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Revegetating weed-infested rangeland with niche-differentiated desirable species

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Abstract

The goal of this study was to determine the potential to revegetate weed-infested rangeland by maximizing niche occupation and resource capture by desirable species. We hypothesized that as desirable species richness increases, weed establishment and growth decrease, provided that the desirable species differ in niche. Three desirable species with differing spatial and temporal growth patterns, [*Agropyron cristatum* (L.) Gaertn., var. Hycrest (crested wheatgrass), *Elytrigia intermedia* (Host) Nevski, var. Rush (intermediate wheatgrass), and *Medicago sativa* L., var. Arrow (alfalfa)], and 1 weed [*Centaurea maculosa* Lam. (spotted knapweed)], were grown in a multiple replacement series. All species were sown simultaneously in spring 1996, simulating revegetation of a site containing spotted knapweed seeds in the seed bank because of prior infestation. Desirable species richness varied among plots, while the total number of desirable seeds sown per plot was held constant. Although the desirable species were shown to differ in niche, desirable species richness or mixture did not affect soil water depletion or spotted knapweed recruitment in 1996 or 1997. These results suggest that revegetation of weed-infested rangeland must also include active control of weeds emerging from the soil seed bank. Only then can other strategies, such as maximizing niche occupation by desirable species, be expected to provide long-term success.

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

Resumen

El objetivo de esta investigación fue determinar el potencial de repoblar pradera infectada con maleza al maximizar la ocupación de nichos y la captación de recursos por especies deseables. Nuestra hipótesis fue que mientras el número de las especies deseables aumenta, el establecimiento y crecimiento de especies no deseables disminuyen con tal de que las especies deseables ocupan diferentes nichos. Tres especies deseables con diferentes patrones de crecimiento, tanto espacial como temporal, [*Agropyron cristatum* (L.) Gaertn., var. Hycrest (crested wheatgrass), *Elytrigia intermedia* (Host) Nevski, var. Rush (intermediate wheatgrass), y *Medicago sativa* L., Arrow (alfalfa)] y 1 especie no deseable [*Centaurea maculosa* Lam. (spotted knapweed)] fueron cultivados en una serie múltiple de reemplazo. Todas las especies fueron sembradas simultáneamente en la primavera de 1996, simulando la recuperación de vegetación de un sitio el cual contenía semillas de spotted knapweed en el banco de semillas causa de una invasión previa. La riqueza de la especie deseable varió entre parcelas experimentales, mientras el número total de semillas deseables sembradas por parcela se mantuvo constante. Aunque las especies deseables se manifestaron en diferentes nichos, la riqueza o mezcla de especies deseables no registró una reducción de agua del subsuelo ni establecimiento de spotted knapweed durante 1996 o 1997. Estos resultados sugieren que la recuperación de vegetación de pradera invadida por maleza también debe incluir un control activo de maleza saliendo del banco de semillas del subsuelo. Solo entonces se puede esperar que otras estrategias, tales como la ocupación de nichos por especies deseables, representen un éxito a largo plazo.

Revegetation of weed-infested rangeland has often failed because of poor establishment of desirable species or because weeds soon reinvade. Cost-effective, sustainable revegetation of weed-infested rangeland must address both successful establishment of desirable species and their ability to resist reestablishment of weed populations. Past revegetation of weed-dominated rangeland that has focused on using broadleaf herbicides to establish grass monocultures has produced variable and unpredictable results (Hubbard 1975, Berube and Myers 1982, Huston et al. 1984, Larson and McInnis 1989). The goal of establishing persistent, biologically diverse plant communities has often been sacrificed to accommodate the short-term goals of plant establishment and soil stabilization (Call and Roundy 1991). Revegetation technology should address spatial and temporal diversity within the community.

During the establishment phase of revegetation, the relative timing of emergence and growth rates of species may be important determinants of community dynamics (Ross and Harper 1972, Harper 1977, Radosevich and Holt 1984). Rehabilitation of yellow starthistle (*Centaurea solstitialis* L.)-dominated rangeland has been attempted by revegetating with desirable grasses. These attempts typically fail because of resource preemption by annual weeds which germinate sooner and have a higher initial growth rate than the desirable grasses (Borman et al. 1991). In an experiment by Harris (1967), the winter annual, cheatgrass (*Bromus tectorum* L.), preempted resources from fall-sown bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. & Smith]. Both species germinated in the fall, but cheatgrass had faster winter root growth than bluebunch wheatgrass, thus allowing it to gain control of the site. Borman et al. (1991) found that established perennial grasses that initiate growth early and maintain some

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growth through the winter can limit reinvasion by weeds.

During the early stages of secondary succession (e.g., revegetation), availability of light, water, and nutrients may be particularly high relative to the demand by a sparse community of establishing plants. In this case, resource preemption may be more important than competition in determining community dynamics (Goldberg 1990). Those plants with the highest growth rates have the highest likelihood of establishing to the exclusion of plants with slower growth rates (Harper 1977). Since establishment is the most critical phase of revegetation, knowledge of the initial growth rate of a species may be the best predictor of the short-term outcome of a revegetation effort (James 1992).

The goal of this study was to determine the potential to revegetate spotted knapweed-infested rangeland by maximizing niche occupation by desirable species that establish well and persist. The overall objective was to determine the relationship among 3 desirable species and spotted knapweed during the first 2 years of establishment. We hypothesized that as desirable species richness increases, spotted knapweed establishment and growth decrease, provided the desirable species differ in niche. We believed that as desirable species richness increased, niche occupation would increase, and resources would be increasingly preempted from spotted knapweed. Specific objectives were to: (1) quantify niche differentiation among 3 desirable species commonly used in revegetation, and (2) determine the relationship between desirable species richness and spotted knapweed establishment.

