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CONTROLLING PERFORMANCE OF BLUEBUNCH WHEATGRASS AND SPOTTED KNAPWEED USING NITROGEN AND SUCROSE AMENDMENTS

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ABSTRACT.—Range- and wildlands are being invaded by nonindigenous plants, resulting in an unprecedented, rapid change in plant community composition across the United States. Successional management predicts that species performance may be modified by resource availability. The objective of this study was to determine whether species performance could be altered by modifying soil nitrate (NO_3^-) and ammonium (NH_4^+) concentrations within an Idaho fescue (*Festuca idahoensis*)/bluebunch wheatgrass (*Pseudoroegneria spicata*) plant association. We planted bluebunch wheatgrass and spotted knapweed (*Centaurea maculosa*) in an addition series at 2 sites in southwestern Montana. Each plot in the addition series matrix was divided into thirds, and we applied nitrogen (N) to a subplot and sucrose to a 2nd subplot. The remaining subplot was not amended and considered a control. Nitrogen amendment tended to enhance the performance of spotted knapweed, while sucrose amendment had no effect. Bluebunch wheatgrass performance was not affected by either amendment. Sucrose treatments only decreased soil NO_3^- at the more productive site. Regression models for predicting bluebunch wheatgrass and spotted knapweed biomass accounted for only about 30% of the variation, suggesting other processes in addition to interference were responsible for explaining relative plant performance. We recommend that land managers prevent activities that increase soil N concentration while the effectiveness of carbon amendments as a means to decrease soil N concentrations and shift interference relationships is further investigated.

Key words: spotted knapweed, bluebunch wheatgrass, Centaurea maculosa, Pseudoroegneria spicata, *succession, competition, carbon amendment, soil impoverishment.*

Ecologists and land managers have attempted to explain mechanistically plant community dynamics to predict their outcome and make more informed management decisions (Connell and Slatyer 1977, Huston 1979, Tilman 1982, Pickett et al. 1987, Davis et al. 2000). Most theories of plant community dynamics focus on ecological processes, such as competition (Tilman 1982) or disturbance (Davis et al. 2000). One emerging phenomenon has caused reconsideration of plant community dynamics. Range- and wildlands are being invaded by nonindigenous plants, resulting in an unprecedented, rapid change in plant community composition across the United States. Invasive plants infest over 40 million hectares in the United States (NISC 2001) and continue to spread at an estimated 14% per year (Westbrooks 1998). The organization, structure, and function of plant communities may be altered when invasive plants dominate (Lacey et al. 1989, Whisenant 1990, D'Antonio and Vitousek 1992, Gerlach and Rice 1996, Olson 1999, LeJeune and Seastedt 2001).

Successional management has been applied theoretically to management of natural resources, including invasive plant–dominated rangelands (Pickett et al. 1987, Luken 1990, Sheley et al. 1996, 2006, Sheley and Rinella 2001, Bard et al. 2003, Krueger-Mangold et al. 2006b). Successional management of invasive plant–dominated rangeland focuses on controlling site availability, species availability, and species performance by using current technology to modify the ecological processes associated with these factors to shift undesirable, weed-infested plant communities toward domination by desired species. We were interested in the potential of controlling species performance through modifying interference between desired species and an invasive plant.

Species performance may be modified by soil nutrient availability. Evidence suggests high nutrient availability, especially nitrogen (N), increases the performance of nonindigenous, invasive species relative to indigenous species (Huenneke et al. 1990, McLendon and Redente 1991, Milchunas and Lauenroth 1995,

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Burke and Grime 1996, Maron and Connors 1996, Kolb et al. 2002, Blumenthal et al. 2003). For example, McLendon and Redente (1991) found that the invasive annual grass cheatgrass (*Bromus tectorum* L.) remained dominant when they applied N to a shrub-steppe community in Colorado. Similarly, Story et al. (1989) found that applications of N fertilizer increased biomass of spotted knapweed (*Centaurea maculosa* Lam.) more than that of competing grasses in western Montana.

