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Integrating disturbance and colonization during rehabilitation of invasive weed-dominated grasslands

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Developing ecological principles applicable to invasive plant management is central to implementing sustainable strategies. We tested portions of a potentially useful successional-based management framework to further our understanding of the relationship between disturbance and colonization during revegetation of invasive weed-dominated grasslands. We hypothesized (1) intermediate wheatgrass density and biomass would be greatest at highest seeding rates, (2) control and tillage procedures that increase the availability of safe sites would increase wheatgrass abundance, and (3) spotted knapweed density and biomass would be lowest in treatments with highest wheatgrass density and biomass. Treatments included three disturbance levels: (1) no disturbance, (2) application of glyphosate, and (3) fall tillage. Colonization treatments were seeding intermediate wheatgrass of 0, 500, 2,500, and 12,500 seeds m^{-2}. Treatments were factorially applied in a randomized complete-block design with four replications at each of two sites located in Montana. Density and biomass of intermediate wheatgrass and spotted knapweed were sampled in 1997 and 2001. At both sites, seeding 2,500 or 12,500 seed m^{-2} increased wheatgrass density over that of the nonseeded control in 1997. The highest seeding rate produced almost three times as many wheatgrass plants as 2,500 seeds m^{-2} that year. By 2001, only the highest seeding rate produced wheatgrass densities greater than that of the nonseeded control at Bozeman. Seeding rates higher than 500 seeds m^{-2} yielded greater wheatgrass biomass than the nonseeded control with or without either tillage or glyphosate. At the highest seeding rate, tillage or glyphosate doubled intermediate wheatgrass biomass compared with no disturbance. Spotted knapweed generally had lower biomass where intermediate wheatgrass density and biomass was highest. One approach to rehabilitation is to design disturbances that favor desired species and then use high seeding rates that overwhelm the pool of available propagules and occupy a high percentage of safe sites.

Nomenclature: Glyphosate; intermediate wheatgrass, *Elytriga intermedia* (Host) Nevski; spotted knapweed, *Centaurea maculosa* Lam.

Key words: Invasive plant management, restoration, successional management, tillage, weeds.

Ecological land rehabilitation is central to replacing and repairing ecosystems damaged by invasive plants (Jacobs et al. 1998). Successional management has been proposed as a theoretical framework for developing ecologically based invasive plant management strategies on rangeland (Sheley et al. 1996). Pickett et al. (1987) provided the ecological basis for successional management by developing a hierarchical model of succession, which includes the general causes, controlling processes, and their modifying factors. Three general causes of succession have been proposed: disturbance, colonization, and species performance (Luken 1990). Within the limits of our knowledge about the conditions, mechanisms, and processes controlling plant community dynamics, these three factors can be modified to allow predictable successional transitions (Bard et al. 2003; Sheley et al. 1996).

The process of disturbance plays an important role in initiating and altering successional pathways, although a unified disturbance theory has not been developed (Pickett and White 1985). Disturbance creates safe sites (Harper et al. 1965) or eliminates site availability (Pickett et al. 1987). The size, severity, frequency, and patchiness of disturbance, and the predisturbance history determine the community organization and successional dynamics. The type and severity of disruption dictate the amount of physical space available for colonization (Bazzaz 1983). Oomes and Elberse (1976) found that the flat-seeded species, such as yarrow (*Achillea millefolium* L.), had highest germination on even surfaces, whereas other species of varying sizes and shape had highest germination on 10- or 20-mm grooved surfaces. Disturbance also greatly influences timing and patterns of resource availability (Bazzaz 1983, 1984). Disturbance may cause a decline in resource use by plants or an increase in resource supply rates, thus leading to fluctuating resource availability (Davis et al. 2000). Light and soil moisture profiles, soil nutrient content, and factors that modify the use of these resources, such as air and soil temperature are dependent on the extent of vegetation damage or removal (Collins et al. 1985; Runkle 1985). In many cases, increased resource availability, especially nitrogen, favors establishment and growth of nonindigenous invasive plants (Herron et al. 2001; McLendon and Redente 1991).

Colonization, the availability and establishment of various species, is another important cause of succession. Factors directing colonization are dispersal, propagule pool, seed weight, time of appearance, and species-specific establishment characteristics (Gross 1999). A major factor modifying colonization is seed output and availability. Failures in establishment of particular species during succession appear more explainable by the absence of viable or sufficient seeds brought in by wind, and their absence in the soil seedbank, than their failure to establish when available (Gross 1980; Gross and Werner 1982). In studies specific to spotted knapweed, Sheley et al. (1999) found that increasing the seeding rate from 500 seeds m^{-2} where no establishment occurred, to 2,500 and 12,500 seeds m^{-2} increased intermediate wheatgrass tiller density to 80 and 140 plants m^{-2}, respectively, at one site and 158 and 710 plants m^{-2} at another site 2 yr after seeding. Long-term dynamics may also be influenced by altering plant densities created by seed availability, thereby shifting the competitive balance among populations (Egler 1954). In a growth chamber study, Jacobs et al. (1996) found that bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh.) Löve] was four times more competitive than spotted knapweed seedlings at densities (1,000 to 5,000 plants m^{-2}) higher than normal for rangeland revegetation. Similarly, Velagala et al. (1997) found that increasing intermediate wheatgrass from < 1,000 plants m^{-2} to > 1,000 plants m^{-2} reduced the competitive effect of spotted knapweed on intermediate wheatgrass biomass where interspecific interference occurred.

