
Enhancing Native Forb Establishment and Persistence Using a Rich Seed Mixture

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Abstract

Establishing native forbs is crucial for invasive plant management and restoring a desirable plant community. Our objectives were to determine (1) if increasing forb seed density results in increased forb establishment; (2) if a species-rich mixture of forbs has greater establishment and survivorship than a single species; and (3) if mixtures of forbs are more competitive with Spotted knapweed (*Centaurea maculosa*) than a forb monoculture. To test our first two objectives, we seeded monocultures of Purple coneflower (*Echinacea angustifolia*), Arrowleaf balsamroot (*Balsamorhiza sagittata*), Annual sunflower (*Helianthus annuus*), Dotted gayfeather (*Liatris punctata*), Western white yarrow (*Achillea millefolium*), Sticky geranium (*Geranium viscosissimum*), as well as a mixture of all forbs. Pots were seeded at 800 or 2,000 seeds/m² and watered twice or thrice weekly. The highest seed density produced

the highest plant density, which averaged 4.35 plants/pot. The density of the mixture was similar to the mean density seen for individual species, and it doubled in response to the highest seed density. To test our third objective, Spotted knapweed and Purple coneflower were arranged in an addition series matrix with a maximum total density of 4,000 seeds/pot. We found that the forb mixture was seven times more competitive with Spotted knapweed than Purple coneflower alone. Using a mixture of forbs rather than a single species enhances forb establishment in various and unpredictable environments because the mixture possesses a variety of traits that may match year-year and site-site conditions. Once established, the mixture may have a greater chance of persisting than a monoculture.

Key words: *Centaurea maculosa*, *Echinacea angustifolia*, native forbs, rangelands, restoration.

Introduction

Non-native invasive plants threaten the diversity, function, and utility of rangelands throughout the western United States and Canada (Sheley & Petroff 1999). Non-native, invasive plants continue to spread and dominate millions of hectares of rangeland and wildland, costing several billions of dollars each year (Pimentel 2002). In addition to controlling invasive weeds, a general objective for invasive plant management is to establish and/or maintain a healthy plant community that is relatively weed resistant while meeting other land-use objectives (Sheley et al. 1996). Invasive plant-dominated rangelands are often void of desirable competitive species. Many weed control procedures open niches that desirable species are not available to occupy (Jacobs et al. 1998; Kedzie-Webb et al. 2002). Introducing and establishing desirable competitive plants is crucial for successful invasive plant management and the reestablishment of a desired plant community (Bottoms & Whitson 1998; Laufenberg 2003).

A number of researchers have suggested that the probability of plant invasion decreases as indigenous species

diversity increases (McGrady-Steele et al. 1997; Tilman 1997), whereas others maintain that species-poor communities resist invasion more than diverse plant communities (Robinson et al. 1995; Levine & D'Antonio 1999; Stohlgren et al. 1999). The studies that actually quantified niche differentiation found invasion of Spotted knapweed (*Centaurea maculosa* Lam.) decreased when species richness and niche occupation increased (Jacobs & Sheley 1999; Carpinelli 2001; Carpinelli et al. 2004). More recently, Pokorny et al. (2005) found that the forb functional group was critical to invasion resistance of species with similar life history traits, such as Spotted knapweed. Establishing indigenous forbs during restoration of native plant communities is central to achieving diverse systems that function sustainably and resist invasion (Pokorny et al. 2004).

In most cases, revegetation or restoration is not included in weed management because of the high cost and risk of failure (Jacobs et al. 1998). Failures occur because of poor germination and emergence (Rose 1998). Where revegetation or restoration is attempted, forbs are usually not included because propagation techniques are highly variable and largely unknown. In many cases, environmental conditions do not coincide with ecological requirements of individual species selected for establishment. For example, Wirth and Pyke (2003) found that only 8% of the seeds of *Astragalus purshii* emerged, whereas 38% of two *Crepis* species emerged across various site preparation treatments in a sagebrush-grassland habitat.