A supporting objective was to quantify the growth rate of spotted knapweed and 3 desirable species commonly used in revegetation of weed-infested rangeland. This information was used to determine the potential of growth analysis to predict the outcome of the revegetation experiment.

Materials and Methods

Study sites

This study was conducted at the Red Bluff Research Ranch and the Arthur Post Research Farm in southwest Montana. Red Bluff Research Ranch (45° 34' N, 111° 40' W; herein referred to as Red Bluff) is located 40 km west of Bozeman, Mont. Elevation at Red Bluff is 1,505 m, and mean annual precipitation is 305 mm. The Red Bluff soil is a Varney clay loam (fine-loamy, mixed, frigid Calcidic Argiustoll). The Arthur H. Post Research Farm (45° 40' N, 111° 09' W; herein referred to as the Post Farm) is located 6 km west of Bozeman, Mont. Elevation at the Post Farm is 1,463 m, and mean annual precipitation is 457 mm. The Post Farm soil is an Amsterdam silty loam (fine-silty, mixed, frigid Typic Haplustoll).

Plant materials

The 3 desirable species used in this study were crested wheatgrass [*Agropyron cristatum* (L.) Gaertn., var. Hycrest], intermediate wheatgrass [*Elytrigia intermedia* (Host) Nevski, var. Rush], and alfalfa (*Medicago sativa* L., var. Arrow). 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 forb with an extended growing period. These 3 introduced perennials are commonly used in revegetation in the West where the management goal is 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 3 desirable species were obtained from the Bridger Plant Materials Center, Bridger, Mont.

The weed species chosen for this experiment was spotted knapweed (*Centaurea maculosa* Lam.), a deeply taprooted Eurasian perennial forb. This species was chosen because of its ecological significance and wide distribution. Spotted knapweed seeds were collected from Deer Lodge County, Mont., in August 1995.

Competition Experiment

Experimental design. Four background densities (blocks) of spotted knapweed (1,250, 2,500, 3,750, and 7,500 seeds m^{-2}) were used in a multiple replacement series (de Wit 1960). Each block contained seven, 4-m^2 plots: 3 plots with 1 desirable species per plot (4,500 seeds m^{-2}), 3 plots with each combination of 2 desirable species (2,250 seeds m^{-2} per species), and 1 plot containing all 3 desirable species (1,500 seeds m^{-2} per species). Nine plots with monocultures of the 3 desirable species at 1 of 3 densities (1,500, 2,250, and 4,500 seeds m^{-2}) accompanied the multiple replacement series (Appendix A). The 37 plots were arranged in a completely randomized design.

All plots 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 Jun. 1996 at Red Bluff and on 28–29 Jun. 1996 at the Post Farm. Seeds were hand sown to minimize aggregated distributions. Plots were then covered with nylon mesh backed straw-mulch (North American Green®, Billings, Mont). To facilitate germination and establishment, plots were watered daily from 29 Jun. to 29 Jul. 1996. On 15 Jul. 1996, when plants averaged approximately 5 cm tall, the mulch was removed from all plots. Nonseeded species were hand-weeded for the duration of the experiment.

1996 Sampling. Harvest at the Post Farm took place from 31 Oct. to 2 Nov. 1996. At the time of sampling, all plants were in the seedling stage (average height about 7 cm). A 510-cm^2 circular frame was placed in the center of a randomly selected quadrant in each plot. Density of each species was counted, and all aboveground biomass was clipped, separated by species, dried (168 hours, 60° C) and weighed. Although Red Bluff was fenced, aboveground biomass at Red Bluff was completely consumed by herbivores (grasshoppers, deer, antelope, rabbits) and was not sampled.

1997 Sampling. Both sites were sampled in 1997. At the time of sampling, average height of all species was about 1 m and 5 cm at the Post Farm and Red Bluff, respectively. At Red Bluff, a 510-cm^2 circular frame was placed in the center of a randomly selected quadrant in each plot. At the Post Farm, the frame was placed in center of a randomly selected, previously unsampled quadrat. Sampling at both sites took place between 11 September and 22 September 1997. Density (stems m^{-2}) of each species was recorded, and all aboveground biomass was clipped, separated by species, dried (168 hours, 60° C) and weighed.

Soil water monitoring. Soil water content was measured weekly during the 1996 growing season and biweekly during the 1997 growing season. A neutron probe was used to measure soil water content in the center of each plot from 10 to 150 cm below the soil surface in 20-cm increments.

Data analysis

Niche differentiation. Niche differentiation between desirable species was quantified using their relative competitive coefficients (Spitters 1983) derived from density and biomass data from the multiple replacement series plots. For each combination of site and year, a model using 3 regressions was used: 1 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 (to linearize exponential growth). Within each model, the same predictor/response combination was used in each of the 3 regressions, and models of different predictor/response combinations were compared. Model preference was given to that which provided the highest cumulative R^2 from its 3 individual regressions (Appendices B-D). The regressions were of the general form:

$$y_i = \beta_{0i} + \beta_{ii}N_i + ... + \beta_{ij}N_j \qquad (1)$$

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). The relative competitive ability of each species is calculated as:

$$RC_i = \beta_{ii}/\beta_{ij} \text{ and } RC_j = \beta_{jj}/\beta_{ji} \qquad (2)$$

where RC_i is the relative competitive ability of species i and j on species i. For example, RC_i is 1/3 where 1 plant of species i and 3 plants of species j have equal influence on the average weight per plant of species i (Spitters 1983). Niche differentiation is calculated from the relative competitive abilities of each species:

$$ND = (\beta_{ii}/\beta_{ij}) / (\beta_{ji}/\beta_{jj}) = RC_i \bullet RC_j = (\beta_{ii}/\beta_{ij}) \bullet (\beta_{jj}/\beta_{ji}) \qquad (3)$$

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).