In many cases, disturbance and colonization alone do not account for successional patterns or species richness (Grubb 1977, 1986). Although ecologists generally acknowledge the importance of disturbance and colonization for the maintenance of desired plant communities, little is known about how disturbances and colonization interact to influence plant community dynamics (Gross 1999).

The overall objective of this study was to test portions of the theory of successional management and to further our understanding of the relationship between disturbance and colonization during revegetation of invasive plant dominated grasslands. The specific objective was to determine whether extraordinarily high seeding rates, combined with the disturbance of tillage or herbicide treatment could be combined to increase the long-term abundance of intermediate wheatgrass in spotted knapweed–infested rangeland. We hypothesized that (1) intermediate wheatgrass density and biomass would be greatest at highest seeding rates, (2) glyphosate and tillage procedures that increase the availability of safe sites would increase wheatgrass abundance, and (3) spotted knapweed density and biomass would be lowest in treatments yielding highest wheatgrass density and biomass.

Materials and Methods

This study was conducted from 1995 through 2001. Data from 1995 through 1997 were published in Sheley et al. (1999) to address the effects of disturbance and colonization on emergence and early establishment. This study compares data collected in 1997 with data collected in 2001 to investigate the medium-term effects of disturbance and colonization on population growth and maintenance and to assess the consistency of short- vs. medium-term conclusions.

Study Sites

The study sites were located about 11 km east–northeast of Hamilton, MT, (46°17′N, 114°1′W) at an elevation of 1,341 m, and about 15 km southwest of Bozeman, MT (45°36′N, 111°11′W) at an elevation of 1,524 m. The Hamilton site is a rough fescue (*Festuca scabrella*)–bluebunch wheatgrass (*Pseudoroegneria spicata*) habitat type and the Bozeman site is a Idaho fescue (*Festuca idahoensis*)–*Pseudoroegneria spicata* habitat type (Mueggler and Stewart 1980). Both sites were dominated by spotted knapweed, with very few desired species present. Spotted knapweed grew in association with downy brome (*Bromus tectorum* L.) more than any other species. Intermediate wheatgrass was not present at either site at the start of the study. Hamilton soils were Stecum stony loamy coarse sand (mixed typic Cryorthenths) and were moderately deep. Bozeman soils were loamy-skeletal over sandy or sandy skeletal (mixed typic Argiboroll). Annual precipitation at both sites ranges from 406 to 457 mm with a bimodal distribution with peaks in the winter and spring. The mean annual temperature at the Hamilton site is 6.6 and 6.1 C at Bozeman. Precipitation and temperature were monitored within 6.5 km of each site during the study period. During the period of the study, precipitation and temperature were near the long-term average.

Experimental Design

The treatments included three disturbance levels: (1) no disturbance, (2) application of the nonselective herbicide glyphosate,[1] and (3) tillage. The four colonization treatments consisted of intermediate wheatgrass seeding rates of 0, 500, 2,500, and 12,500 seeds m^{-2}. The herbicide killed plants present at the time of application. No further soil disturbance occurred. The tillage disturbance created safe sites by killing plants present at the time of tillage, and by creating a seedbed that may have favored species with large seeds. Treatments were factorially applied in a randomized complete-block design with four blocks (replications) at each site (128 total plots). Each plot was 3 by 3 m.

Procedures

Disturbances

Glyphosate, a nonselective herbicide, which is rapidly deactivated by binding to soil particles, was applied at 1.16 kg ae ha^{-1} using a CO_2-pressurized backpack sprayer calibrated to deliver a total volume of 410 L ha^{-1} during the fall of 1995. Because most plants were not completely dormant, this treatment provided about 95% vegetation control for the month after application and about 50% plant control during the next year. By 1997, spotted knapweed density was greater in the glyphosate treatment than in that of the control at Hamilton (Sheley et al. 1999). Tillage was accomplished using a tractor-mounted rototiller that mixed the soil to a depth of about 200 mm. This shallow tillage was aimed at preparing a seedbed for establishment while minimizing the release of nutrients from plant material. The most significant differences between the two disturbance treatments were that tillage exposed more bare soil and incorporated the litter into the soil profile than did the glyphosate treatment.

Colonization

Seeds of 'Oahe' intermediate wheatgrass were broadcast on the soil surface of each plot immediately after application of disturbances and were covered with a small amount of soil (< 2 mm). Intermediate wheatgrass seeds were purchased from Circle S Seeds Inc., Three Forks, MT, in October 1995. Intermediate wheatgrass is an important grass species used for revegetating spotted knapweed–infested rangeland because it establishes easily and produces abundant forage for cattle and wildlife without invading onto adjacent habitat types (Holzworth and Lacey 1991). Ninety-four percent of the seeds germinated in a standard test. Treatments were applied during November 4 through November 8, 1995, at Bozeman and November 11 through November 14, 1995, at Hamilton.

