

Restoring Species Richness and Diversity in a Russian Knapweed (*Acroptilon repens*)-Infested Riparian Plant Community Using Herbicides

Roger L. Sheley, Stephen M. Laufenberg, James S. Jacobs, and John Borkowski*

Species richness and diversity are important indicators of ecosystem function and may be related to plant community resistance to invasion by nonindigenous species. 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 nonnative species within a Russian knapweed-infested plant community. Twenty-eight treatments (3 herbicides by 3 rates by 3 application timings, and an untreated control) were applied to two sites located along the Missouri River riparian corridor in Montana. Clopyralid plus 2,4-D, glyphosate, and fosamine 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). Herbicide rates were clopyralid plus 2,4-D at 0.08 (clopyralid) + 0.42 (2,4-D), 0.13 + 0.67, and 0.18 + 0.92 kg ai ha⁻¹; glyphosate at 0.6, 1.2, and 1.8 kg ai ha⁻¹; fosamine at 3.6, 7.2, and 10.8 kg ai ha⁻¹. Density of each species was recorded during June and August of 2001 and 2002. Species richness and Simpson's Reciprocal Index (1/D) were calculated. By 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). At that time, diversity after applying clopyralid plus 2,4-D remained similar to that of the control (1.4), but glyphosate (2.3) and fosamine (2.0) increased total species diversity. Nonnative grasses and forbs accounted for the increases in richness and diversity. Glyphosate may be appropriate for enhancing ecosystem function and possibly niche occupation to preempt reinvasion by Russian knapweed, but restoring native species seems unlikely using any of these herbicides alone.

Nomenclature: Clopyralid; fosamine; glyphosate; 2,4-D; Russian knapweed; *Acroptilon repens* (L.) DC. CENRE.

Key words: Wildland weed management, riparian weed management, wildlife habitat, rehabilitation, desired plant communities, native plants.

Invasions of nonnative plant species, such as Russian knapweed, can displace native vegetation and decrease plant diversity, thereby altering the structure and function of ecological systems (Tilman 1997). Russian knapweed, a rhizomatous perennial forb, invades disturbed sites and often forms monocultures after becoming established. Introduced to North America in the early 1900s, Russian knapweed is widespread in the United States, most commonly in the semiarid portions of the West and adjacent Canada. Additionally, this species invades river bottoms and riparian woodlands throughout the United States (Whitson 1999).

Russian knapweed has an aggressive rate of spread, a competitive advantage over native species, and contains allelopathic compounds (Whitson 1999). Consequently, land managers are recognizing the importance and difficulty of controlling this weed. Previous research indicates that a number of herbicides can provide short-term suppression of Russian knapweed (Whitson 1999). However, further research on controlling Russian knapweed with herbicides appropriate for use in wet areas and river bottoms is needed. In a companion study, we tested the efficacy of three herbicides (clopyralid plus 2,4-D, glyphosate, and fosamine), at different application rates and timings, for controlling Russian knapweed (Laufenberg et al. 2004). Our data indicated that medium (0.13 plus 0.67 kg ai ha⁻¹) and high (0.18 plus 0.92 kg ai ha⁻¹) rates of clopyralid plus 2,4-D provided the most effective control of Russian knapweed 2 yr after treatment were applied, irrespective of application timing. At that time, 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 the plant community 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-scale importance of species richness and diversity (Pokorny et al. 2005). The opinion that plant richness (number of species) and diversity (relative abundance of species) play a major role in contributing to human welfare is emerging in land management. Naeem et al. (1999) suggested that biodiversity, including the earth's living organisms, benefit human welfare through market (economy-based) and nonmarket 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. Nonmarket 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 (Chapin 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. 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. 1997). 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

DOI: 10.1614/WS-07-001.1

* First author: United States Department of Agriculture, Agricultural Research Service, Burns, OR 97720; second and third authors: Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717; fourth author: Mathematical Sciences, Montana State University, Bozeman, MT 59717. Corresponding author's E-mail: Roger.Sheley@oregonstate.edu

richness and diversity may improve the efficiency of ecosystem function.