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One method for enhancing forb establishment may be increasing the availability of seeds to increase the probability that they reach a safe site. Seabloom et al. (2003) found that native annual forbs were strongly seed limited, and a single seeding increased the abundance of native forbs even in the presence of high densities of exotic species. Sheley et al. (1999) found that Bluebunch wheatgrass (*Pseudoroegneria spicata*) was four times more competitive than Spotted knapweed when planted at higher densities than normal for rangeland restoration (1,000–5,000 plants/m²). Because species differ in traits and ranges of tolerances, seeding mixtures with greater species richness are more likely to contain a species within a functional group that will germinate and emerge under varying and unpredictable environmental conditions (Tilman 1994). In addition, establishing multiple species mixtures may maximize resource uptake (Brown 1998; Carpinelli 2001; Pokorny et al. 2004).

Long-term invasive plant management requires the development of ecological strategies for establishing forbs during revegetation and restoration of invasive plant-dominated rangeland. Our objectives were to determine (1) if increasing forb seed density results in increased forb establishment; (2) if a species-rich mixture of forbs has greater establishment and survivorship than a single species; and (3) if a mixture of forbs is more competitive with Spotted knapweed than a monoculture. Our hypotheses were (1) highest forb density would occur at the highest seed density; (2) a species-rich mixture of forbs would establish at a density equal to or greater than the average densities of all the species seeded as monocultures, regardless of watering frequency, because species with varying traits would average their response in varying moisture regimes; and (3) a mixture of forbs would be more competitive with Spotted knapweed than a monoculture of Purple coneflower (*Echinacea angustifolia* L.).

Methods

Germination, Dormancy, and Viability Test

Four replications of 100 seeds of each species were used to test the germination and dormancy of Spotted knapweed, Purple coneflower, Arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt), Annual sunflower (*Helianthus annuus* L.), Dotted gayfeather (*Liatris punctata* Hook), Western white yarrow (*Achillea millefolium* L.), and Sticky geranium (*Geranium viscosissimum* Fisch). Each group of 100 seeds were placed on two sheets of pre-soaked Whatman No. 1 filter paper, spread evenly in 100 by 15-mm petri dish, and were covered with parafilm. For the germination test, seeds were sown on 20 November 2002 and counted between 3 December 2002 and 4 December 2002. Germination occurred in an alternate controlled environment set at 15°C at night and 25°C during the day in 16 hr in dark and 8 hr in light. Emergence of the radicle was the indication of seedling emergence. After two weeks of incubation, the germinated seeds were

counted and removed from each petri dish. The remaining ungerminated seeds were then used in the dormancy test. Tetrazolium chloride test was used to test seed viability. The test includes two replications of 100 seeds of each species. Seeds were placed in 100 by 15-mm petri dish lined with Kimpak material, which was soaked in a 1% tetrazolium chloride solution (AOSA 2000).

Data Analysis

Differences among percent germination, dormancy, and viability were tested by analysis of variance (ANOVA). Mean separations were achieved with Fisher's protected least significance difference (LSD) comparisons ($p \leq 0.05$) (Peterson 1985).

Emergence Study

Experimental Design. This experiment was conducted in a plant growth room at the USDA-Agricultural Research Station in Burns, Oregon. Monocultures of Purple coneflower, Arrowleaf balsamroot, Annual sunflower, Dotted gayfeather, Western white yarrow, and Sticky geranium and a mixture of all the indigenous forbs were used to test emergence of each individual plant species and the combination of forbs at two densities and under two watering frequencies. Seeding densities were 800 or 2,000 seeds/m². Pots were misted with about 50 ml of water two (Tuesday and Friday) and three times (Sunday, Tuesday, and Friday) weekly beginning on 12 December 2003 and ending on 11 February 2004. This study included 28 treatments (two seed density, two misting frequencies, six monocultures, and one mixture). Pots were arranged in split-split plot design with seeding density and watering as whole plots and monocultures or mixtures as subplots. The experiment was replicated 10 times.

Procedures. Pots were filled with "A" horizon soil from an Idaho fescue and Bluebunch wheatgrass habitat type located at Placidea Butte about 58 km west of Burns, Oregon. Soils are classified as Madeline-Decantel Variant complex, which is a very cobbly sandy loam (Lentz & Simonson 1986). The soil was saturated with water and allowed to equilibrate to pot capacity in the growth room. Because invasive plants possess large and persistent seed banks (Davis 1990), we seeded a background density of 2,000 seeds/m² of Spotted knapweed in all pots. Seeds of all species were manually broadcasted in plastic pots, each with a 1,540-mm² soil surface area and 111 mm deep. About 2-mm depth of soil was used to cover the surface of the soil following seeding. Room temperature was set at a constant temperature of 22°C. Plants were allowed to emerge and grow for 62 days.