Plant Characteristics

Spotted knapweed is a taprooted perennial Asteraceae of Eurasian origin that depends primarily on seeds for reproduction. Spotted knapweed seeds are spherical in shape, have a smooth seed coat with a short plume, and weigh about 5 mg. Intermediate wheatgrass is an introduced, perennial, rhizomatous grass. Intermediate wheatgrass seeds are cylindrical in shape and weigh about 8 mg.

Sampling

The study was sampled at peak standing crop (July) in 1996, 1997, and 2001. Density of intermediate wheatgrass and spotted knapweed were determined by counting the number of plants in one randomly placed 0.44-m^2 circular hoop in each plot. If the hoop landed on an area that had earlier sampling, it was rerandomized to avoid multiple samplings within the same area. Biomass was determined by clipping plants to ground level. Plants were separated by species, dried (60 C, 48 h), and weighed.

Analysis

Initially, data were pooled and tested for homogeneity of variances. This test indicated that data met the assumption for analysis of variance. Analysis of variance was used to determine the effects of intermediate wheatgrass seeding rate, tillage, and glyphosate on the density and biomass of intermediate wheatgrass and spotted knapweed. Data were analyzed as a split plot in time. The model included site, year, seeding rate, tillage, glyphosate, and their factorial combinations. Year and interactions including year were tested using the rep by site by tillage by glyphosate by seeding rate interaction as the error term. Other main effects and interactions were tested using the error mean square from the overall model. Analysis of variance P values from *F*-tests are presented and individual means were compared using a least significant difference test at the 5% level of confidence when P values were significant at the 5% level (Peterson 1985). Data presented in Figures 1–8 are averaged over factors that were not significant and did not interact.

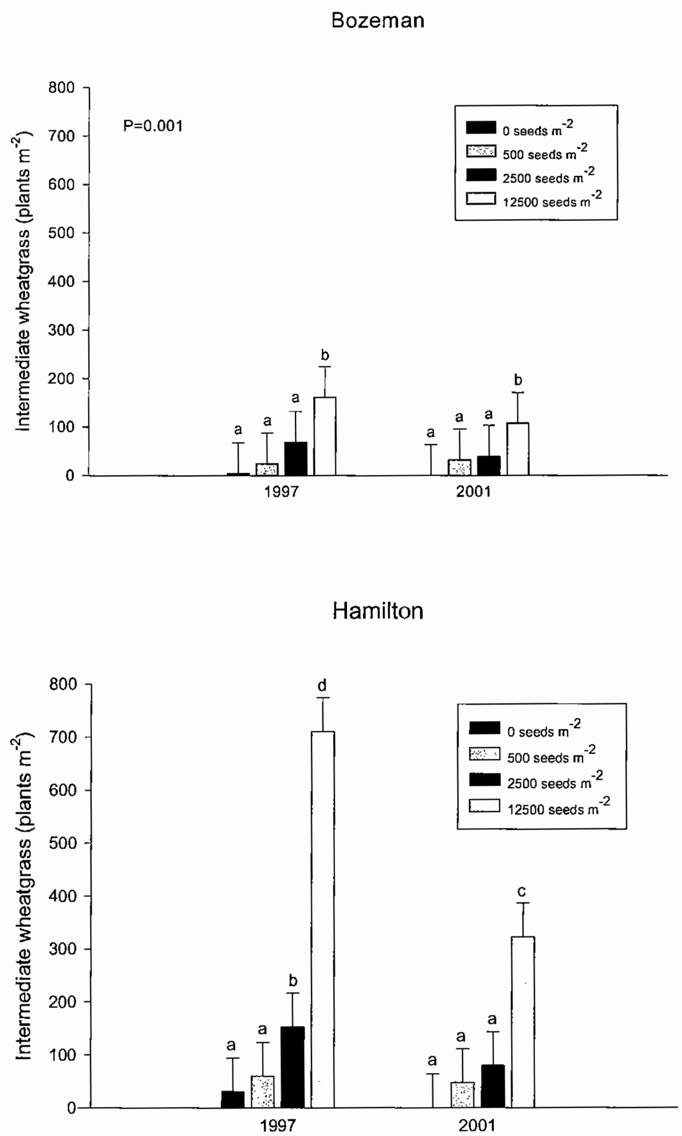

FIGURE 1. Interaction of seeding rate, year, and site on intermediate wheatgrass density. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across tillage and glyphosate treatments. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

Results

Intermediate Wheatgrass

Density

The effect of wheatgrass seeding on intermediate wheatgrass density depended on the site and year of sampling (Figure 1; Table 1). At Bozeman, wheatgrass seeding at 12,500 seed m^{-2} increased intermediate wheatgrass density over that of the control in 1997 whereas seeding either 2,500 or 12,500 seed m^{-2} increased wheatgrass density at Hamilton. The highest seeding rate in 1997 produced almost two to three times as many wheatgrass plants as seeding 2,500 seeds m^{-2}. By 2001, only the highest seeding rate produced wheatgrass densities greater than that of the control at both sites. At both sites and years, the highest seeding rate produced the highest wheatgrass density.