Carbon may be applied to reduce N availability and alter the performance of invasive species during restoration projects (Morgan 1994, Alpert and Maron 2000, Paschke et al. 2000, Blumenthal 2003, Svejcar 2003). Carbon addition increases soil microbial biomass, and N is immobilized by the microbial community, creating a temporary depletion of plant-available N and soil N concentrations more indicative of late successional stages (Redente et al. 1992, Morgan 1994). To date, studies testing the effectiveness of carbon additions as a management tool for nonindigenous species have produced mixed conclusions (Seastedt et al. 1996, Hopkins 1998, Reever Morghan and Seastedt 1999, Alpert and Maron 2000, Lowe et al. 2002, Blumenthal 2003, Brockington 2003).

Addition series interference studies have been used increasingly in weed-infested range and wildland systems to quantify interference between desired vegetation and invasive plants (Sheley and Larson 1995, Jacobs et al. 1996, Velagala et al. 1997, Radosevich et al. 1997, Young and Mangold 2008). We conducted a study that quantified interference between bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh) and spotted knapweed when treated with carbon and N amendments. An earlier study suggested that for spotted knapweed to maintain its biomass, it required a soil nitrate (NO_3^-) concentration 10 times greater than what bluebunch wheatgrass required, indicating that its performance should be decreased relative to bluebunch wheatgrass as soil NO_3^- decreases (Krueger-Mangold et al. 2006a). Based on those results, we hypothesized that spotted knapweed would increase its biomass and interference ability relative to bluebunch wheatgrass with increasing soil NO_3^- and ammonium (NH_4^+) concentration (i.e., with N amendment). We hypothesized that bluebunch wheatgrass would increase its interference ability relative to spotted knapweed with decreasing soil NO_3^- and NH_4^+ concentration (i.e., with sucrose amendment).

STUDY SITES

The study was conducted on 2 sites in western Montana characterized as an Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass habitat type (Mueggler and Stewart 1980). Site 1 is at Red Bluff Research Ranch about 2 km east of Norris, Montana (45°35′N, 111°39′W; hereafter referred to as Red Bluff). Elevation is 1505 m, and annual precipitation is 305 mm. Soils are a fine-loamy, mixed, frigid Calcidic Argiustoll. Site 2 is in Story Hills about 5 km northeast of Bozeman, Montana (45°36′N, 111°34′W; hereafter referred to as Story Hills). Elevation at Story Hills is 1478 m, with 432 mm annual precipitation. Soils are a clayey-skeletal, mixed Typic Argiboroll.

METHODS

Experimental Design

Sites were plowed to a 15-cm depth with a moldboard plow and lightly tilled on 15 September (Red Bluff) and 16 September (Story Hills) 2000. We applied glyphosate [N-(phosphonomethyl)glycine] at 2.3 kg a.i. $\cdot$ ha^{-1} on 24 October 2000 to kill vegetation that germinated or resprouted following plowing and tilling. Rocks were removed by hand raking. Dead plant material was also removed to minimize the potential for N leaching in the soil.

We arranged monocultures and mixtures of bluebunch wheatgrass and spotted knapweed in an addition series matrix (Spitters 1983). Annual sunflower (*Helianthus annuus* L.) was initially included as a 3rd species, but it did not persist throughout the duration of the study and was therefore not included in the analysis. Four densities of each species were factorially arranged in combinations of 0, 1000, 2000, and 4000 seeds $\cdot$ m^{-2} for a total of 64 whole plots in each replication. In October 2000 we hand-broadcasted seeds of each species on 1.5 × 1.5-m plots. Density combinations were established in a randomized complete-block design and replicated 3 times at each site for a total of 192 experimental whole plots at each site. Plants were allowed to grow for 2 years prior to sucrose and N

TABLE 1. Treatment application dates in 2003 for Red Bluff and Story Hills.

Treatment	Red Bluff	Story Hills
Sucrose and N	27 April	28 April
Sucrose	12 May	14 May
Sucrose and N	27 May	28 May
Sucrose	09 June	12 June
Sucrose and N	25 June	26 June

amendments. During 2001 and 2002, 2% glyphosate solution was wiped onto nonseeded species in an attempt to maintain desired combinations.

