Creating Weed-Resistant Plant Communities Using Niche-Differentiated Nonnative Species

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Abstract

Enhancing desired species establishment and persistence is central to rehabilitating invasive plant–infested rangeland. We hypothesized that nonnative desired species (alfalfa [*Medicago sativa* L., var. Arrow], intermediate wheatgrass [*Thinopyrum intermedium* {Host} Barkworth & D.R. Dewey], and crested wheatgrass [*Agropyron cristatum* {L.} Gaertn., var. Hycrest]) increase as desired species richness within seeding mixture increases, and spotted knapweed (*Centaurea maculosa* Lam.) decrease as desirable species richness increases. We simultaneously tested the degree of niche differentiation among desired species. Experiments consisted of 7 seeding monocultures and combinations. Treatments were monocultures of each desired species (3 plots), all combinations of 2 desirable species (2 250 seeds $\cdot$ m^{-2} per species; 3 plots), and 1 plot containing all 3 desirable species (1 500 seeds $\cdot$ m^{-2} per species). Monocultures or mixtures were replicated 4 times by seeding each treatment with four background densities of spotted knapweed (1 250, 2 500, 3 750, and 7 500 seeds $\cdot$ m^{-2}; 7 treatments $\times$ 4 background densities = 28 plots). Analysis included regression with the 7 desired species monocultures or mixtures as a fixed effect and spotted knapweed sowing density as a continuous effect. All desired species established had either low or no negative influence on their neighbor, and differed in niche after 7 years of growing in association. Increasing richness of desired species led to increased productivity. Spotted knapweed density and biomass were low across all monocultures and mixtures at the productive site because shade and litter of desired species reduced light availability to the rosette-forming invasive weed. Combining crested wheatgrass and alfalfa provided lower spotted knapweed density and biomass more than did monocultures or grass mixtures because these 2 species appeared to occupy complementary niches. Increased niche occupation by nonnative desirable species may increase resource use and productivity, thus minimizing establishment and dominance of unwanted invasive plants during rehabilitation on arid, marginally productive rangeland sites.

Resumen

Aumentar el establecimiento y persistencia de especies deseables es un punto central para rehabilitar pastizales infestados con plantas invasoras. Hipotetizamos que especies deseables no nativas (“Alfalfa” [*Medicago sativa* L., var. Arrow], “Intermediate wheatgrass” [*Thinopyrum intermedium* {Host} Barkworth & D.R. Dewey] y “Crested wheatgrass” [*Agropyron cristatum* {L.} Gaertn., var. Hycrest]) aumentan conforme la riqueza de especies deseables aumenta dentro de una siembra de mezcla de especies y el “Spotted knapweed”(*Centaurea maculosa* Lam.) disminuye al aumentar la riqueza de especies deseables. Simultáneamente probamos el grado de diferenciación del nicho entre las especies deseables. Los experimentos consistieron en sembrar siete monocultivos y combinaciones. Los tratamientos fueron monocultivos de cada especie (3 parcelas), todas las combinaciones de dos especies deseables (2 250 semillas $\cdot$ m^{-2} por especie; 3 parcelas), y una parcela conteniendo las tres especies deseables (1 500 semillas $\cdot$ m^{-2} por especie). Los monocultivos y las mezclas fueron repetidos cuatro veces sembrando cada tratamiento con cuatro densidades base de “Spotted knapweed”(1 250, 2 500, 3 750 y 7 500 semillas $\cdot$ m^{-2}; 7 tratamientos $\times$ 4 densidades base = 28 parcelas). Los análisis estadísticos incluyeron regresiones con los 7 monocultivos de especies deseables o mezclas como efecto fijo y la densidad de siembra del “Spotted knapweed” como un efecto continuo. Todas las especies deseables establecidas tuvieron poca, o no tuvieron, influencia negativa con sus vecinos y difirieron en el nicho después de siete años de crecer en asociación. Aumentando la riqueza de especies deseables, aumentó la productividad. En el sitio productivo, la densidad y biomasa de “Spotted knapweed” fue baja en todos los monocultivos y mezclas de ellos debido a que la sombra y mantillo de las especies deseables reducen la disponibilidad de luz para esta maleza invasora. La combinación de “Crested wheatgrass”y “Alfalfa” produjo la mas baja densidad y biomasa de “Spotted knapweed”, más que los monocultivos o las mezclas de zacates, porque estas dos especies parecen ocupar nichos complementarios. El aumento en la ocupación de nichos por especies no nativas deseables puede aumentar el uso de recursos y productividad, minimizando así el establecimiento y dominancia de especies invasoras no deseadas durante la rehabilitación de sitios de pastizal áridos o marginalmente productivos.

Key Words: species richness, niche occupation, invasion, spotted knapweed, intermediate wheatgrass, crested wheatgrass, alfalfa

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INTRODUCTION

Nonnative invasive plants threaten the diversity, function, and usefulness of rangelands throughout the western United States (Sheley and Petroff 1999). Invasive weeds dominate millions of hectares and continue to spread rapidly. Although controlling weeds is important, Sheley et al. (1996) proposed that a generalized objective for invasive plant management is to either establish or maintain (or both) a healthy plant community that is relatively weed-resistant while meeting other land-use objectives such as forage production, wildlife habitat, or recreational land maintenance. One impediment to achieving this objective is that highly degraded rangelands dominated by invasive weeds are often devoid of competitive desirable plants (Kedzie-Webb et al. 2001). On these sites, weed control is often short-lived because desirable species are not available to occupy niches opened by weed control procedures (Kedzie-Webb et al. 2002). Introducing and establishing desirable competitive plants is essential for successful management of invasive plants and the reestablishment of desirable plant communities (Bottoms and Whitson 1998; Laufenberg 2003).