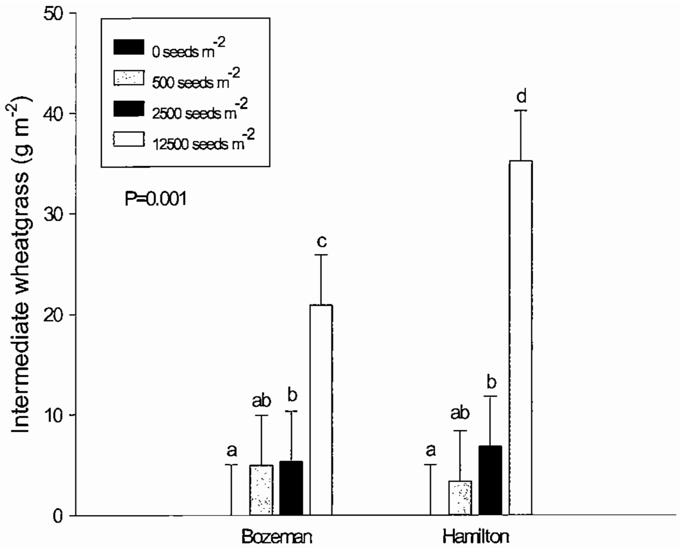

FIGURE 2. Interaction of site and seeding rate on intermediate wheatgrass biomass. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across year, tillage, and glyphosate. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

Biomass

The influence of seeding rate on intermediate wheatgrass depended upon the site or year sampled (Figures 2 and 3; Table 1). Intermediate wheatgrass biomass was highest in plots receiving the highest seeding rate. At the highest seeding rate, Hamilton produced 15 g m^{-2} more biomass than Bozeman, which accounted for the site by seeding rate interaction (Table 1). In 1997, only the highest seeding rate yielded biomass greater than that of the control (Figure 3; Table 1). By 2001, all seeding rates produced biomass greater than that of the control, with the highest rate producing over six times the biomass of any other treatment.

The effect of seeding on intermediate wheatgrass biomass also depended on tillage or glyphosate (Figure 4; Table 1). Seeding rates higher than 500 seeds m^{-2} yielded greater wheatgrass biomass than the nonseeded control with or without either tillage or glyphosate. Intermediate wheatgrass biomass was greatest in the plots receiving the highest seeding rate. At the highest seeding rate, tillage or glyphosate doubled intermediate wheatgrass compared with no disturbance.

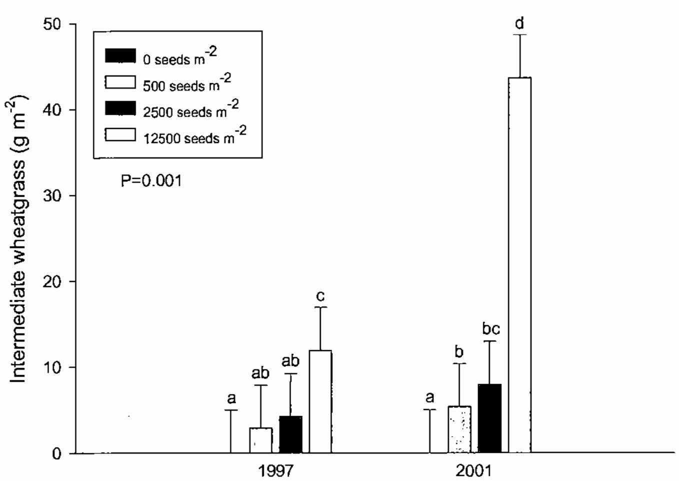

FIGURE 3. Interaction of year and seeding rate on intermediate wheatgrass biomass. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across site, tillage, and glyphosate. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