The response variable and the sign (+ or -) of the coefficients are important in interpreting niche differentiation ratios. Where the response is the inverse of the average weight per plant, a positive sign denotes negative interference (e.g., competition, amensalism), and a negative sign denotes positive interference (e.g., mutualism, commensalism). The opposite is true where the response is average weight per plant.

An estimate of niche differentiation for each 2-species combination was made that accounted for the variability in the estimate of each predictor. For each predictor, a population of 1,000 coefficient values was created by randomly selecting from a normal distribution with mean and standard error equal to that of its respective predictor. From these populations of coefficients, a population of 1,000 niche differentiation values was calculated for each 2-species combination. A 2-tailed t-test was performed to quantify the difference between each population of niche differentiation values and a population of 1,000 values of unity (no niche separation). The resultant P-value represents the degree of niche separation. For example, a small P-value indicates a small probability that the 2 species overlapped in niche, while a P-value of unity indicates complete niche overlap (no niche differentiation).

Spotted knapweed recruitment. The effects of desirable species richness on spotted knapweed recruitment [(spotted knapweed density/spotted knapweed sowing density) x 100%] were compared using one-tailed t-tests ($P \leq 0.05$). Analysis of variance was used to test the effect of desirable species mixture on spotted knapweed recruitment (PROC GLM, SAS Institute Inc. 1991). Means were compared ($P \leq 0.05$) using Fisher's protected LSD test (Peterson 1985).

Spotted knapweed biomass and density. Linear regression was used to quantify the relationship between desirable species richness and spotted knapweed biomass and density. An ANOVA was used to compare mean aboveground biomass of spotted knapweed to mean aboveground biomass of the desirable species.

Soil water. Soil water content (average content of all depths, averaged over the entire season) was used to predict spotted knapweed growth using linear regression. Total aboveground biomass was used to predict season-long soil water depletion ([beginning soil water content] - [ending soil water content]). ANOVA was used to compare the effects of desirable species mixture and richness on soil water depletion (average of all depths, averaged over the entire season).

Growth Analysis Experiment

Isolated plants of spotted knapweed, crested wheatgrass, intermediate wheatgrass, and alfalfa were arranged in a randomized-complete-block design. Each of 4 blocks contained 20 plants (4 species x 5 harvest dates). Plants were grown in pots in an environmental chamber (12° C, 12-hour daylength, 500 $\mu E\ m^{-2}\ sec^{-1}$ visible radiation measured at pot height). The pots (10 cm diameter x 1 m length polyvinyl chloride tubes) were split vertically and taped back together to facilitate post-harvest root removal. The pots were filled with sterilized Farland silt loam (fine-silty, mixed Typic Argiboroll; A horizon), water-saturated, and allowed to drain to pot capacity. Ten seeds of a given species were evenly spaced on the soil surface of each pot and covered lightly with soil (< 2 mm). The surface was lightly misted with water once daily and covered with clear plastic until emergence (7 days), after which no further watering occurred. Pots were thinned to a single individual per pot (10 days).

Seed weight of each species was determined by taking the mean of 4 subsamples of 100 seeds. First plant harvest occurred 14 days after emergence (DAE). Harvests continued on 14-day intervals until final harvest (70 DAE). Soil was manually rinsed from roots. Root systems were extracted from each pot, separated from shoots, and washed. All plant material (root and shoots) was dried (48 hours, 60° C) and weighed.

A regression analysis was used to estimate the instantaneous relative growth rate (RGR) calculated over the 70-day period (Hunt 1982). Slopes were compared using the extra sums of squares procedure ($P \leq 0.05$, Ratkowski 1983).

Results

Competition Experiment

The desirable species were significantly niche-differentiated from each other at the

Table 1. Niche differentiation (ND) mean values for the desirable species pairs. An ND of unity represents complete niche overlap. P represents the probability that ND = 1. P for all means was less than 0.01. Numbers in parentheses = lower and upper limits of the 95% confidence interval.

Site	Year	Intermediate-Crested	Intermediate-Alfalfa	Crested-Alfalfa
Red Bluff	1997	1.010 (1.010, 1.010)	0.531 (0.436, 0.625)	0.501 (0.403, 0.599)
Post Farm	1996	0.934 (0.933, 0.934)	1.005 (1.004, 1.007)	1.167 (1.135, 1.199)
Post Farm	1997	–0.938 (–1.057, –0.820)	–1.163 (–1.401, –0.924)	1.342 (1.094, 1.590)