In April 2003 we divided each whole plot in the addition series matrix into 3 subplots. Nitrogen was applied to a randomly chosen subplot in each whole plot (N amended). Sucrose was applied to a 2nd subplot in each plot (sucrose amended). The remaining subplot of each plot was not amended and considered a control (control). The N amendment consisted of 112 kg N · ha^{-1} applied as granular ammonium nitrate (NH_4NO_3) in 3 increments every 30 days (Table 1). Sucrose was applied approximately every 14 days at 100 g C · m^{-2} (Table 2), based upon data provided by Brockington (2003). We hand-broadcasted both chemicals on the soil surface of each subplot.

Sampling

We sampled plant density and biomass of bluebunch wheatgrass and spotted knapweed in mid-July 2003. Density of plants and grass tillers was determined by counting the number of plants or grass tillers in a 30-cm × 130-cm frame placed randomly on the ground within each subplot. Biomass was determined by clipping and separating species within the frame used for counting density. Clipped samples were dried at 60°C for 48 hours and weighed.

Concurrent with plant sampling, we collected three 2-cm-wide soil cores from within the area where plants were sampled to a depth of 12–15 cm from each subplot. We composited subsamples for inorganic nitrogen analyses. Soil samples were dried at 42°C and sieved through a 2-mm screen prior to chemical analyses. Inorganic soil nitrogen (NO_3^- and NH_4^+) was determined on 1 M KCl extracts from soil (5 g soil:50 mL extractant). Aliquots of filtered extracts were analyzed for NO_3^- and NH_4^+ using Cd reduction and salicylate colorimetric methods, respectively (Mulvaney 1996).

At Red Bluff we sampled all 3 replications. At Story Hills we sampled 2 replications and left the 3rd replication undisturbed for future sampling and quantification of long-term community dynamics.

Statistical Analysis

REGRESSION ANALYSIS.—Multiple linear regression models were fit using densities of bluebunch wheatgrass and spotted knapweed as the independent variable and biomass of bluebunch wheatgrass or spotted knapweed as the dependent variable (Spitters 1983). Density and biomass of bluebunch wheatgrass and spotted knapweed from those plots that initially contained annual sunflower were included in the models of the following form:

bluebunch wheatgrass:
$$y_b = \beta_{b0} + \beta_{bb}N_b + \beta_{bs}N_s$$
spotted knapweed: $y_s = \beta_{s0} + \beta_{ss}N_s + \beta_{sb}N_b$,

where y_b is bluebunch wheatgrass mean biomass per plant, y_s is spotted knapweed mean biomass per plant, N_b is bluebunch wheatgrass density, N_s is spotted knapweed density, and β_{b0}, β_{s0}, β_{bb}, β_{ss}, β_{bs}, β_{sb} are regression coefficients. The regression coefficients are interpreted as β_{b0} and β_{s0} = biomass of an individual bluebunch wheatgrass or spotted knapweed plant grown in isolation, β_{bb} and β_{ss} = intensity of intraspecific interference, and β_{bs} and β_{sb} = intensity of interspecific interference. Data from each treatment were fit to the model to generate regression coefficients for each treatment at both sites (SAS Institute Inc. 1990). Models for each treatment from Red Bluff included 192 observations (64 × 3 replications) while those from Story Hills included 128 observations (64 × 2 replications).

Slopes of the regressions were compared between treatments by calculating variance ratios using the equation

$$\text{Variance ratio}_i = [(RSS_i - RSS_1) / (df_i - df_1)] / (RSS_1 / df_1) ,$$

where RSS_i is the residual sums of squares from pooling data from the 2 treatments being compared, RSS_1 is the residual sums of squares of 1 treatment plus the residual sums of squares of the other treatment, df_i is the error degrees

TABLE 2. Regression analysis for the prediction of bluebunch wheatgrass biomass (mg · tiller^{-1}) at Story Hills[a]. β_{b0} = mean biomass of an individual bluebunch wheatgrass tiller grown in isolation, β_{bb} = effect of bluebunch wheatgrass density on bluebunch wheatgrass biomass per tiller, β_{bs} = effect of spotted knapweed density on bluebunch wheatgrass biomass per tiller. Numbers in parentheses are standard errors for coefficients that were significantly different from zero ($P = 0.05$); NS = not significant.