Sampling. Species density was recorded by counting seedlings of each species in each pot. Species richness was determined for each pot. Richness was measured as the total number of species (Purple coneflower, Arrowleaf balsamroot, Annual sunflower, Dotted gayfeather, Western white yarrow, and Sticky geranium) per experimental

pot. Species richness can be considered the same as frequency in pots only seeded within a single species.

Data Analysis. Seedling density data were analyzed using ANOVA for a split-split plot procedures described by Cody and Smith (1997). Whole plots were tested using the replication \times main effect interaction as the error term. The interaction of seed density and watering was tested using the replication \times seed rate \times watering frequency as the error term. All other main effects or interactions were tested using the error term for the overall model. Means were separated using Fisher's protected LSD comparisons at the 0.05 level of significance (Peterson 1985).

Survivorship and Competition

Experimental Design. We used Spotted knapweed, Purple coneflower, and a mixture of Purple coneflower and associated forbs (Arrowleaf balsamroot, Annual sunflower, Dotted gayfeather, Western white yarrow, and Sticky geranium) as a model system to test our hypotheses that a mixture would be more competitive than a monoculture against Spotted knapweed. Varying densities and proportions of Spotted knapweed and Purple coneflower were arranged to provide one addition series matrix (Radosевич 1987). In another matrix, Spotted knapweed was seeded with the mixture of forbs in the same densities and proportions. Densities of both matrices were 0:0, 0:100, 0:400, 0:700, 0:1,000, 100:0, 100:100, 100:400, 100:700, 100:1,000, 400:0, 400:100, 400:400, 400:700, 400:1,000, 700:0, 700:100, 700:400, 700:700, 700:1,000, 1,000:0, 1,000:400, 1,000:700, and 1,000:1,000 seeds per pot based on pure live seeds. Initial density ranged from 0 to 1,200 plants/m², whereas final density ranged from 0 to about 1,000 plants/m². Each matrix and density combination was replicated four times, and pots were completely randomized and placed in a growth room at 22°C.

Procedures. Seeds were sown in 1,824 mm² (surface area) \times 400 mm (depth)-polyvinyl chloride tubes from 7 November 2002 to 12 November 2002. Tubes were filled with nonpasteurized soil that had been sieved through a 2-mm screen. The soil was a Calcic arguistoll, which is a Varny clay loam (consisting only of "A" horizon soil) from Red Bluff Research Ranch, located near Norris, Montana. The soil was saturated with water and allowed to equilibrate to pot capacity. Seeds were broadcast on the soil surface and manually arranged until a uniform distribution was achieved. A small amount (<2-mm depth) of dry soil was used to cover the seeds. Soil was evenly misted on alternate days until emergence. No further misting or watering occurred after emergence. Tubes were placed randomly in a growth chamber (10°C, 12-hr day length, 500 μ E m⁻² s⁻¹ spectral light). Plants were allowed to grow for 85 days after seeding. Conditions of this study were within the range of those found during establishment of forbs within the Bluebunch wheatgrass/Idaho fescue habitat type (Mueggler & Stewart 1980).

Sampling. Three weeks after initial seeding, density by species was counted in each pot to determine initial emergence density. Density was also counted at the term of the experiment (final density). Plants were harvested at ground level and separated by species on day 85. Plant material was then dried for one week at 60°C and weighed.

Data Analysis

Survivorship. Data were incorporated into simple linear regression models using initial density to predict final density for Purple coneflower and the mixture at each Spotted knapweed density (0, 100, 400, 700, and 1,000 plants/m²). Differences in intercepts (β_0) and survivorship rates (β_i) were determined by calculating regression coefficients for each replication ($n = 4$) and comparing beta coefficients for Purple coneflower with that of the mixture using ANOVA (Neter et al. 1989).