Rehabilitating invasive plant-infested rangeland is costly, and managers are reluctant to attempt it because of the high likelihood of failure. A procedure that simultaneously applies herbicides and no-till drills seeds has been developed for spotted knapweed (*Centaurea maculosa* Lam.)–infested rangeland. In this procedure, a fall dormant seeding of various grass species is conducted simultaneously with an application of picloram (4-amino-3,5,6-trichloropicolinic acid) (0.28 kg/ha), a broadleaf herbicide (Jacobs et al. 1999). This single-entry procedure is less costly than multientry approaches, and pubescent wheatgrass (*Thinopyrum intermedium* [Host] Barkworth & D.R. Dewey), Russian wildrye (*Psathyrostachys juncea* [Fisch.] Nevski), and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Love) stands were well established in all years and at both sites tested (Sheley et al. 2001). Although establishing grass monocultures, mixtures, or both may be feasible using this system, it fails to address the structural and functional diversity needed for a healthy plant community because picloram prevents the establishment of forbs (Pokorny 2002; Denny 2003).

Species richness and diversity have been recognized as valuable indicators of ecosystem function (McNaugthton 1993; Vitousek and Hooper 1993). Processes such as nutrient and water cycling, as well as energy flow, are directly influenced by the structure and organization of ecosystems. For example, greater species richness and diversity increased the uptake of limited soil nitrogen (N) and decreased N leaching in Minnesota grasslands (Tilman et al. 1996), and experimental grasslands with the greatest species richness also had the greatest biomass (Spehn et al. 2000).

There is an ongoing debate about the relationship between species richness and weed invasion. Increasing evidence indicates that where desired species are complementary in niche, plant communities with high species richness and diversity may resist invasion more effectively than those with low species richness and diversity (Naeem and Li 1997; Tilman et al. 1997a). In a short-term study, Carpinelli (2000) found that as species richness and niche occupation increased, invasion by spotted knapweed decreased. However, no long-term study has attempted to measure the degree of niche-differentiation among species while simultaneously testing the relationship between richness and invasion. Pokorny (2002) found that forbs play a central role in minimizing invasion of *Festuca idahoensis/ Agropyron spicatum* plant communities by spotted knapweed. In that study, invasion increased where forbs were removed and resource use decreased.

Where rehabilitation of plant community function (e.g., N-cycling, H_2O cycling, energy flow), enhanced wildlife and livestock forage, and invasion resistance are primary land-use objectives, establishing and maintaining nonnative desirable species may be useful. These species can be easier to establish than natives (Sheley et al. 2001; Wirth and Pyke 2003) and very competitive once established (Borman et al. 1991; Bottoms and Whitson 1998). Nonnative species also are generally more available, less costly, and produce high quantities of forage for livestock and wildlife. In highly disturbed systems, nonnative species may be better adapted because the original site has been modified and does not resemble the environment of functional characteristics under which the native species evolved (Jones 2003). Thus, species with the highest genetic identity (native ecotypes) may not be ultimately successful, and higher order gene pools, such as those of nonnative species, may be substituted and successful because they possess aggressive traits allowing exploitation of newly available resources created by the disturbances.

Our overall objective was to determine the potential to establish and maintain a diverse plant community of desirable nonnative species in invasive plant–dominated rangeland where the seed bank consists of various amounts of weed seeds. In our short-term study, we hypothesized that as desirable species richness increases, weed establishment and growth decreases, provided that the desirable species differ in niche (Carpinelli et al. 2004). In that study, the desirable species were shown to differ in niche, although desirable species richness did not affect spotted knapweed recruitment 1 or 2 years after seeding. Those results suggested that revegetation of weed-infested rangeland must also include active control of weeds emerging from the soil seed bank.

In this long-term study, we tested the hypotheses that density and biomass of desired species increase as desired species richness within seeding mixture increases, and spotted knapweed density and biomass decrease as desirable species richness increases. We also tested for a trend in desired species density and biomass with respect to spotted knapweed sowing density, and whether differences in the density or biomass, or both, across the desired species monocultures or mixtures depends on the knapweed sowing density. Finally, we tested the hypotheses that as species richness increases, desirable plant biomass increases; and as desirable plant productivity increases, spotted knapweed density and biomass decrease.

METHODS

Study Sites

This study was conducted at the Arthur Post Research Farm and the Red Bluff Research Ranch in southwest Montana, from 1996 to 2002. The Arthur H. Post Research Farm (latitude 45°40′N, longitude 111°09′W; herein referred to as the Post

Farm) is located 6 km west of Bozeman, Montana and is considered the more productive site. Elevation at the Post Farm is 1 463 m, and the long-term (59-year) mean annual precipitation is 457 mm. During the study period, mean annual temperatures and mean annual precipitation ranged from 5.68° to 7.89°C and 238 to 537 mm, respectively, at the Post Farm (Fig. 1). The Post Farm soil is an Amsterdam silty loam (fine-silty, mixed, frigid Typic Haplustoll). Red Bluff Research Ranch (latitude 45°34′N, longitude 111°40′W; herein referred to as Red Bluff) is located 40 km west of Bozeman, Montana, and is considered the least productive site. Elevation at Red Bluff is 1 505 m, and mean annual precipitation is 305 (59-year) mm. The Red Bluff soil is a Varney clay loam (fine-loamy, mixed, frigid Calcidic Argiustoll). Mean annual temperatures and mean annual precipitation ranged from 7.94° to 9.44°C and 286 to 602 mm, respectively, during the study at Red Bluff (Fig. 1).