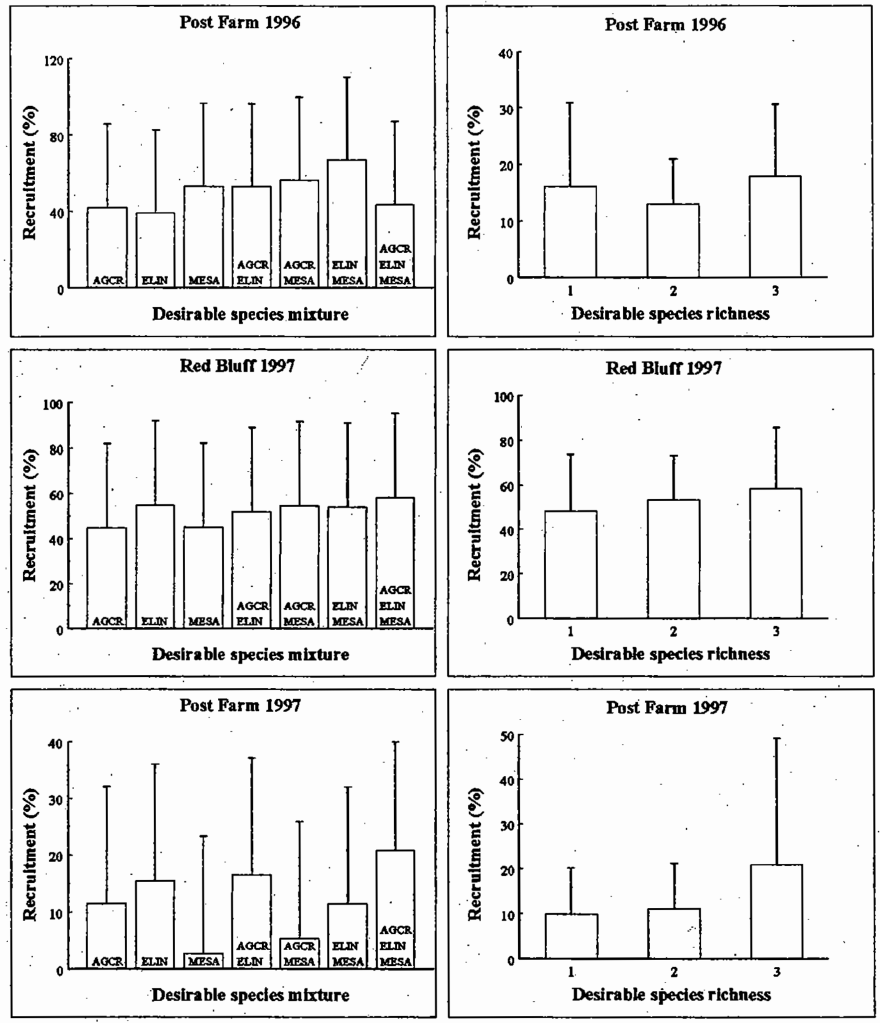

Fig. 1. Effect of desirable species mixture (error bars = 1 LSD) and desirable species richness (error bars = 1 SE) on spotted knapweed recruitment by site and year. Neither desirable species mixture nor desirable species richness significantly affected spotted knapweed recruitment. ELIN = intermediate wheatgrass; AGCR = crested wheatgrass; MESA = alfalfa.

Post Farm in 1996 and at both sites in 1997 (Table 1). However, spotted knapweed recruitment was not affected by desirable species mixture or richness at the Post Farm in 1996 or at either site in 1997 ($P \leq 0.05$, Fig. 1).

Total desirable plant sowing density was the same in all plots containing spotted knapweed. Because spotted knapweed sowing density varied among plots, relationships among desirable species richness and spotted knapweed may have been influenced by spotted knapweed sowing density. Regressions of spotted knapweed measured density on its sowing density were highly significant ($P < 0.001$) for the Post Farm in 1996 and Red Bluff in 1997; however, this relationship was not significant for the Post Farm in 1997 (Table 2). Therefore, the relationships between desirable species richness and spotted knapweed biomass and density were not confounded by spotted knapweed sowing density at the Post Farm in 1997, and these relationships were quantified. Neither relationship was significant (Table 3). At the Post Farm in 1997, mean biomass of spotted knapweed was at least 5 times greater than the mean biomass of each of the desirable species, which were similar (Fig. 2). Biomass of desirable species monocultures grown in the absence of spotted knapweed was similar to spotted knapweed biomass and total biomass (all species) of mixtures at the Post Farm in 1997 (Fig. 3). There was no significant relationship between spotted knapweed biomass and desirable species biomass in plots where spotted knapweed was sown (Fig. 4).

For reasons stated above, relationships between spotted knapweed biomass and total plot biomass were not confounded by spotted knapweed sowing density at the Post Farm in 1997. This allowed for the quantification of the following 2 relationships for the Post Farm in 1997: (1) between spotted knapweed biomass production and soil water content, and (2) between total biomass production by all species and soil water depletion. Neither relationship was significant (Table 4). Neither desirable species mixture nor richness affected season-long soil water depletion at the Post Farm in 1997 (Fig. 5). Season-long soil water depletion by depth increment showed no consistent trends or differences by species mixture at either site or in either year (data not shown). Soil water depletion by sampling date and species mixture showed no consistent trends or differences for any depth increment at either site or in either year (data not shown).

Table 2. Linear regression of spotted knapweed measured density on its sowing density.

Year	Site	P Model	R^2 Model
1996	Post Farm	< 0.01	0.45
1997	Red Bluff	< 0.01	0.44
1997	Post Farm	0.63	0.01

Table 3. Linear regression of spotted knapweed biomass and density on desirable species richness for the Post Farm in 1997.

Independent variable	Dependent variable	P_{Model}	R^2 Model
Desirable species richness	Spotted knapweed biomass	0.76	0.004
	Spotted knapweed density	0.31	0.04

Table 4. Linear regressions of spotted knapweed biomass production on season-average soil water content and season-long soil water depletion on total biomass production by all species for the Post Farm in 1997.

