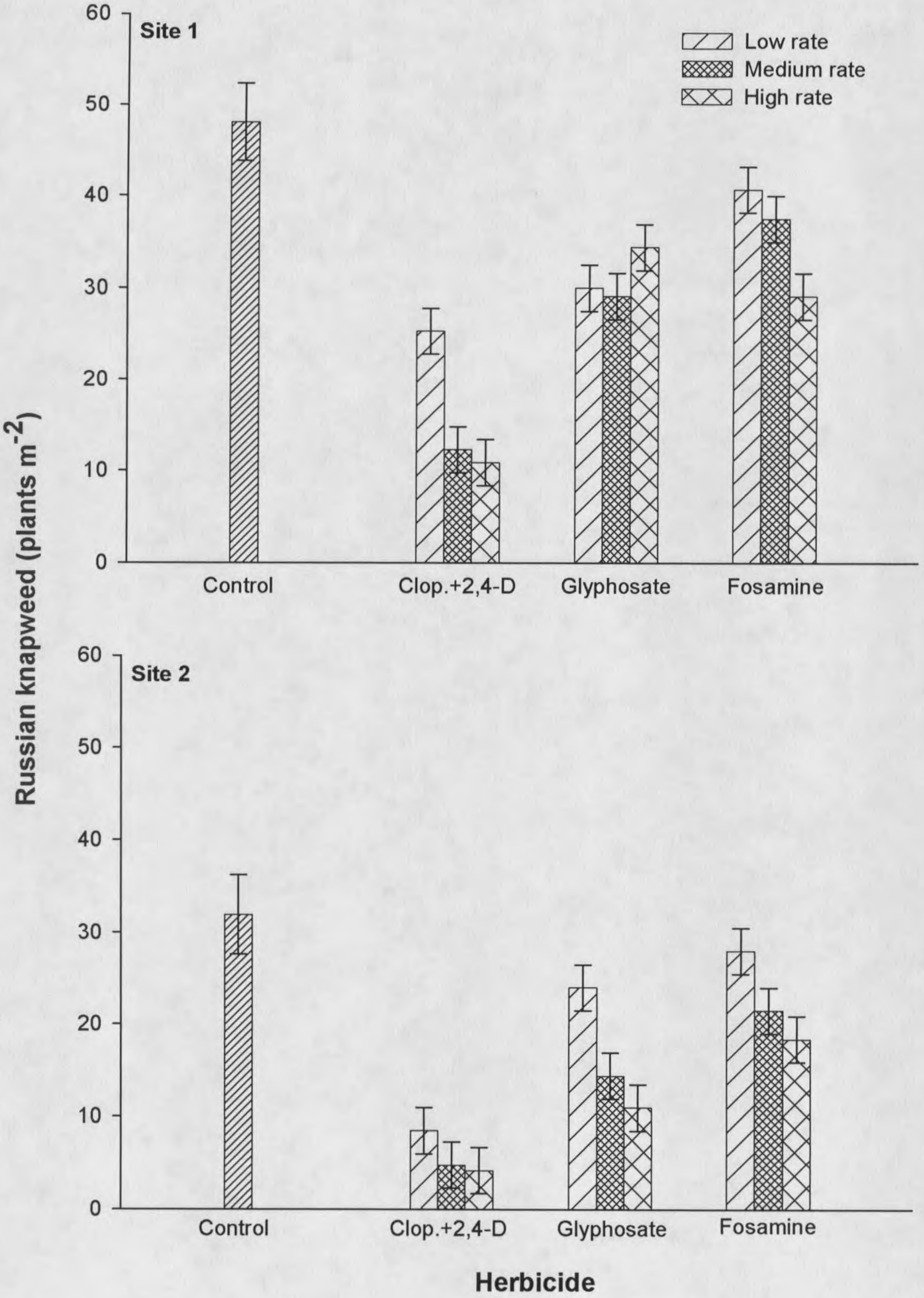

Figure 2.3. The effect of herbicide by application rate at sites 1 and 2. Error bars represent a SE of 4.3 (controls) and 2.5 (treatments).

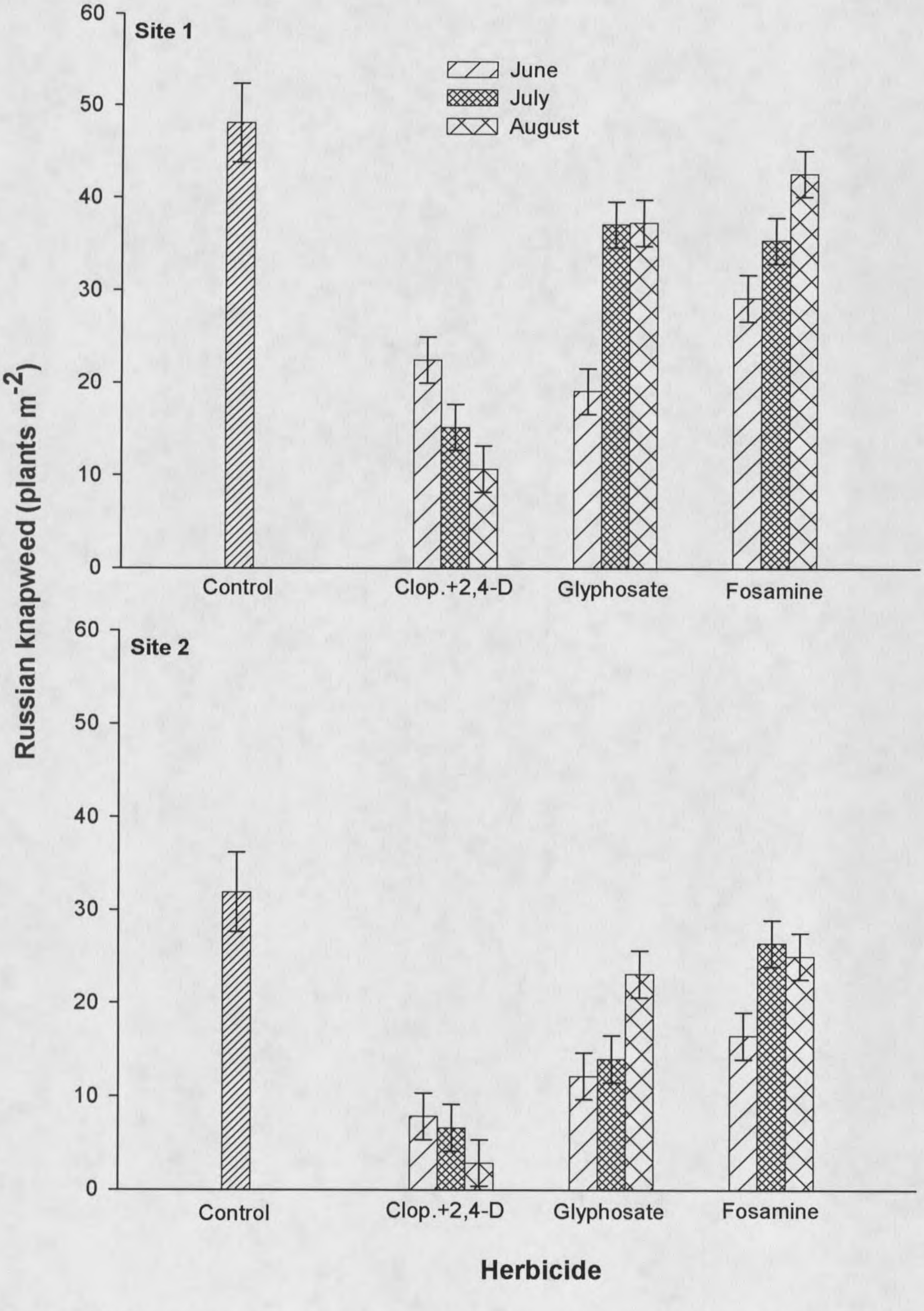

Figure 2.4. The effect of herbicide by application timing on Russian knapweed density at sites 1 and 2. Error bars represent a SE of 4.3 (controls) and 2.5 (treatments).

biomass (44 to 56 g m^{-2}) than the fall application (81 g m^{-2}). The June application of fosamine yielded about half as much (44 g m^{-2}) Russian knapweed biomass as did the July and August applications, which averaged 88 g m^{-2}. The effect of timing on Russian knapweed biomass was also site dependent ($P = 0.03$). At site 1, for the June application of herbicides, the average reduction in biomass was from 161 g m^{-2} in the untreated control to 37 g m^{-2} (Figure 2.5b). The July and August applications of herbicides provided similar biomass control, averaging 73 g m^{-2}. At site 2, no significant differences were detected for the effects of herbicide application timings on Russian knapweed biomass. All application timings reduced biomass values, ranging from 40 to 49 g m^{-2}, below that of the control (90 g m^{-2}).

Grass Density and Biomass

Native grass density was affected by a site*herbicide*rate interaction ($P = 0.001$). At site 1, all three rates of clopyralid plus 2,4-D maintained native grass tiller density relative to the control (about 64 tillers m^{-2}; Figure 2.6). But the high rate of clopyralid plus 2,4-D yielded the highest native grass density (67 tillers m^{-2}) compared to all other treatments. All rates of glyphosate decreased native grass density, averaging about 7 tillers m^{-2}, under that of the control. With fosamine, the low and medium rates maintained native grass density relative to the control, while the high rate reduced density to about 11 tillers m^{-2}. At site 2, only rates of clopyralid plus 2,4-D increased native grass density over that of the control. The clopyralid plus 2,4-D rates averaged 465 tillers m^{-2}, compared to the 305 tillers m^{-2} in the untreated control. For all rates of glyphosate, native grass density (ranging from 72 to 236 tillers m^{-2}) was less than that of the control.

The low rate of fosamine had no effect on native grass density, while the medium and high rates of fosamine reduced tillers below that of the control.

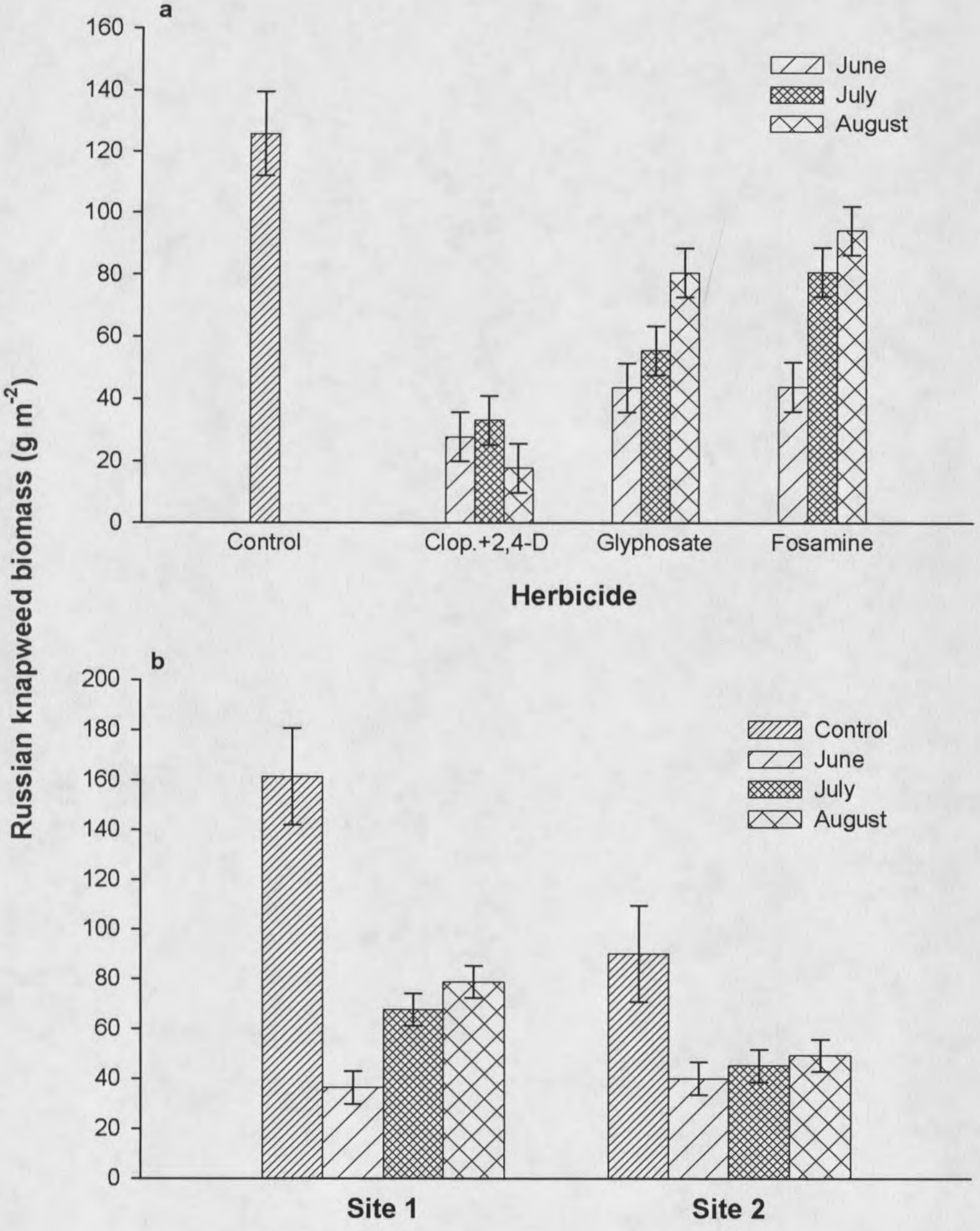

Figure 2.5. The effect of application timing by herbicide (a) and at sites 1 and 2 (b), on Russian knapweed biomass. Error bars in (a) represent a SE of 13.8 (control) and 7.9 (treatments). Error bars in (b) represent a SE of 19.4 (controls) and 6.5 (treatments).

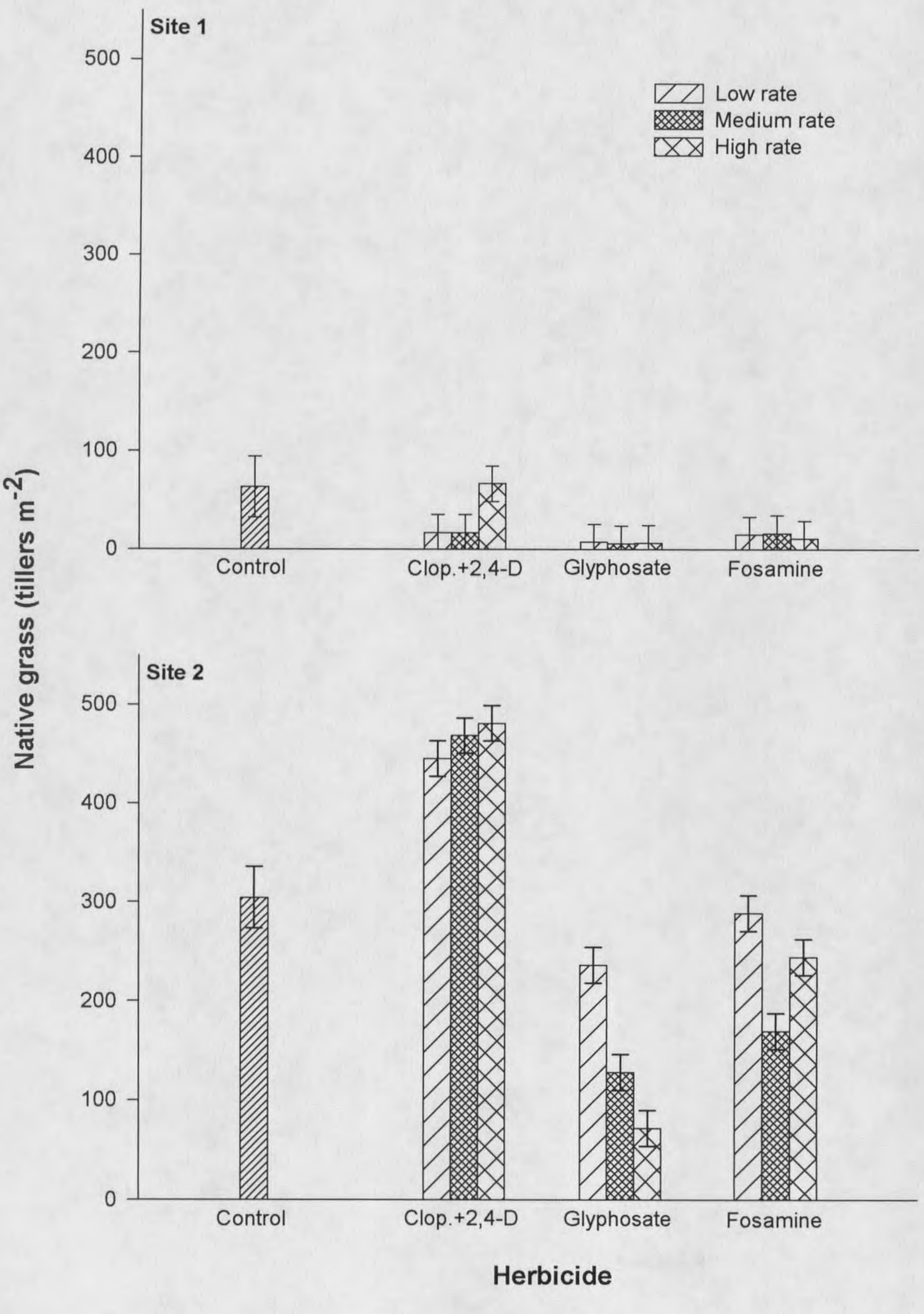

Figure 2.6. The effect of herbicide by application rate at sites 1 and 2 on native grass density. Error bars represent a SE of 31.2 (controls) and 18.0 (treatments).

There was also a significant site*herbicide*rate interaction ($P = 0.02$) affecting non-native grass density. Results from site 1 indicate that only for the clopyralid plus 2,4-D rates, non-native grass density (averaging 466 tillers m^{-2}) was greater than that of the control (374 tillers m^{-2}; Figure 2.7). All rates of glyphosate reduced non-native grass density to less than 87 tillers m^{-2}. The low rate of fosamine did not affect non-native grass density, but the medium and high rates decreased it to an average of 228 tillers m^{-2}. At site 2, where the control yielded 36 non-native grass tillers m^{-2}, no rates of herbicides significantly affected non-native grass density, excluding the medium rate of glyphosate, which increased non-native grass density to 105 tillers m^{-2}.

Biomass of native grasses was affected by a site*herbicide*rate interaction ($P < 0.001$). At site 1, the greatest native grass biomass (17 g m^{-2}) was detected for the high rate of clopyralid plus 2,4-D (Figure 2.8). However, no treatment effects were significantly different from the control (5 g m^{-2}). Among all treatments at site 2, only the medium and high rates of clopyralid plus 2,4-D had greater native grass biomass (averaging 98 g m^{-2}) than the 71 g m^{-2} for the control. Native grass biomass was unaffected by both the low rates of clopyralid plus 2,4-D and glyphosate at this site. Furthermore, for the medium and high rates of glyphosate, as well as for all rates of fosamine, native grass biomass was less than that of the control.