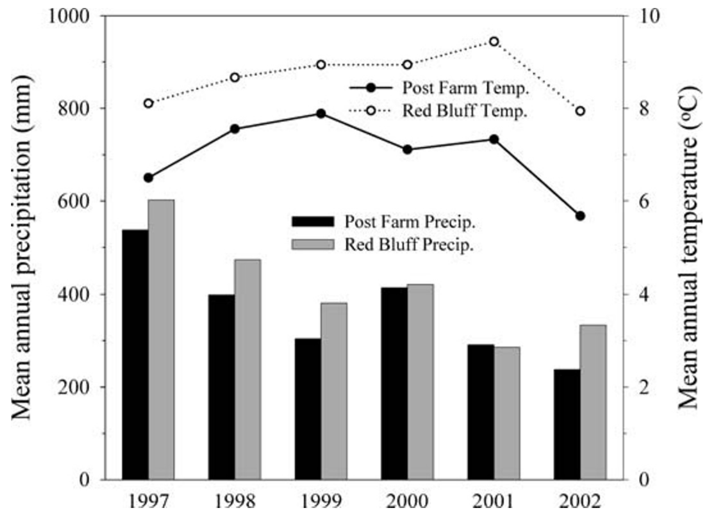

Figure 1. Mean annual temperature and total annual precipitation for the Post Farm and Red Bluff.

Plant Materials

The 3 nonnative desirable species used in this study were crested wheatgrass (*Agropyron cristatum* [L.] Gaertn., var. Hycrest), intermediate wheatgrass (*Thinopyrum intermedium* [Host] Barkworth & D. R. Dewey), and alfalfa (*Medicago sativa* L.). Crested wheatgrass is an early emerging, cool-season bunchgrass. Intermediate wheatgrass is a cool-season, sod-forming grass that matures later than crested wheatgrass (Asay and Jensen 1996). Alfalfa is a deeply taprooted broadleaf with a comparatively long growing period. These 3 introduced perennials are commonly used in revegetation throughout the western United States in areas where the management goal is rehabilitation and forage production. They were chosen because of their differing growth habits, potentially allowing them to collectively occupy multiple niches when used together in a revegetation seed mix (Holzworth and Lacey 1991). Seeds of these species were obtained from the Bridger Plant Materials Center, Bridger, Montana. Spotted knapweed, a deeply taprooted Eurasian perennial forb, was used because of its ecological significance and wide distribution. Spotted knapweed seeds were collected from Deer Lodge County, Montana, in August 1995. Although this model system has very few species, based on studies by Tilman et al. (1997b, 1998), very few species may account for a majority of the response.

Experimental Design

The experiment consisted of monocultures of each desired species (4 500 total seed$\cdot$m^{-2}; 3 plots), all combinations of 2 desirable species (2 250 seeds$\cdot$m^{-2} per species; 3 plots), and 1 plot containing all 3 desirable species (1 500 seeds$\cdot$m^{-2} per species). Each monoculture and mixtures were replicated 4 times at each site by seeding each density combination with 4 background densities of spotted knapweed (1 250, 2 500, 3 750, and 7 500 seeds$\cdot$m^{-2}; 7 treatments $\times$ 4 background densities = 28 plots) as blocks. Desired species and spotted knapweed were seeded simultaneously. Plot locations were completely randomized.

Procedures

All plots (2 $\times$ 2 m) were tilled to a depth of 10 cm within 2 weeks prior to sowing to remove existing vegetation and prepare the seedbed. Sowing occurred on 24–25 June 1996 at Red Bluff, and on 28–29 June 1996 at the Post Farm. Seeds were carefully hand-sown to achieve uniform distribution. Plots were then covered with nylon-mesh backed straw-mulch (North American Green®, Billings, Montana). Because the study was initiated in late spring, plots were watered daily from 29 June to 29 July 1996 to facilitate germination and establishment. On 15 July 1996, when plants averaged approximately 5 cm tall, the mulch was removed from all plots. Species emerging that were not an intended portion of the study were removed by hand twice monthly throughout the growing period.

Sampling

Sampling was conducted between 11 September and 22 September 1997 and 2002. At the time of sampling, average height across all species was about 1 m and 0.5 m at the Post Farm and Red Bluff, respectively. In 1997, a 510-cm^2 circular frame was placed in the center of a randomly selected quadrant in each plot. In 2002, a 20 $\times$ 50-cm frame was placed in center of a randomly selected, previously nonsampled quadrant. The smaller quadrant was used in subsequent years to maintain maximum nonclipped area for future sampling events. In both years, density (stems$\cdot$m^{-2}) of each species was recorded, and all aboveground biomass was clipped, separated by species, dried (168 hours, 60°C), and weighed.

Data Analysis

Data were analyzed by site and year because of a general lack of homogeneity of variances among these factors. Various transformations were tested in an attempt to improve data normality and model fit. The inverse of weight was used as the dependent variable in most competition analyses because this transformation increased linearity of the data. Best fitting models were generated using nontransformed data for all other analyses.

Niche Differentiation. Niche differentiation between desirable species was quantified using their relative competitive coefficients derived from density and biomass data from the multiple replacement series plots (Spitters 1983). For each combination of site and year, a model using 3 regressions was used; one for each desirable species (response) being predicted by all 3 desirable species. The predictor variable was sown density or measured density, and the response variable was the average shoot weight per plant or its inverse. Model preference was given to that which provided the highest cumulative R^2 from its 3 individual regressions. The regressions were of the general form:

$$y_i = \beta_{0i} + \beta_{ii}N_i + \cdots + \beta_{ij}N_j \quad [1]$$

where y_i is the response (average weight of an individual or its inverse) of species i, β_{0i} is the y-intercept (interpreted as the weight of an isolated individual), $\beta_{ii}N_i$ is the product of the coefficient of intraspecific competition of species i (β_{ii}) and its density (N_i), and $\beta_{ij}N_j$ is the product of the coefficient of interspecific competition of species j on species i (β_{ij}) and the density of species j (N_j). Where the response is the inverse of the average weight per plant, a positive sign denotes negative interference, and a negative sign denotes positive interference.