Independent variable	Dependent variable	P_{Model}	R^2 Model
Soil water content	Spotted knapweed biomass	0.36	0.03
Total biomass production	Soil water depletion	0.51	0.01

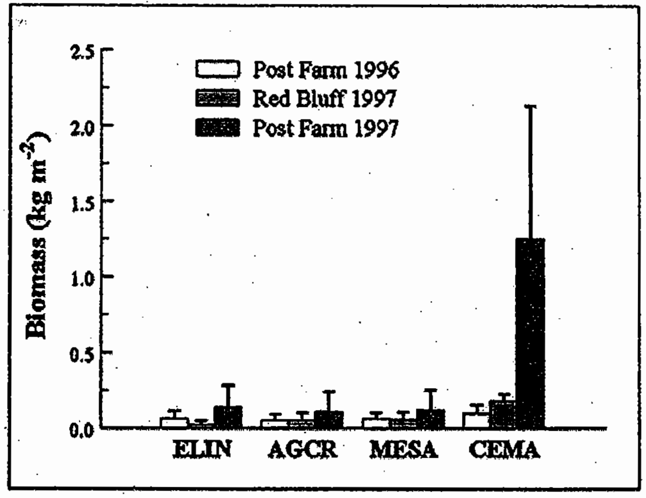

Fig. 2. Mean shoot biomass per species by site and year. For each desirable species, data represent its mean biomass per plot in the multiple replacement series plots where it was sown (mean sowing density per desirable species = 2625 seeds m^{-2}; total desirable species sowing density = 4500 seeds m^{-2}; mean spotted knapweed sowing density = 3750 seeds m^{-2}). Data for spotted knapweed represent all 28 multiple replacement series plots. At the Post Farm in 1997, biomass of spotted knapweed was greater than each of the desirable species, which were similar. Error bars = 1 SE. ELIN = intermediate wheatgrass; AGCR = crested wheatgrass; MESA = alfalfa; CEMA = spotted knapweed.

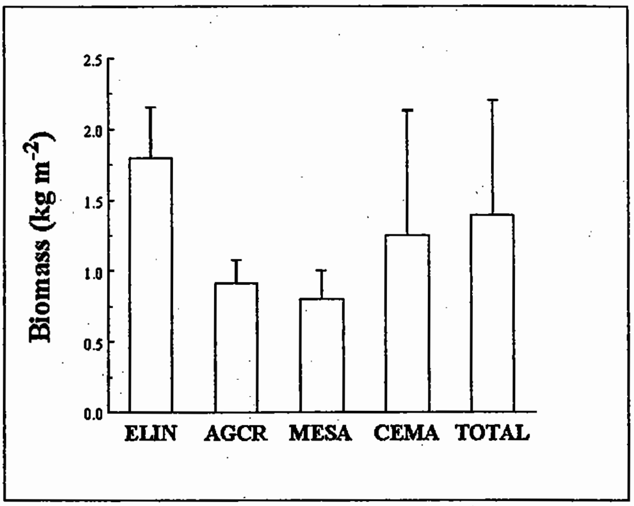

Fig. 3. Mean shoot biomass of monocultures of intermediate wheatgrass (ELIN), crested wheatgrass (AGCR), and alfalfa (MESA) in plots where spotted knapweed was not sown; mean biomass of spotted knapweed (CEMA) in mixtures; and mean total biomass of all species in mixtures (TOTAL) for the Post Farm in 1997. Mean sowing density of desirable species monocultures was 2750 seeds m^{-2}. Mean sowing density of spotted knapweed in mixtures was 3750 seeds m^{-2}. Total sowing density of desirable species in mixtures was 4500 seeds m^{-2}. There were no significant differences among biomass means. The difference between CEMA and TOTAL represents desirable species biomass in plots where spotted knapweed was sown. Error bars = 1 SE.

Growth Analysis

Relative growth rates of intermediate and crested wheatgrasses were similar to each other, and approximately twice that of alfalfa and spotted knapweed, which were similar to each other (Fig. 6).

Discussion and Conclusions

Increasing species richness with species that are niche-differentiated would be expected to increase resource use because niche occupation increases. Hooper and Vitousek (1998) found that increasing functional group diversity increased resource use, and Tilman et al. (1997) and Brown (1998) found increasing functional group diversity increased aboveground biomass. Carpinelli (2000) has shown that in well-established communities, increasing species richness with niche-differentiated species increased overall biomass production and reduced spotted knapweed invasion, suggesting resources were preempted from establishing spotted knapweed. In this study, however, where all species established simultaneously, increasing desirable species richness had no effect on spotted knapweed even though the desirable species were niche-differentiated. This may be because this study was limited to the first 2 years of establishment, when occupation of 'biological space' may be more important than competition for resources (Harper 1977). However, the fact that biomass of desirable species monocultures was similar to total biomass of mixtures containing spotted knapweed (Fig. 3) indicates that spotted knapweed was able to preempt resources from desirable species in the second growing season, or that spotted knapweed was able to outcompete the desirable species regardless of the degree of niche occupation by desirable species.