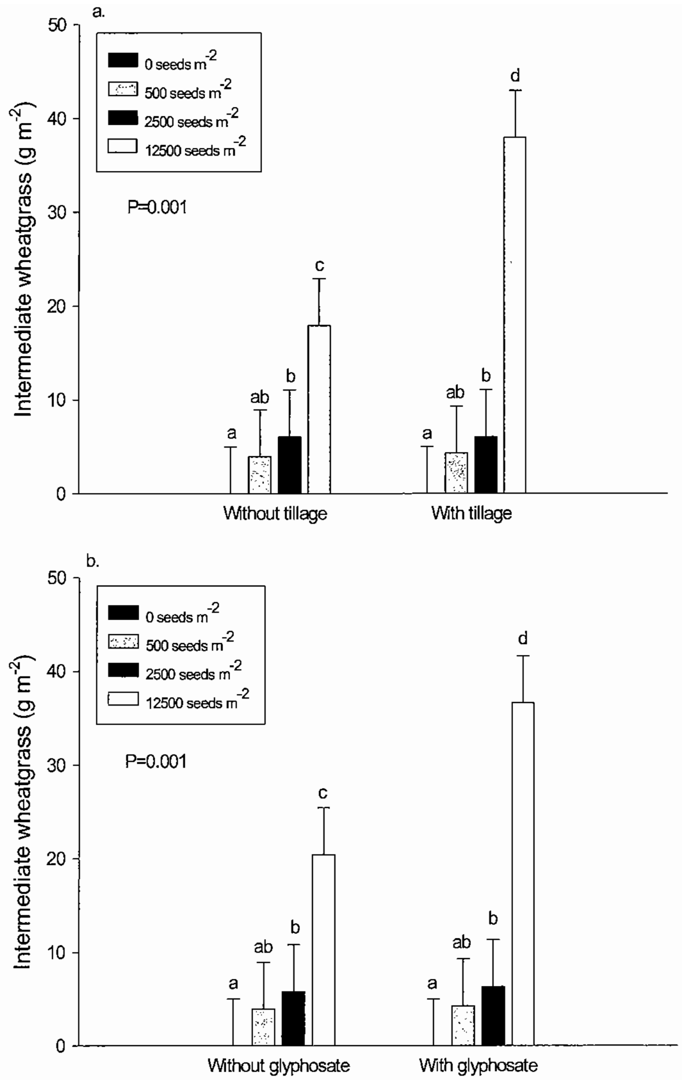

FIGURE 4. Interaction of seeding rate tillage (a) and glyphosate (b) on intermediate wheatgrass biomass. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across site, year, and seeding rate. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

Spotted Knapweed

Density

The effect of glyphosate on spotted knapweed density depended upon the site and year sampled (Figure 5; Table 2). At Bozeman, spotted knapweed increased on plots sprayed with glyphosate from 305 to 419 plants m^{-2} in 1997. By 2001, spotted knapweed density was reduced to about 105 plants m^{-2}, with or without glyphosate. At Hamilton, treating with glyphosate did not affect spotted knapweed density in 1997. By 2001, spotted knapweed density

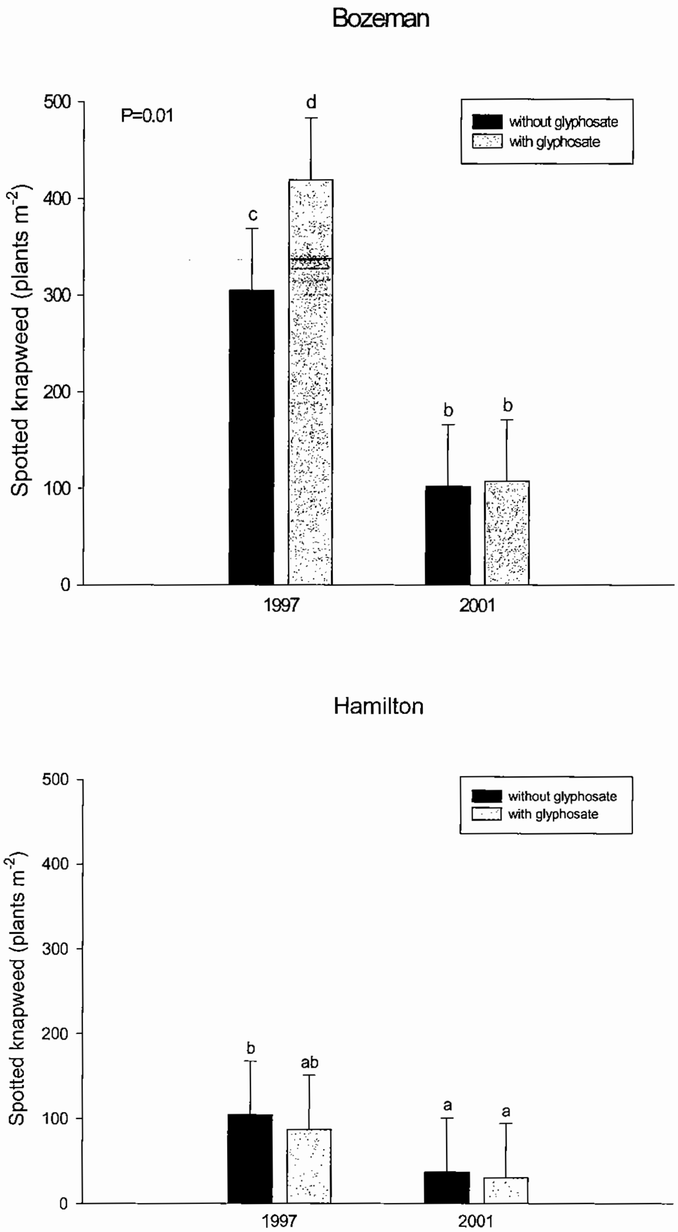

Figure 5. Interaction of site, year, and glyphosate on spotted knapweed density. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across year, tillage, and glyphosate. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

was reduced from 104 to about 33 plants m^{-2}, with or without glyphosate.