Effects on non-native grass biomass were dependent upon a site*herbicide*application timing interaction ($P = 0.002$). At site 1, increases in non-native grass biomass, relative to the untreated control (63 g m^{-2}), were detected for the three application timings of clopyralid plus 2,4-D (100 to 128 g m^{-2}; Figure 2.9). By

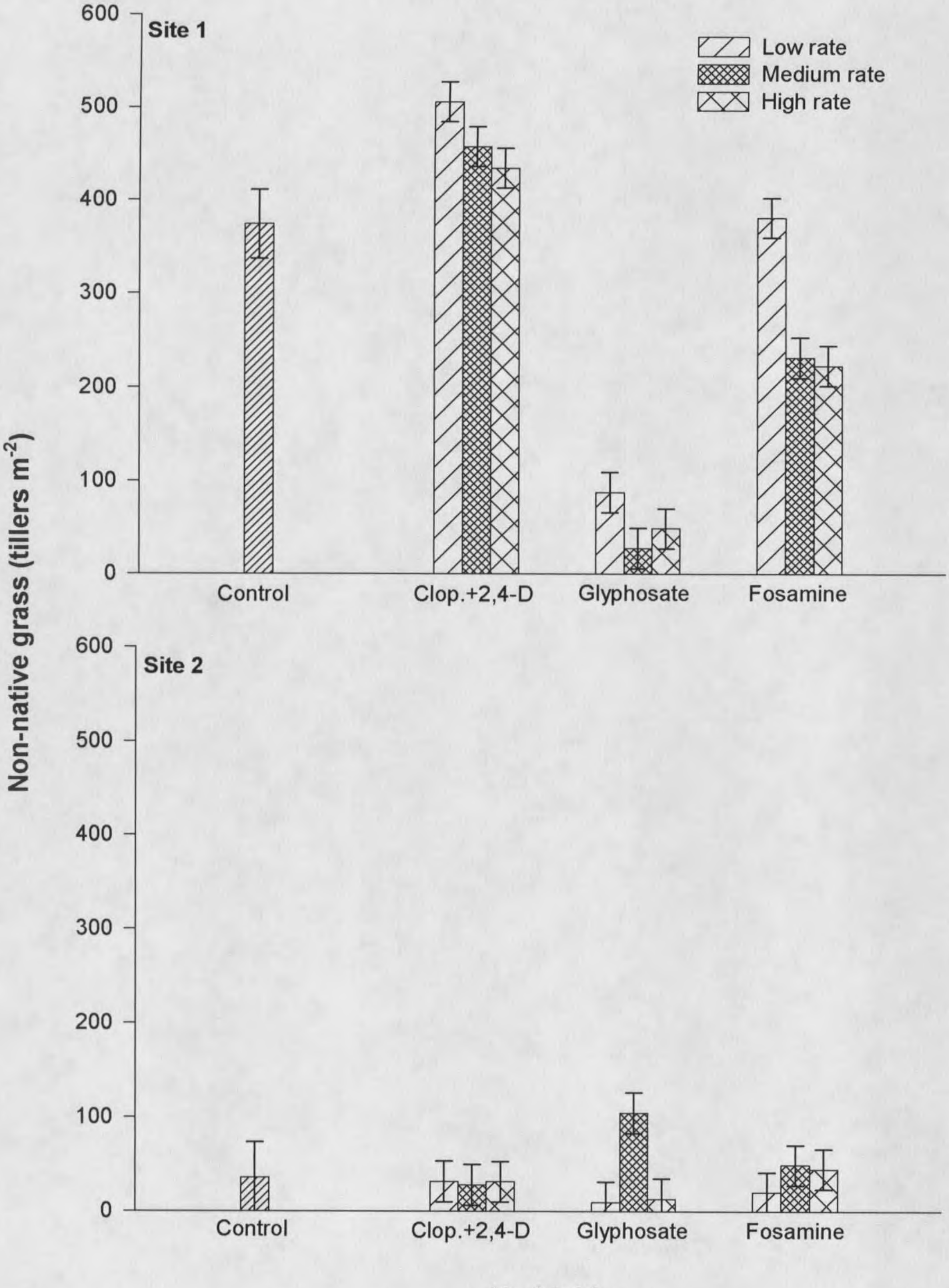

Figure 2.7. The effect of herbicide by application rate at sites 1 and 2 on non-native grass density. Error bars represent a SE of 37.3 (controls) and 21.5 (treatments).

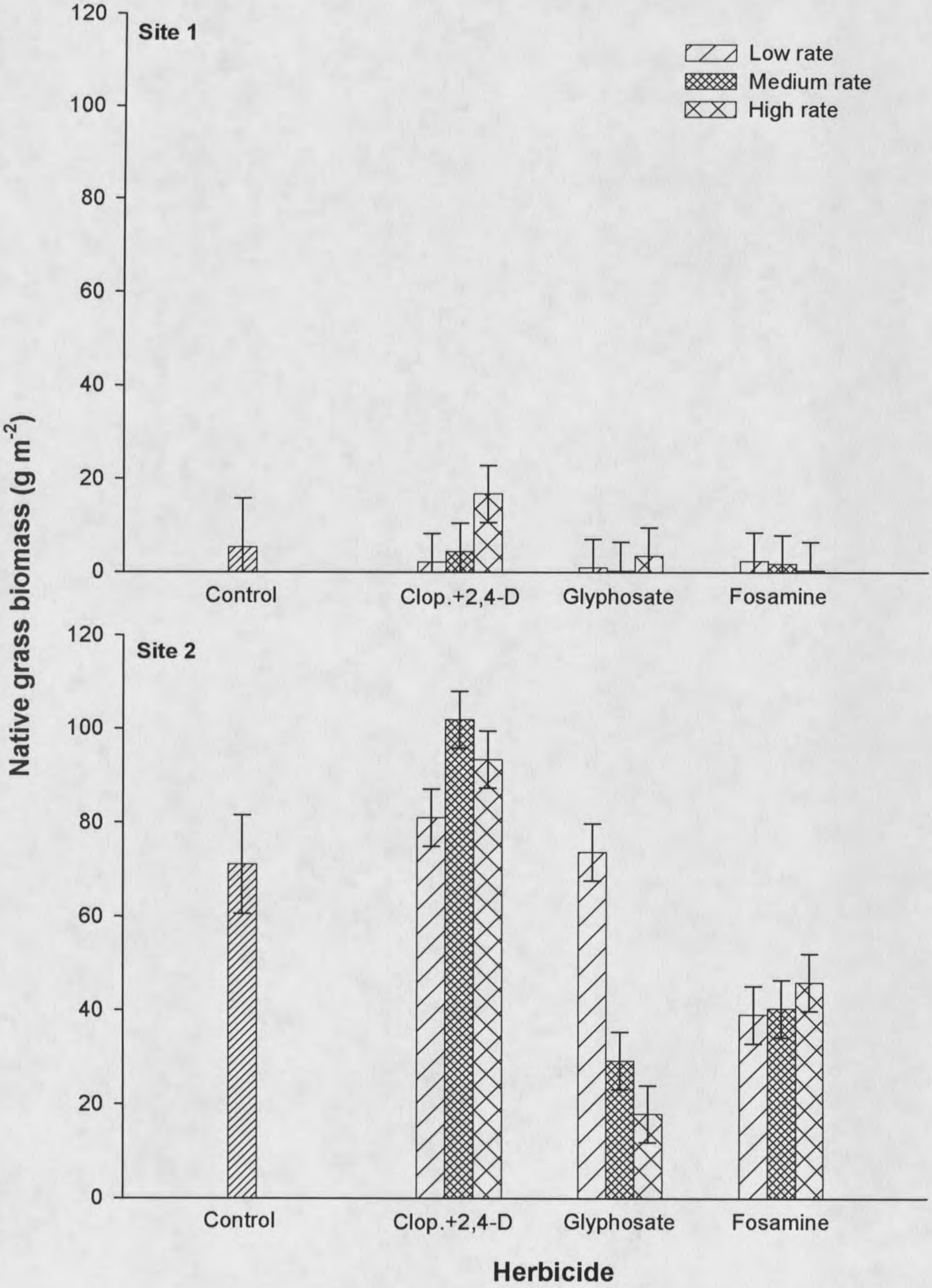

Figure 2.8. The effect of herbicide by application rate on native grass biomass at sites 1 and 2. Error bars represent a SE of 10.5 (controls) and 6.1 (treatments).

contrast, for all glyphosate timings, non-native grass biomass (averaging 21 g m^{-2}) was less than that of the control. Similar to the clopyralid treatments, fosamine applied in June and August increased non-native grass biomass. The July application of fosamine did not affect biomass of this plant group. At site 2, there were no significant differences in non-native grass biomass between the control (17 g m^{-2}) and any treatment. Among all treatments, the only significant difference in biomass occurred between the July application of clopyralid plus 2,4-D (2 g m^{-2}) and the June application of fosamine (19 g m^{-2}).

Non-native Forb Density and Biomass

Non-native forb density was affected by a herbicide*rate*application timing interaction ($P = 0.02$). Relative to the control (27 plants m^{-2}), non-native forb density increased for all rates of glyphosate applied in June, and ranged from 89 to 137 plants m^{-2} (Figure 2.10). Effects of the other two herbicides varied according to application rates. For clopyralid plus 2,4-D, the June-applied low and medium rates maintained non-native forb density, while it increased (54 plants m^{-2}) for the high rate. The low rate of fosamine applied in June had no effect on non-native forb density, while an increase was detected for the medium (50 plants m^{-2}) and high (106 plants m^{-2}) rates. Unlike the June applications, no rates of clopyralid plus 2,4-D applied in July increased non-native forb density relative to the control. For the medium rate of clopyralid plus 2,4-D, non-native forb density (37 plants m^{-2}) was less than that of the control. With glyphosate applied in July, only the medium and high rates increased non-native forb density (averaging 110 plants m^{-2}). The low and medium rates of fosamine applied in July also yielded more

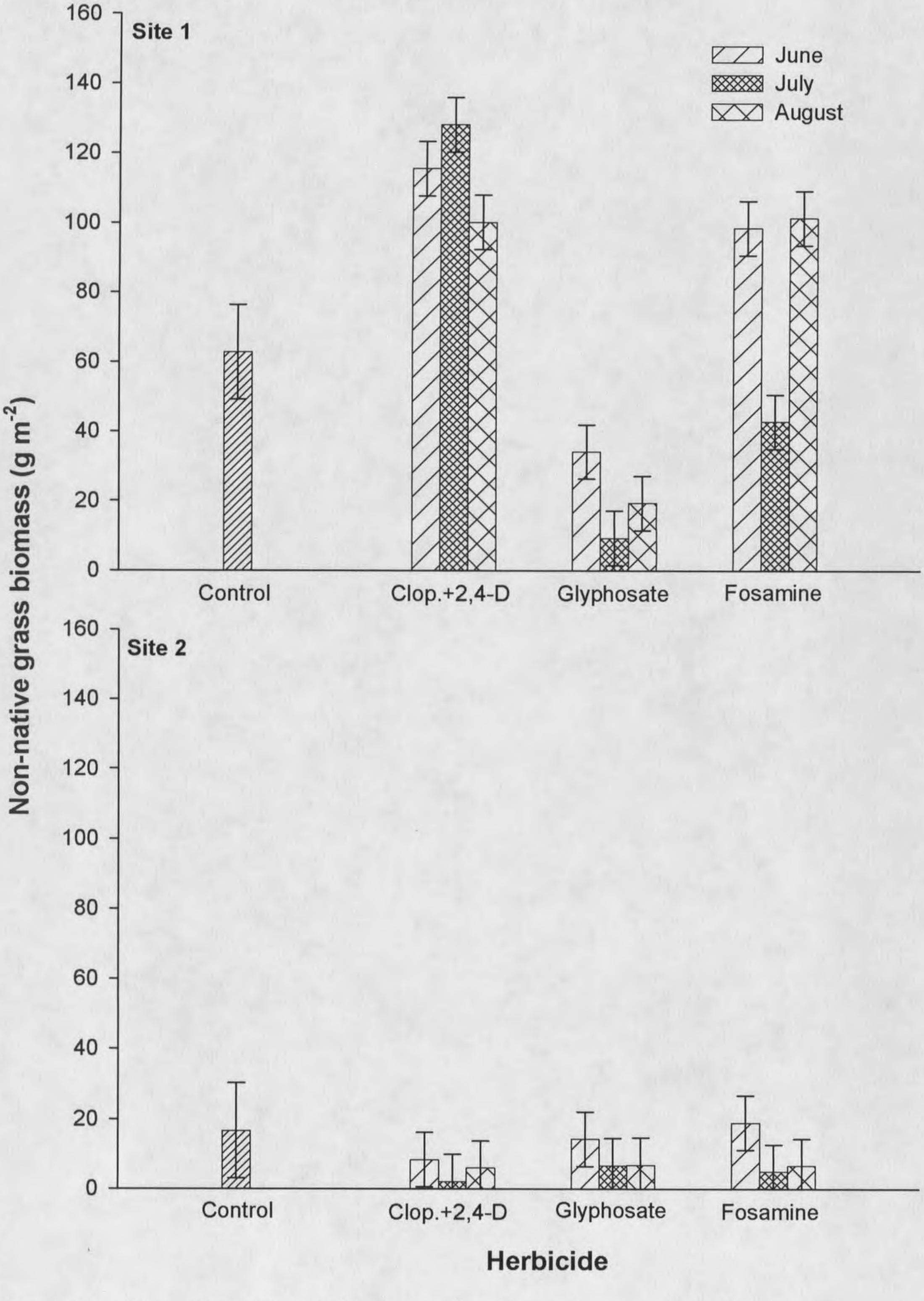

Figure 2.9. The effect of herbicide by application timing on non-native grass biomass at sites 1 and 2. Error bars represent a SE of 13.6 (controls) and 7.8 (treatments).

non-native forbs than the control. For glyphosate rates applied in August, non-native forbs were greater than that of the control. All rates of fosamine and the medium and high rates of clopyralid plus 2,4-D, applied in August, maintained non-native forb density. The only August treatment indicating a reduction in non-native forb density relative to the control was the low rate of clopyralid plus 2,4-D (24 plants m^{-2}).

Non-native forb biomass was dependent upon a site*herbicide*timing of application interaction ($P = 0.04$). No treatments at either site had non-native forb biomass less than the control. At site 1, for all timings of clopyralid plus 2,4-D and the August timing of fosamine, there were no significant effects on non-native forb biomass relative to the control (4 g m^{-2}; Figure 2.11). All timings of glyphosate increased non-native forb biomass, which ranged from 26 to 69 g m^{-2}. Also, for the June (22 g m^{-2}) and July (35 g m^{-2}) applications of fosamine, non-native forb biomass was greater than that of the control. Treatment effects were similar at site 2 to those at site 1.

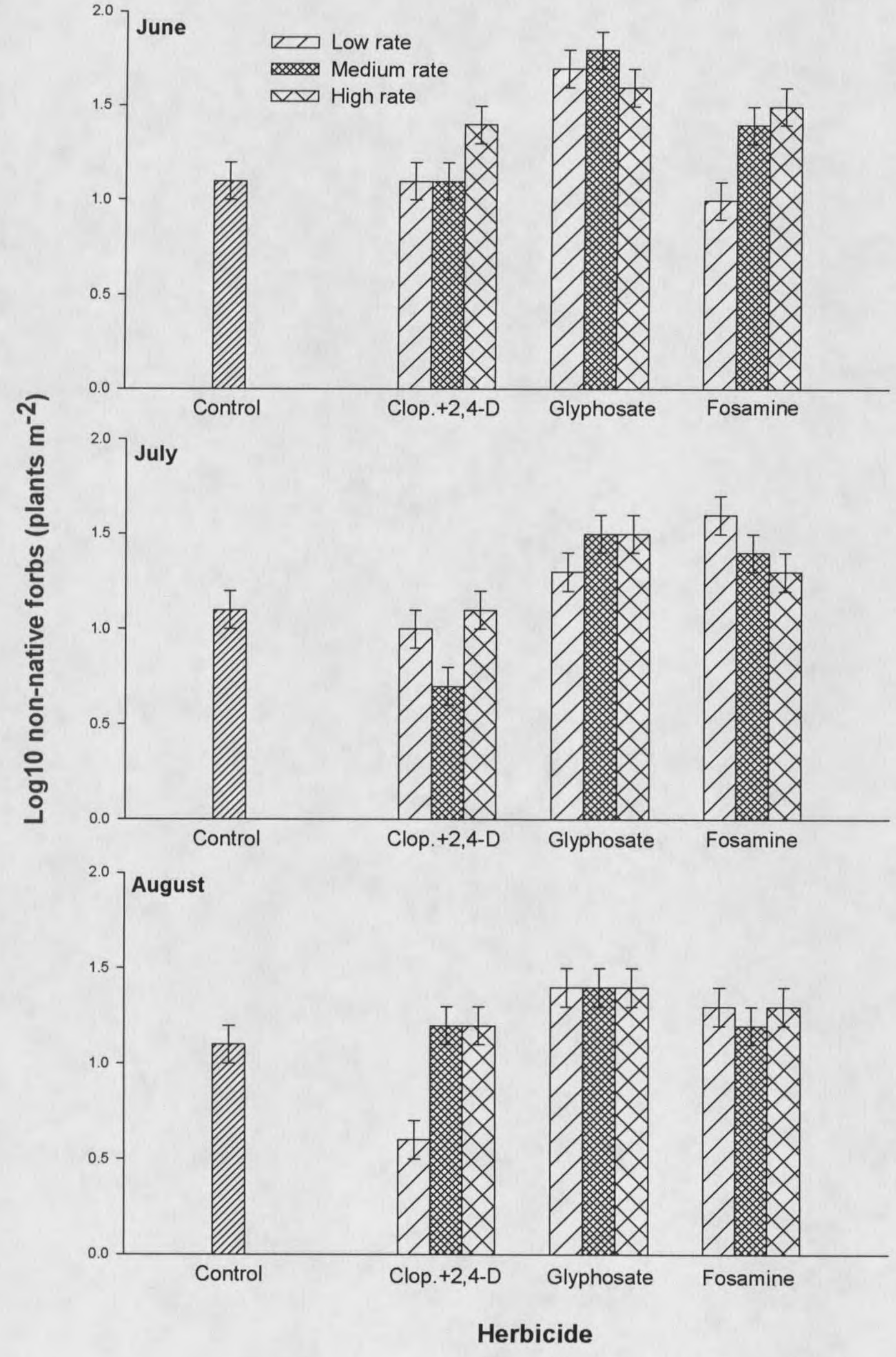

Figure 2.10. The effect of herbicide by application timing on log10 non-native forb density (+0.1). Error bars represent a SE of 0.1 for controls and all treatments.