Spotted knapweed germination is positively related to light (Nolan and Upadhyaya 1988, Lindquist et al. 1991), and spotted knapweed germination and

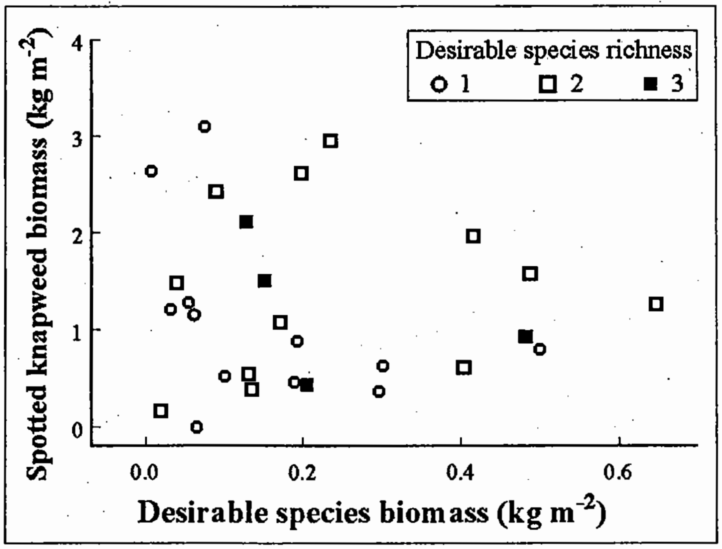

Fig. 4. Regression of spotted knapweed biomass on total desirable species shoot biomass for the Post Farm in 1997. The regression model was not significant.

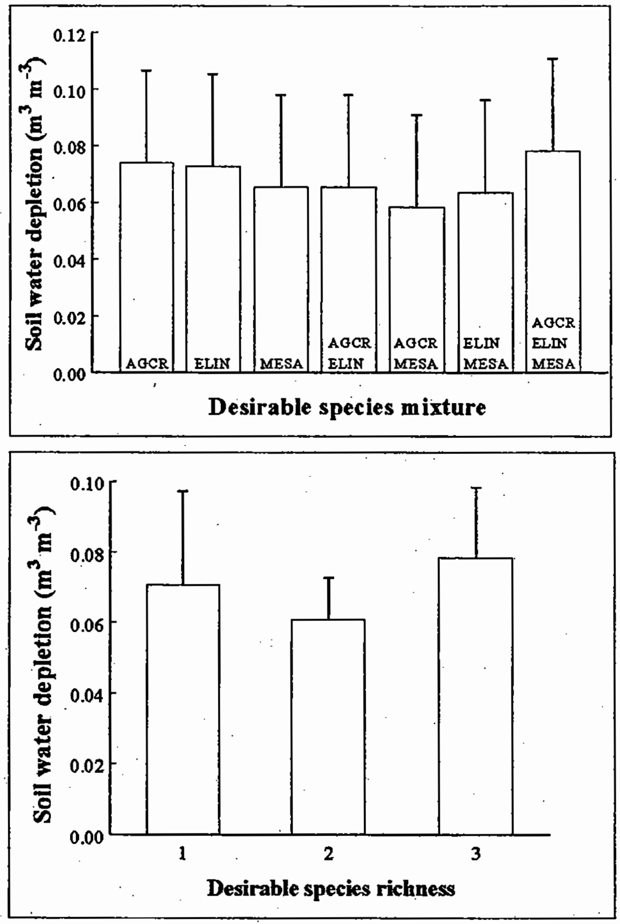

Fig. 5. Effects of desirable species mixture and desirable species richness on season-long soil water depletion (10 to 150 cm soil depth average) for the Post Farm in 1997. Neither effect was significant. ELIN = intermediate wheatgrass; AGCR = crested wheatgrass; MESA = alfalfa.

growth is positively related to soil water content (Eddleman and Romo 1988, Jacobs and Sheley 1997, Carpinelli 2000). In this study, the lack of effect of mean soil water content on spotted knapweed growth, and the lack of effect of spotted knapweed growth on soil water depletion, indicate water was neither limiting to, nor influenced by, spotted knapweed, at least for the depth increments monitored in this study. In addition, the lack of effect of desirable species richness on soil water depletion indicates that the desirable species were not limited by soil water. This suggests niche differentiation among desirable species may have resulted from competition for a resource other than water, and that same resource may not have been limiting to spotted knapweed.

Brown (1998) found that plants grown in containers in low-density monocultures showed similar morphology to plants of those same species when grown in high-density monocultures under field conditions. The growth analysis results in this study led us to expect intermediate wheatgrass and crested wheatgrass may be capable of preempting resources from spotted knapweed in the competition experiment (Fig. 6). However, the reduction in desirable species biomass from monocultures to mixtures containing spotted knapweed (Fig. 3) suggests: (1) competition by spotted knapweed appears to have been responsible for its dominance over the desirable species, and (2) growth characteristics of a plant grown in isolation may not be reflective of that species' growth characteristics grown in populations or communities. This is supported by the work of Huber-Sannwald et al. (1996), who found that *Pseudoroegneria spicata* differed morphologically when grown in monoculture vs. grown in mixtures with *Agropyron desertorum.*

In this study, the ability of spotted knapweed to dominate the desirable species, regardless of species richness, demonstrates the necessity to consider site history in revegetation. If revegetation of weed-infested rangeland is to be successful, it must address potential weed reestablishment from seeds or other propagules in the soil. For broadleaf weeds, this may be