Competition. Data were incorporated into multiple linear regression models using initial and final density of each species to predict their biomass (Spitters 1983). Regressions predicted the biomass of an isolated individual of Purple coneflower, forb mixture, and Spotted knapweed as dependent variables using initial and final densities of Purple coneflower, forb mixture, and Spotted knapweed as independent variables. The predictor variable was the measured densities, and the response variable was biomass per plant. The r^2 values from the three individual regressions were evaluated to determine the most suitable model (Spitters 1983). The regressions were of the form

$$y_s = \beta_{0s} + \beta_{sp}N_p + \beta_{sm}N_m + \beta_{ss}N_s$$

$$y_m = \beta_{0m} + \beta_{mp}N_p + \beta_{mm}N_m + \beta_{ms}N_s$$

$$y_p = \beta_{0p} + \beta_{pp}N_p + \beta_{pm}N_m + \beta_{ps}N_s$$

where y_s , y_m , and y_p are the response of each species (average weight or biomass of Purple coneflower, forb mixture, and Spotted knapweed); β_{0s} , β_{0m} , and β_{0p} is the y -intercept (intercept as the weight of individuals in a pot); $\beta_{ss}N_s$, $\beta_{mm}N_m$, and $\beta_{pp}N_p$ are the coefficients of intraspecific competition of species s , m , and p and their density (N_s , N_m , and N_p); β_{sp} , β_{sm} , β_{pm} , β_{ps} , β_{mp} , and β_{ms} are the interspecific competition coefficients and their density (N_s , N_m , and N_p). Because the data were not transformed, a positive response denotes positive interference and a negative response denotes negative interference. The relative competitive ability of each species is calculated as

$$RC_s = \beta_{ss}/\beta_{pm} \quad \text{and} \quad RC_m = \beta_{mm}/\beta_{mp}$$

$$RC_m = \beta_{mm}/\beta_m \quad \text{and} \quad RC_s = \beta_{ss}/\beta_{sm}$$

$$RC_p = \beta_{pp}/\beta_{ps} \quad \text{and} \quad RC_s = \beta_{ss}/\beta_{sp}$$

where RC_s , RC_m , and RC_p are the relative competitive abilities of all the species on species s , m , and p . Relative competitive abilities of each species are used to calculate niche differentiation (Spitters 1983):

$$ND = (\beta_{pp}/\beta_{pm})/(\beta_{mp}/\beta_{mm}) = RC_p/RC_m$$

$$= (\beta_{pp}/\beta_{pm})/(\beta_{mm}/\beta_{mp})$$

$$ND = (\beta_{mm}/\beta_{ms})/(\beta_{sm}/\beta_{ss}) = RC_m/RC_s$$

$$= (\beta_{mm}/\beta_{ms})/(\beta_{ss}/\beta_{sm})$$

$$ND = (\beta_{pp}/\beta_{ps})/(\beta_{sp}/\beta_{ss}) = RC_p/RC_s$$

$$= (\beta_{pp}/\beta_{ps})/(\beta_{ss}/\beta_{sp})$$

where ND = niche differentiation. Niche differentiation increases as ND departs from unity, that is, species s , m , and p are decreasingly limited by the same resources. Nonsignificant competition coefficients indicate complete niche differentiation in which there is no interaction between species.

Results

Germination, Dormancy, and Viability

All species differed in germination (Fig. 1). Arrowleaf balsamroot had the lowest germination, which was about 2%. Sticky geranium seeds had slightly higher germination (14%) than Arrowleaf balsamroot. Annual sunflower germination was about 22%. Purple coneflower and Dotted gayfeather seeds had moderate germination of 47 and 60%. Western white yarrow and Spotted knapweed seeds both had high germination, which was 95 and 98%, respectively.

Seeds that did not germinate were used to quantify dormancy (Fig. 1). Spotted knapweed had zero dormancy because 98% of the seeds germinated and about 2% of

the seeds were unfilled. The same was true for Western white yarrow seeds, which had 95% germination, 0.5% of the seeds were dormant, and about 4% were unfilled. Of the ungerminated Purple coneflower, only 23% of the seeds were dormant. Annual sunflower, Dotted gayfeather, and Sticky geranium all averaged about 33% dormancy. Of the ungerminated Arrowleaf balsamroot seeds, about 77% were dormant.

Species also varied in seed viability (Fig. 1). The lowest viable seeds were the Sticky geranium (45%) and Annual sunflower (59%). Purple coneflower and Arrowleaf balsamroot both had moderately viable seeds, which was 70 and 79%, respectively. Dotted gayfeather, Western white yarrow, and Spotted knapweed seeds were 93, 95, and 98% viable, respectively.