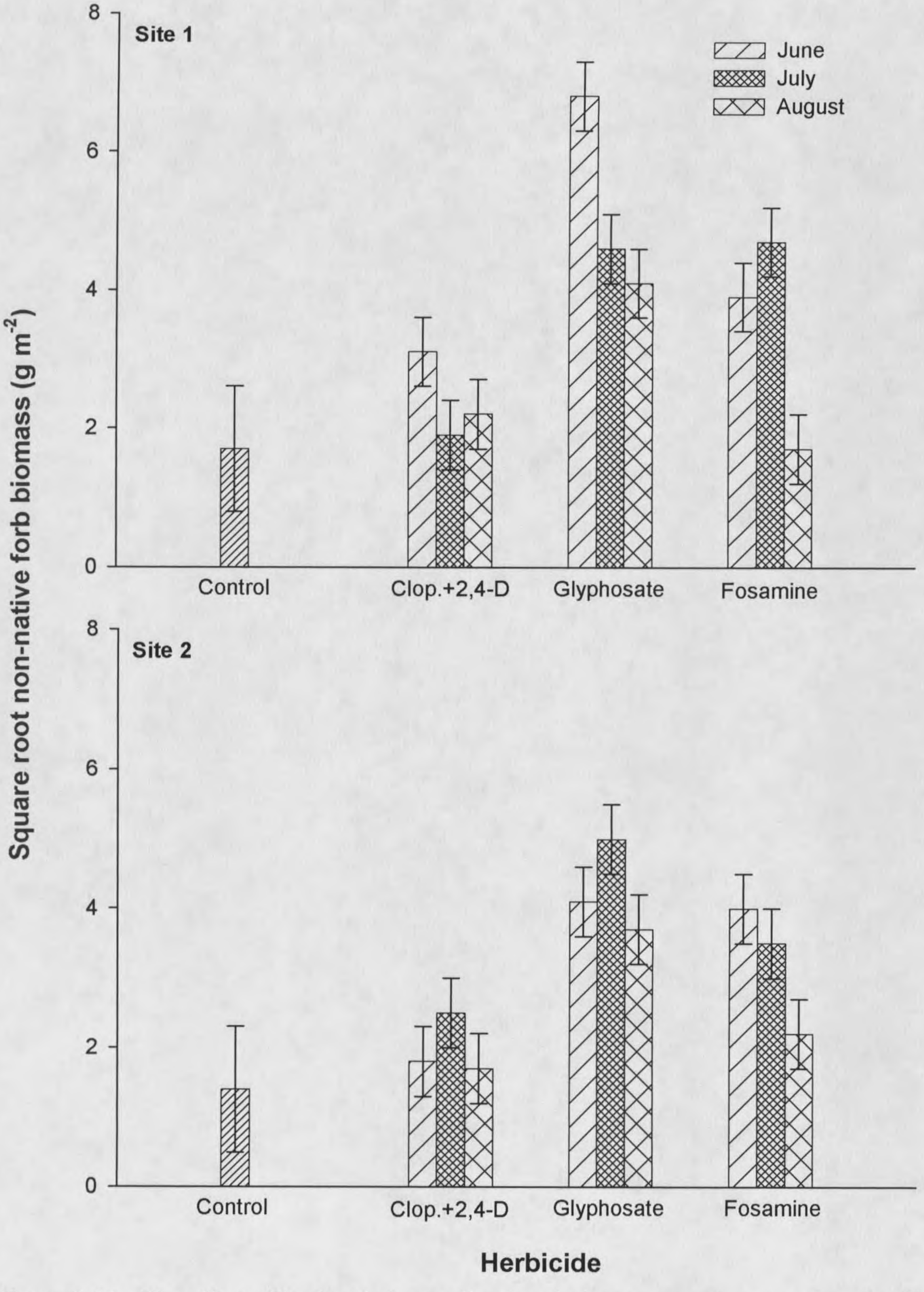

Figure 2.11. The effect of herbicide by application timing on square root non-native forb biomass at sites 1 and 2. Error bars represent a SE of 0.9 (controls) and 0.5 (treatments).

Discussion

Using herbicides can provide effective short-term suppression of invasive weeds, including Russian knapweed. Clopyralid (0.28 kg a.i. ha^{-1}) plus 2,4-D (1.49 kg a.i. ha^{-1}) provided 94% control of Russian knapweed in north-central Wyoming two years after application (Whitson et al. 1991). Similarly, in this study Russian knapweed biomass was reduced from 125 g m^{-2} to about 25 g m^{-2} using this herbicide, but irrespective of rate. Clopyralid plus 2,4-D also reduced Russian knapweed density by more than half (35 to 13 plants m^{-2}) two years after treatment. We rejected our hypothesis that the highest rate of clopyralid plus 2,4-D would provide the best control of Russian knapweed density and biomass. In general, both medium and high rates of clopyralid plus 2,4-D provided the best Russian knapweed control, but that result was site dependent.

The timing of herbicide application is important for weed control, and literature suggests that clopyralid plus 2,4-D is most effective controlling Russian knapweed when applied from full bloom to the first killing frost (Bussan et al. 2001). In our study, the effect of clopyralid plus 2,4-D on Russian knapweed biomass or density did not depend upon the timing of application. Therefore, we rejected our hypothesis that the August application would provide the lowest density and biomass of Russian knapweed. The only exception was the June application, which reduced Russian knapweed biomass the most at site 1. Targeting Russian knapweed juveniles in the spring can greatly reduce the productivity of an infestation. Whitson et al. (1991) found that applying clopyralid plus 2,4-D to Russian knapweed rosettes in May provided 76 to 81% control one year after treatment.

Glyphosate reduced Russian knapweed density and biomass, but only temporarily, as Russian knapweed density was equal to that of the control by August 2002. However, a timing of application interaction indicates that June and possibly July applications appear to provide effective short-term suppression. Previous research showed that glyphosate applied at the bud stage and again to remaining live plants two months later provided no Russian knapweed control two years after treatment (Benz et al. 1999). Spring applications of glyphosate can prevent pre-emergent desirable species from being affected. However, sequential glyphosate treatments during one growing season may reduce desirable species populations to levels at which they cannot effectively compete with Russian knapweed. Although glyphosate has minimal environmental impact on aquatic ecosystems, it appears to lack the desired efficacy for Russian knapweed control.

Fosamine is a selective herbicide that targets woody and herbaceous plants. However, the impacts of fosamine vary and can be unreliable (Barring 1982). We found no published data that have examined the effects of fosamine on Russian knapweed. Based on this herbicide's low impact to aquatic systems and some success controlling leafy spurge (Tu et al. 2001), we wanted to determine if fosamine could control Russian knapweed in a riparian area. In general, fosamine treatments did not provide consistent control of Russian knapweed. However, higher rates applied in June appear to have some potential for controlling Russian knapweed in riparian bottomlands. Because fosamine does not easily penetrate the leaves of mature plants (Hernandez et al. 1978), the efficacy of the June application may be attributed to the vulnerability of the juveniles.

Neither glyphosate nor fosamine provided substantial Russian knapweed control or increases in grasses. However, application of clopyralid plus 2,4-D has increased grass abundance (Rice et al. 1997). Similarly, the medium and high rates of clopyralid plus 2,4-D increased native grass density and biomass on the site with a dominant residual understory of native grasses. Non-native grasses were unaffected by clopyralid plus 2,4-D at this site. On the site co-dominated with non-native grasses, clopyralid plus 2,4-D maintained native grass density and biomass regardless of rate, and non-native grasses increased in density and biomass from all rates of clopyralid plus 2,4-D. Because the highest density and biomass of grasses did not result exclusively from the highest rate and the August application of clopyralid plus 2,4-D, we rejected our hypothesis. The treatment effects on grasses appeared to be associated with the dominant grass composition at each site, i.e. native vs. non-native grasses. We believe that the most abundant species capture the majority of resources, which allow them to usurp those resources faster than species occurring with less frequency.

Determining community level effects from herbicides can be difficult when species frequency and abundance varies. Our native forb and shrub data could not be analyzed by ANOVA because of normality and homogeneity of variance violations. Marrs (1985) encountered similar difficulty because many species were not present in all the plots, and occurred at low frequency where they did exist. By the inception of this study, we believe Russian knapweed and other non-native forbs had already reduced the native forb and shrub populations so low that they did not meet statistical requirements for ANOVA. We doubt any herbicide treatments could have facilitated a positive response because of the initial paucity of native forbs and shrubs.

Our study sites consisted of many non-native forbs considered by land managers to be invasive species. Therefore, we were interested in treatments that reduced the density and biomass of this plant group. Rice et al. (1997) found that a June application of clopyralid plus 2,4-D caused a large reduction in non-target forb cover. In our study, only the medium rate of clopyralid plus 2,4-D in July and low rate in August decreased non-native forb density. No treatments reduced non-native forb biomass. Again, we rejected our hypothesis that the highest rate of clopyralid plus 2,4-D applied in August would provide the lowest density and biomass of non-native forbs.

Of the herbicides tested in this study, clopyralid plus 2,4-D provided the best control of Russian knapweed. Although suppression two years after treatments does not infer long-term control, we hoped to observe increases in the density and biomass of all desirable plant groups. These increases would have had the potential to direct the existing plant community on a positive trajectory towards meeting our wildlife production objectives. Because we detected increases only in grasses, we believe that the rehabilitation of the plant community's structure was not successful. Without sufficient community structure and competition from other critical plant groups, Russian knapweed will most likely recover from suppression treatments (Pokorny 2002). Therefore, we believe that herbicides alone are inadequate for the restoration or rehabilitation of desirable plant communities infested with Russian knapweed.

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CHAPTER 3

HERBICIDE EFFECTS ON SPECIES RICHNESS AND DIVERSITY IN A RUSSIAN KNAPWEED-INFESTED PLANT COMMUNITY

Introduction

Invasions of non-native plant species, such as Russian knapweed [*Acroptilon repens* (L.) DC.], can displace native vegetation and decrease plant diversity, thereby altering the structure and function of ecological systems (Olson 1999). Russian knapweed, a rhizomatous perennial forb, invades disturbed sites and often forms monocultures after becoming established (Whitson 1999). Introduced to North America in the early 1900's, it is widespread in the United States, most commonly in the semiarid portions of the West and adjacent Canada. Additionally, this species invades riverbottoms and riparian woodlands throughout the U.S. (Carpenter and Murray 1999).

Russian knapweed has an aggressive rate of spread (Whitson 1999), a competitive advantage over native species (Watson 1980), and allelopathic compounds (Fletcher and Renny 1963). Consequently, land managers are recognizing the importance and difficulty of controlling this weed. Previous research indicates that a variety of herbicide formulations can provide short-term suppression of Russian knapweed (Whitson et al. 1992, Sebastian and Beck 1993, Benz et al. 1999). However, further research on controlling Russian knapweed with herbicides appropriate for use in wet areas and riverbottoms is needed. My companion study tested the efficacy of three herbicides (clopyralid plus 2,4-D, glyphosate, and fosamine), at different application rates and timings, for controlling Russian knapweed (Chapter 2). Our data indicated that medium (0.13 plus 0.67 kg a.i. ha^{-1}) and high (0.18 plus 0.92 kg a.i. ha^{-1}) rates of clopyralid plus 2,4-D provided the most effective control of Russian knapweed, irrespective of application timing. Two years after treatments, Russian knapweed density was reduced from 35 to 13 plants m^{-2} and biomass was reduced from 125 to 25 g m^{-2}. That study also investigated the effects of these herbicides on density and biomass of desirable species to determine the influence of a single herbicide application on plant productivity and wildlife habitat. Data indicated that clopyralid plus 2,4-D increased density and biomass of grasses, but not forbs or shrubs. We concluded that plant productivity and wildlife habitat would consist primarily of grasses and would therefore lack key plants needed for many wildlife species.

Plant density and biomass data can provide insight to community structure and dynamics. More recently, ecologists have emphasized the community- to global-scale importance of species richness and diversity (Chapin et al. 1997, Vitousek et al. 1997). As components of overall biodiversity, plant richness (number of species) and diversity (relative abundance of species) play a major role in contributing to human welfare. Naeem et al. (1999) suggested that biodiversity, including the earth's living organisms, benefit human welfare through market (economy-based) and non-market values. They define market values as goods and services such as food, medicine, industrial products, genetic resources for crop breeding, and natural pest control services. Non-market values (e.g. knowledge and aesthetics) are difficult to quantify, but are equally strong justifications for the preservation of biodiversity (Naeem et al. 1999).

Species richness and diversity have also been recognized as valuable indicators of ecosystem function (McNaughton 1993, Vitousek and Hooper 1993, Naeem et al. 1994). Ecosystem processes such as plant productivity, nutrient cycling, and energy and material flow are directly influenced by the structure and organization of those systems. For example, in a Minnesota grassland study, greater plant diversity increased the uptake of limiting soil nitrogen and decreased leaching loss of nitrogen, which could result in greater soil fertility (Tilman et al. 1996). In another study, Spehn et al. (2000) found that experimental grassland communities with the greatest richness (32 species) produced 143% more biomass than the average biomass of all monocultures. These studies indicate that greater species richness/diversity may improve the efficiency of ecosystem function.

Previous research has focused on the relationship between species richness/diversity and resilience/resistance of native plant communities (McNaughton 1977, Chapin and Shaver 1985, Rejmanek 1989, Woods 1993, Naeem and Li 1997, Tilman et al. 1997). With high species richness and diversity, plant communities will more likely include species important in successional dynamics following disturbance (Elton 1958). In many cases, plant communities with higher species diversity that are subjected to disturbances tend to resist change more strongly than those with lower diversity (Crawley 1987, Lawton and Brown 1993, Naeem 1998). For example, in a comparison of eight grasslands in Yellowstone National Park, Frank and McNaughton (1991) found that grassland community composition with greater plant diversity was more stable in response to drought.

Evidence for stronger resistance to non-native plant invasion as a function of plant diversity is increasing (Robinson et al. 1995, Levine and D'Antonio 1999). Communities with high species diversity may have greater niche occupation and enhanced resource capture (Pyke and Archer 1991, Jacobs and Sheley 1999a). Resource capture by desirable species preempts their use by invasive plants (Sheley and Larson 1995). Carpinelli (2000) found as species richness and niche occupation increased, invasion by spotted knapweed (*Centaurea maculosa* Lam.) decreased. In fact, including three desired species in the plant community, all differing in niche requirements, nearly prevented establishment of this invasive weed.

Knowledge about the influence of various strategies on species richness and diversity is central to making wise weed management decisions. Goals of invasive weed management should include the establishment of structurally diverse plant communities that may lead to more complete ecosystem processes such as nutrient cycling. To achieve these goals, community level effects must be better understood. The overall objective of this study was to investigate the effects of three herbicides on plant community species richness and diversity. Our specific objective was to determine the influence of clopyralid plus 2,4-D, glyphosate, and fosamine, at different application rates and timings, on richness and diversity of total species, total native species, and total non-native species within a Russian knapweed-infested plant community. We hypothesized that clopyralid plus 2,4-D or fosamine treatments, regardless of application rate or timing, would provide greater species richness and diversity in all plant groups than those of glyphosate because these two broadleaf herbicides would create sufficient niches for desirable species to occupy without creating the moonscape-type disturbance, indicative of glyphosate treatments, that would favor Russian knapweed spread.

Materials and Methods

Study Sites

This study was conducted in north-central Montana on the Charles M. Russell (CMR) National Wildlife Refuge, about 105 kilometers north (22°29'N, 23°29'E) of Lewistown, Montana. Two study sites were located on a floodplain known as Knox Bottom along the Missouri River, near the western boundary of the refuge. Sites were on a north aspect of 0-2% slopes at 670 m elevation with an annual average precipitation of 30 cm and an annual average temperature of 7° C. Soils at both sites were Kobar silty clay loams (fine, montmorillonitic Borollic Camborthids). These soils were formed in alluvium material and have slow permeability (USDA 1978).

Study sites were located within the silver sage/western wheatgrass (*Artemisia cana/Agropyron smithii*) habitat type (Hansen et al. 1995). Similar habitat types have been described for the northern Great Plains by Hanson and Whitman (1938), Mackie (1970), and Jorgensen (1979). This habitat type, common in central and eastern Montana, represents one of the driest extremes of the riparian zone. Plant communities at both sites consist of native and non-native species. The non-native invader Russian knapweed was abundant at the study area and had displaced desirable plant species. Study sites were chosen based on similarities of habitat type as well as obvious differences in predominant graminoid species. Grass species at site 1 were dominated by quackgrass [*Elytrigia repens* (L.) Desv. ex Nevski], a non-native grass, while the native western wheatgrass (*Pascopyrum smithii* P.A. Love) was the dominant grass species at site 2.

The silver sage/western wheatgrass habitat type typically occurs as a result of disturbance, where site potential has changed, possibly due to prolonged heavy grazing (Hansen et al. 1995). Land use at these sites over the past century (approximately 1920's - 1980's) has included crop production and cattle grazing. Throughout that period, cattle were moved from upland summer pastures to the river bottoms for winter grazing. In addition, flooding from the Missouri River occurs with varying frequency and intensity. Because of its location within the CMR National Wildlife Refuge, Knox Bottom provides critical wildlife habitat and continues to be managed for wildlife production.

Experimental Design

In a randomized complete block design at both sites, 28 treatments (3 herbicides x 3 herbicide rates x 3 herbicide application timings, and a control) were applied from June through August 2000 to 4.3 m x 4.6 m plots. Treatments were replicated four times at both sites for a total of 224 plots. Clopyralid plus 2,4-D (3,6-dichloropicolinic acid + 2,4-dichlorophenoxyacetic acid), glyphosate [N- (phosphonomethyl) glycine], and fosamine [ethyl hydrogen (aminocarbonyl) phosphonate] were applied in June (spring rosette stage of Russian knapweed), July (bud to bloom stage of Russian knapweed), and August (flowering stage of Russian knapweed) in accordance with CMR National Wildlife Refuge and U.S. Fish and Wildlife Service restrictions. Low, medium, and high rates [clopyralid plus 2,4-D at 0.08 (clopyralid) + 0.42 (2,4-D), 0.13 + 0.67, and 0.18 + 0.92 kg a.i. ha^{-1}; glyphosate at 0.6, 1.2, and 1.8 kg a.i. ha^{-1}; fosamine at 3.6, 7.2, and 10.8

kg a.i. ha^{-1}] were applied based on label rates for Russian knapweed. These herbicides were chosen because of their low environmental risk in areas near water and wildlife (Table 3.1). Herbicides were applied using a 4-nozzle backpack sprayer delivering 130 liters ha^{-1} of spray solution.

Table 3.1. Properties, soil and water behavior, and fish toxicity of herbicides (Tu et al. 2001).

Herbicide	Mode of Action	Average Soil Half-Life	Soil Sorption (Koc)	Soil Mobility	Water Solubility	LC-50 (bluegill sunfish)
Clopyralid	Auxin mimic	40 days	avg. 6 mL/g	Moderate-High.	1,000 mg/L (acid)	125 mL/g (moderate)
2,4-D	Auxin mimic	10 days	20 mL/g (acid)	Moderate-High	900 mg/L (acid)	263 mL/g (moderate)
Glyphosate	Inhibits the shikimac acid pathway depleting aromatic amino acids	47 days	24,000 mL/g	Low	900,000 mg/L (IPA salt)	120 mL/g (moderate)
Fosamine	Mitotic inhibitor	8 days	150 mL/g	Moderate	1,790,000 mg/L	670 mL/g (low)

Sampling

Species richness was recorded for all existing plant species during June and August of 2001 and 2002. Richness was measured as the total number of species (grasses, forbs, and shrubs) per experimental plot. A Daubenmire frame (0.10 m^2) was randomly placed three times within each plot for data collection. Grasses were identified using Cronquist et al. (1977), while forbs and shrubs were classified according to Dorn (1984).

Species diversity was derived from the number of individuals (density) of each species. Species density was also recorded during June and August of 2001 and 2002. A Daubenmire's frame ($0.10\ m^2$) was randomly placed three times within each plot. Species diversity was then calculated using Simpson's Reciprocal Index (1/D), where $D = \sum (n/N)^2$ (Begon et al. 1996). In this equation, n = the total number of individuals of a particular species, and N = the total number of individuals of all species. Simpson's Diversity Index (D) is the probability that two individuals randomly selected from a sample will belong to the same species. Therefore, the Simpson's Reciprocal Index (1/D) represents the number of equally common species that will give the observed Simpson's Diversity Index (D). The value of 1/D can range from 1 to the total number of species (richness) in the sample. A value of 1 represents no diversity, while a value equal to the species richness indicates maximum diversity, where each species has the same number of individuals.