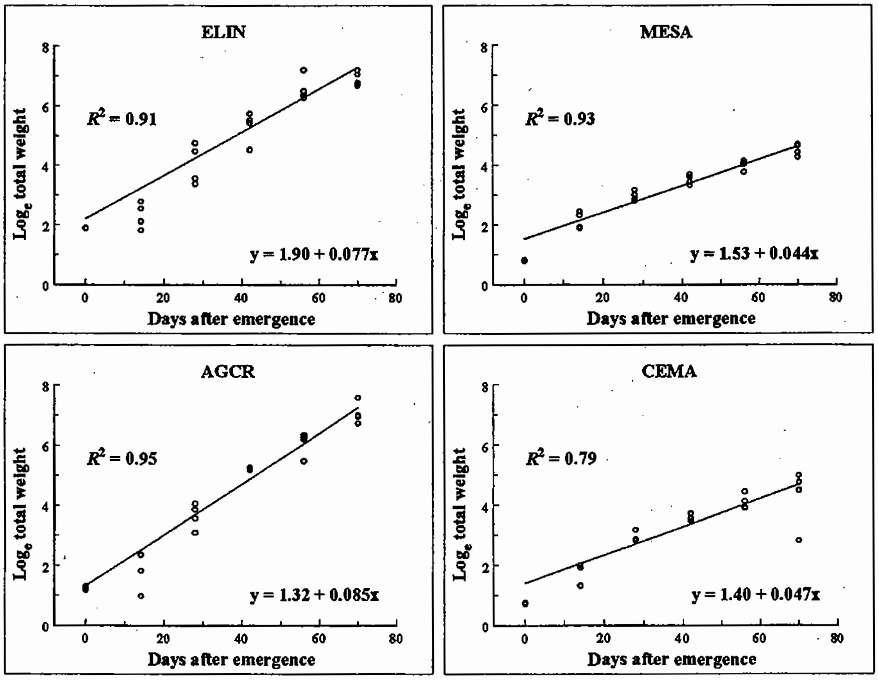

Fig. 6. Relative growth rates of isolated individuals of intermediate wheatgrass (ELIN), crested wheatgrass (AGCR), alfalfa (MESA), and spotted knapweed (CEMA). Plant weight at 0 days after emergence = seed weight.

accomplished by using a persistent broadleaf herbicide to provide a weed-free window of establishment for desirable grass species, followed by a delayed seeding of desirable broadleaf species. For either grass or broadleaf weeds, it may be possible to deplete the soil seed bank prior to revegetation by allowing weed seeds to germinate, removing the emerging weeds by tilling or applying a non-specific, non-persistent herbicide such as glyphosate, and then seeding with a diverse mix of desirable species. The desirable species may dominate the site by preempting resources from weeds that may later emerge. Only after controlling weeds emerging from the soil seed bank, may long-term revegetation success be achieved by maximizing niche occupation by desirable species.

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Appendix A. Plot plan for multiple replacement series (upper) and monocultures (lower). Each cell represents 1 mixture; field location of all plots was complete randomized. AGCR = crested wheatgrass; ELIN = intermediate wheatgrass; CEMA = spotted knapweed; MESA = alfalfa. CEMA$_0$, CEMA$_1$, CEMA$_2$, CEMA$_3$ and CEMA$_4$, represent background spotted knapweed sowing densities of 0, 1,250, 2,500, 3,750 and 7,500 seeds m^{-2}, respectively. Subscripted proportions of 0, 1/3, 1/2, and 1 represent sowing densities of desirable species: 0, 1,500, 2,250, and 4,500 seeds m^{-2}, respectively.

AGCR$_{1/3}$ ELIN$_{1/3}$ MESA$_{1/3}$ CEMA$_1$	AGCR$_1$ ELIN$_0$ MESA$_0$ CEMA$_1$	AGCR$_0$ ELIN$_1$ MESA$_0$ CEMA$_1$	AGCR$_0$ ELIN$_0$ MESA$_1$ CEMA$_1$
AGCR$_{1/2}$ ELIN$_{1/2}$ MESA$_0$ CEMA$_1$	AGCR$_{1/2}$ ELIN$_0$ MESA$_{1/2}$ CEMA$_1$	AGCR$_0$ ELIN$_{1/2}$ MESA$_{1/2}$ CEMA$_1$	
AGCR$_{1/3}$ ELIN$_{1/3}$ MESA$_{1/3}$ CEMA$_2$	AGCR$_1$ ELIN$_0$ MESA$_0$ CEMA$_2$	AGCR$_0$ ELIN$_1$ MESA$_0$ CEMA$_2$	AGCR$_0$ ELIN$_0$ MESA$_1$ CEMA$_2$
AGCR$_{1/2}$ ELIN$_{1/2}$ MESA$_0$ CEMA$_2$	AGCR$_{1/2}$ ELIN$_0$ MESA$_{1/2}$ CEMA$_2$	AGCR$_0$ ELIN$_{1/2}$ MESA$_{1/2}$ CEMA$_2$	
AGCR$_{1/3}$ ELIN$_{1/3}$ MESA$_{1/3}$ CEMA$_3$	AGCR$_1$ ELIN$_0$ MESA$_0$ CEMA$_2$	AGCR$_0$ ELIN$_1$ MESA$_0$ CEMA$_3$	AGCR$_0$ ELIN$_0$ MESA$_1$ CEMA$_3$
AGCR$_{1/2}$ ELIN$_{1/2}$ MESA$_0$ CEMA$_3$	AGCR$_{1/2}$ ELIN$_0$ MESA$_{1/2}$ CEMA$_3$	AGCR$_0$ ELIN$_{1/2}$ MESA$_{1/2}$ CEMA$_3$	
AGCR$_{1/3}$ ELIN$_{1/3}$ MESA$_{1/3}$ CEMA$_4$	AGCR$_1$ ELIN$_0$ MESA$_0$ CEMA$_4$	AGCR$_0$ ELIN$_1$ MESA$_0$ CEMA$_4$	AGCR$_0$ ELIN$_0$ MESA$_1$ CEMA$_4$
AGCR$_{1/2}$ ELIN$_{1/2}$ MESA$_0$ CEMA$_4$	AGCR$_{1/2}$ ELIN$_0$ MESA$_{1/2}$ CEMA$_4$	AGCR$_0$ ELIN$_{1/2}$ MESA$_{1/2}$ CEMA$_4$	