Emergence

Total Density. The influence of seed density on resulting forb density depended on the watering frequency ($p = 0.0054$). Seeding at 800 seeds/m² while watering twice produced about 0.5 seedlings per pot (Fig. 2). Increasing water from two to three times per week increased seedling density to 2.2 plants/pot at this seeding rate. The highest seed density produced highest plant density, which averaged 4.35 plants per pot, regardless of water frequency.

The effects of seed density or watering frequency on plant density depended on the particular species or mixture ($p = 0.0001$). Seeding at 2,000 seeds/m² increased the seedling density of most species by 3- or 4-fold over those pots seeded with 800 seeds/pot (Fig. 3). The exception was Arrowleaf balsamroot, which did not establish. The density of the mixture was similar to the mean density for the individual species and it almost doubled in response to the highest seed density. Arrowleaf balsamroot (0.0 plants/pot) and Sticky geranium (0.8 plants/pot) produced the

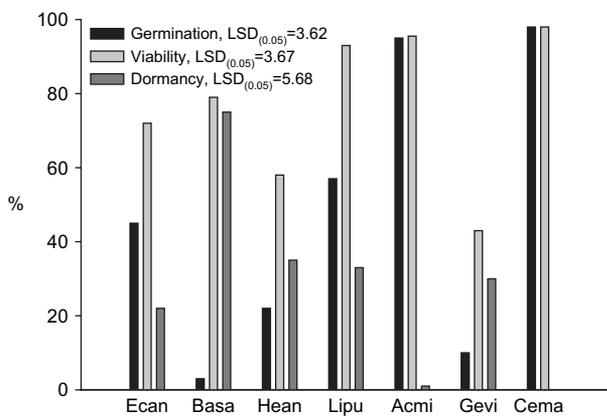


Figure 1. Percent germination (G), viability (V), and dormancy (D) of Purple coneflower (Ecan), Arrowleaf balsamroot (Basa), Annual sunflower (Hean), Dotted gayfeather (Lipu), Western white yarrow (Acmi), Sticky geranium (Gevi), and Spotted knapweed (Cema).

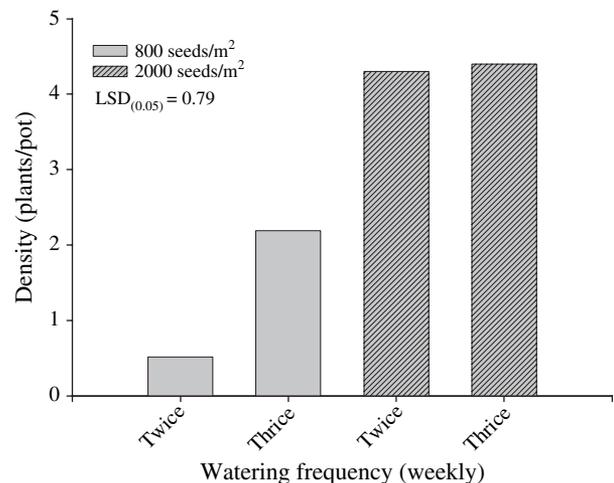


Figure 2. The influence of watering frequency and seed density on density across all species, except Spotted knapweed.

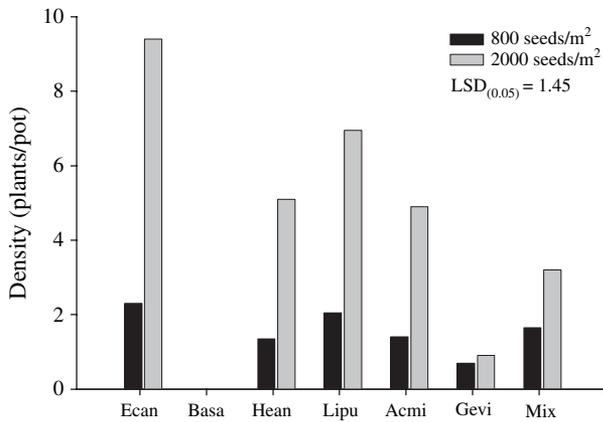


Figure 3. The influence of seed density on Purple coneflower (Ecan), Arrowleaf balsamroot (Basa), Annual sunflower (Hean), Dotted gayfeather (Lipu), Western white yarrow (Acmi), Sticky geranium (Gevi), and the mixture on desired forbs density.