Data Analysis

Analysis of variance (ANOVA) was used to determine the effects of site, year (following treatments), herbicide, application rate, and application timing on desirable plant species richness and diversity. Treatment main effects and all interactions were included in the model. Five-way, 4-way, and non-significant ($P > 0.05$) 3-way interactions were pooled and included in the error term to improve the sensitivity of the analysis to detect important effects. When a significant P-value ($P \leq 0.05$) was observed, mean separations for main effects and interactions were achieved based on standard errors (SE). Each SE was calculated by determining the square root of the quotient

MSE/N, where MSE is the model mean square error, and N is the number of experimental units associated with a main effect or interaction. Detecting mean differences with this SE calculation was appropriate because the number of experimental units (N) differed among treatments and controls, and it was necessary to incorporate varying sample sizes in the formula.

Due to the infrequent occurrence and low abundance of native species, ANOVA models were inappropriate for statistical analysis of total native species diversity data. Because the Simpson's Reciprocal Diversity Index (1/D) is based on species richness and their relative abundance (evenness), index values for native species were consistently low and differences were statistically negligible. Because ANOVA models were inappropriate for total native species diversity data, observed trends for treatment main effects will be discussed in the Results section.

Results

Total Species Richness and Diversity

Total species richness was affected by a year*site interaction ($P = 0.02$). In June 2001, site 1 (3.1 species m^{-2}; SE = 0.1) had lower richness than site 2 (3.8 species m^{-2}; SE = 0.1). By August 2002, no significant difference in richness was found between site 1 (3.9 species m^{-2}; SE = 0.1) and site 2 (4.1 species m^{-2}; SE = 0.1). From June 2001 to August 2002, there was an increase in total species richness at both sites; site 1 increased by 0.8 species m^{-2}, and a 0.3 species m^{-2} increase was detected at site 2.

The effect of herbicide on total species richness depended upon the year after treatment ($P < 0.001$). In June 2001, there were no significant differences in richness between the control and the herbicide treatments (Figure 3.1a). In August 2002, only the glyphosate treatment (4.6 species m^{-2}) yielded greater total richness over that of the control (3.5 species m^{-2}). Plots that received glyphosate and fosamine treatments had increased richness from June 2001 to August 2002, but no significant differences in richness were detected for clopyralid plus 2,4-D or the controls during this time period. The influence of herbicide on total species richness also differed by site ($P = 0.03$). At site 1, reductions in total richness were detected for all herbicide treatments, relative to the control (4.3 species m^{-2}; Figure 3.1b). At site 2 however, glyphosate and fosamine treatments increased total richness, and no significant difference existed between the control and clopyralid plus 2,4-D treatments.

Differences in total species richness were also attributed to a herbicide*rate interaction ($P = 0.01$). For all rates of clopyralid plus 2,4-D, total richness decreased (averaging 3.3 species m^{-2}) below that of the control (3.9 species m^{-2}; Figure 3.2a). No differences were detected among the control and any rates of glyphosate or fosamine. The effect of herbicide on total richness was also dependent upon timing of application ($P = 0.001$). For the three timings of clopyralid plus 2,4-D, the June application produced similar total species richness as the control (3.9 species m^{-2}), but the July and August applications reduced richness by 0.8 species m^{-2} (Figure 3.2b). Effects from glyphosate timings on total species richness varied. The June application yielded greater richness than the control, while the July application decreased richness. The August application of glyphosate indicated no significant difference in richness from the control. For all application timings of fosamine, no differences in total richness were detected relative to the control.

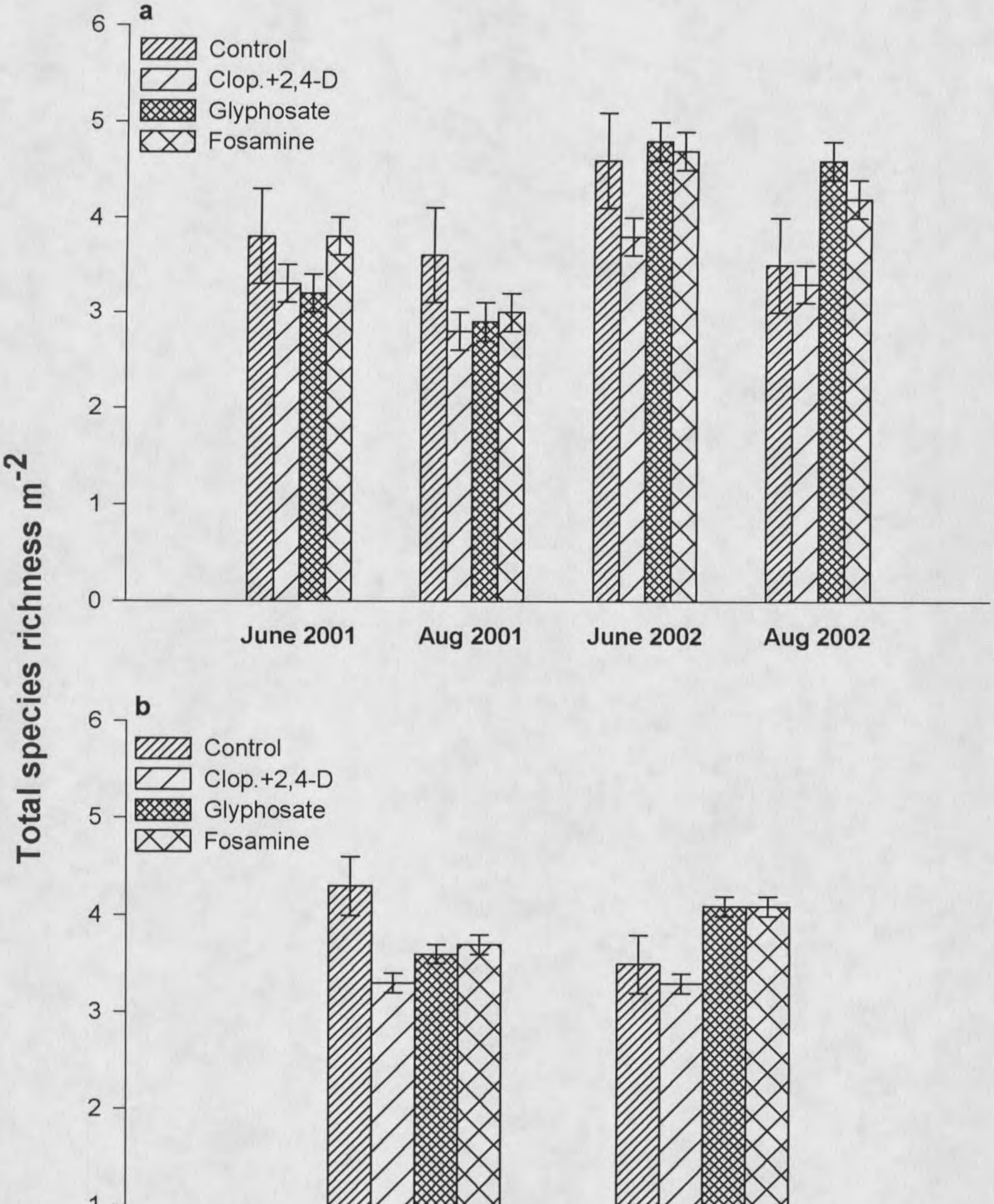

Figure 3.1. The effect of herbicide by year (a) and site (b) on total species richness. Error bars in (a) represent a SE of 0.5 (controls) and 0.2 (treatments). Error bars in (b) represent a SE of 0.3 (controls) and 0.1 (treatments).

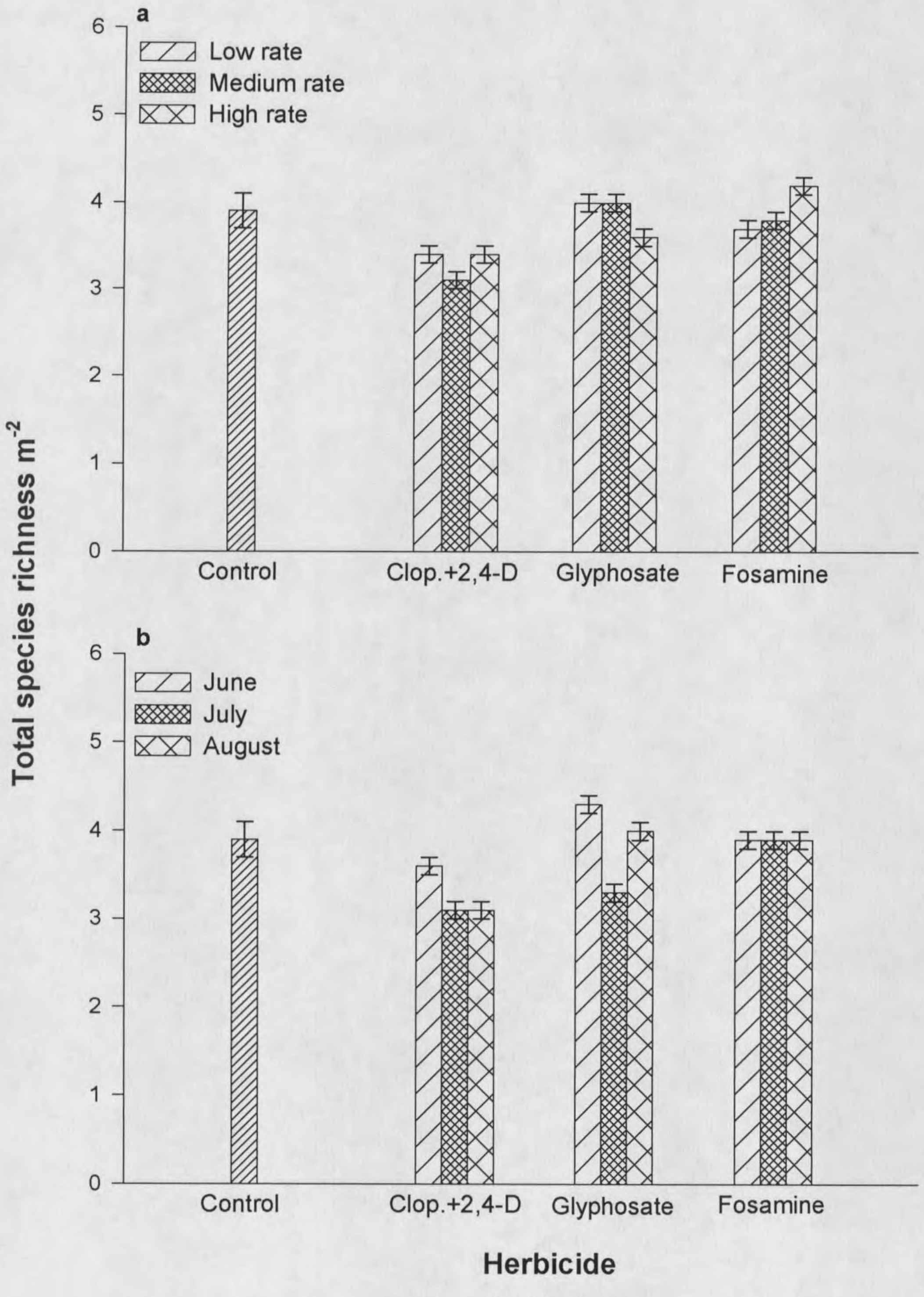

Figure 3.2. The effect of herbicide by application rate (a) and timing (b) on total species richness. Error bars in (a) and (b) represent a SE of 0.2 (controls) and 0.1 (treatments).

Total species diversity was affected by a year*herbicide interaction (P = 0.02). Sampling in June 2001 indicated no differences in diversity from any herbicides and the control (Figure 3.3). In August 2002, diversity from clopyralid plus 2,4-D remained similar to that of the control (1.4), but increases in total species diversity were detected for glyphosate (2.3) and fosamine (2.0). Between June 2001 and August 2002, total species diversity for glyphosate treatments increased from 1.9 to 2.3.

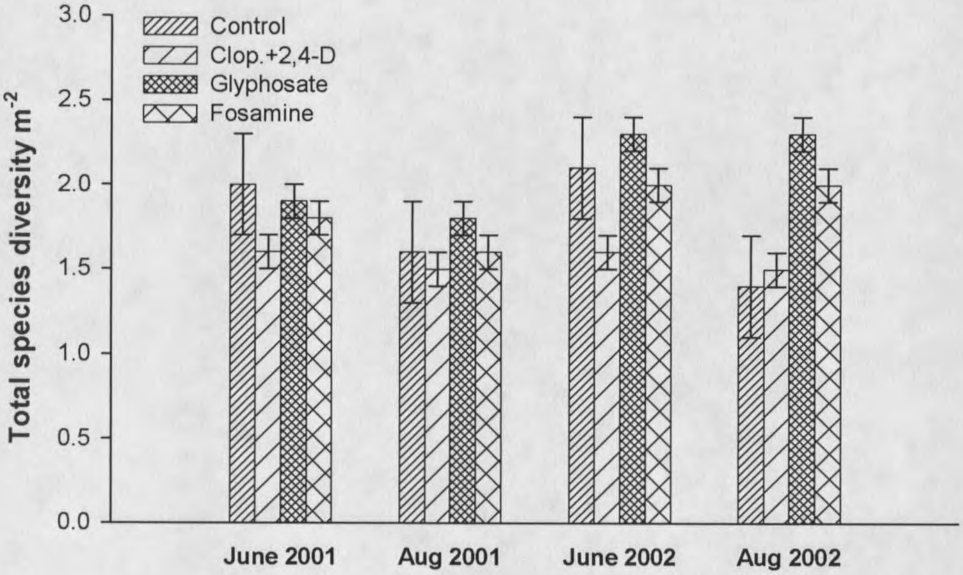

Figure 3.3. The effect of herbicide by year on total species diversity. Error bars represent a SE of 0.3 (controls) and 0.1 (treatments).

Total species diversity also depended upon a site*herbicide*rate interaction (P = 0.03). At site 1, most treatments had no significant effect on total diversity relative to the control (Figure 3.4). However, the low rate of glyphosate produced greater total diversity (2.3) than that of the control (1.8). At site 2, all clopyralid plus 2,4-D rates decreased total diversity; the high rate of glyphosate (2.2) increased total diversity, and the low and medium rates of glyphosate and all fosamine rates were not significantly different from the control.

The effect of herbicide on total species diversity was affected by application rate and timing ($P = 0.02$). For June applications, the high rate of glyphosate yielded greater total diversity (2.3) than the control (1.8), while significant differences were not detected from other treatments (Figure 3.5). In July, all rates of clopyralid plus 2,4-D decreased total diversity, and the low rate of glyphosate and medium and high rates of fosamine increased diversity. For August applications, the low rate of clopyralid plus 2,4-D reduced total species diversity (1.5), whereas the high rate of glyphosate resulted in an increased diversity (2.3) over that of the control.

Total Native Species Richness and Diversity

Total native species richness depended upon an application rate main effect ($P = 0.003$). All herbicide rates (averaging 0.8 species m^{-2}; SE's = 0.03) reduced total native species richness below that of the control (1.3 species m^{-2}; SE = 0.1). A year*site interaction ($P < 0.001$) also affected total native species richness. For each sampling date, richness remained unchanged at site 1. At site 2, total native plant richness increased from June 2001 (1.0 species m^{-2}; SE = 0.1) to August 2002 (1.4 species m^{-2}; SE = 0.1). The effect of site on total native richness was also influenced by herbicide ($P = 0.03$). Results from the controls at both sites indicated that richness was lower at site 1 (0.9 species m^{-2}) than at site 2 (1.6 species m^{-2}; Figure 3.6a). Furthermore, reductions in total native plant richness were detected for all herbicide treatments at both sites, relative to their respective controls. Total native species richness was also affected by the

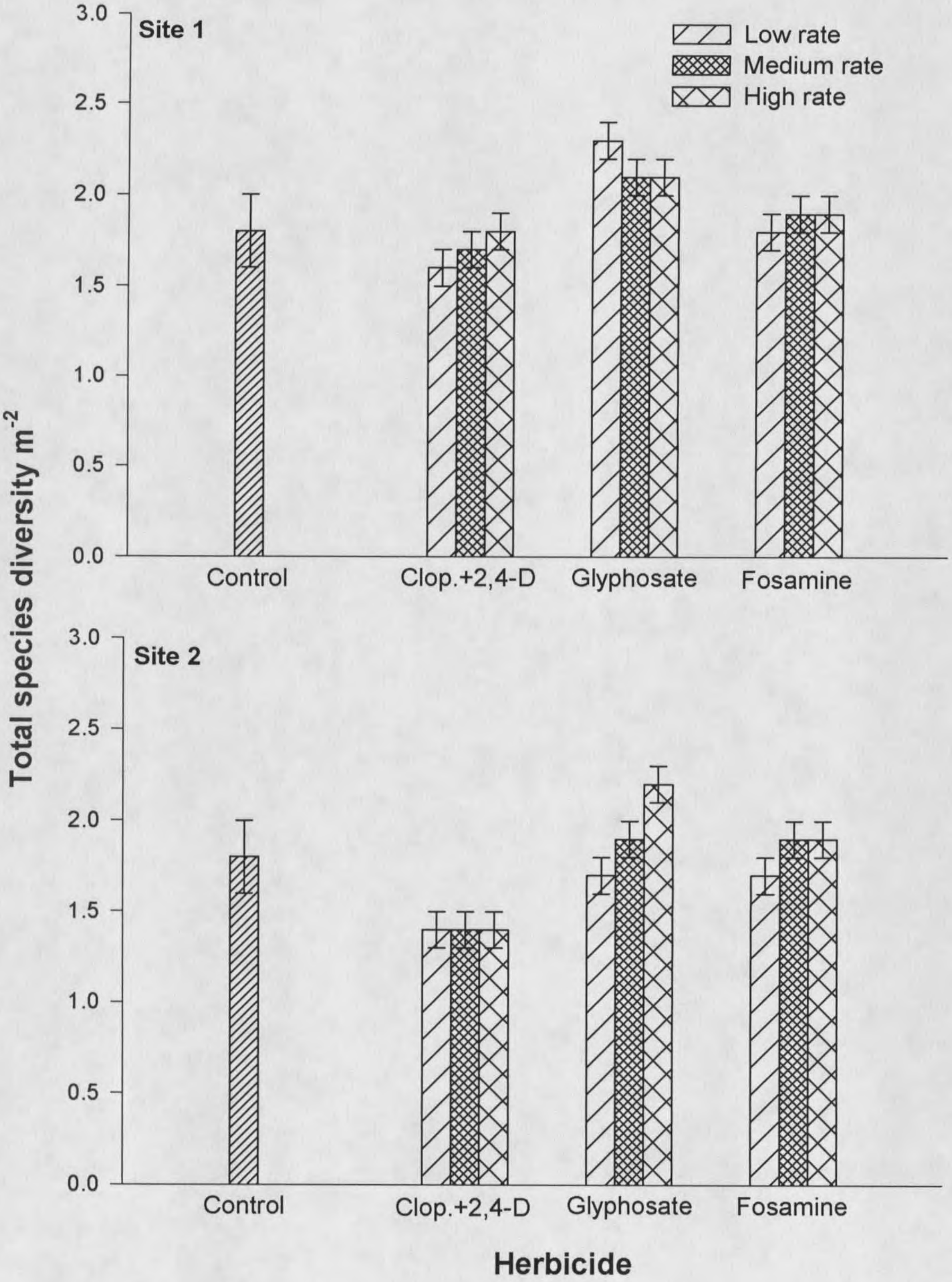

Figure 3.4. The effect of herbicide by application rate on total species diversity at sites 1 and 2. Error bars represent a SE of 0.2 (controls) and 0.1 (treatments).