Previous research has focused on the relationship between species richness and diversity and the resilience and resistance of native plant communities (Symstad 2000; Tilman 1997). With high species richness and diversity, plant communities will more likely include species important in successional dynamics following disturbance (Egler 1954). 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. 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 nonnative plant invasion as a function of plant diversity is increasing (Carpinelli 2000; Sheley and Carpinelli 2005). Communities with high species diversity may have greater niche occupation and enhanced resource capture (Carpinelli 2000). Resource capture by desirable species preempts their use by invasive plants. 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 during restoration. 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 of management must be better understood. The overall objective of this study was to investigate the effects of three herbicides on plant species richness and diversity of the community. 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 nonnative 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. These broadleaf herbicides may 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 km north (22°29'N, 23°29'E) of Lewistown, MT. 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 to 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.

Study sites were located within the silver sage–western wheatgrass (*Artemisia cana* Pursh–*Agropyron smithii* Rydb.) habitat type. 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 nonnative species. The nonnative 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.) Nevski], a nonnative grass, whereas 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 because of disturbance, where site potential has changed, possibly because of prolonged heavy grazing. Land use at these sites over the past century (approximately 1920s to 1980s) 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 by 3 herbicide rates by 3 herbicide application timings, and a control) were applied from June through August 2000 to 4.3 by 4.6 m plots. Treatments were replicated four times at both sites for a total of 224 plots. Clopyralid plus 2,4-D, glyphosate, and fosamine 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 ai ha⁻¹; glyphosate at 0.6, 1.2, and 1.8 kg ai ha⁻¹; fosamine at 3.6, 7.2, and 10.8 kg ai 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. Herbicides were applied using a four-nozzle backpack sprayer delivering 130 L ha⁻¹ of spray solution.

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 m²) was randomly placed three times within each plot for data collection. Grasses were identified using Cronquist et al. (1977), whereas forbs and shrubs were classified according to Dorn (1984).

Species density was also recorded during June and August of 2001 and 2002. Species diversity was derived from the number of individuals (density) of each species. Species diversity was then calculated using Simpson's Reciprocal Index (1/D), where $D = \sum (n/N)^2$. In this equation, n is the

total number of individuals of a particular species, and N is 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, whereas a value equal to the species richness indicates maximum diversity, where each species has the same number of individuals.

Data Analysis. 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, four-way, and nonsignificant ($P > 0.05$) three-way interactions were pooled and included in the error term to improve the sensitivity of the analysis. 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.

Because of 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 by 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 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

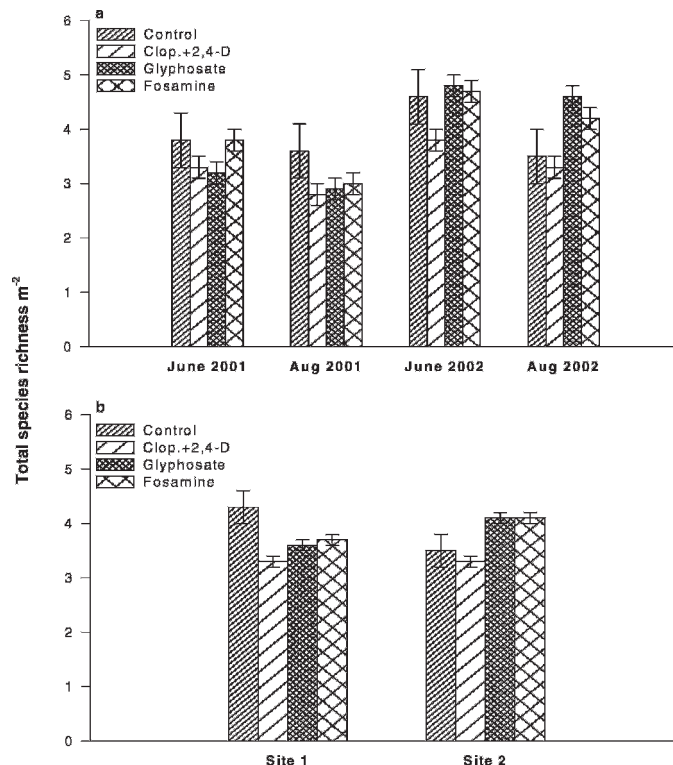


Figure 1. The effect of herbicide (a) by year and (b) by site on total species richness. Error bars in (a) represent a standard error of 0.5 (controls) and 0.2 (treatments). Error bars in (b) represent an SE of 0.3 (controls) and 0.1 (treatments).

clopyralid plus 2,4-D or the controls during that 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 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 an herbicide by 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 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 2b). Effects from glyphosate timings on total species richness varied. The June application yielded greater richness than the control, whereas 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.