The relative competitive ability of each species is calculated as:

$$RC_i = \beta_{ii}/\beta_{ij} \quad \text{and} \quad RC_j = \beta_{jj}/\beta_{ji} \quad [2]$$

where RC_i is the relative competitive ability of species i and j on species i (Spitters 1983). Niche differentiation is calculated from the relative competitive abilities of each species:

$$ND = (\beta_{ii}/\beta_{ij})/(\beta_{ji}/\beta_{jj}) = RC_i \cdot RC_j = (\beta_{ii}/\beta_{ij}) \cdot (\beta_{jj}/\beta_{ji}) \quad [3]$$

where ND = niche differentiation. Niche differentiation increases as ND departs from unity; that is, species i and j are decreasingly limited by the same resources (Spitters 1983). Complete niche differentiation is indicated where regression (competition) coefficients are nonsignificant because there is no interaction between species.

Density and Biomass. Data were analyzed using regression with the 7 desired species monocultures or mixtures as a fixed effect and spotted knapweed sowing density as a continuous effect. Initially, an expanded model was used. In these expanded models, the response of spotted knapweed to desired species monocultures and mixtures was tested with 6 degrees of freedom, the trend in response to spotted knapweed sowing density was tested with a single degree of freedom, and the test to determine whether differences in the response across desired species monocultures or mixture depend on knapweed sowing density was allocated 6 degrees of freedom. There were 14 degrees of freedom in the error term. The effects of desired species monocultures or mixtures on their own density and biomass were tested by excluding plots where the desired species in the response variable was not included in the species sown. This was required to normalize the data. In these cases, the response of desired species to desired species monocultures or mixtures and the interaction term were tested with 3 degrees of freedom. In cases where the expanded model indicated that the desired species monoculture or mixture did not interact with knapweed sowing density, a reduced model was used to test the main effects. In these cases, the interaction was included in the error term. All models assume that the trends across spotted knapweed sowing density were linear for all desired species monocultures and mixtures. Scatter plots indicated that linear models were appropriate descriptions of the relationships. Tests also indicated homogeneity of variances among desired species monocultures and mixtures across levels of spotted knapweed sowing density. Where treatment effects were not detected with either model, the expanded model with means averaged across all treatments are presented to provide a comprehensive description of the data. Where the fixed effect was significant, reduced models and means are presented. Species not included in the seeding mixture were not included in the analysis. Means were separated using Fisher's Protected LSD test at $\alpha = 0.05$ level of significance (Peterson 1985). If the continuous variable or the interaction including the continuous variable was significant, regressions were presented in the text.

Richness/Productivity and Spotted Knapweed. Linear regression was used to quantify the relationships between desirable species richness and spotted knapweed density and biomass, the relationship between desired species richness and total desired species productivity, and the relationship between total desired species productivity and spotted knapweed. Interpreting these regressions should be performed with caution because the x-axis has only 3 independent variables along the regression plane.

RESULTS

Niche Differentiation

The desirable species differed in niche at both sites in both years. The only exception was that there appeared to be niche overlap (ND = 0.90) between intermediate wheatgrass and crested wheatgrass during establishment (1997) at Red Bluff.

Nonnative Desired Species

Post Farm. In both years, spotted knapweed sowing density did not influence desired species density or biomass at the Post Farm (Table 1). Intermediate wheatgrass density was about 3 times greater where sown as a monoculture than where sown in a 2-species mixture, and 10 times greater than where sown in a 3-species mixture (Fig. 2). Desired species sowing-treatments did not influence density or biomass of crested wheatgrass or alfalfa in either year at this site. In 1997, intermediate wheatgrass produced an average biomass of 139 $g \cdot m^{-2}$ across all treatments at this site. Crested wheatgrass produced 353 $tillers \cdot m^{-2}$ and 105 $g \cdot m^{-2}$, while alfalfa produced 204 $plants \cdot m^{-2}$ and 120 $g \cdot m^{-2}$ across all plots at this site in 1997. In 2002, intermediate wheatgrass and crested wheatgrass produced 189 and 12.5 $tillers \cdot m^{-2}$ and 277 and 54.7 $g \cdot m^{-2}$, respectively. Alfalfa produced 15.1 $plants \cdot m^{-2}$ and 145 $g \cdot m^{-2}$ across all plots at the Post Farm in 2002.

Red Bluff. In both years, spotted knapweed sowing density did not influence the density or biomass of intermediate wheatgrass or crested wheatgrass at the Red Bluff. Desired species composition affected the density and biomass of intermediate wheatgrass at this site in 1997 (Table 1). Intermediate wheatgrass produced about 789 tillers m^{-2} where grown as a monoculture, but the density was reduced to 29.5 and 0 where grown with crested wheatgrass or in the 3-species mixture, respectively (Fig. 3a). Sowing intermediate wheatgrass with alfalfa produced

Table 1. *P* values for the influence of desired species monocultures or mixtures, or both (D); spotted knapweed sowing density (K); and their interactions (D × K) on desired species density and biomass.[1]