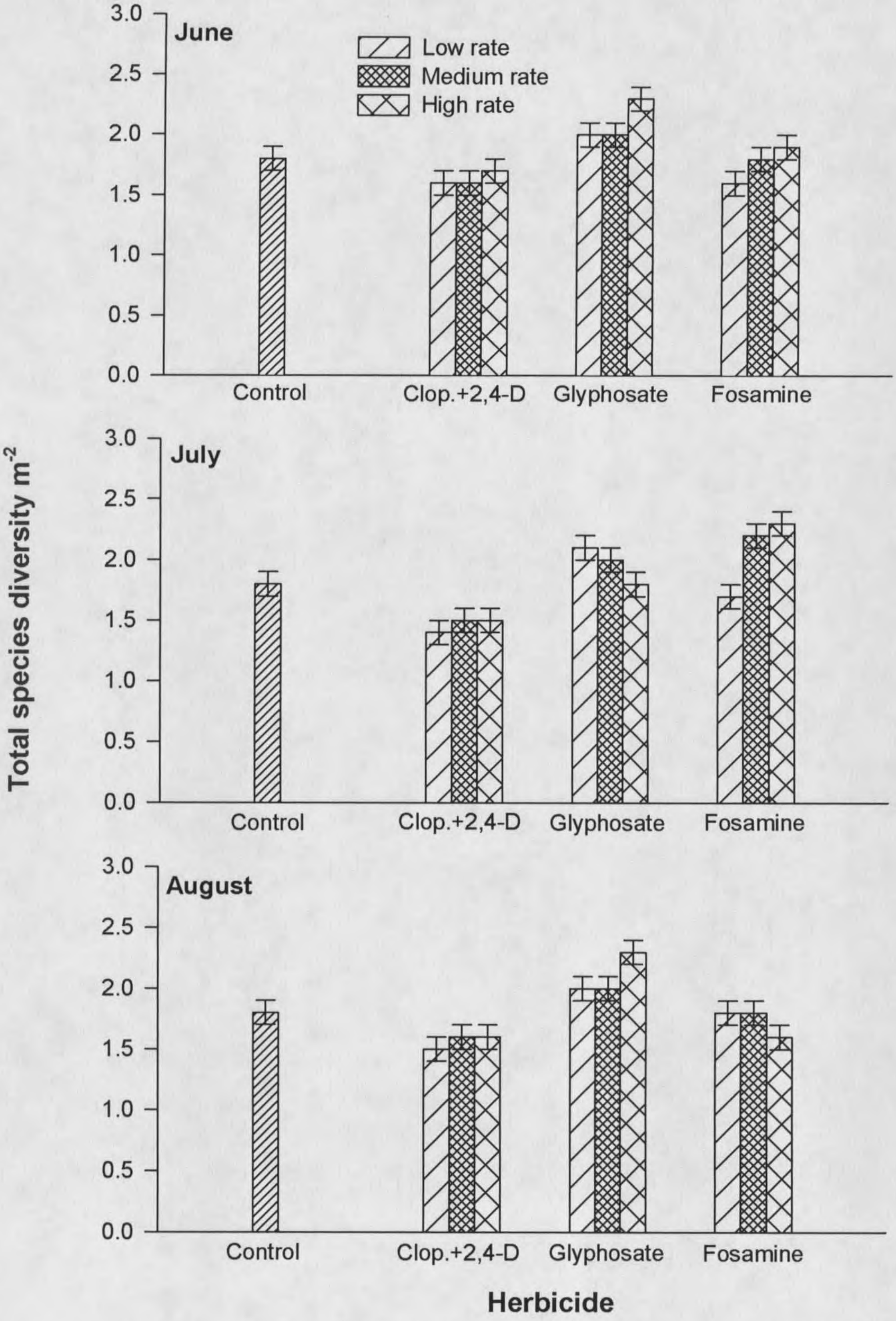

Figure 3.5. The effect of herbicide by application rate and timing on total species diversity. Error bars represent a SE of 0.1 for controls and all treatments.

application timing of herbicides ($P = 0.03$). All timings of each herbicide reduced richness below that of the control (1.3 species m^{-2}; Figure 3.6b).

Diversity data for total native species violated ANOVA assumptions of normality and homogeneity of variance. Therefore, discussion will be restricted to the analysis of trends associated with treatment main effects. For the effect of year, a slight increase in total native species diversity was observed from June 2001 (1.0) to August 2002 (1.1). Diversity among sites appeared to vary slightly, as site 1 (1.0) had a lower diversity index than site 2 (1.1). All herbicide treatments (1.0 to 1.1) tended to reduce total native species diversity, relative to the control (1.2). Similarly, all herbicide application rates and timings appeared to produce diversity indices (1.0 to 1.1) below that of the control (1.2).

Total Non-native Species Richness and Diversity

Richness of total non-native species was affected by a year*site interaction ($P < 0.001$). In June 2001, there was no difference in richness between site 1 (2.7 species m^{-2}; SE = 0.1) and site 2 (2.8 species m^{-2}; SE = 0.1). By August 2002, site 1 had greater richness, by 0.8 species m^{-2}, than site 2. Also, richness at site 1 increased from June 2001 to August 2002 (2.7 to 3.6 species m^{-2}; SE's = 0.1), but site 2 indicated no change among sampling dates, as both had 2.8 species m^{-2} (SE's = 0.1).

The effect of herbicide on total non-native richness depended upon year ($P < 0.001$). In June 2001, plots treated with fosamine (3.1 species m^{-2}) produced higher richness than the control (2.5 species m^{-2}), but clopyralid plus 2,4-D and glyphosate did not affect richness (Figure 3.7a). Total non-native species richness, as a result of

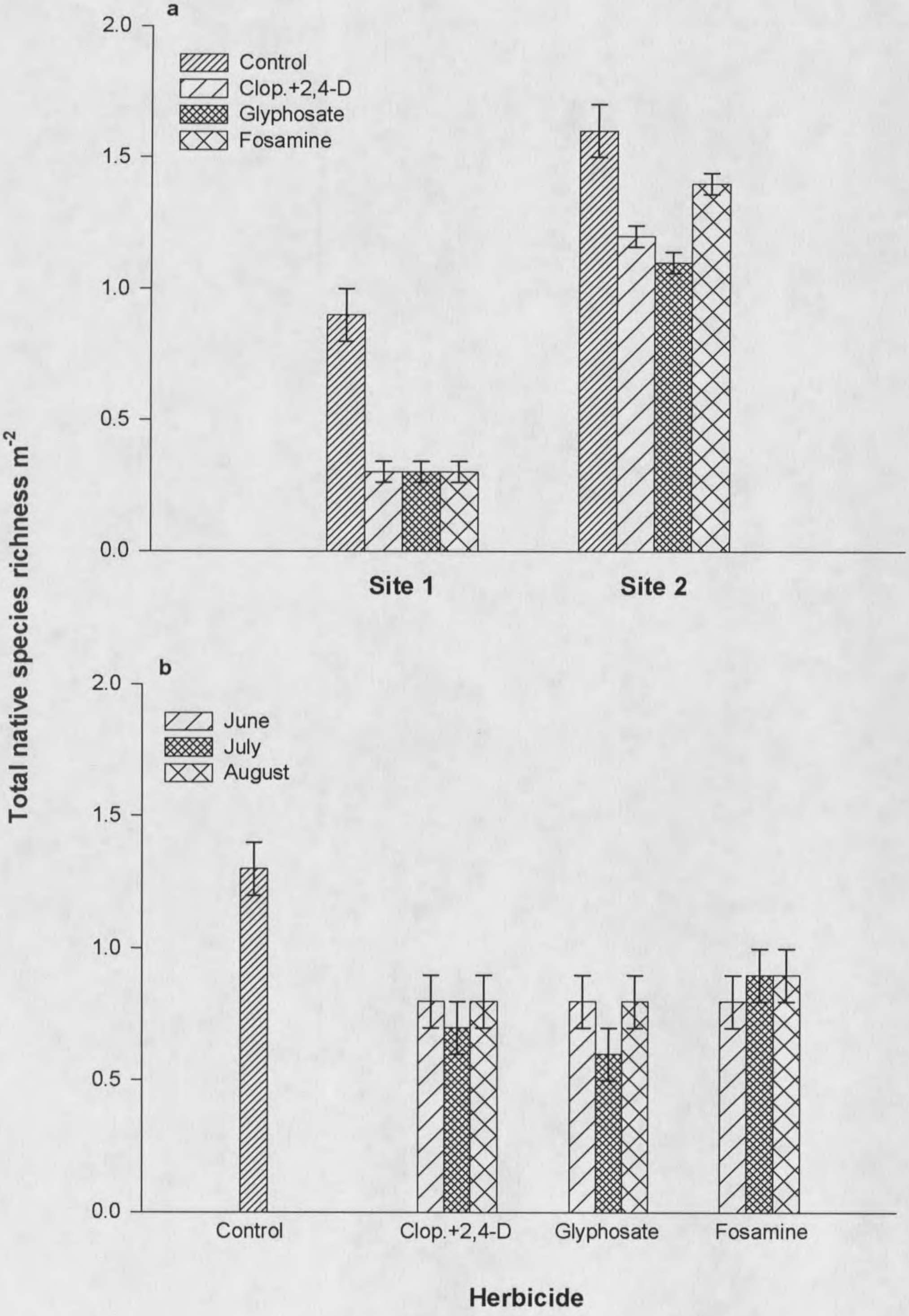

Figure 3.6. The effect of herbicide by site (a) and application timing (b) on total native species richness. Error bars in (a) represent a SE of 0.1 (controls) and 0.04 (treatments). Error bars in (b) represent a SE of 0.1 for the control and all treatments.

clopyralid plus 2,4-D, remained similar to the control in August 2002, but glyphosate and fosamine increased richness. From June 2001 to August 2002, richness resulting from the untreated controls, clopyralid plus 2,4-D, or fosamine did not differ. However, glyphosate increased non-native species richness between June 2001 (2.6 species m^{-2}) and August 2002 (3.9 species m^{-2}). The effect of herbicide on total non-native species richness was also influenced by application timing ($P = 0.03$). For clopyralid plus 2,4-D, only the June application (3.0 species m^{-2}) increased richness above that of the control (2.6 species m^{-2}; Figure 3.7b). Additionally, June and August applications of glyphosate and all timings of fosamine increased non-native species richness.

Total non-native species richness was also affected by a site*herbicide*rate interaction ($P = 0.03$). Relative to the control (3.3 species m^{-2}) at site 1, no significant differences in richness were detected among the treatments (Figure 3.8). At site 2, the high rate of clopyralid plus 2,4-D increased richness over the control (2.5 vs. 1.9 species m^{-2}). Greater richness was also produced from all rates of glyphosate, as well as the medium and high rates of fosamine.

The effect of herbicide on total non-native diversity depended upon year ($P = 0.05$). In June 2001, glyphosate and fosamine increased diversity over that of the control (1.8 for both herbicide treatments vs. 1.4; Figure 3.9a). In August 2002, all herbicide treatments produced greater diversity than the control. Between June 2001 and August 2002, only diversity indices from glyphosate were significantly different; an increase from 1.8 to 2.3 was detected. rate ($P = 0.02$). For clopyralid plus 2,4-D, the high rate (1.7) increased diversity over that of the control (1.4; Figure 3.9b). Greater diversity

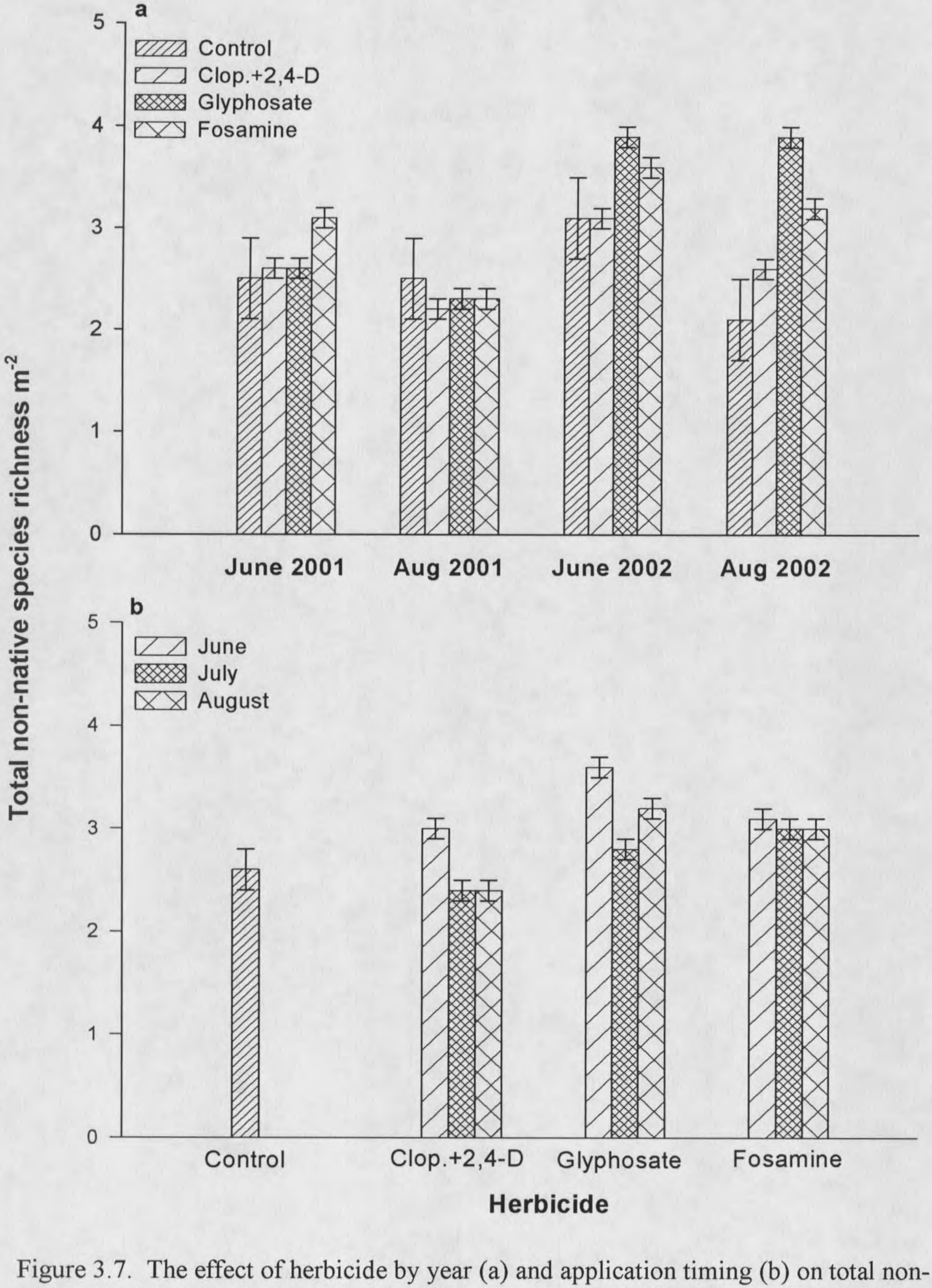

Figure 3.7. The effect of herbicide by year (a) and application timing (b) on total non-native species richness. Error bars in (a) represent a SE of 0.4 (controls) and 0.1 (treatments). Error bars in (b) represent a SE of 0.2 (control) and 0.1 (treatments).

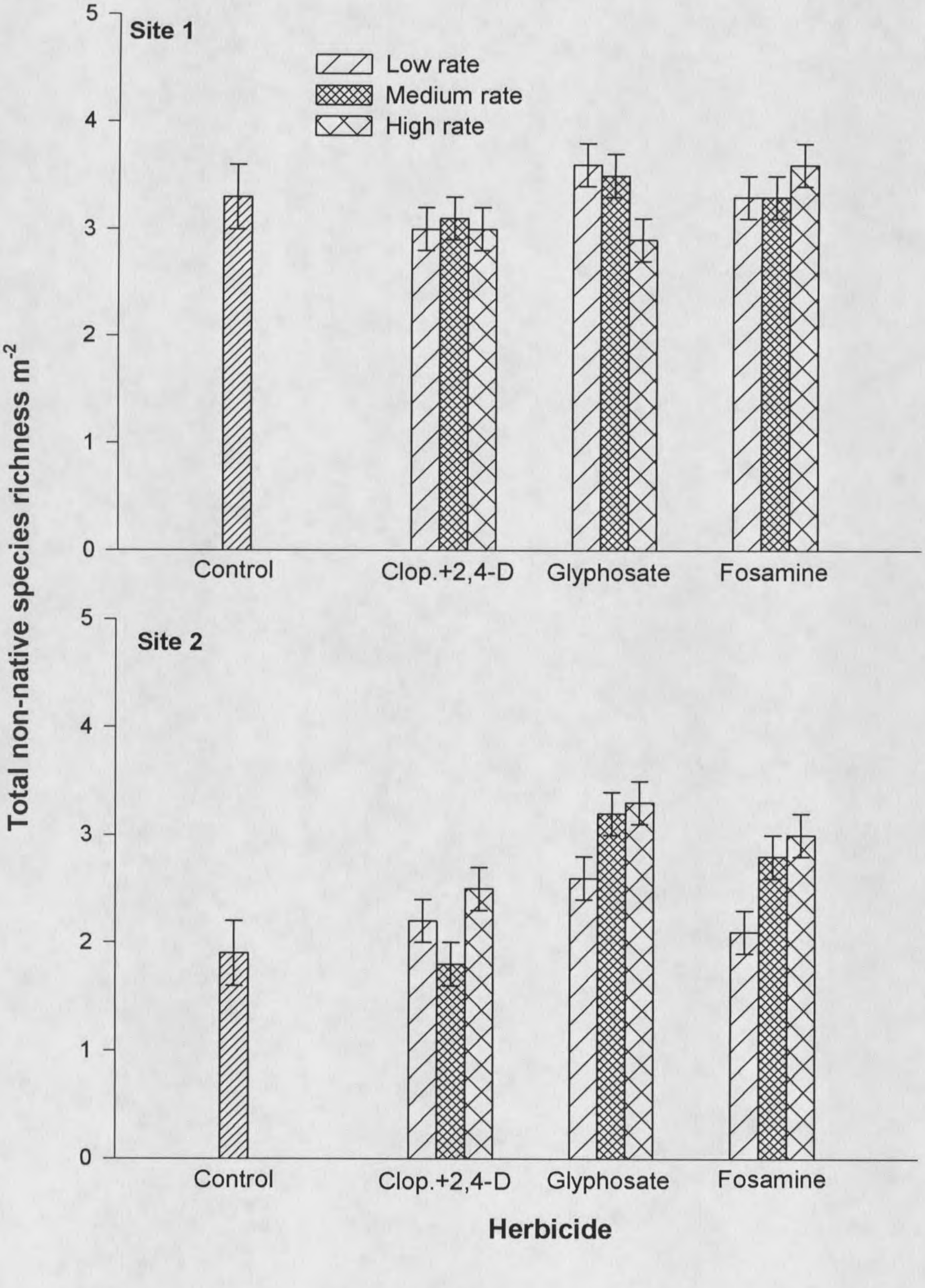

Figure 3.8. The effect of herbicide by application rate on total non-native species richness at sites 1 and 2. Error bars represent a SE of 0.3 (controls) and 0.2 (treatments).

indices were found for all rates of glyphosate (1.9 to 2.0) relative to the control. The medium (1.8) and high (1.9) rates of fosamine also increased diversity above the control.