Total species diversity was affected by a year by herbicide interaction ($P = 0.02$). Sampling in June 2001 indicated no differences in diversity from any herbicides and the control (Figure 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

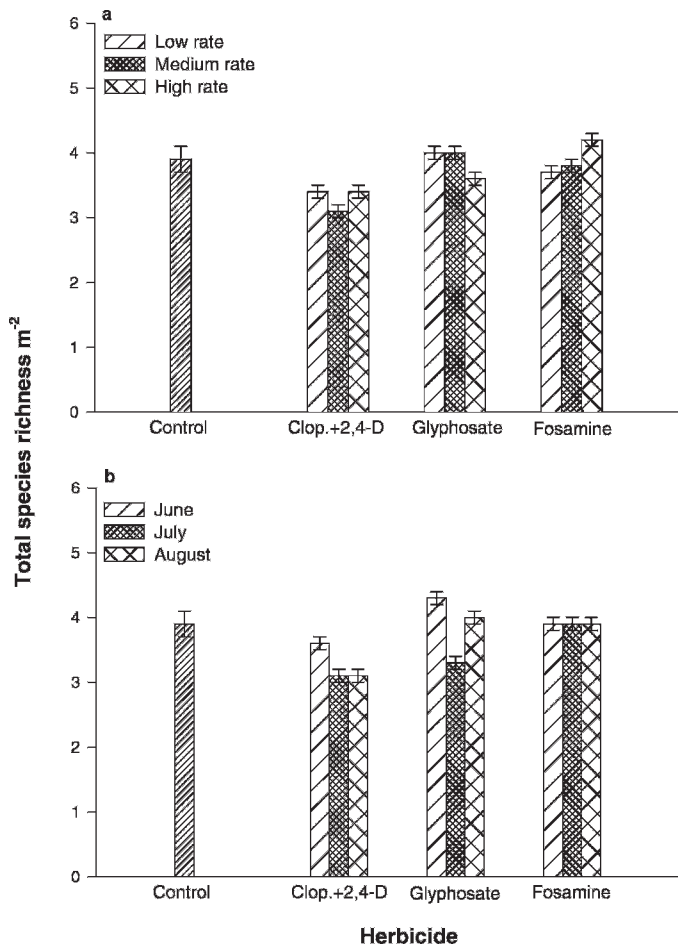


Figure 2. The effect of herbicide (a) by application rate and (b) by timing on total species richness. Error bars in (a) and (b) represent a standard error of 0.2 (controls) and 0.1 (treatments).

(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.

Total species diversity also depended upon a site by herbicide by rate interaction ($P = 0.03$). At site 1, most treatments had no significant effect on total diversity relative to the control (Figure 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

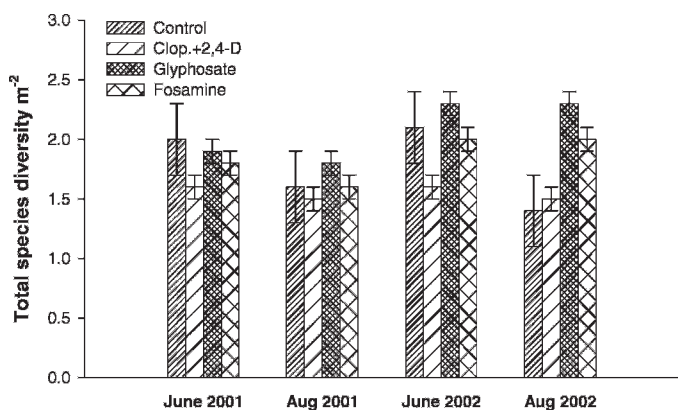


Figure 3. The effect of herbicide by year on total species diversity. Error bars represent a standard error of 0.3 (controls) and 0.1 (treatments).