AGCR$_{1/3}$ ELIN$_0$ MESA$_0$ CEMA$_0$	AGCR$_0$ ELIN$_{1/3}$ MESA$_0$ CEMA$_0$	AGCR$_0$ ELIN$_0$ MESA$_{1/3}$ CEMA$_0$
AGCR$_{1/2}$ ELIN$_0$ MESA$_0$ CEMA$_0$	AGCR$_0$ ELIN$_{1/2}$ MESA$_0$ CEMA$_0$	AGCR$_0$ ELIN$_0$ MESA$_{1/2}$ CEMA$_0$
AGCR$_1$ ELIN$_0$ MESA$_0$ CEMA$_0$	AGCR$_0$ ELIN$_1$ MESA$_0$ CEMA$_0$	AGCR$_0$ ELIN$_0$ MESA$_1$ CEMA$_0$

Appendix B. Regressions used in calculating niche differentation for the Post Farm in 1996. The y-intercept (y_{max}) is interpreted as the weight of an isolated individual. Numbers in parentheses = 1 SE.

Response: average shoot weight per plant (mg)	Predictor: sown density (seeds m^{-2})	Coefficient $\beta_{\text{response predictor}}$
Intermediate wheatgrass (I) $R^2 = 0.83$ $y_{max} = 407$ (39.1)	Intermediate wheatgrass	$\beta_{II} = -0.077$ (0.010)
	Crested wheatgrass	$\beta_{IC} = -0.070$ (0.010)
	Alfalfa	$\beta_{IA} = -0.078$ (0.010)
Crested wheatgrass (C) $R^2 = 0.68$ $y_{max} = 342$ (51.9)	Intermediate wheatgrass	$\beta_{CI} = -0.069$ (0.014)
	Crested wheatgrass	$\beta_{CC} = -0.065$ (0.013)
	Alfalfa	$\beta_{CA} = -0.069$ (0.014)
Alfalfa (A) $R^2 = 0.50$ $y_{max} = 280$ (55.0)	Intermediate wheatgrass	$\beta_{AI} = -0.051$ (0.015)
	Crested wheatgrass	$\beta_{AC} = -0.015$ (0.015)
	Alfalfa	$\beta_{AA} = -0.051$ (0.014)

Appendix C. Regressions used in calculating niche differentiation for the Post Farm in 1997. The y-intercept (y_{max}) is interpreted as the inverse of the weight of an isolated individual. Numbers in parentheses = 1 SE.

Response: inverse of the average shoot weight per plant (mg^{-1})	Predictor: measured density (plants m^{-2})	Coefficient $\beta_{\text{response predictor}}$
Intermediate wheatgrass (I) $R^2 = 0.58$ $y_{max} = 12.6$ (2.97)	Intermediate wheatgrass	$\beta_{II} = -0.005$ (0.003)
	Crested wheatgrass	$\beta_{IC} = -0.006$ (0.008)
	Alfalfa	$\beta_{IA} = 0.033$ (0.011)
Crested wheatgrass (C) $R^2 = 0.53$ $y_{max} = 32.6$ (35.1)	Intermediate wheatgrass	$\beta_{CI} = -0.137$ (0.227)
	Crested wheatgrass	$\beta_{CC} = -0.009$ (0.017)
	Alfalfa	$\beta_{CA} = 0.616$ (0.215)
Alfalfa (A) $R^2 = 0.36$ $y_{max} = 18.6$ (9.47)	Intermediate wheatgrass	$\beta_{AI} = 0.0347$ (0.057)
	Crested wheatgrass	$\beta_{AC} = 0.130$ (0.090)
	Alfalfa	$\beta_{AA} = -0.022$ (0.016)

Appendix D. Regressions used in calculating niche differentiation for Red Bluff in 1997. The y-intercept (y_{max}) is interpreted as the weight of an isolated individual. Numbers in parentheses = 1 SE.

Response: average shoot weight per plant (mg)	Predictor: sown density (seeds m^{-2})	Coefficient $\beta_{\text{response predictor}}$
Intermediate wheatgrass (I) $R^2 = 0.74$ $y_{max} = 1729$ (254)	Intermediate wheatgrass	$\beta_{II} = -0.366$ (0.064)
	Crested wheatgrass	$\beta_{IC} = -0.391$ (0.068)
	Alfalfa	$\beta_{IA} = -0.383$ (0.068)
Crested wheatgrass (C) $R^2 = 0.98$ $y_{max} = 1417$ (52.4)	Intermediate wheatgrass	$\beta_{CI} = -0.310$ (0.014)
	Crested wheatgrass	$\beta_{CC} = -0.297$ (0.013)
	Alfalfa	$\beta_{CA} = -0.312$ (0.014)
Alfalfa (A) $R^2 = 0.22$ $y_{max} = 608$ (250)	Intermediate wheatgrass	$\beta_{AI} = -0.117$ (0.067)
	Crested wheatgrass	$\beta_{AC} = -0.120$ (0.067)
	Alfalfa	$\beta_{AA} = -0.087$ (0.063)