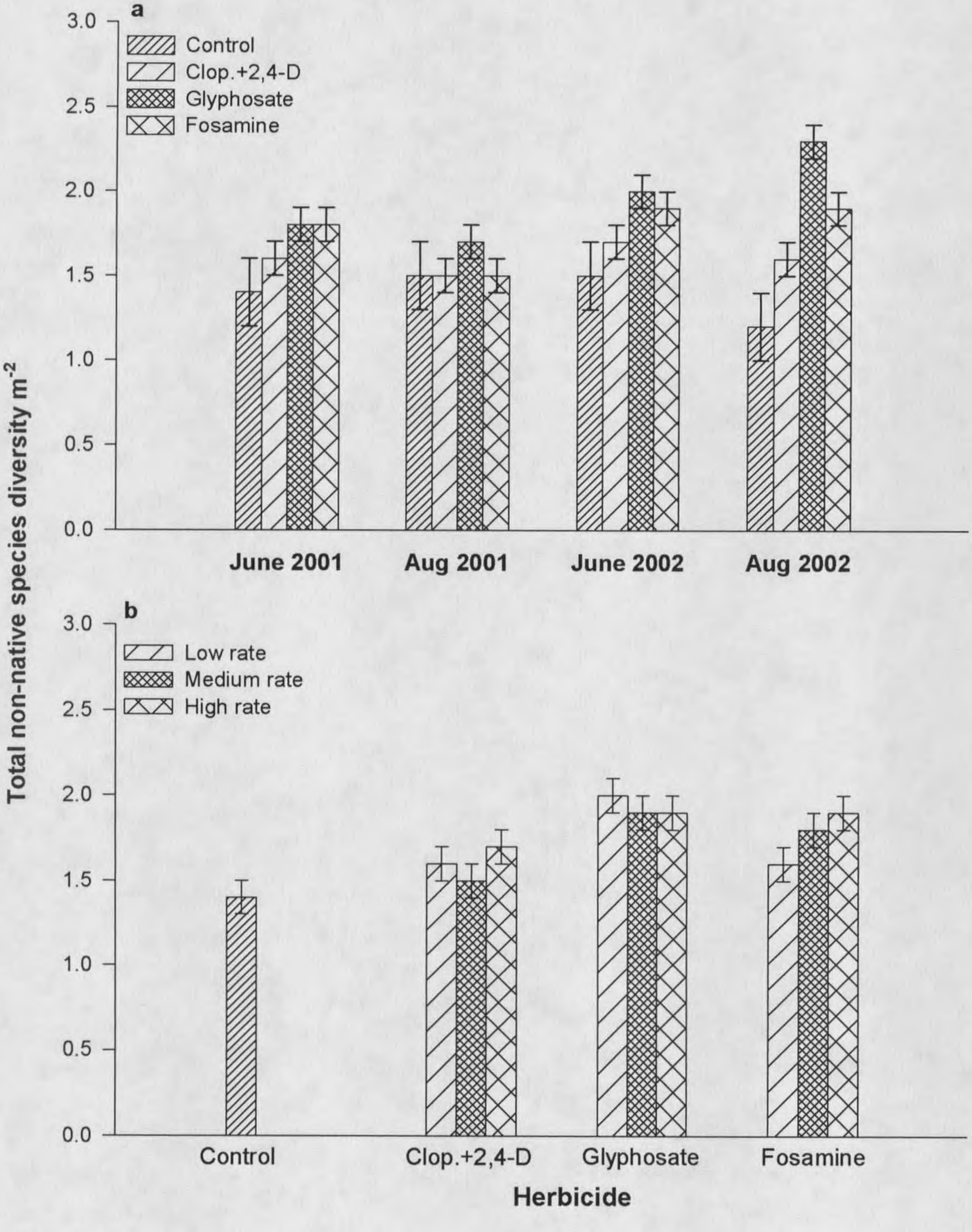

Figure 3.9. The effect of herbicide by year (a) and application rate (b) on total non-native species diversity. Error bars in (a) represent a SE of 0.2 (controls) and 0.1 (treatments). Error bars in (b) represent a SE of 0.1 for the control and all treatments.

Discussion

Consistent with other studies investigating community response to herbicides (Marrs 1985, Rice et al. 1997), our data indicated that effects on plant communities varied among treatments. Rice et al. (1997) found that the largest decrease in species richness occurred in plots treated with picloram and clopyralid plus 2,4-D applied in early spring, and little or no decrease occurred with clopyralid alone and clopyralid plus 2,4-D applied in late summer. Denny (2003) found that among several herbicides, picloram decreased forbs more than any other treatment. In that study, no treatments increased species richness. In this study, glyphosate caused an increase in total species richness above untreated control levels. Although the majority of these species were non-native annual forbs, they may play an important role in recovering the functions of the system (Pokorny 2002). My companion study (Chapter 2) indicated that controlling Russian knapweed with glyphosate was effective for only one year post-application. Therefore, glyphosate may be more useful for increasing desired species richness in communities infested by non-rhizomatous or annual weeds.

Application rates of herbicides are important determinants of community response (Boyd et al. 1995) because species vary in their ability to tolerate herbicide amounts. Marrs (1985) found that a single application of picloram, the most commonly used herbicide on rangeland, reduced non-target desired species to unacceptable levels when applied at high rates necessary to control scrub in lowland heath vegetation. Fosamine applied at 4.8 kg a.i. ha^{-1} was found to be suitable for scrub control without causing significant damage to the heath vegetation. In our study, herbicide rate did not influence total species richness. However, the influence of herbicide rate on species diversity depended upon the time of application and/or the site. This suggests that herbicide rates have less impact on the loss or gain of new species, but may have substantial impact on the abundance of these species present at the time of application.

In this study, glyphosate seemed to increase richness and diversity regardless of timing of application, while fosamine applied in July increased diversity, but had no effect at any other application timing. It has been suggested that short-lived herbicides, such as clopyralid plus 2,4-D or 2,4-D alone can be applied late in the growing season to avoid negative impacts on non-target forbs (Hitchmough et al. 1994, Jacobs and Sheley 1999b). Although applying clopyralid plus 2,4-D during June had no effect on total richness and diversity, applications during July and August consistently decreased both diversity parameters. These results are surprising because herbicides with low soil activity require uptake by actively growing foliar tissue to maximize absorption (Bussan and Dyer 1999). One potential explanation is that later applications provided poor Russian knapweed control. However, our companion study indicated effective control of this weed with later applications. Therefore, we believe that translocation from shoots to roots in non-target species during late application of clopyralid plus 2,4-D occurred with the movement of carbohydrates (Bussan and Dyer 1999), reducing species richness and diversity.

Herbicide application recommendations tend to be provided for broad geographic areas. The Pacific Northwest Weed Management Handbook (William et al. 2002) and the Montana/Utah/Wyoming Weed Management Handbook (Bussan et al. 2001) provide examples of regional herbicide recommendations that encompass multiple states within regions. Broad geographic recommendations may be appropriate for weed control, but our data suggests that herbicide recommendations considering post-application richness and diversity may be site-specific. In our study, nearly all response parameters vary between sites. For example, clopyralid plus 2,4-D did not influence total species diversity at site 1, but decreased it at site 2. At site 1, Russian knapweed was associated with a high presence of quackgrass, which responded positively to this broadleaf herbicide. Site 2 had limited associated grasses that could respond to the clopyralid plus 2,4-D treatment. Herbicide treatments aimed at enhancing richness and diversity will require improved predictive capability that considers pre-treatment plant assemblage composition to increase the probability that the treatments meet long-term management objectives (Kedzie-Webb et al. 2002).

The success of any management program depends on how closely the post-application plant community approximates that stated in the objectives (Sheley and Krueger-Mangold 2003). In this study, non-native species accounted for the majority of the richness and diversity in areas where they were dominant prior to application, whereas native species tended to decrease. Management strategies aimed at enhancing ecosystem function and possibly niche occupation to preempt re-invasion by Russian knapweed may possibly meet their goals, however restoring plant communities with native species using these herbicides seems less likely.

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CHAPTER 4

SEEDING METHOD AND HERBICIDE EFFECTS ON NATIVE SPECIES ESTABLISHMENT IN A RUSSIAN KNAPWEED-INFESTED PLANT COMMUNITY

Introduction

The ecological integrity of native plant communities in North America is being degraded by invasions of non-native species (Olson 1999). These invasions can alter the structure and function of ecosystems by displacing species, thereby reducing the diversity of plant communities. Russian knapweed [*Acroptilon repens* (L.) DC.] is a non-native perennial forb that has invaded about 630,344 hectares in the western U.S. and adjacent Canada (Duncan 2001). This rhizomatous weed can establish as monocultures in a variety of habitat types and plant communities, and is common in areas with shallow water tables or excess moisture (Whitson 1999, Zouhar 2001). Impacts from Russian knapweed infestations include reductions in wildlife habitat, livestock forage, crop yields, and overall rangeland biodiversity (Watson 1980, Kurz et al. 1995).

Effective control of Russian knapweed is vital to the restoration of infested plant communities and ecosystem processes. Herbicide use has been a common method for controlling this weed, but research has shown that this approach typically provides only short-term suppression (Bottoms and Whitson 1998). In addition, my companion studies (Chapters 2 and 3) indicated that while clopyralid plus 2,4-D, glyphosate, or fosamine may reduce Russian knapweed density and biomass, they are inadequate for restoring the structure and function of native plant communities. For example, we found that clopyralid plus 2,4-D provided effective control of Russian knapweed two years after treatment, but this herbicide increased only the density and biomass of grasses and not forbs or shrubs (Chapter 2). Furthermore, glyphosate treatments increased richness and diversity of non-native species but decreased those of native species (Chapter 3). While herbicides are an important component of weed management, evidence suggests that the implementation of alternative strategies is necessary to achieve native plant community restoration goals.

Previous research has indicated that competition from seeded plant species can provide effective control of Russian knapweed (Sulima 1968, Dall'Armellina and Zimdahl 1988). For example, various grass species seeded as monocultures after a clopyralid plus 2,4-D application produced 66 to 93% less Russian knapweed biomass two years after treatments than when no grass was sown (Benz et al. 1999). While this study supports the widespread acceptance that grass competition can be an effective method of weed control (Bottoms and Whitson 1998), it fails to address structural diversity of the plant community and ecosystem functioning.

Revegetation techniques promoting monoculture establishment may meet rehabilitation (partial restoration) goals, but most likely will not produce plant community traits necessary for ecological restoration. It has been suggested that sustainable management of ecosystems infested by weedy species must focus on establishing desirable species with plant traits that maximize niche occupation (Larson et al. 1994). The establishment of desirable species with diverse above- and belowground life forms may minimize interspecific competition, maximize spatial and temporal structure, and enhance their resource capture (Pyke and Archer 1991, Tilman 1996). We believe that addressing community structure and ecosystem processes will increase the potential for successful restoration of native systems.

Seedling establishment is the most critical phase of revegetation (James 1992). Revegetation efforts in Russian knapweed-infested plant communities have focused on both native and non-native perennial grasses. Some research suggests that non-native grasses have higher establishment success in stands of Russian knapweed than native grasses. For example, 'Ephraim' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], 'Oahe' intermediate wheatgrass [*Agropyron intermedium* (Host.) Beauv.], and 'Bozoisky' Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] had 20-45% cover in Russian knapweed stands two years after seeding without initial herbicide treatments, while the native 'Sherman' big bluegrass (*Poa ampla* Presl.) failed to establish (Whitson et al. 1993). In another study testing competition between five perennial grasses (three native species and two non-native species) and Russian knapweed, the native species 'Critana' thickspike wheatgrass [*Elymus lanceolatus* (Scribn. & Smith) Gould] and 'Sodar' streambamk wheatgrass [*Elymus lanceolatus* (Scribn. & Smith) Gould] produced the highest average percent live grass cover five years after seeding (Bottoms and Whitson 1998).

Although revegetation with non-native grasses can provide benefits such as ability to out-compete weeds, high forage production, and high nutritional value, their use is inappropriate in areas where management goals include the restoration of native plant communities. To increase the probability of restoring native systems, revegetation must include a diverse assemblage of native species that promote the enhancement of ecological functioning and resistance to invasion by exotic species. The objective of this study was to determine the influence of four seeding methods, two herbicides, and a non-treated control on the density, cover, biomass, richness, and diversity of ten native species seeded simultaneously into a Russian knapweed-infested plant community. We hypothesized that the combination of clopyralid plus 2,4-D and till and drill seeding would provide the greatest establishment of native seeded species. Our rationale was that this herbicide would create adequate safe sites for seedling establishment by suppressing Russian knapweed and other broadleaf plants. In addition, tillage would further reduce weed competition and provide a nutrient flush for seedlings, and drilling seeds would improve seed-to-soil contact and enhance safe site availability.

Materials and Methods

Study Site

This study was conducted in north-central Montana on the Charles M. Russell (CMR) National Wildlife Refuge, about 105 kilometers north (22°29'N, 23°29'E) of Lewistown, Montana. The study site was located on a floodplain known as Knox Bottom along the Missouri River, near the western boundary of the refuge. The site's aspect was negligible with 0% slope at 670 m elevation, with an annual average precipitation of 30 cm and an annual average temperature of 7° C. Soil at the site was a Kobar silty clay loam (fine, montmorillonitic Borollic Camborthid). This soil was formed in alluvium material and has slow permeability (USDA 1978).

The study site was located within the silver sage/western wheatgrass (*Artemisia cana/Agropyron smithii*) habitat type (Hansen et al. 1995). Similar habitat types have been described for the northern Great Plains by Hanson and Whitman (1938), Mackie

(1970), and Jorgensen (1979). This habitat type, common in central and eastern Montana, represents one of the driest extremes of the riparian zone. The plant community consists of native and non-native grasses and forbs. The non-native invader Russian knapweed was abundant at the study area and had displaced desirable plant species.

The silver sage/western wheatgrass habitat type typically occurs as a result of disturbance, where site potential has changed, possibly due to prolonged heavy grazing (Hansen et al. 1995). Land use at this area over the past century (approximately 1920's - 1980's) has included crop production and cattle grazing. Throughout that period, cattle were moved from upland summer pastures to the river bottoms for winter grazing. In addition, flooding from the Missouri River occurs with varying frequency and intensity. Because of its location within the CMR National Wildlife Refuge, Knox Bottom provides critical wildlife habitat and continues to be managed for wildlife production.

Experimental Design

In a split-plot design, 15 treatments (4 seeding methods with an unseeded control, and 2 herbicides with an untreated control) were applied in 2001 to 4.3 m x 4.6 m plots, where the five seeding methods were the whole plots and the three herbicide treatments were the sub-plots. The 15 treatments were replicated six times at one site for a total of 90 plots. Clopyralid (0.08 kg a.i. ha^{-1}) plus 2,4-D (0.42 kg a.i. ha^{-1}) and glyphosate (1.2 kg a.i./ha^{-1}) were applied in August (flowering stage of Russian knapweed) 2001 based on herbicide label rates and in accordance with CMR National Wildlife Refuge and U.S. Fish and Wildlife Service restrictions. Herbicides were chosen because of their low environmental risk in areas near water and wildlife. Herbicides were applied using a 4-nozzle backpack sprayer delivering 130 liters ha^{-1} of spray solution.

Plots were seeded in October 2001 with an equal mixture of ten native species at a seeding rate of 22 kg ha^{-1}. Species consisted of Sandberg's bluegrass (*Poa secunda* Presl.), 'Mandan' Canada wildrye (*Elymus canadensis* L.), 'Lodorm' green needlegrass [*Nassella viridula* (Trin.) Barkworth], 'Secar' bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve], 'Rosana' western wheatgrass (*Pascopyrum smithii* P.A. Love), 'Critana' thickspike wheatgrass [*Elymus lanceolatus* (Scrib. & Smith) Gould], 'Birds eye' blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], 'Texoka' buffalo grass [*Buchloe dactyloides* (Nutt.) Engelm.], western snowberry (*Symphoricarpos occidentalis* Hook.), and silver sage (*Artemisia cana* Pursh). Seeded native species were chosen based on adaptability to regional climatic and soil characteristics of the study area. Although this study investigated short-term (i.e. establishment) effects, seeded species were selected based on long-term goals of sustainable structure and function of the plant community. The ten seeded species represent some diversity of physiological and morphological parameters, and were subjectively classified into five different functional groups of species (Table 4.1).

Species were seeded using four different seeding methods: broadcast, imprint, no-till drill, or till and drill. Due to abundant litter and post-herbicide aboveground biomass, plots receiving seeding method treatments were initially mowed and harrowed. The broadcast method included rototilling the upper 10 cm of soil surface, hand broadcasting seeds uniformly throughout the plot, and gently raking the soil surface to ensure sufficient seed-to-soil contact. The imprint method represents small depressions (imprints) in the soil surface designed to provide "pools" of water and nutrients that will potentially enhance seedling germination. In plots receiving this seeding method, an AerWay® was pulled behind a tractor, creating approximately eighteen 9x9x9 cm divots per m^2 of soil surface. Seeds were then hand broadcast uniformly throughout the plot without bias to the location of the divots, and the soil surface was lightly raked. The no-till drill method consisted of drill seeding the species mixture after plots had been mowed and harrowed. A rangeland drill was calibrated to deliver 22 kg of seed mixture ha^{-1} for each plot at a depth of 12 mm. The till and drill method was similar to the no-till drill method except that the upper 10 cm of the soil surface was rototilled prior to drill seeding.

Table 4.1. Seeded species and associated functional group parameters.

Native seeded species	Seral stage	Photosynthetic pathway	Rooting structure	Life form
Sandberg's bluegrass Canada wildrye	early-mid	C3	shallow	bunchgrass
green needlegrass bluebunch wheatgrass	late	C3	deep	bunchgrass
western wheatgrass thickspike wheatgrass	mid-late	C3	rhizomatous	grass
blue grama buffalo grass	mid	C4	rhizomatous	grass
western snowberry silver sage	mid	C3	rhizomatous	shrub

Sampling

Density, cover, and biomass were recorded for total native seeded species, total existing plant community species (hereafter referred to as "residual species"), and

Russian knapweed in August 2002 (one year after treatments). Cover and biomass of plant litter, and bareground cover, were also recorded. For density and cover, a Daubenmire frame (0.10 m^2) was randomly placed three times within each plot. Grasses were identified using Cronquist et al. (1977), while forbs and shrubs were classified according to Dorn (1984). Biomass was collected using a 0.44 m^2 hoop randomly placed once within each plot. Plants were harvested at ground level and separated by species in the field. Plant material was then dried to a constant weight and biomass was recorded.

Species richness and diversity were calculated for total seeded species in August 2002. Richness was measured as the total number of seeded species (grasses and shrubs) per experimental plot. A Daubenmire frame (0.10 m^2) was randomly placed three times within each plot for data collection. Species diversity was derived from the number of individuals (density) of each species. Species diversity was calculated using Simpson's Reciprocal Index (1/D), where $D = \sum (n/N)^2$ (Begon et al. 1996). In this equation, n = the total number of individuals of a particular species, and N = the total number of individuals of all species. Simpson's Diversity Index (D) is the probability that two individuals randomly selected from a sample will belong to the same species. Therefore, the Simpson's Reciprocal Index (1/D) represents the number of equally common species that will give the observed Simpson's Diversity Index (D). The value of 1/D can range from 1 to the total number of species (richness) in the sample. A value of 1 represents no diversity, while a value equal to the species richness indicates maximum diversity, where each species has the same number of individuals.

Data Analysis

Analysis of variance (ANOVA) was used to determine the effects of seeding method and herbicide on: 1) density, cover, biomass, richness, and diversity of total seeded species, 2) density, cover, and biomass of total residual species and Russian knapweed, 3) cover and biomass of plant litter,and 4) bareground cover. Replication, seeding method, and herbicide main effects and the seeding method*herbicide interaction were included in the model. Because the initial plot design accounted for potential environmental variations/gradients, replication interaction estimates were pooled into the model error term. Therefore, rep*seeding method (df = 20), rep*herbicide (df = 10), and rep*seeding method*herbicide (df = 40) represented the 70 degrees of freedom in the model error term.