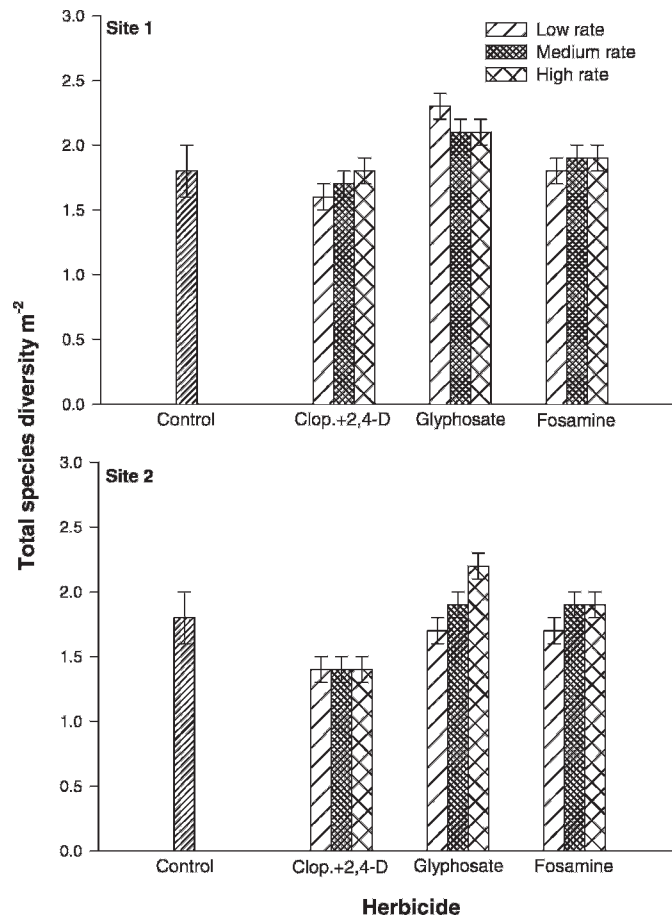


Figure 4. The effect of herbicide by application rate on total species diversity at sites 1 and 2. Error bars represent a standard error of 0.2 (controls) and 0.1 (treatments).

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), whereas significant differences were not detected from other treatments (Figure 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 on an application rate main effect ($P = 0.003$). All herbicide rates (averaging 0.8 species m^{-2} ; $SE = 0.03$) reduced total native species richness below that of the control (1.3 species m^{-2} ; $SE = 0.1$). A year by 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

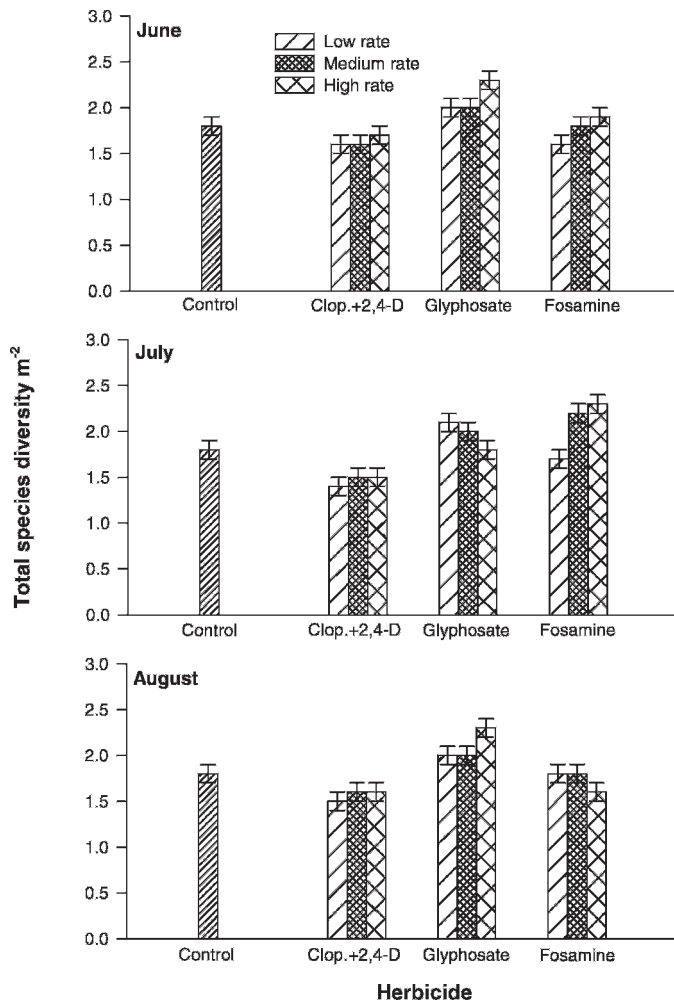


Figure 5. The effect of herbicide by application rate and timing on total species diversity. Error bars represent a standard error of 0.1 for controls and all treatments.