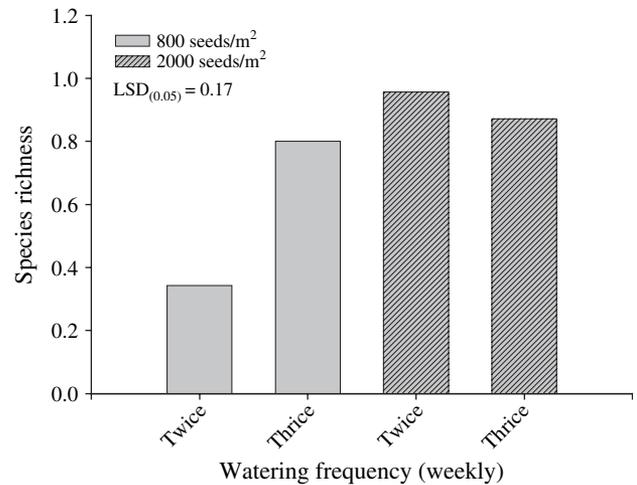


Figure 5. The influence of seed density and watering frequency on species richness.

lowest plant density and were unaffected by watering frequency (Fig. 4). Annual sunflower and Western white yarrow produced intermediate emergence densities, regardless of watering frequency, ranging from 2.4 to 3.9 plants/pot. Plant densities of these two species were lower than those of Purple coneflower when watered twice weekly. In the most frequent watering regime, Purple coneflower yielded the highest density, which was 7.3 plants/pot. The mixture produced 2.3 and 2.6 plants/pot when watered twice and thrice weekly, respectively.

Species Richness. The influence of seed density on species richness depended on either water frequency and the particular species or mixture ($p = 0.0001$). Seeding at 800 seeds/m² combined with watering twice weekly yielded the lowest species richness (Fig. 5). All other seed density and watering treatments yielded similar species richness,

which was two or three times greater than that yielded by the lowest seed density and watering frequency.

Arrowleaf balsamroot did not establish. Purple coneflower, Annual sunflower, Western white yarrow, and Sticky geranium yielded similar mean richness when seeded at 800 plants/m², which ranged from 0.45 to 0.60 species per pot (Fig. 6). Dotted gayfeather yielded higher richness than Sticky geranium at this seed density, indicating that plants did not always establish in all replications. The mixture yielded higher richness than any monocultures when seeded at 800 seeds/m². At 2,000 seeds/m², Purple coneflower, Annual sunflower, Dotted gayfeather, and Western white yarrow yielded similar richness, which neared 1.0. Sticky geranium richness was 0.55 at the highest seed density, which was the lowest of any species that emerged. The mixture yielded a richness of 3.2 when seeded at 2,000 seeds/m², which was higher than any other treatment.

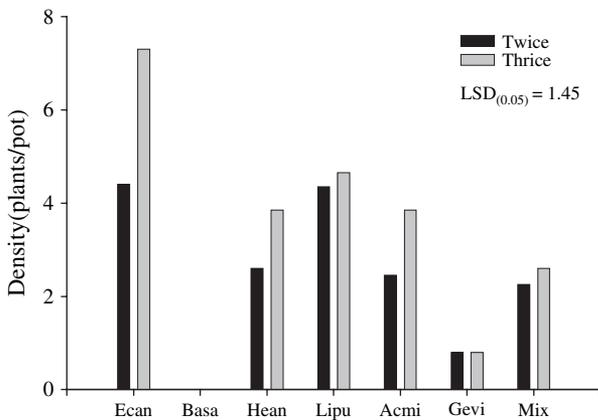


Figure 4. The influence of watering frequency on Purple coneflower (Ecan), Arrowleaf balsamroot (Basa), Annual sunflower (Hean), Dotted gayfeather (Lipu), Western white yarrow (Acmi), Sticky geranium (Gevi), and the mixture on desired forbs density.