Biomass

The effect of tillage on spotted knapweed biomass depended upon the year of sampling (Figure 6; Table 2). In 1997, tillage reduced spotted knapweed biomass by about 26 g m^{-2} below that of plots not tilled. In 2001, the spotted knapweed biomass was lower than in 1997, with or without tillage.

The effects of wheatgrass seeding rate on spotted knapweed biomass depended on the interaction of site and year of sampling (Figure 7; Table 2). At Bozeman, all seeding rates yielded similar spotted knapweed biomass in 1997. In

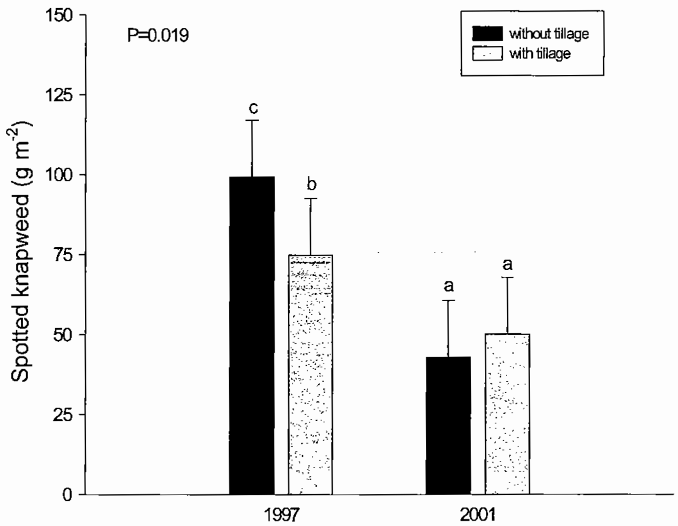

Figure 6. Interaction of year and tillage on spotted knapweed biomass. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across site, seeding rate, and glyphosate. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

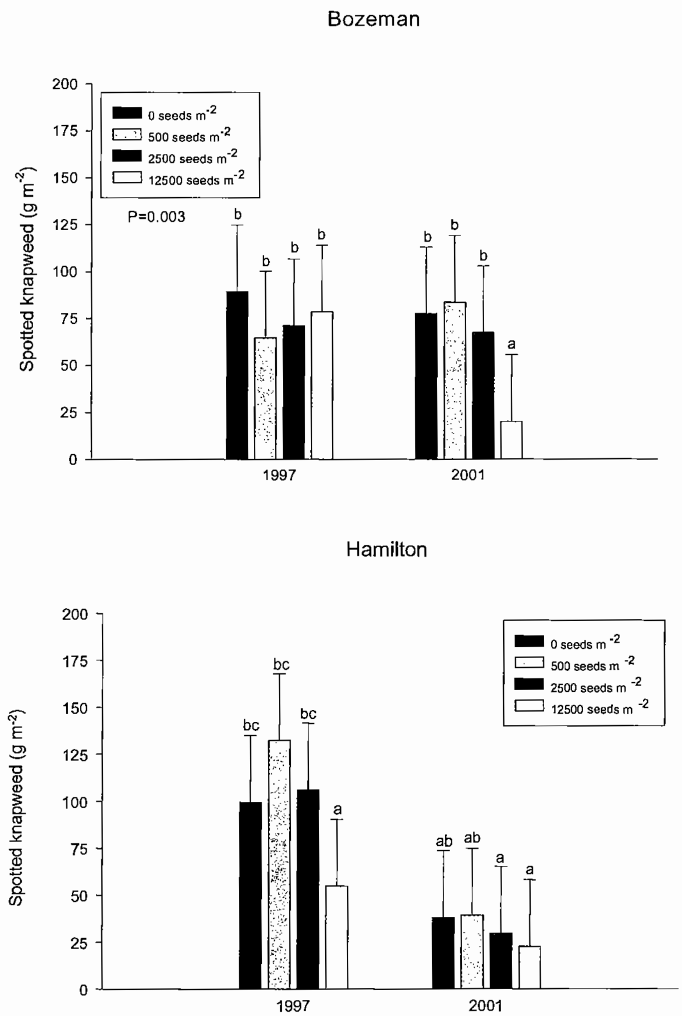

Figure 7. Interaction of site, year, and seeding rate on spotted knapweed biomass. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across tillage and glyphosate. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