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 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 richness below that of the control (1.3 species m⁻²; Figure 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 Nonnative Species Richness and Diversity. Richness of total nonnative species was affected by a year by site

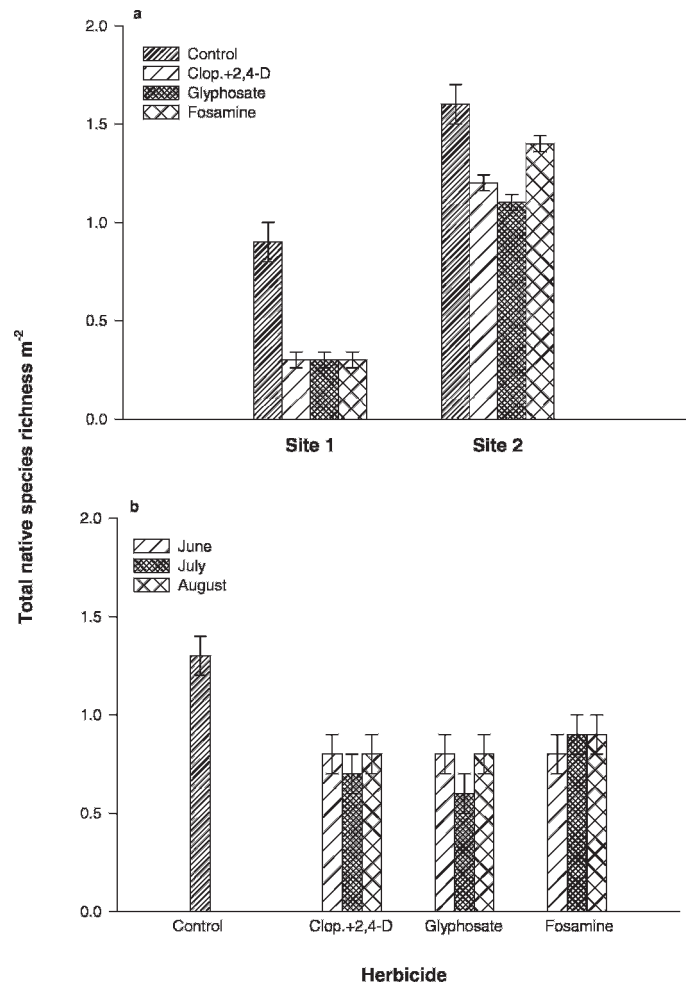


Figure 6. The effect of herbicide (a) by site and (b) by application timing on total native species richness. Error bars in (a) represent a standard error of 0.1 (controls) and 0.04 (treatments). Error bars in (b) represent a standard error of 0.1 for the control and all treatments.

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 = 0.1).

The effect of herbicide on total nonnative 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 cloyralid plus 2,4-D and glyphosate did not affect richness (Figure 7a). Total nonnative species richness, as a result of cloyralid 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, cloyralid plus 2,4-D, or fosamine did not differ. However, glyphosate increased nonnative species richness between June 2001 (2.6 species m⁻²) and August 2002 (3.9 species m⁻²). The effect of herbicide on total nonnative species richness was also influenced by application timing ($P = 0.03$). For cloyralid plus 2,4-D, only the June application (3.0 species m⁻²) increased richness above that of the control