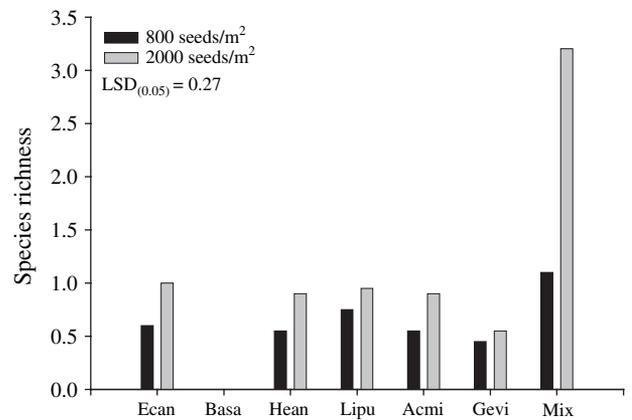


Figure 6. The influence of seed density on Purple coneflower (Ecan), Arrowleaf balsamroot (Basa), Annual sunflower (Hean), Dotted gayfeather (Lipu), Western white yarrow (Acmi), Sticky geranium (Gevi), and the mixture on species richness.

Survivorship

Regression and ANOVA indicated that Purple coneflower and the mixture had similar intercepts, regardless of the background density of Spotted knapweed (Fig. 7). The only exception was that Purple coneflower had a higher intercept than the mixture where Spotted knapweed was not seeded. All intercepts approached zero, except that of Purple coneflower in pots not seeded with Spotted knapweed, where the final density was about 200 plants/m².

Based on the beta coefficient, there was a positive relationship between initial and final density for Purple coneflower and the mixture in all cases (Fig. 7). Survivorship of Purple coneflower and the mixture did not significantly differ where either 0 or 100 seeds per pot of Spotted knapweed were seeded as a background. In pots where Spotted knapweed was seeded with 400, 700, or 1,000 seeds, survivorship was higher for the mixture than for Purple coneflower. For example, at 400 Spotted knapweed seeds per pot, it required 11 ($\beta = 0.09$) initial plants of Purple coneflower for a single plant at the final count, whereas a single surviving plant resulted from two plants of the mixture ($\beta = 0.52$).