Treatment	β_{b0}	β_{bb}	β_{bs}	β_{bb}/β_{bs}	r^2
Control	7.0 (10.0)	0.04 (0.01)	–0.09 (0.04)	0.44	0.27
Nitrogen	9.0 (10.0)	0.01 (NS)	–0.19 (0.06)	5.0×10^{-4}	0.16
Sucrose	8.0 (10.0)	0.02 (NS)	–0.08 (0.04)	1.3×10^{-3}	0.07

[a] Comparison of slopes: $F = 1.31$ (control vs. N), 0.63 (control vs. sucrose), 0.70 (N vs. sucrose); critical $F_{(0.05,\,5,\,137)} \geq 2.21$ for rejecting the null hypothesis.

of freedom from the pooled treatments, and df_1 is the error degrees of freedom of 1 treatment plus the error degrees of freedom for the other treatment. A variance ratio larger than the critical $F_{(\alpha,\,\text{df numerator},\,\text{df denominator})}$ value rejects the null hypothesis that the slopes are the same (Ratkowski 1983).

The ratio of the intra- to interspecific interference coefficient was used to determine the relative influence of each species on the response variable. For example, if $\beta_{bb}/\beta_{bs} = 2$, then the density of bluebunch wheatgrass has twice as much influence on bluebunch wheatgrass biomass as spotted knapweed density has on bluebunch wheatgrass biomass. Zero was used for all nonsignificant coefficients and a constant of 0.0001 was used for ratio calculations (Roush 1988, Jacobs et al. 1996). The $[\beta_{bb}{:}\beta_{bs}/\beta_{ss}\beta_{sb}]$ double ratio was used to determine partitioning of resources between species (Spitters 1983). Deviations from unity (1.0) indicated increased resource partitioning (niche differentiation).

PLANT AVAILABLE SOIL N CONCENTRATION AND SPECIES BIOMASS.—We used a mixed model to determine the effects of site, replication, and soil amendment (control, nitrogen, and sucrose) on soil NO_3^- and NH_4^+ concentrations (SAS Institute, Inc. 2006). Soil amendment was treated as a fixed factor and site and replication were treated as random factors. We also analyzed bluebunch wheatgrass and spotted knapweed absolute biomass with PROC MIXED in a similar manner to soil inorganic N concentration. Each subplot within a replication was included as an observation for analysis, making a total of 576 at Red Bluff and 384 observations at Story Hills across soil amendment treatments. Soil NO_3^- was reciprocal transformed to normalize the data and homogenize variances. Nontransformed means are presented.

RESULTS

Regression Analysis

Regression analysis provided significant models for predicting bluebunch wheatgrass biomass per plant at Story Hills ($P < 0.01$ control, $P < 0.01$ N amended, $P = 0.03$ sucrose amended), but not at Red Bluff ($P = 0.07$ control, $P = 0.38$ N amended, $P = 0.49$ sucrose amended). Models for predicting spotted knapweed biomass per plant were significant for all treatments at both sites ($P < 0.01$).

Bluebunch wheatgrass density at Story Hills influenced its biomass in the control only, and the effect was positive (Table 2). Spotted knapweed density negatively influenced bluebunch wheatgrass biomass in the control and amended plots. Based upon this model, every increase of 10 spotted knapweed plants decreased bluebunch wheatgrass biomass per tiller by 1–2 mg. The adjusted r^2 for the models ranged from 0.07 to 0.27. Soil amendments had no effect on the slopes of the regressions.