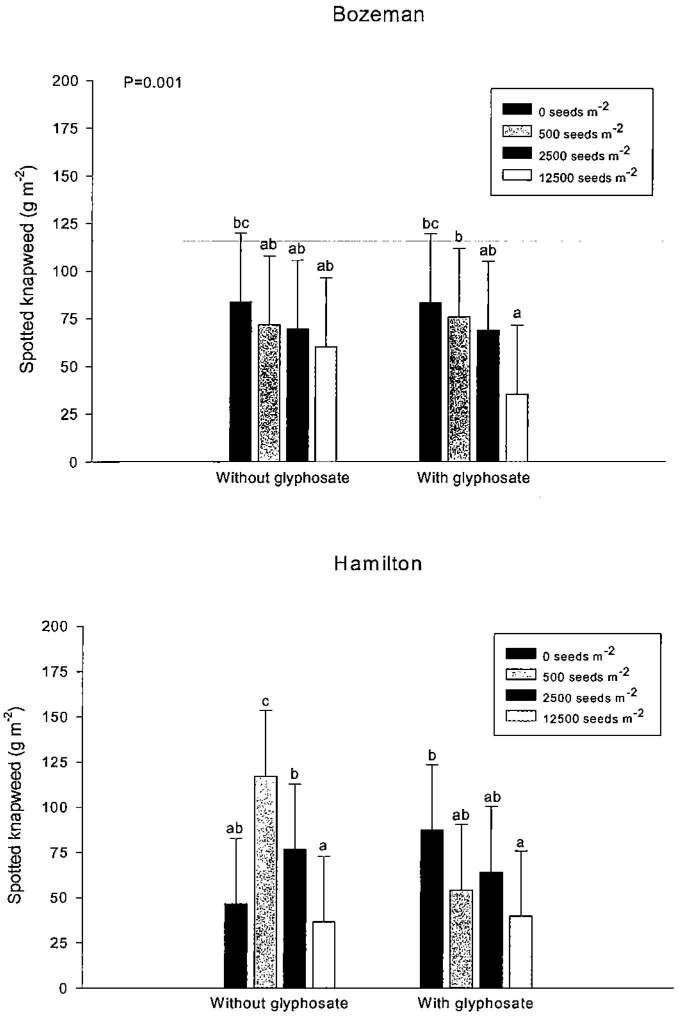

FIGURE 8. Interaction of site, seeding rate, and glyphosate on spotted knapweed biomass. P values indicate the level of significance of the interaction from analysis of variance. Means are averaged across year and tillage. Means followed by the same letter were not significantly different, and LSD bars provide indication of the overall experimental variance.

2001, the highest seeding rate reduced spotted knapweed biomass by about one third that of any other treatment at this site. At Hamilton, the highest seeding rate reduced spotted knapweed biomass by about half that of all other treatments in 1997; by 2001 there was no seeding rate effect.

At Bozeman, all seeding rates yielded similar spotted knapweed biomass without glyphosate (Figure 8; Table 2). Including glyphosate with the highest seeding rate reduced spotted knapweed biomass below the nonseeded control and those seeded with 500 seed m^{-2} at this site. At Hamilton, seeding at 500 seeds m^{-2} without glyphosate actually increased spotted knapweed biomass. Seeding at 12,500 seeds m^{-2} without glyphosate produced similar knapweed biomass as that of the nonseeded control.

Discussion

Most revegetation trials are short-term studies that focus on seedling establishment, and reevaluation of persistence and abundance after years of climatic fluctuation is rare. A substantial number of conclusions presented in Sheley et al. (1999) for seedling emergence remain consistent several

TABLE 1. P values from analysis of variance for intermediate wheatgrass density and biomass during 1997 and 2001 at Hamilton and Bozeman, MT.

Source	Density	Biomass
Replication	0.001**	0.147
Site	0.001**	0.006**
Year	0.001**	0.001**
Tillage	0.129	0.001**
Glyphosate	0.267	0.003**
Seeding rate	0.001**	0.001**
Site by year	0.001**	0.824
Site by tillage	0.897	0.891
Site by glyphosate	0.933	0.296
Site by seeding rate	0.001**	0.001**
Year by tillage	0.789	0.097
Year by glyphosate	0.682	0.344
Year by seeding rate	0.001**	0.001**
Tillage by glyphosate	0.736	0.839
Tillage by seeding rate	0.854	0.001**
Glyphosate by seeding rate	0.067	0.001**
Site by year by tillage	0.419	0.623
Site by year by glyphosate	0.849	0.270
Site by year by seeding rate	0.001**	0.961
Site by tillage by glyphosate	0.869	0.882
Site by tillage by seeding rate	0.985	0.277
Year by tillage by glyphosate	0.173	0.929
Year by tillage by seeding rate	0.869	0.116
Year by glyphosate by seeding rate	0.695	0.284
Tillage by glyphosate by seeding rate	0.866	0.142

* Significant at $P \leq 0.01$; ** significant at $P < 0.05$.

TABLE 2. P values from analysis of variance for spotted knapweed density and biomass during 1997 and 2001 at Hamilton and Bozeman, MT.