Site	Treatment	df	1997 Intermediate wheatgrass Density (plants · m^{-2})	1997 Intermediate wheatgrass Biomass (g · m^{-2})	1997 Crested wheatgrass Density (plants · m^{-2})	1997 Crested wheatgrass Biomass (g · m^{-2})	1997 Alfalfa Density (plants · m^{-2})	1997 Alfalfa Biomass (g · m^{-2})	2002 Intermediate wheatgrass Density (plants · m^{-2})	2002 Intermediate wheatgrass Biomass (g · m^{-2})	2002 Crested wheatgrass Density (plants · m^{-2})	2002 Crested wheatgrass Biomass (g · m^{-2})	2002 Alfalfa Density (plants · m^{-2})	2002 Alfalfa Biomass (g · m^{-2})
Post Farm	D	3	0.031	0.087	0.166	0.286	0.180	0.412	0.199	0.445	0.768	0.245	0.807	0.842
	K	1	0.696	0.735	0.642	0.065	0.387	0.603	0.732	0.763	0.741	0.716	0.837	0.193
	D × K	3	0.514	0.065	0.124	0.107	0.135	0.352	0.282	0.672	0.996	0.650	0.937	0.474
	Mean		—[3]	139	353	105	205	120	189	277	12.5	54.7	15.1	145
	SE[2]			27.5	97.6	27.1	44.6	34.7	21.7	48.0	4.20	13.4	6.40	26.6
Red Bluff	D	3	0.002	0.012	0.434	0.256	0.008	0.399	0.145	0.059	0.751	0.441	0.063	0.982
	K	1	0.489	0.169	0.564	0.620	0.860	0.117	0.352	0.456	0.960	0.988	0.908	0.062
	D × K	3	—[4]	—[4]	0.668	0.473	0.013	0.611	0.396	0.235	0.935	0.970	0.040	0.218
	Mean		—[5]	—[6]	871	47.4	—	57.3	32.0	10.1	20.5	45.2	—	36.6
	SE[2]		—	—	144	13.1	—	11.5	20.1	6.20	5.10	9.80	—	4.16

[1]Means are averaged across treatments where all treatments were nonsignificant.
[2]SE indicates standard error.
[3]Data are presented in Figure 2.
[4]*P* values were generated from model including only main effects. The interaction was nonsignificant and included in the error term. Expanded models are shown where treatment effects were nonsignificant in all models.
[5]Data are presented in Figure 3a.
[6]Data are presented in Figure 3b.

about 330 intermediate wheatgrass tillers·m^{-2}. Intermediate wheatgrass biomass responded with a similar trend to that of density at this site in 1997 (Fig. 3b). In 1997, crested wheatgrass produced about 871 tillers·m^{-2} and 47.4 g·m^{-2} at this site across all treatments. Alfalfa yielded about 57.3 g·m^{-2} across all treatments at Red Bluff in 1997. In 2002, intermediate wheatgrass produced 32.0 plants·m^{-2} and 10.1 g·m^{-2} across all plots at this site. Crested wheatgrass produced 20.5 tillers m^{-2} and 45.2 g·m^{-2} at Red Bluff that year. Alfalfa yielded 34.6 g·m^{-2} across all plots at this site in 2002.

Spotted knapweed seeding density interacted with desired species treatments to influence alfalfa density at Red Bluff in both years (Table 1). Regression analysis indicated that the maximum predicted density of alfalfa was about 509 and 10 plants m^{-2} in 1997 and 2002, respectively. For each single seed increase in spotted knapweed sowing density, alfalfa density decreased by 0.230 (SE = 0.079) plants/m^{-2} in 1997 and increased by 0.005 (SE = 0.0017) plants/m^{-2} in 2002, where alfalfa was sown as a monoculture. Regressions predicting alfalfa density using spotted knapweed sowing density were nonsignificant for all desired species combinations that included alfalfa.

Total Desired Species Biomass

Neither spotted knapweed sowing density nor spotted knapweed sowing density × desired species interaction significantly influenced the total desired species biomass at either site during either year (Table 2). At Red Bluff in 2002, the total desired species biomass depended on the species sown. Intermediate wheatgrass and crested wheatgrass monocultures and the mixture of these 2 species yielded the lowest total desired species biomass (Fig. 4). Of the monocultures, alfalfa yielded the highest biomass. Mixtures of species including alfalfa yielded greater biomass than all monocultures and the 2-species grass mixture. At Red Bluff, crested wheatgrass combined with alfalfa yielded more than 100 g·m^{-2}, which was the highest biomass of any combination.

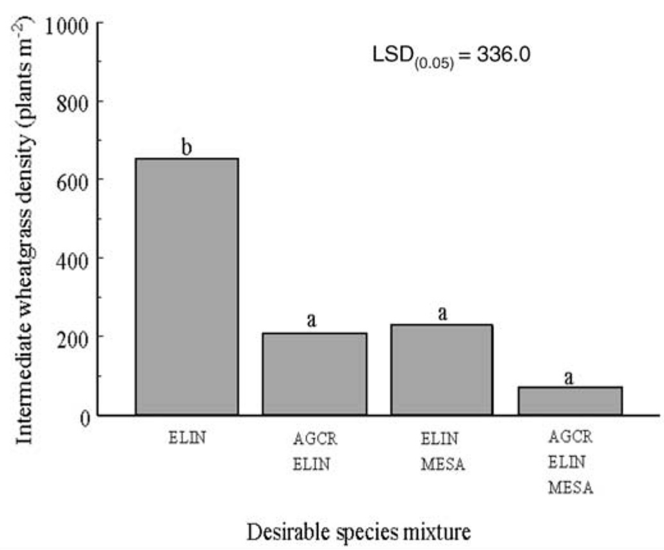

Figure 2. Effect of desired species monoculture and mixtures on intermediate wheatgrass density at the Post Farm in 1997. Analysis did not include treatments for which intermediate wheatgrass was not sown. ELIN indicates intermediate wheatgrass; AGCR, crested wheatgrass; and MESA, alfalfa.