Spotted knapweed biomass per plant was negatively influenced by spotted knapweed density in the control and with soil amendments at both sites (Table 3). The negative influence of spotted knapweed density on its biomass was nearly 10 times greater at Story Hills than at Red Bluff. At Red Bluff an increase of 1 spotted knapweed plant was associated with a 4–6-mg decrease in spotted knapweed biomass per plant across treatments. At Story Hills an increase of 1 spotted knapweed plant was associated with a 20–30 mg decrease in spotted knapweed biomass per plant across treatments. Bluebunch wheatgrass density influenced spotted knapweed biomass in the control and N-amended plots at Red Bluff, where an increase of 3 to 6 bluebunch wheatgrass tillers decreased spotted knapweed biomass by 1 mg. Adjusted r^2's for Red Bluff were 0.17–0.22 and 0.24–0.32 for Story Hills.

TABLE 3. Regression analysis for the prediction of spotted knapweed biomass (mg · plant^{-1}) at Red Bluff[a] and Story Hills[b]. β_{s0} = mean biomass of an individual spotted knapweed plant grown in isolation, β_{ss} = effect of spotted knapweed density on spotted knapweed biomass per plant, β_{sb} = effect of bluebunch wheatgrass density on spotted knapweed biomass per plant. Numbers in parentheses are standard errors for coefficients that were significantly different from zero ($P = 0.05$); NS = not significant.

Treatment	β_{s0}	β_{ss}	β_{sb}	β_{ss}/β_{sb}	r^2
Red Bluff					
Control	2880 (350)	–3.8 (1.0)	–5.7 (3.0)	0.67	0.17
Nitrogen	3560 (363)	–4.7 (1.0)	–3.3 (2.0)	1.42	0.22
Sucrose	3490 (393)	–5.8 (1.0)	–3.4 (NS)	5.8×10^4	0.18
Story Hills					
Control	8800 (788)	–17.7 (3.0)	–3.4 (NS)	1.8×10^5	0.32
Nitrogen	11900 (1179)	–31.4 (6.0)	–6.4 (NS)	3.1×10^5	0.24
Sucrose	8090 (802)	–16.9 (2.0)	–1.3 (NS)	1.7×10^5	0.24

[a] Comparison of slopes: $F = 1.46$ (control vs. N), 0.72 (control vs. sucrose), 0.79 (N vs. sucrose); critical $F_{(0.05, 3, 163)} \geq 2.60$ for rejecting null hypothesis.
[b] Comparison of slopes: $F = 2.00$ (control vs. N), 0.19 (control vs. sucrose), 2.54 (N vs. sucrose); critical $F_{(0.05, 3, 183)} \geq 2.60$ for rejecting null hypothesis, critical $F_{(0.10, 3, 183)} \geq 2.13$.

The slopes of the regressions were not affected by soil amendments at either site (Table 3). However at Story Hills the slope of the N- and sucrose-amended regressions differed at the $\alpha = 0.10$ level.

Ratios of interference coefficients clearly demonstrate that spotted knapweed density influenced spotted knapweed biomass more than bluebunch wheatgrass density influenced spotted knapweed biomass (Table 3). This influence was especially large at Story Hills, where the density of spotted knapweed was almost 200–300 times more influential than bluebunch wheatgrass density in determining spotted knapweed biomass per plant. The relative influence of spotted knapweed was greatest when N was added.

The $[\beta_{bb}{:}\beta_{bs}/\beta_{ss}\beta_{sb}]$ double ratio used to determine partitioning of resources between species was calculated at Story Hills where significant models were available for both species. Strong deviations from unity occurred in all treatments. Double ratios equaled 2.4×10^{-6}, 1.6×10^{-9}, and 7.6×10^{-10} for the control, N-amended, and sucrose-amended models, respectively, suggesting strong resource partitioning (i.e., niche partitioning) between bluebunch wheatgrass and spotted knapweed.

Absolute Biomass

Absolute biomass differed between sites ($P \leq 0.01$). Absolute biomass was lower at Red Bluff than at Story Hills. Spotted knapweed absolute biomass was 359.8 g · m^{-2} at Red Bluff and 487.2 g · m^{-2} at Story Hills. Bluebunch wheatgrass absolute biomass was 3.2 g · m^{-2} at Red Bluff and 27.1 g · m^{-2} at Story Hills.