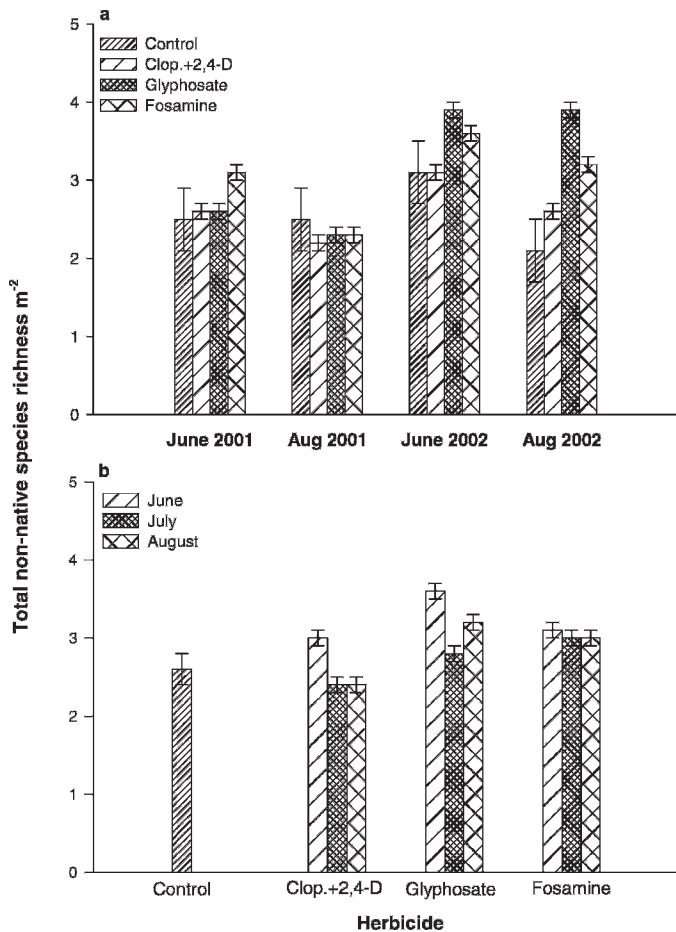


Figure 7. The effect of herbicide (a) by year and (b) by application timing on total nonnative species richness. Error bars in (a) represent a standard error of 0.4 (controls) and 0.1 (treatments). Error bars in (b) represent a standard error of 0.2 (control) and 0.1 (treatments).

(2.6 species m^{-2} ; Figure 7b). Additionally, June and August applications of glyphosate and all timings of fosamine increased nonnative species richness.

Total nonnative species richness was also affected by a site by herbicide by 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 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 nonnative 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 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. For clopyralid plus 2,4-D, the high rate (1.7) increased diversity over that of the control (1.4; Figure 9b). Greater diversity 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.

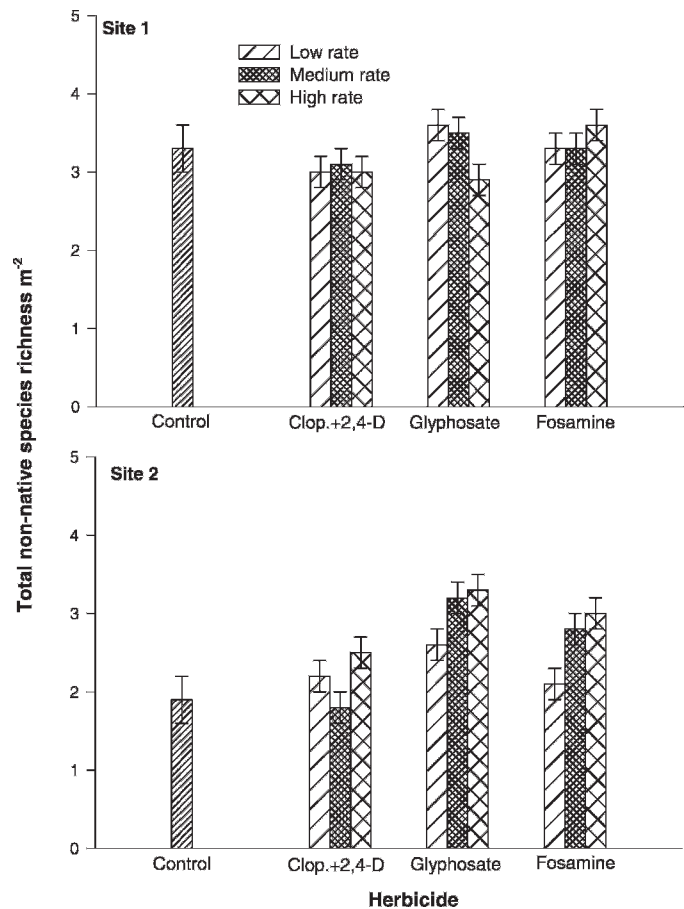


Figure 8. The effect of herbicide by application rate on total nonnative species richness at sites 1 and 2. Error bars represent a standard error of 0.3 (controls) and 0.2 (treatments).