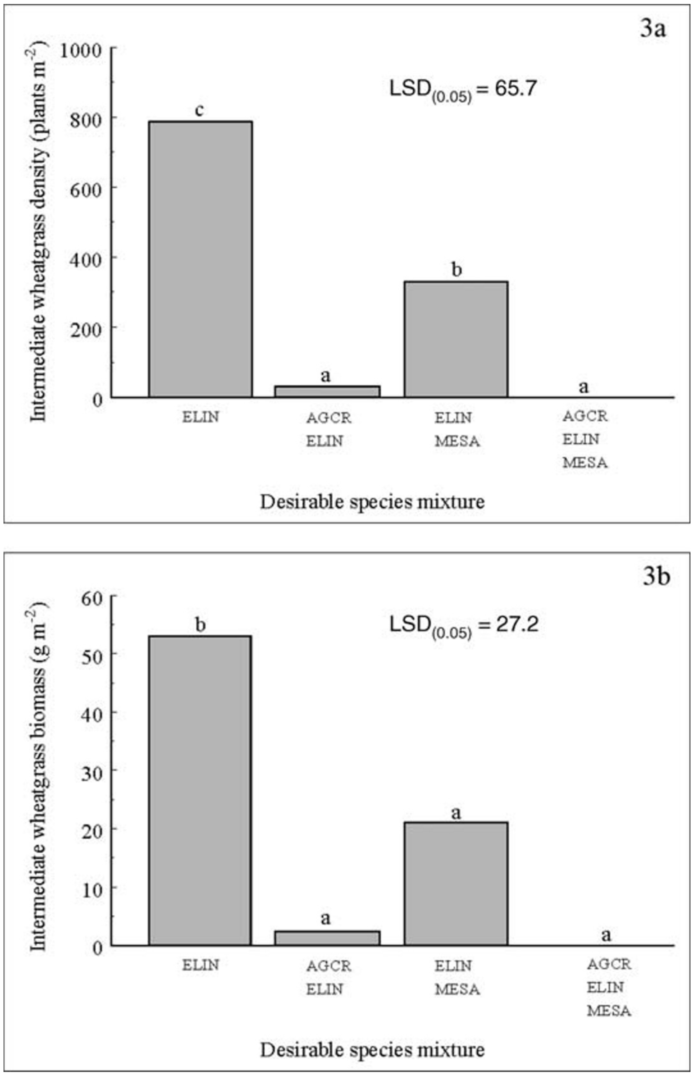

Figure 3. Effect of desired species monoculture and mixtures on intermediate wheatgrasss density **a,** and biomass **b,** at the Red Bluff in 1997. Analysis did not include treatments for which wheatgrass was not sown. ELIN indicates intermediate wheatgrass; AGCR, crested wheatgrass; and MESA, alfalfa.

Spotted Knapweed

Post Farm. Neither seeding mixtures, spotted knapweed sowing density, or their interaction influenced spotted knapweed density or biomass at the Post Farm in either year (Table 3).

Red Bluff. In 1997, the influence of desired species monocultures or mixtures on spotted knapweed density depended upon spotted knapweed sowing density (Table 3). Regression analysis indicated that the maximum predicted density of spotted knapweed was 1826 plants $\cdot$ m^{-2}. Where crested wheatgrass was sown alone, spotted knapweed density was decreased by 0.833 (SE = 0.214) plants $\cdot$ m^{-2} for each additional spotted knapweed sown. Where alfalfa was sown alone, each additional spotted knapweed sown reduced knapweed density by 0.775 (SE = 0.214) plants $\cdot$ m^{-2}. Spotted knapweed density was not associated with any other treatments or desired species combinations.

Table 2. *P* values and means for the effect of desired species monocultures or mixtures (or both) (D); spotted knapweed sowing density (K); and their interactions (D $\times$ K) on total biomass of desired species.[1]

		Post Farm		Red Bluff	
Treatment	df	1997	2002	1997	2002
D	6	0.254	0.605	0.530	<0.001
K	1	0.346	0.074	0.220	0.535
D $\times$ K	6	0.122	0.110	0.799	—[2]
Mean		208	1552	70.9	—[3]
SE[4]		29.5	1063	10.6	—

[1]Means are averaged across treatments where all treatments were nonsignificant.
[2]*P* values were generated from model including only main effects. The interaction was nonsignificant and included in the error term. Expanded models are shown where treatment effects were nonsignificant in all models.
[3]Data are presented in Figure 4.
[4]SE indicates standard error.

The reduced model indicated that the desired species affected spotted knapweed plant density at Red Bluff in 2002 (Fig. 5a). Mixtures including crested wheatgrass and alfalfa had the lowest spotted knapweed density at this site in 2002, but crested wheatgrass combined with alfalfa had similar spotted knapweed density as plots sown with intermediate wheatgrass and alfalfa. Intermediate wheatgrass sown alone produced the greatest spotted knapweed density. Plots with crested wheatgrass, alfalfa, or the combination of crested wheatgrass and intermediate wheatgrass averaged about 132 spotted knapweed plants $\cdot$ m^{-2}.

Desired species affected spotted knapweed plant biomass at Red Bluff in 2002 (Table 3). Combinations of crested wheatgrass with alfalfa and the 3-species mixture yielded lower spotted knapweed biomass than did the monocultures (Fig. 5b). Spotted knapweed biomass was similar among all monocultures at Red Bluff that year.

Species Richness

Regression analysis showed that as desired species richness increased, total desired species biomass increased at both sites in 2002 (Post Farm: $y = 146.8 + 109.7x$, $R^2 = 0.22$; Red Bluff: $y = -18.5 + 41.5x$, $R^2 = 0.33$). Using total desired species biomass to predict spotted knapweed biomass indicated that as total desired species biomass increased, spotted knapweed biomass decreased (Post Farm: $y = 99.5 - 0.20x$, $R^2 = 0.13$; Red Bluff: $y = 89.7 - 0.42x$, $R^2 = 0.32$).