Data from several response variables were transformed to meet normality and homogeneity of variance assumptions of ANOVA. Total seeded species density, cover, and biomass data (+0.1) were transformed to the log10 scale, and diversity data were transformed to the log10 scale. Total residual species biomass data (+0.1) were transformed to the log10 scale. Russian knapweed density, cover, and biomass data were transformed to the square root scale. Litter biomass data (+0.1) were transformed to the log10 scale, and bareground cover data were transformed to the square root scale. When a significant P-value ($P \leq 0.05$) was calculated, mean separations for main effects were achieved using Fisher's protected $LSD_{(\alpha=0.05)}$ comparisons (Peterson 1985). For transformed data, untransformed means are presented with P-values referring to transformed mean comparisons.

Results

Total Seeded Species Density, Cover, and Biomass

Total seeded species density was affected by seeding method ($P < 0.001$). The till and drill method produced higher seeded species density than the control or imprint or no-till drill methods, but was not different than the density produced by broadcast seeding (Figure 4.1a). Seeded species density resulting from imprint or no-till drill treatments was not significantly different from the unseeded control. Seeded species density was also influenced by herbicide ($P < 0.001$). The density for plots receiving glyphosate was about 60% greater than the density for those plots treated with clopyralid plus 2,4-D, and was 78% greater than the density for the untreated control (Figure 4.1b). There was no significant difference in seeded species density between the control and clopyralid plus 2,4-D treatments.

Percent cover of total seeded species was affected by seeding method ($P = 0.002$). Till and drill treatments yielded the highest cover (5%) compared to the other seeding methods and the control (Figure 4.1c). Broadcast, imprint, and no-till drill seeding methods (1-4% cover) were not significantly different than the control (1% cover). A herbicide main effect also significantly influenced seeded species percent cover ($P < 0.001$). Plots receiving glyphosate had the highest (4%) total seeded species cover compared to clopyralid plus 2,4-D and the control (Figure 4.1d). Seeded species cover data between the control (1%) and clopyralid plus 2,4-D (2%) were not significantly different.

Total seeded species biomass was affected by seeding method ($P = 0.04$). Biomass levels from broadcast and till and drill seeding (1.3-2.0 g m^{-2}), which were not significantly different from each other, were the only treatments that produced higher seeded species biomass than the unseeded control (0.8 g m^{-2}; Figure 4.1e). Seeded species biomass was also influenced by a herbicide main effect ($P < 0.001$). Plots receiving glyphosate yielded almost four times more seeded species biomass than the untreated control and those receiving clopyralid plus 2,4-D (Figure 4.1f). Seeded species biomass in the control (0.3 g m^{-2}) and from clopyralid plus 2,4-D treatments (0.8 g m^{-2}) did not differ.

Total Seeded Species Richness and Diversity

Total seeded species richness was affected by seeding method ($P < 0.001$). Plots receiving till and drill treatments yielded the highest richness (1.5 species m^{-2}) compared to the other three seeding methods and the control (Figure 4.2a). There was no significant difference in seeded species richness between the broadcast, imprint, and no-till drill methods (0.6-0.8 species m^{-2}), and richness from the imprint method was not significantly different from that of the control (0.2 species m^{-2}). Herbicide also affected total seeded species richness ($P < 0.001$). Plots receiving glyphosate (1.3 species m^{-2}) yielded higher richness than the control (0.4 species m^{-2}) and clopyralid plus 2,4-D treatments (0.5 species m^{-2}; Figure 4.2b).

Seeded species diversity was affected by seeding method ($P = 0.005$). Till and drill (1.4) was the only seeding method that produced a higher Simpson's diversity index than the control (1.0; Figure 4.2c). Diversity indices from broadcast, imprint, and no-till

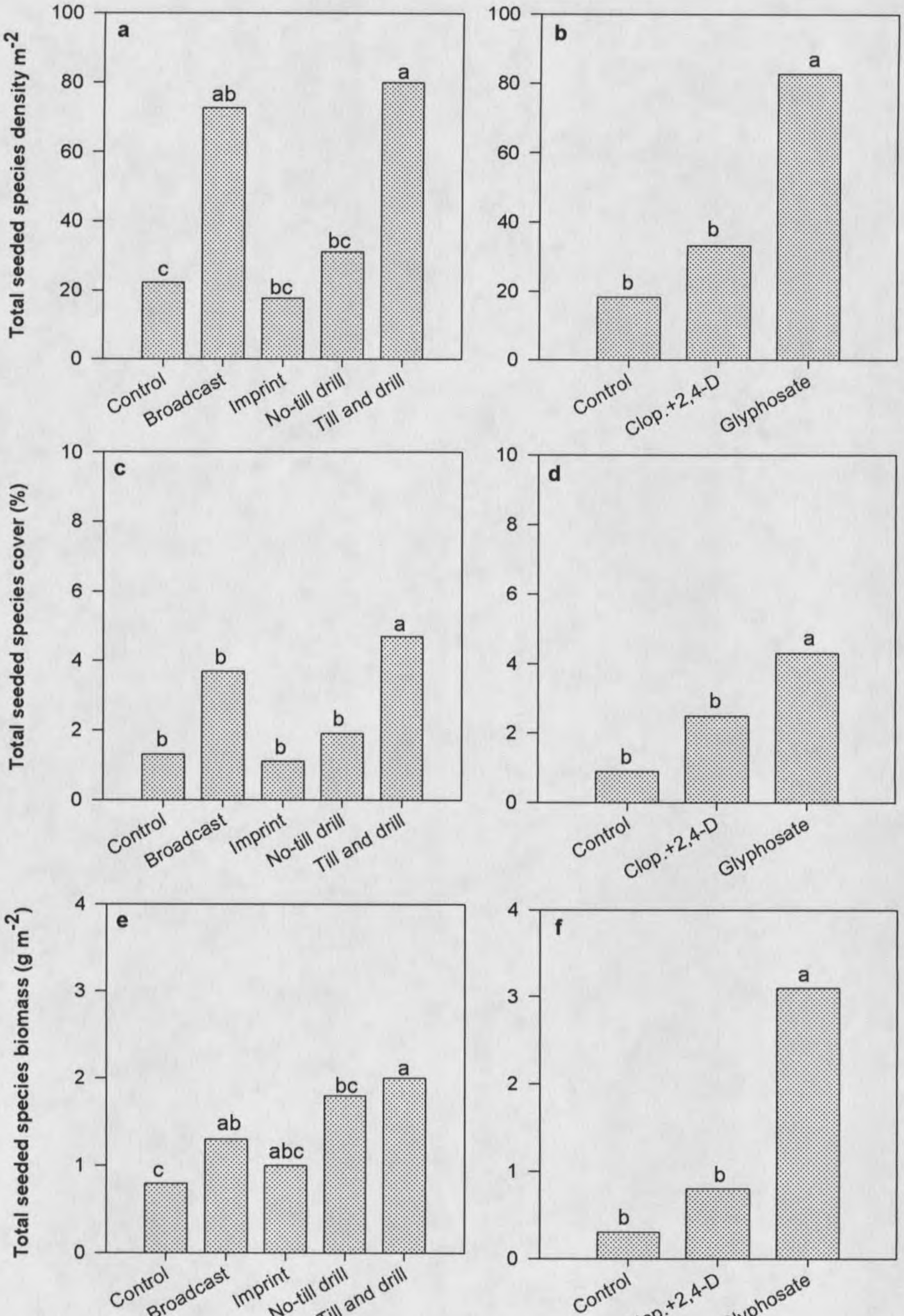

Figure 4.1. The effects of seeding methods and herbicides on total seeded species density (a, b), cover (c, d), and biomass (e, f). Different letters above bars represent significant differences (α=0.05) in treatment main effects within each graph.

drill (1.1-1.2) were not significantly different from each other or from the control. Total seeded species diversity was also influenced by herbicide treatments ($P = 0.02$). Higher seeded species diversity was detected from glyphosate treatments (1.3) than from clopyralid plus 2,4-D treatments (1.1) and the control (1.1; Figure 4.2d).

Total Residual Species Density, Cover, and Biomass

Total residual species density was influenced by seeding method ($P < 0.001$). The highest residual species density was detected in the unseeded control (372.1 individuals m^{-2}) and those plots receiving imprint (400.7 individuals m^{-2}) or no-till drill (365.3 individuals m^{-2}) seeding treatments (Figure 4.3a). Residual species density between broadcast and till and drill treatments (averaging 230.7 individuals m^{-2}) was not significantly different. Herbicide also affected total residual species density ($P < 0.001$). Clopyralid plus 2,4-D treatments yielded the highest residual species density, which was about 14% greater than the untreated control (Figure 4.3b). Furthermore, the control plots had about 67% greater residual species density than those receiving glyphosate treatments.

Seeding method had a significant effect on total residual species cover ($P < 0.001$). The highest residual species percent cover was detected from the imprint (36%) and no-till drill (31%) treatments, as well as the control (34%; Figure 4.3c). Plots that received broadcast or till and drill seeding treatments had 20-22% residual species cover, and were not significantly different from each other. Residual species cover was also influenced by herbicide treatments ($P < 0.001$). Plots sprayed with clopyralid plus 2,4-D (38%) yielded the highest percent cover of residual species, followed by the control

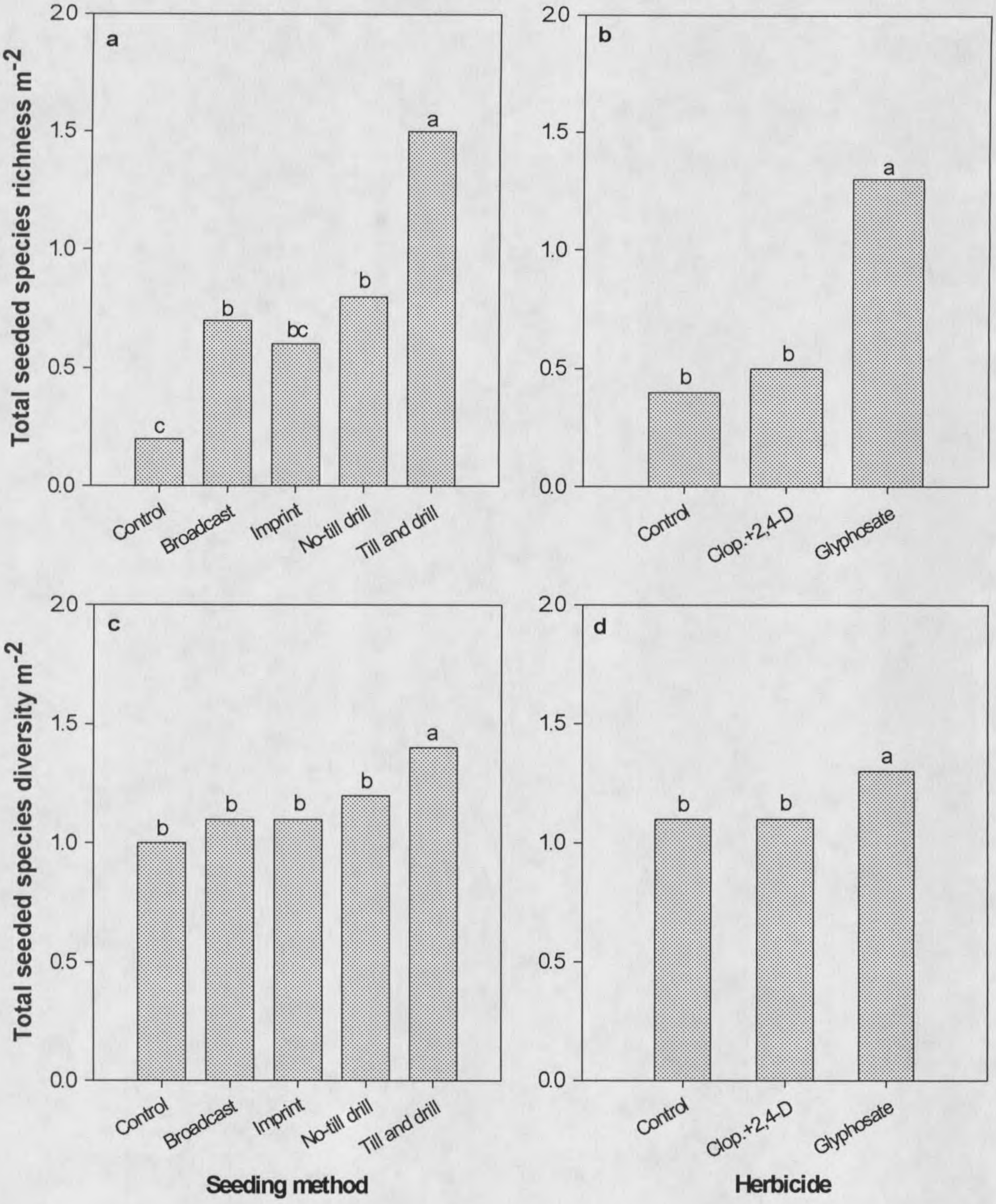

Figure 4.2. The effects of seeding methods and herbicides on total seeded species richness (a, b) and diversity (c, d). Different letters above bars represent significant differences (α=0.05) in treatment main effects within each graph.

(30%) and glyphosate (18%; Figure 4.3d). Total residual species biomass was affected only by herbicide treatments ($P < 0.001$). Plots receiving clopyralid plus 2,4-D (120.2 g m^{-2}) yielded similar residual species biomass to those that were untreated (114.8 g m^{-2}), and these values were not significantly different from each other (Figure 4.3e). Glyphosate treatments produced the lowest amount of total residual species biomass (110.4 g m^{-2}).

Russian Knapweed Density, Cover, and Biomass

Russian knapweed density was influenced by seeding method ($P = 0.004$). The greatest Russian knapweed density occurred in plots that were broadcast seeded (105.5 plants m^{-2}; Figure 4.4a). All other seeding methods and the control yielded similar densities of Russian knapweed, averaging 59.3 plants m^{-2}. There was also a herbicide effect on Russian knapweed density ($P < 0.001$). Glyphosate reduced Russian knapweed density 77% below that of the control (129.7 plants m^{-2}), and clopyralid plus 2,4-D reduced it by 65% (Figure 4.4b).

Russian knapweed cover was affected by seeding method ($P = 0.01$). Broadcast treatments (11%) yielded the highest Russian knapweed cover, compared to the other three seeding methods and the control, all of which produced 6% Russian knapweed cover (Figure 4.4c). A herbicide main effect influenced Russian knapweed cover ($P < 0.001$). Similar to Russian knapweed density data, the highest reduction in Russian knapweed cover relative to the control (13%) was caused by glyphosate (Figure 4.4d). Glyphosate reduced cover by 10% and clopyralid plus 2,4-D reduced it by 8%.

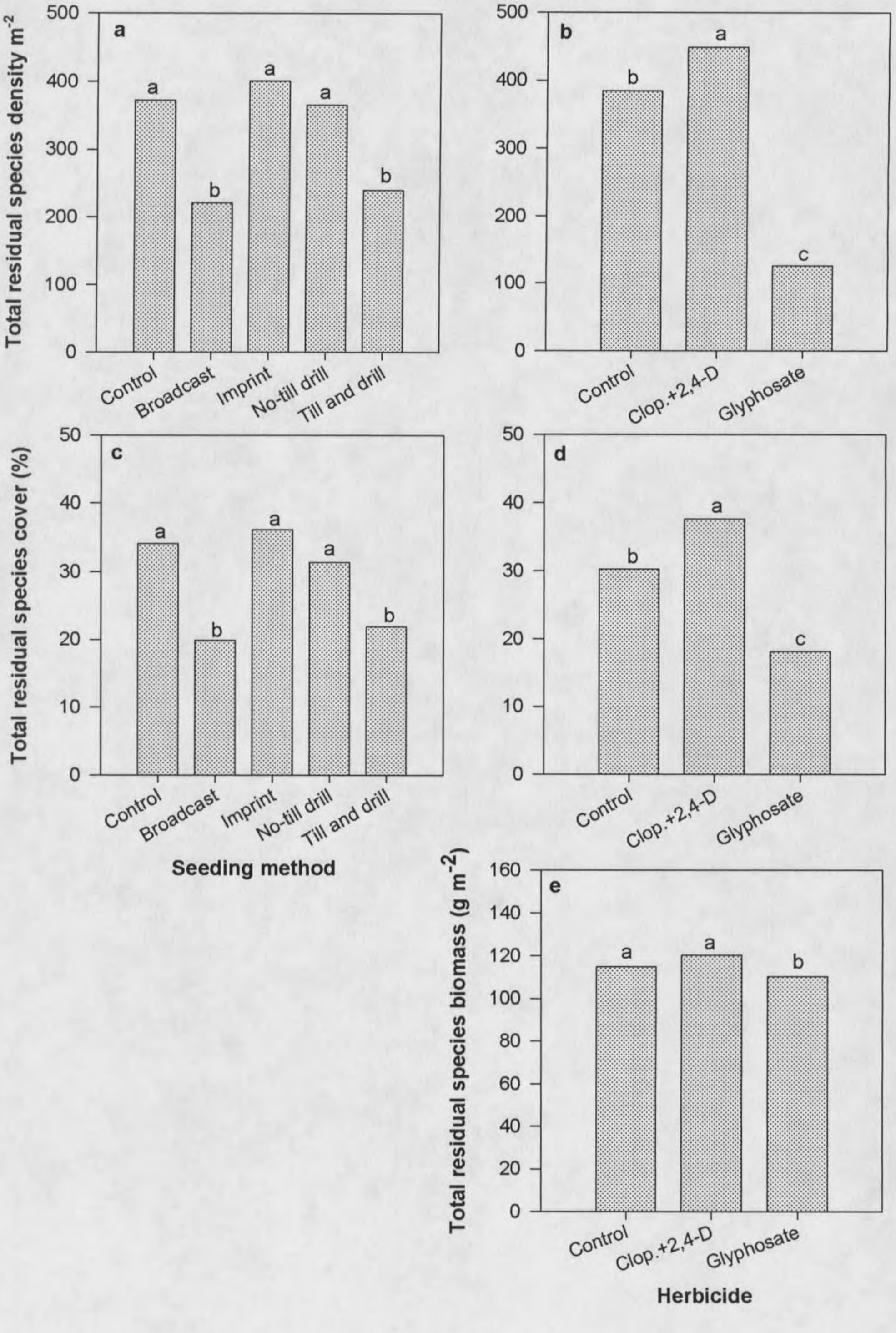

Figure 4.3. The effects of seeding methods and herbicides on total residual species density (a, b), cover (c, d), and the effect of herbicide on total residual species biomass (e). Different letters above bars represent significant differences (α=0.05) in treatment main effects within each graph.

Russian knapweed biomass was affected by seeding method ($P = 0.04$). Plots receiving till and drill or broadcast treatments (45.2 - 47.1 g m^{-2}) yielded more Russian knapweed biomass than those where imprint or no-till drill methods (23.6 – 27.4 g m^{-2}) were used (Figure 4.4e). However, none of the seeding methods yielded Russian knapweed biomass values that were significantly different from that of the control (32.8 g m^{-2}). Herbicide also influenced Russian knapweed biomass ($P < 0.001$). Clopyralid plus 2,4-D or glyphosate treatments produced similar Russian knapweed biomass (averaging 14.4 g m^{-2}), which reduced biomass about 81% below that of the control (Figure 4.4f).