Source	Density	Biomass
Replication	0.017*	0.470
Site	0.001**	0.411
Year	0.001**	0.001**
Tillage	0.317	0.273
Glyphosate	0.076	0.276
Seeding rate	0.044*	0.001**
Site by year	0.001**	0.002**
Site by tillage	0.101	0.190
Site by glyphosate	0.007**	0.619
Site by seeding rate	0.067	0.406
Year by tillage	0.098	0.019*
Year by glyphosate	0.033	0.185
Year by seeding rate	0.439	0.969
Tillage by glyphosate	0.320	0.101
Tillage by seeding rate	0.549	0.863
Glyphosate by seeding rate	0.189	0.153
Site by year by tillage	0.121	0.488
Site by year by glyphosate	0.010*	0.834
Site by year by seeding rate	0.375	0.003**
Site by tillage by glyphosate	0.054	0.494
Site by tillage by seeding rate	0.242	0.681
Year by tillage by glyphosate	0.939	0.447
Year by tillage by seeding rate	0.445	0.957
Year by glyphosate by seeding rate	0.061	0.198
Tillage by glyphosate by seeding rate	0.964	0.350

* Significant at $P \leq 0.01$; ** significant at $P < 0.05$.

years after the initial assessment. This lends credibility to the notion that seedling emergence and establishment data provide valuable information regarding long-term population dynamics during revegetation. The main and consistent conclusion of both the short- and medium-term analysis was that our study provides evidence that disturbances, such as tillage or glyphosate application (or both), that create safe sites (Harper et al. 1965) and open niches, interact with seed availability to, in part, control plant population and community dynamics.

On invasive plant–dominated grasslands, broadcast seeding often fails to successfully produce vigorous grass stands because of the lack of soil moisture, weed competition, or both (James 1992; Velagala et al. 1997). Recommended seeding rates for intermediate wheatgrass ranges from 170 seeds m^{-2} (Granite Seed Co., Lehi, Utah) to 430 seed m^{-2} (Goodwin and Sheley 2002). Sheley et al. (1999) indicated that intermediate wheatgrass establishment did not occur at 500 seeds m^{-2} under tillage, glyphosate, or their combined treatment by the second growing season. In addition, this analysis confirms that this seeding rate is too low for broadcast seeding because, in most cases, 500 seeds m^{-2} failed to produce a grass stand even 6 yr after the seeding. We believe that too few seeds were available to reach the limited naturally occurring safe sites. Failures in revegetation may be overcome by increasing seeding rates, thereby increasing the chances of a seed reaching a safe site. In most cases, increasing intermediate wheatgrass seeding rate increased intermediate wheatgrass abundance in our study. On the basis of the disturbance–colonization relationship observed in this study, it may also be possible to assess the availability of safe sites before seeding and match seed size and other seed characteristics (e.g., shape) with safe site characteristics to maximize safe site occupation. For example, choosing small seeded species that can take advantage of small and infrequent safe sites may enhance broadcast seeding success (Oomes and Elberse 1976).

In addition to the results found by Sheley et al. (1999), we found evidence supporting our hypothesis that intermediate wheatgrass biomass would be greatest at highest seeding rates where glyphosate and tillage procedures increase the availability of safe sites. Middle seeding rates combined with disturbances tended to increase the abundance of intermediate wheatgrass, but only slightly, whereas extraordinarily high seeding rates combined with disturbance produced the highest abundance of intermediate wheatgrass. In this case, we believe that the disturbance created safe sites and niches (Kocher and Stubbendieck 1986) that could be exploited by increasing the availability of seeds (Call and Roundy 1991).

Our data also support the hypothesis that spotted knapweed density and biomass would be negatively affected by intermediate wheatgrass. In another study, increasing niche occupation with desired species (including intermediate wheatgrass) nearly prevented the establishment of spotted knapweed (Carpinelli et al. 2004). Although spotted knapweed was not completely removed in this study, it was reduced in areas where intermediate wheatgrass became well established. We speculate that these results are associated with competitive effects of establishment at high seeding rates. Velagala et al. (1997) found that the competitive influence of spotted knapweed on intermediate wheatgrass was drastically reduced at high seeding rates.

Successional management provides a theoretical framework that can be used to guide the implementation of augmentative rehabilitation and integrated weed management (Bard et al. 2002; Sheley et al. 1996). By accepting the hypothesis that disturbances that create safe sites and open niches interact with seed availability to, in part, control plant population and community dynamics, we provide evidence supporting the theory of successional management (Luken 1990; Pickett et al. 1987). Our ability to use this framework depends on our understanding of the processes causing successional dynamics, and knowledge about the interactions among these processes. Rehabilitation of invasive plant–infested sites will require steps that favor establishment and persistence of the desired species. One approach to rehabilitation is to design disturbances that favor desired species and then use high seeding rates that overwhelm the pool of available propagules and occupy a high percentage of safe sites. For long-term successful rehabilitation, it will be important that disturbances or desired species (or both) limit nutrients available to invasive species (Herron et al. 2001; Pokorny 2002). These rehabilitation procedures can be designed to augment naturally occurring variation in disturbances, seed banks, and seed sources across the landscape to repair damaged processes and replace missing portions of the plant community (Bard et al. 2002).

Sources of Materials

[1] Glyphosate, Roundup®, Monsanto Company, 800 North Lindbergh Boulevard, St. Louis, MO 63167.

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