Discussion

Consistent with other studies investigating community response to herbicides, 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 nonnative annual forbs, they may play an important role in recovering the functions of the system. Our companion study indicated that controlling Russian knapweed with glyphosate was effective for only one year postapplication (Laufenberg et al. 2004). Therefore, glyphosate may be more useful for increasing desired species richness in communities infested by nonrhizomatous or annual weeds.

Because species vary in their tolerance to herbicides, application rates are important determinants of community response. Marrs (1985) found that a single application of picloram, the most commonly used herbicide on rangeland,

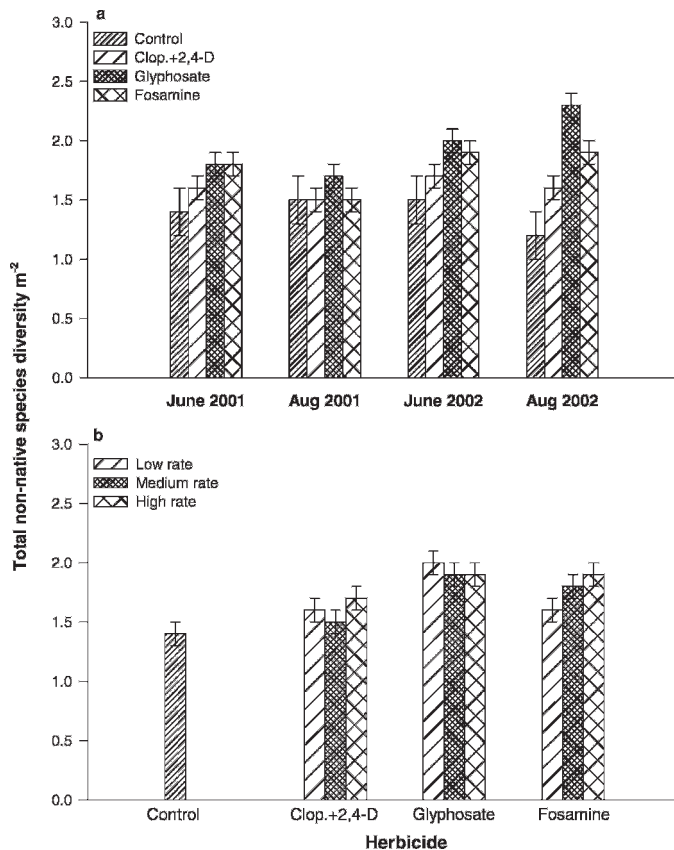


Figure 9. The effect of herbicide (a) by year and (b) by application rate on total nonnative species diversity. Error bars in (a) represent a standard error of 0.2 (controls) and 0.1 (treatments). Error bars in (b) represent a standard error of 0.1 for the control and all treatments.

reduced nontarget desired species to unacceptable levels when applied at rates necessary to control scrub in lowland heath vegetation. Fosamine applied at $4.8 \text{ kg ai ha}^{-1}$ 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 the site. This suggests that herbicide rates have less effect on the loss or gain of new species but may have substantial effect 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, whereas 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 nontarget forbs. 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. One possible explanation is that later applications provided poor Russian knapweed control. However, our companion study indicated effective control of this weed with later applications (Laufenberg et al. 2004). Therefore, we believe that translocation from shoots to roots in nontarget species during late application of

clopyralid plus 2,4-D occurred with the movement of carbohydrates, reducing species richness and diversity.

Herbicide application recommendations tend to be provided for broad geographic areas. The Pacific Northwest Weed Management Handbook and the Montana/Utah/Wyoming Weed Management Handbook provide examples of regional herbicide recommendations that encompass multiple states within regions. Broad geographic recommendations may be appropriate for weed control, but our data suggest that herbicide recommendations considering post-application richness and diversity may be site-specific. In our study, nearly all response parameters varied 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 pretreatment plant assemblage composition to increase the probability that the treatments meet long-term management objectives.