Soil amendments affected absolute biomass of spotted knapweed at both sites ($P < 0.01$), but bluebunch wheatgrass absolute biomass remained unaffected ($P = 0.69$). Across sites the N treatment resulted in more spotted knapweed biomass than the sucrose-amended treatment and the control, which did not differ from one another. At Red Bluff spotted knapweed biomass was highest in the N-amended (441.1 g · m^{-2}) and lowest in the sucrose-amended (310.5 g · m^{-2}) and control (327.8 g · m^{-2}) plots. The N amendment at Story Hills resulted in spotted knapweed biomass of 577.6 g · m^{-2}, compared with 455.7 g · m^{-2} in the control and 428.3 g · m^{-2} in the sucrose-amended plots.

Soil NO_3^- and NH_4^+ Concentrations

Soil NO_3^- differed between sites ($P < 0.01$), while soil NH_4^+ concentrations were similar ($P = 0.22$). Averaged across all treatments, soil NO_3^- was lower at Red Bluff than at Story Hills. Nitrate concentration was 1.3 ± 0.4 mg · kg^{-1} at Red Bluff and 2.3 ± 0.4 mg · kg^{-1} at Story Hills. Ammonium concentration was 2.9 ± 0.5 mg · kg^{-1} at Red Bluff and 4.1 ± 0.6 mg · kg^{-1} at Story Hills.

Soil NO_3^- ($P < 0.01$) and NH_4^+ ($P < 0.01$) concentrations were affected by amendments at both sites. At Red Bluff the N amendment increased NO_3^- concentration from 0.04 mg · kg^{-1} in the control to 3.82 mg · kg^{-1}. The sucrose amendment resulted in an NO_3^- concentration of 0.03 mg · kg^{-1}, which was lower than the N amendment but similar to the control. At Story Hills the highest NO_3^- concentration was found in the N-amended plots (6.57

$mg \cdot kg^{-1}$), followed by the control ($0.23\ mg \cdot kg^{-1}$), followed by the sucrose-amended plots ($0.11\ mg \cdot kg^{-1}$). Averaged across both sites, the N amendment increased NH_4^+ concentration to $8.22\ mg \cdot kg^{-1}$ compared with the control at $1.16\ mg \cdot kg^{-1}$. The sucrose amendment ($1.15\ mg \cdot kg^{-1}$) had no effect on NH_4^+ concentration compared with the control.

DISCUSSION

Sucrose and N amendments did not influence plant performance as strongly as we hypothesized they would. Amending the soil with N tended toward favoring the performance of spotted knapweed at Story Hills relative to bluebunch wheatgrass, and consistently increased spotted knapweed absolute biomass as hypothesized. Our results for spotted knapweed are supported by other studies where high N availability was found to facilitate invasion by nonindigenous, weedy species (Story et al. 1989, Huenneke et al. 1990, Maron and Connors 1996, Alpert and Maron 2000, Blumenthal et al. 2003). However, spotted knapweed performance did not decrease when N availability was decreased by the sucrose treatment at Story Hills. This result lends support to the suggestion that spotted knapweed's success may be explained by its genetic variation and plasticity in N requirements; it appears to colonize disturbed sites by rapidly acquiring surplus N, and yet compete with late successional species for limited N on undisturbed sites (Blicker et al. 2002).

In contrast to spotted knapweed, bluebunch wheatgrass performance was not affected by soil amendments. Even at Story Hills where the sucrose amendment decreased soil NO_3^- concentration below that of the control, bluebunch wheatgrass performance was not increased relative to the performance of spotted knapweed. Late successional, native species have displayed various responses to N availability. In some cases the application of N fertilizer increased late successional, native grass biomass (Owensby et al. 1972, Krueger-Mangold et al. 2004). Other studies have found an increase in late successional, native grass biomass when N availability is decreased (Paschke et al. 2000, Ewing 2002, Blumenthal et al. 2003). Nitrogen availability has also been found to have no effect on late successional, native grass biomass (Morgan 1994, Alpert and Maron 2000). Differences in response may be due to the timing or level of N addition, species composition and life form, and past and current management (Huberty et al. 1998).