DISCUSSION

The general supposition for using nonnative species is that they are often easier to establish and, in some cases, establish more quickly than native species (Holzworth and Lacey 1991), and once established, are very competitive with invasive weeds (Borman et al. 1991). In our study, the 3 nonnative species became well established, both as monocultures and mixtures. Our data indicate that increasing density of desired species either had little or no influence on desired species biomass. We found little evidence that establishment and persistence of our nonnative desired species were related to weed density. Our data

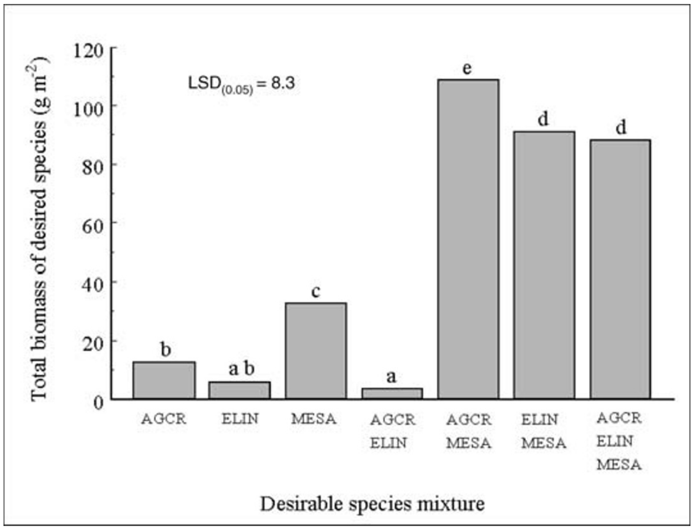

Figure 4. Effect of desired species monoculture and mixtures on the total biomass of desirable species at Red Bluff in 2002. ELIN indicates intermediate wheatgrass; AGCR, crested wheatgrass; and MESA, alfalfa.

support the hypothesis that some nonnative species possess aggressive plant traits that allow establishment and dominance even in the presence of high densities of invasive plants. In some cases, nonnative species may establish because they possess aggressive traits that are required for rehabilitation of invasive plant-dominated rangeland (Jones 2003).

Understanding niche differentiation among species used in rehabilitation may provide valuable information that can be used to favorably influence plant community dynamics and reduce invasion. Plant community dynamics and the susceptibility of plant communities to invasion are influenced by resource availability (Elton 1958; Burke and Grime 1996; Stohlgren et al. 1999) and the relative ability of plants to capture resources (Reever-Morghan and Seastedt 1999; Herron et al. 2001; Mangold 2004). Niche differentiation has been suggested as the mechanism for resource depletion (Naeem et al. 1994; Tilman et al. 1996; Hooper and Vitousek 1997), and maximizing niche occupation has been associated with invasion resistance (Brown 1998; Carpinelli 2000). Our data indicate that crested wheatgrass, intermediate wheatgrass, and alfalfa overlapped in niche during the initial years of establishment at the less productive site. In this case, soil resources may have been somewhat limited because competition was intense among all 3 species. Based on the R^2 from the competition models predicting intermediate wheatgrass (0.74) and crested wheatgrass (0.92), competition was an important process in controlling growth (Weldon and Slausen 1986). After 7 years of growth in association, crested wheatgrass, intermediate wheatgrass, and alfalfa exhibited little detectable competition and were strongly niche-differentiated. Plant traits and characteristics have been good predictors of performance in ecological restoration (Pywell et al. 2003), and selecting species with differing root and growth structure, phenology, leaf morphology, photosynthetic pathways, or a combination of these, may maximize niche occupation and resource capture by desirable species during rehabilitation. A high degree of niche occupation may enhance ecosystem function by ensuring N-cycling and that hydrologic cycling is sustainable (McNaugthton 1993; Vitousek and Hooper 1993).

Our data also partially support the contention that greater species richness is positively correlated with greater overall biomass (Anderson and Inouye 2001; Tilman et al. 2001). Spehn et al. (2000) found experimental grasslands with the greatest species richness also had the greatest biomass. In our study, the desired species were niche-differentiated at both sites in 2002. Regression models using species richness to predict total biomass were weakly significant at both sites. These data showed that an increase in biomass in species-rich plots was detected only at the less productive site (Red Bluff), and there it occurred only where alfalfa was included in the mixture. Theoretically, increased niche occupation provides more complete use of resources (Levine and D'Antonio 1999). In our case, the more productive site may have had ample soil resources, and growth was not limited by a lack of below-ground resources. This speculation is supported by high overall productivity and the lack of intense competition among these species. In this case, full niche differentiation may be a result of high nutrient status of the soil that minimized competition, combined with

Table 3. *P* values for the influence of desired species monocultures, or mixtures, or both (D); spotted knapweed sowing density (K); and their interactions (D × K) on spotted knapweed density and biomass.[1]

		Post Farm				Red Bluff			
		1997		2002		1997		2002	
Treatment	df	Density (plants · m^{-2})	Biomass (g · m^{-2})	Density (plants · m^{-2})	Biomass (g · m^{-2})	Density (plants · m^{-2})	Biomass (g · m^{-2})	Density (plants · m^{-2})	Biomass (g · m^{-2})
D	6	0.466	0.833	0.332	0.619	0.258	0.601	<0.001	0.004
K	1	0.745	0.487	0.381	0.657	<0.001	0.844	0.912	0.175
D × K	6	0.866	0.787	0.639	0.963	0.005	0.473	—[2]	—[2]
Mean		284	1254	24.5	25.5		179	—[3]	—[4]
SE[5]		36.3	172	9.90	19.0		8.60	—	—

[1]Means are averaged across treatments where all treatments were significant. Reduced model for Red Bluff 2002 density; D × K is included in the error term.
[2]*P* values were generated from model including only main effects. The interaction was nonsignificant and included in the error term. Expanded models are shown where treatment effects were nonsignificant in all models.
[3]Data are presented in Figure 5a.
[4]Data are presented in Figure 5b.
[5]SE indicates standard error.