Litter Biomass and Cover

Litter biomass was affected by seeding method ($P < 0.001$). The imprint and no-till drill treatments and the control all produced similar litter biomass (158.0 – 188.0 g m^{-2}), which was higher than the litter biomass yielded as a result of broadcast or till and drill seeding methods (Figure 4.5a). Litter biomass from the broadcast (60.4 g m^{-2}) and till and drill (45.3 g m^{-2}) methods was not significantly different from each other. Litter biomass was also influenced by herbicide application ($P = 0.01$). The highest litter biomass occurred in plots treated with glyphosate (164.4 g m^{-2}), which was about 34% more litter biomass than was yielded from the control and clopyralid plus 2,4-D (Figure 4.5b).

Litter percent cover was affected only by seeding method ($P < 0.001$). The control (51%) and no-till drill treatment (54%) yielded the highest litter cover, and were not significantly different from each other (Figure 4.5c). Plots receiving the imprint seeding method (42%) produced more litter cover than those receiving the till and drill

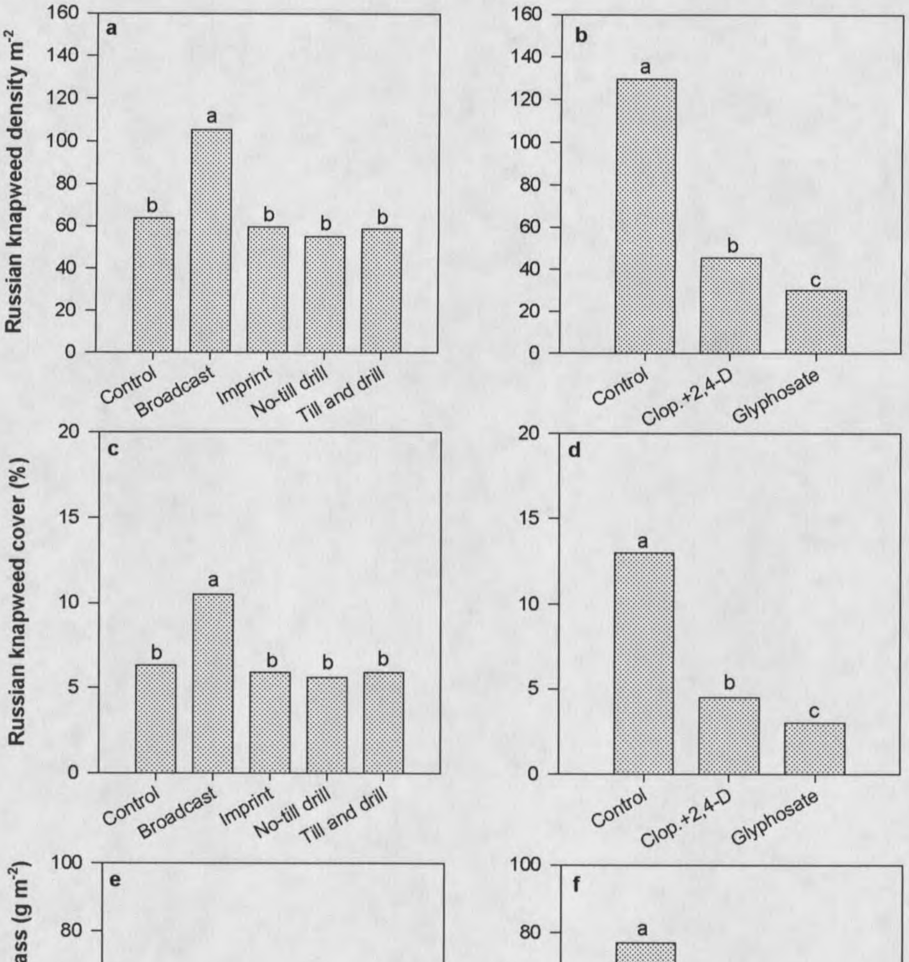

Figure 4.4. The effects of seeding methods and herbicides on Russian knapweed density (a, b), cover (c, d), and biomass (e, f). Different letters above bars represent significant differences (α=0.05) in treatment main effects within each graph.

method (32%), and both of these values were not significantly different than that caused by broadcast seeding (36%).

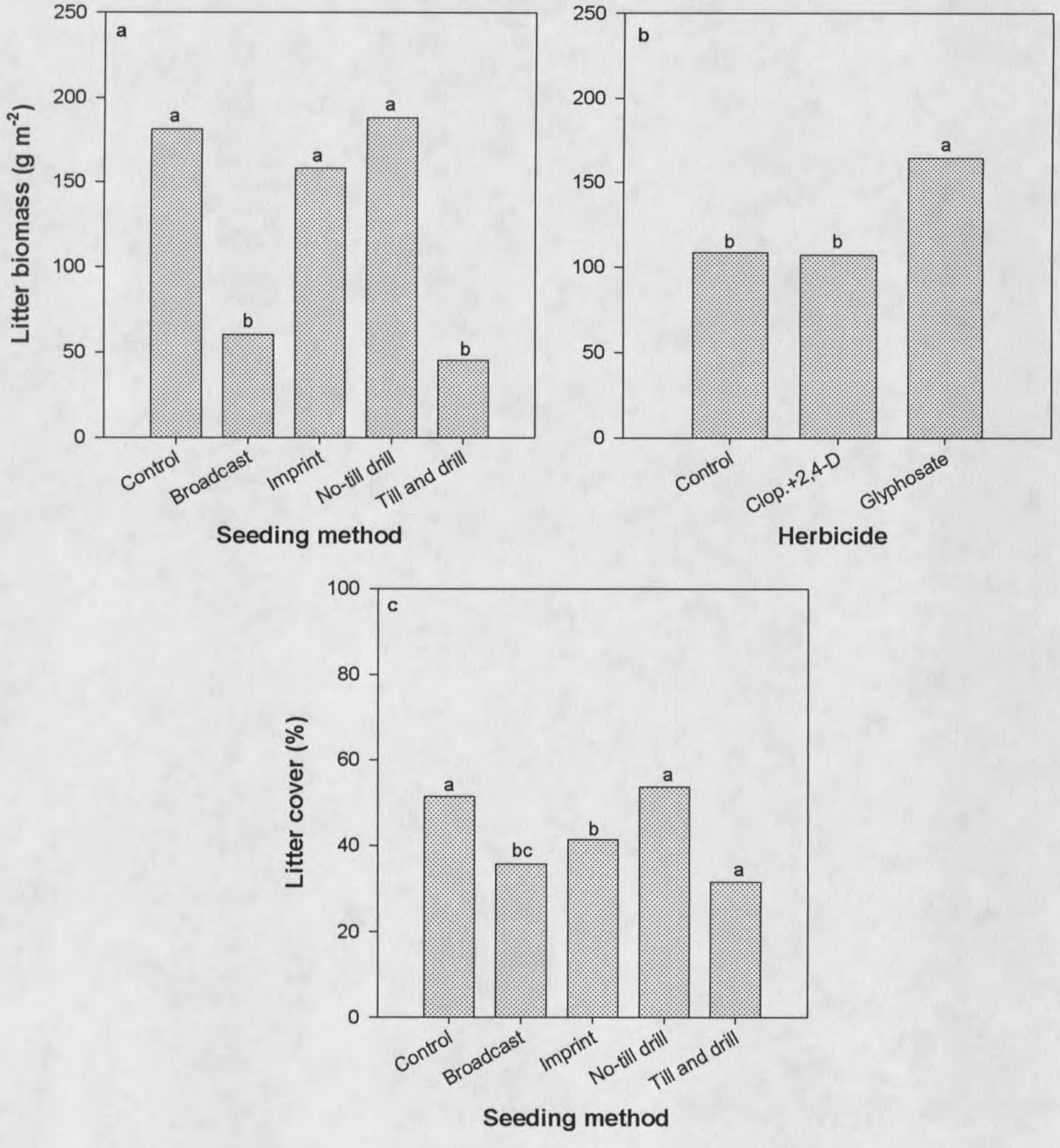

Figure 4.5. The effects of seeding method and herbicide on litter biomass (a, b), and the effect of seeding method on litter cover (c). Different letters above bars represent significant differences (α=0.05) in treatment main effects within each graph.

Bareground Cover

Bareground cover was affected by seeding method (P < 0.001). The till and drill treatment (32%) yielded the highest percent bareground cover, compared to all other treatments, and was 8% greater than the cover produced by broadcast seeding (Figure 4.6a). The control and imprint and no-till drill treatments produced bareground cover values (4-7%) that were not significantly different from each other. Herbicide treatments also influenced bareground cover (P = 0.04). Glyphosate applications (17%) yielded more bareground cover than that of the control (12%), but both of these cover values were not significantly different from that of clopyralid plus 2,4-D (14%; Figure 4.6b).

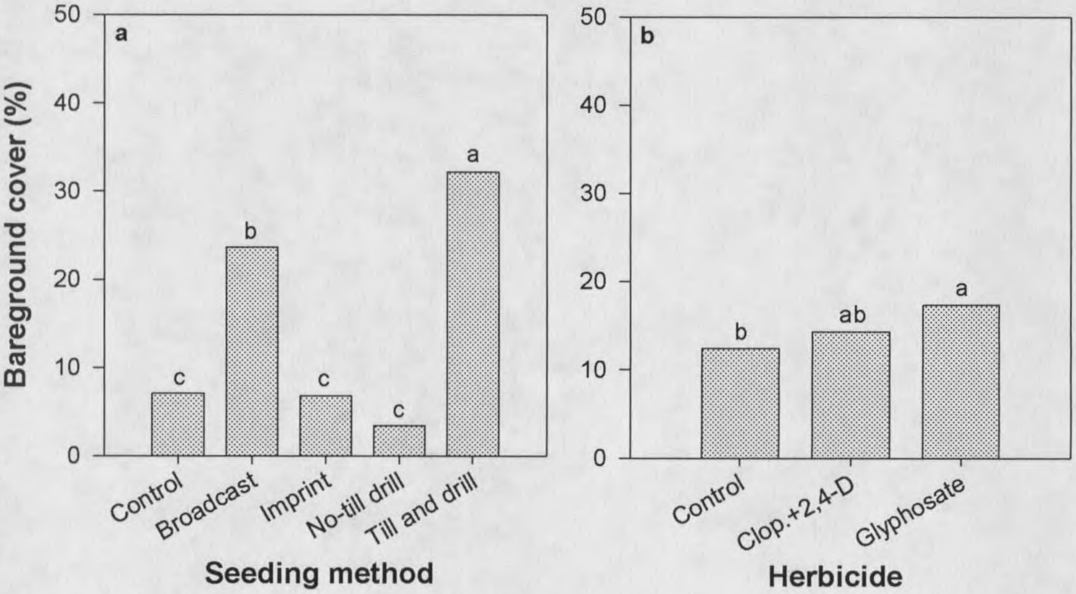

Figure 4.6. The effects of seeding method and herbicide on bareground cover (a, b). Different letters above bars represent significant differences (α=0.05) in treatment main effects within each graph.

Discussion

Revegetation of weed-infested rangeland often fails because of insufficient moisture and intense weed competition (Velagala et al. 1997). Seedling establishment appears to be associated with the availability of safe sites (Harper et al. 1965, Wright et al. 1978) and the availability of seeds (Pickett et al. 1987). In this study, the greatest establishment of seeded species generally occurred in plots receiving either glyphosate or till and drill treatments.

Glyphosate, a non-selective herbicide, is often recommended for weed control prior to fall-dormant seeding with the objective of suppressing all undesirable vegetation for a brief period (Jacobs et al. 1998, Bussan et al. 2001). Our study indicates that glyphosate applied at 1.2 kg a.i. ha^{-1} in late summer reduced Russian knapweed density 71% and biomass 80% one year after treatment. This herbicide treatment also reduced residual species density and cover 67% and 40%, respectively. Not surprisingly, glyphosate increased percent bareground cover above that of the control. These data suggest that glyphosate reduced the ability of Russian knapweed and other residual species to compete for resources with seeded species during establishment. In addition, increased bareground cover appeared to provide additional safe sites necessary for improved seedling establishment. Our data indicated that litter biomass was 34% greater in plots treated with glyphosate than in plots receiving clopyralid plus 2,4-D or no herbicide. Because litter decomposition provides nutrients to soil and associated vegetation (Begon et al. 1996), we speculate that higher litter biomass from glyphosate application resulted in more nutrients for the system, thus increasing establishment of seeded species (Stauffer and Brooks 1997).

Seedbed preparation affects the establishment and survival of seedlings. Plowing, or tilling, the soil surface is the most effective method for preparing an ideal seedbed (Jacobs et al. 1999). Tilling removes competitive vegetation, increases the number of safe sites by roughening the soil surface, and loosens the upper layer of soil, thereby facilitating root extension of establishing seedlings (Jacobs et al. 1999). Furthermore, Bottoms and Whitson (1998) propose that in areas infested with Russian knapweed, tillage is necessary to remove allelopathic residues which inhibit the survival of grass seedlings. Seeding depth can also affect the success of seedling establishment. Drill seeding, compared to the broadcast method, drops seeds in a furrow at a specified rate and depth, improving seed distribution and decreasing predation by rodents and birds (Fenner 1985).

In this study, the till and drill method generally provided the highest establishment of seeded species. However, broadcast seeding produced similar levels of seeded species density and biomass. These two methods, which included tillage prior to seeding, also yielded the lowest density and percent cover of residual species. Data suggest that tilling the soil surface reduced competition from residual species, thus increasing seedling establishment. Data also indicated that broadcast and till and drill treatments produced higher bareground percent cover than those of imprint and no-till drill, which supports the assertion that tilling also increases the number of safe sites for seedlings. The only implementation difference between the broadcast method and till and drill was seed distribution. Because of similar seeded species responses (i.e. density and biomass) to these methods, our data suggest that seedbed preparation may be more important than seeding depth as determinants of seedling establishment.

Although this study investigated the short-term establishment phase of revegetation techniques, our native seed mixture was designed to enhance the structural diversity of the plant community. While glyphosate or till and drill generally provided the highest density, cover, and biomass of seeded species, the greatest richness and diversity of seeded species were also produced with either treatment. Higher species richness and diversity enhance the efficiency of ecosystem function (Vitousek and Hooper 1993) and increase a plant community's resistance to invasion (Levine and D'Antonio 1999), and we believe successful establishment of this diverse assemblage of native species provides the necessary foundation for complete restoration.

In areas where persistent herbicides cannot be used, there is increased risk that recovering weed populations will prevent the survival of established seedlings. For example, Sheley et al. (2001) found that glyphosate applied at 0.5 kg a.i. ha^{-1} in the fall reduced spotted knapweed (*Centaurea maculosa* Lam.) and increased grass establishment (via no-till drill) the first year after treatment. However, spotted knapweed density increased in subsequent years and grass establishment decreased, suggesting that short-term weed suppression with glyphosate was adequate for seedling establishment but not seedling survival. We propose that the combination of glyphosate and tillage may reduce weed competition enough for established seedlings to persist in subsequent years. Our study provides evidence that this revegetation technique facilitates establishment of native species in a plant community infested by Russian knapweed, thereby increasing the potential for complete restoration of the system.

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CHAPTER 5

SUMMARY

This study investigated the potential for restoring Russian knapweed-infested plant communities in a riverbottom floodplain. The overall objectives of this research were: 1) to determine whether herbicides alone could control Russian knapweed and increase the density and biomass of associated plant community species, 2) to determine whether herbicides alone could increase the richness and diversity of existing plant species within a community dominated by Russian knapweed, and 3) to determine whether a seeding method, herbicide, or seeding method/herbicide combination could facilitate the establishment of native species seeded simultaneously into a Russian knapweed-infested plant community.

In Chapter 2, we hypothesized that clopyralid plus 2,4-D, applied at the highest rate in August, would provide the lowest density and biomass of Russian knapweed and forbs/shrubs, and the highest density and biomass of grasses. We investigated the potential of increasing the productivity of desirable plant species with different life forms with a single herbicide application, and therefore meeting land use objectives such as wildlife habitat enhancement. Our data indicated that clopyralid plus 2,4-D provided the best control of Russian knapweed, reducing density 63% and biomass 80% two years after treatment. However, we rejected our hypothesis because these results were not dependent upon timing of application, and both the medium and high rates of clopyralid plus 2,4-D provided the best control of Russian knapweed.

Clopyralid plus 2,4-D also increased the density and biomass of grasses, but application rate or timing generally did not influence these results. We were not able to test our hypothesis regarding herbicide effects on the density and biomass of native forbs and shrubs because the paucity of these plant groups prevented appropriate statistical analyses or the observation of trends. Because many of the non-native forbs in this study are considered by managers to be invasive, we were interested in treatments that reduced this component of the plant community. Our data indicated that the medium rate/July application and the low rate/August application of clopyralid plus 2,4-D decreased only the density of non-native forbs, while no treatments reduced their biomass. Although clopyralid plus 2,4-D provided the greatest control of Russian knapweed and increased the density and biomass of grasses, we did not detect an increase in desirable forbs or shrubs. Without sufficient community structure and competition from forbs/shrubs, Russian knapweed will most likely recover from suppression treatments. Therefore, we believe that herbicides alone are inadequate for the restoration or rehabilitation of Russian knapweed-infested plant communities.

While testing the potential for herbicides to recover the structure and function of a plant community degraded by Russian knapweed, we hypothesized in Chapter 3 that clopyralid plus 2,4-D or fosamine treatments would provide greater species richness and diversity than those of glyphosate. However, our data indicated that glyphosate generally caused the greatest increase in total species richness and diversity two years after treatments. Our data in Chapter 2 indicated that Russian knapweed density and biomass recovered from glyphosate suppression by the second year after treatment. Therefore, this herbicide may be more effective for increasing and sustaining species richness and diversity in a plant community infested with an annual or non-rhizomatous weed. In addition, nearly all response parameters varied between our two sites, which differed in dominant species compositions. This suggests that herbicide treatments aimed at enhancing species richness and diversity will require improved predictive capability that considers pre-treatment plant assemblage composition, to increase the success of achieving long-term management objectives. Because the majority of increased richness and diversity was attributed to non-native species, this management strategy may be appropriate for enhancing ecosystem function and possibly niche occupation to preempt re-invasion by Russian knapweed. However, it seems less likely that the herbicides we tested can restore native plant communities associated with Russian knapweed infestations.

In Chapter 4, we investigated the potential for native species establishment in plant communities dominated by Russian knapweed by testing the effects of different seeding methods and herbicide applications. We hypothesized that the combination of clopyralid plus 2,4-D and till and drill seeding would provide the greatest establishment of our native seed mixture. Our data indicated that the highest establishment was generally achieved with either the glyphosate application or the till and drill method one year after treatment. We speculated that glyphosate increased seeded species establishment by: 1) decreasing Russian knapweed/residual species and thus reducing competition for resources, 2) increasing bareground and therefore safe sites, and 3) increasing nutrient availability from higher litter biomass. Broadcast seeding produced similar results to the till and drill method in some seeded species response parameters. Because these two methods involved tillage prior to seeding, our data suggested that seedbed preparation was more important than seed distribution as determinants of native species establishment in this system. This revegetation strategy facilitated the short-term establishment of a diverse assemblage of native species in this study, and therefore we believe it has the potential for achieving complete restoration.

This research suggests that herbicides alone cannot increase and sustain the productivity of desirable species representing varying life forms within a Russian knapweed-infested plant community. Furthermore, it appears that herbicides cannot increase the richness and diversity of native species in this system, and therefore are also inadequate for restoring its structure and function. As a result, alternative weed management strategies seem necessary to achieve restoration goals. Because we identified a revegetation method that provided establishment of a native species seed mixture, this strategy has the potential to restore native plant communities infested with Russian knapweed.