In this study soil N concentration was very low. Late successional, native species accustomed to low nutrient environments often show a limited response to fluctuations in soil nutrients as a consequence of adaptations which promote conservative nutrient use, loss, and uptake (Chapin 1991, Chapin et al. 1993). In an earlier study we found that bluebunch wheatgrass maintained its biomass even when soil NO_3^- concentration was less than 0.05 ppm (Krueger-Mangold et al. 2006a). In this study NO_3^- concentrations were well above 0.05 ppm even when sucrose was added. Therefore, soil NO_3^- concentration may not have been low enough to promote the dominance of bluebunch wheatgrass over that of spotted knapweed as we hypothesized it would. The failure of the sucrose treatment to significantly lower soil NO_3^- concentration calls into question the applicability of carbon additions in low-nutrient, arid, and semiarid systems as a means to enhance the performance of native plants relative to invasive weeds.

The importance of interference relative to other processes that may influence dynamics between bluebunch wheatgrass and spotted knapweed, as indicated by r^2 (Weldon and Slauson 1986), was low in this study, typically accounting for less than one-third of the variation. Spotted knapweed and bluebunch wheatgrass appeared to coexist with little interference because their niches may not have overlapped to a very large degree. This is further supported by results which suggest that intraspecific interference was more intense than interspecific interference when predicting spotted knapweed biomass. This is similar to results of Jacobs and Sheley (1999), who found that intraspecific competition was more important in determining spotted knapweed shoot weight than interspecific competition. Also, Lindquist et al. (1996) found that bluebunch wheatgrass had no effect on spotted knapweed growth when the two species were grown together.

We believe that abiotic factors influencing establishment, such as disturbance created by tilling and droughty conditions (precipitation was 70%, 52%, and 84% of 40-year average during 2001–2003, respectively; WRCC 2007) during the study, may have been more important than interference. Because spotted knapweed possesses traits typical of colonizing species, such as high seed production and rapid growth rate (Bazzaz 1986), it may have been favored by establishment conditions more so than bluebunch wheatgrass. Spotted knapweed may possess traits that allow it to colonize and persist even in the presence of late-seral species. For example, Blicker et al. (2002) found that spotted knapweed was capable of exploiting readily available resources following a disturbance in addition to being tolerant of low nutrient conditions. Some invaders, including spotted knapweed, exhibit a large degree of physiological plasticity which may provide some explanation of their success.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our results suggest that spotted knapweed may capitalize on increases in N availability more so than the native, late-seral species bluebunch wheatgrass. Results concerning interference dynamics when soil N concentration is decreased are less clear. If soil N concentration could have been lowered even further through either increased quantities of sucrose additions or more frequent sucrose applications, bluebunch wheatgrass may have increased in dominance. Other studies suggest that the effectiveness of carbon additions and the amount of carbon necessary to decrease soil N availability vary (Morgan 1994, Wilson and Gerry 1995, Reever Morghan and Seastedt 1999, Alpert and Maron 2000, Blumenthal et al. 2003, Brockington 2003). However, inorganic soil N concentrations were already extremely low, and lowering them even further is a question of practicality. Further research on the effectiveness of carbon amendments is necessary. Efforts should focus on identifying practical sources of carbon, determining appropriate quantities and frequencies of application, longevity of effectiveness, and amount of labor involved in application (Reever Morghan and Seastedt 1999). In addition to carbon amendments, other methods of decreasing soil N concentration, such as seeding cover crops and plant litter management, should be further investigated.

Although successional management predicts that altering resource availability may be a way to influence species performance, this study suggests this may not be as straightforward as predicted. Adding N enhanced the performance of spotted knapweed, consistent with the findings of others (Story et al. 1989, Herron et al. 2001). However, decreasing soil N availability proved difficult and even when it was lowered, spotted knapweed performance was not decreased and bluebunch wheatgrass performance was not increased. In areas currently infested with spotted knapweed, we suggest that land managers prevent activities that increase plant available N, such as direct fertilization, burning, and cultivation. During restoration of weed-infested lands, seeding a cover crop along with desirable species that will sequester N released by disturbance may facilitate establishment of late successional, desirable species (Herron et al. 2001).

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