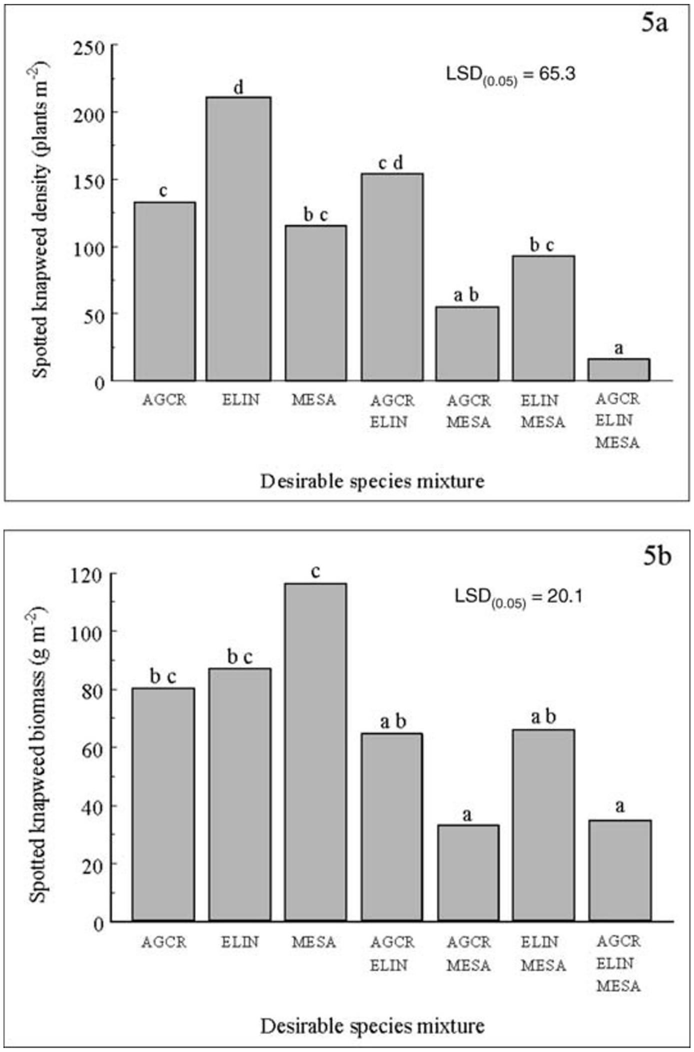

Figure 5. Effect of desired species monoculture and mixtures on the spotted knapweed density **a,** and biomass **b,** at Red Bluff in 2002. ELIN indicates intermediate wheatgrass; AGCR, crested wheatgrass; and MESA, alfalfa.

niche-differentiating traits of the desired species. We believe that niche differentiation was a result of plant traits at Red Bluff, where soil resources appeared to limit plant growth.

The theory that species-rich communities resist invasion through competitive exclusion is being debated in the ecological literature (D'Antonio 1999; Tilman 1999; Kennedy et al. 2002; Levine and Stohlgren et al. 2003). The discrepancy among studies may be scale-dependent (Prieur-Richard and Lavorel 2000). It is also possible that species are redundant in niche, whereas unoccupied niches remain unfilled and receptive to invasion (Lawton and Brown 1993; Diaz and Cabido 2001). We tested the hypothesis that spotted knapweed density and biomass decrease as desirable species richness increases, while simultaneously determining the degree of niche differentiation occurring among desired species. Regressions indicated a negative relationship between species richness and spotted knapweed biomass, but the relationship was very weak at the Post Farm. At the Post Farm, where soil nutrients and production were highest, mean comparisons confirmed that no combination sowing of desired species exhibited differences in spotted knapweed density or biomass. However, the invasive weed occurred in very low amounts. In this case, we believe that spotted knapweed was limited by light because of shading by tall (1 m), productive, desirable species; or by their litter; or both. Foliage, root, and crown growth of spotted knapweed increased significantly when plants received full light, rather than one-half light (Kennett et al. 1992). Crops such as alfalfa produce dense shade under irrigation and have been used to suppress Russian knapweed (*Acroptilon repens* L.) in cropping systems (Roché and Roché 1991).

Conversely, we found evidence for niche differentiation among desired species based on resources other than light at Red Bluff. Because the aboveground biomass was lower at Red Bluff than at the Post Farm, we speculate that most competition was for belowground resources at Red Bluff. We also believe that the clay loam soil combined with higher mean annual temperatures may create lower plant available soil moisture. Limited soil moisture can limit nutrient uptake and create conditions for intense plant competition (Brady and Weil 2002). Our data indicated that those communities that included the combination of crested wheatgrass and alfalfa seemed to resist invasion more so than monocultures or other combinations. Our data suggest that crested wheatgrass and alfalfa occupy complementary niches, and the 2-species combined competitively excluded spotted knapweed at Red Bluff (Grime 1973).

MANAGEMENT IMPLICATIONS

Although seeding nonnative species is somewhat controversial, where rehabilitation of plant community function, enhanced wildlife and livestock forage, and invasion resistance are primary land-use objectives, establishing and maintaining a diversity of nonnative desirable species may be useful. We believe that seeding a rich mixture of niche-differentiated desirable species may facilitate the establishment of a desirable plant community and enhance plant productivity. Although establishing a species-rich plant community appears less important on highly productive sites, increased niche occupation by desirable species may increase resource use and productivity, thus minimizing establishment and dominance of unwanted invasive plants during rehabilitation on arid, marginally productive sites typical of many rangeland ecosystems.

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