The success of any restoration program depends on how closely the postapplication plant community approximates that stated in the objectives. In this study, nonnative species accounted for the majority of the richness and diversity in areas where they were dominant before herbicide application, whereas native species tended to decrease. Management strategies aimed at enhancing ecosystem function and niche occupation to preempt reinvasion by Russian knapweed can, possibly, meet their goals; however, restoring plant communities with native species using these herbicides seems less likely.

Literature Cited

- Carpinelli, M.F. 2000. Designing weed-resistant plant communities by maximizing niche occupation and resource capture. Ph.D. dissertation. Bozeman, MT: Montana State University.
- Chapin, F.S.I. 1993. Functional role of growth forms in ecosystem and global processes. Pages 287–312 in J.R. Ehleringer and C.B. Field, eds. *Scaling Physiological Processes: Leaf to Globe*. San Diego, CA: Academic.
- Cronquist, A., A.H. Holmgren, N.H. Holmgren, J.L. Reveal, and P.K. Holmgren. 1977. *Intermountain Flora; Vascular Plants of the Intermountain West, U.S.A.* New York, NY: Columbia University Press.
- Denny, M.K. 2003. Maintaining and establishing culturally important plants after landscape scale disturbance. M.S. thesis. Bozeman, MT: Montana State University.
- Dorn, R.D. 1984. *Vascular Plants of Montana*. Cheyenne, WY: Mountain West.
- Egler, F.E. 1954. Vegetation science concepts, I: initial floristic composition—a factor in old-field vegetation development. *Vegetatio* 4:412–417.
- Frank, D.A. and S.J. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the Yellowstone drought. *Oikos* 62:360–362.
- Hanson, H.C. and W.C. Whitman. 1938. Characteristics of major grassland types in western North Dakota. *Ecol. Monogr.* 8:57–114.
- Jorgensen, H.E. 1979. *Vegetation of the Yellow Water Triangle, Montana*. Billings, MT: Montana Department of Fish and Game, U.S. Bureau of Land Management Unnumbered Publication. 57 p.
- Laufenberg, S.M., R.L. Sheley, J.S. Jacobs, and J. Borkowski. 2004. Herbicide effects on density and biomass of Russian knapweed (*Acroptilon repens*) and associated plant species. *Weed Technol.* 19:62–72.
- Mackie, R.J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. *Wildlife Monograph* 20. Bethesda, MD: The Wildlife Society. 79 p.
- Marrs, R.H. 1985. The effects of potential bracken and scrub control herbicides on lowland Calluna and grass heath communities in East Anglia, UK. *Biol. Conserv.* 32:13–32.

- Naem, S., F.S. Chapin III, R. Costanza, et al. 1999. Biodiversity and ecosystem functioning: maintaining natural life support processes. *Issues in Ecology* 4. Washington, DC: Ecological Society of America.
- Pokorny, M.L., R.L. Sheley, C.A. Zabinski, R.E. Engel, T.J. Svejcar, and J.J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restor. Ecol.* 13:448–459.
- Rice, P.M., J.C. Toney, D.J. Bedunah, and C.E. Carlson. 1997. Plant community diversity and growth form responses to herbicide applications for control of *Centaurea maculosa*. *J. App.Ecol.* 34:1397–1412.
- Sheley, R.L. and M.F. Carpinelli. 2005. Creating weed-resistant plant communities using niche-differentiated nonnative species. *Range. Ecol. Manag.* 58: 480–488.
- Spehn, E., J. Joshi, B. Schmid, M. Diemer, and C. Korner. 2000. Aboveground resource use increases with plant species richness in experimental grassland ecosystems. *Funct. Ecol.* 14:326–337.
- Symstad, A.J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81:99–109.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 87:81–92.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1305.
- Whitson, T.D. 1999. Russian knapweed. Page 438 in Sheley, R. and J. Petroff, eds. *Biology and Management of Noxious Rangeland Weeds*. 1999. Corvallis, OR: Oregon State University Press.

Received December 28, 2006, and approved March 9, 2007.