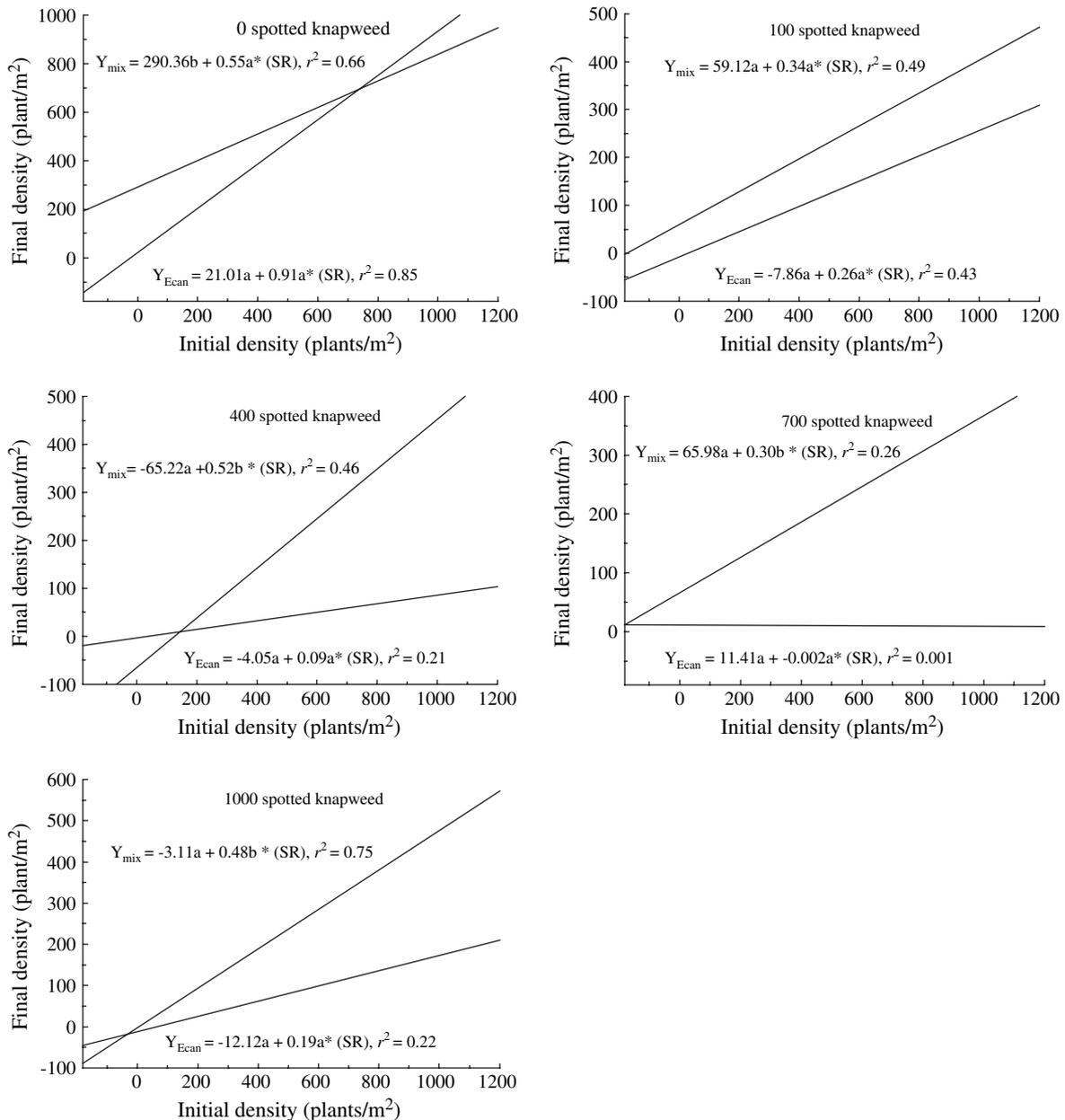


Figure 7. Regressions comparing survivorship of Purple coneflower (Ecan) and a mixture of forbs (mix). Regression coefficients by the same letters indicate they are not significantly different at $\alpha = 0.05$.

Competition

Initial Density versus Biomass. The maximum predicted biomass of an isolated individual was 183.5, 12.2, and 46.7 g/plant for Spotted knapweed, Purple coneflower, and the forb mixture (treated as an isolated individual for the analysis), respectively (Table 1). Adding a single Purple coneflower reduced Spotted knapweed biomass by 0.0038 g/plant. An increase by one unit in the forb mixture reduced Spotted knapweed by 0.0295 g/plant. Adding an individual Spotted knapweed plant increased Spotted knapweed biomass by 0.0118 g/plant. Adding a Purple coneflower plant increased Purple coneflower biomass by 0.0366 g/plant. An increase by one unit in the forb mixture reduced Purple coneflower by 0.0057 g/plant. Adding an individual Spotted knapweed decreased Purple coneflower by 0.0015 g/plant. Adding an individual Purple coneflower decreased the forb mixture by 0.0455 g/plant. Adding one unit to the forb mixture increased the forb mixture by 0.066 g/plant. Adding an individual Spotted knapweed plant reduced the forb mixture by 0.005 g/plant.

Final Density versus Biomass. The maximum predicted biomass of an isolated individual was 176, 31.2, and 4.3 g/plant for Spotted knapweed, forb mixture (treated as an isolated individual for the analysis), and Purple coneflower, respectively (Table 2). Adding an individual Purple coneflower plant decreased Spotted knapweed biomass by 0.06 g/plant. Adding one unit to the forb mixture reduced Spotted knapweed by 0.07 g/plant. Adding an individual Spotted knapweed plant increased Spotted knapweed biomass by 0.04 g/plant. Adding a Purple coneflower plant increased Purple coneflower biomass by 0.1 g/plant. Adding one unit to the forb mixture reduced Purple coneflower by 0.004 g/plant. Adding an individual Spotted knapweed decreased Purple coneflower by 0.001 g/plant. Adding an individual Purple coneflower decreased the forb mixture by 0.06 g/plant. Adding one unit to the forb mixture increased the forb mixture by 0.14 g/plant. Adding an individual Spotted knapweed plant reduced the forb mixture by 0.01 g/plant.

Niche Differentiation. The double ratio (niche differentiation) analysis indicates that resource partitioning occurred with respect to initial and final density to the total biomass of Purple coneflower versus mixture, mixture versus Spotted knapweed, and Purple coneflower versus Spotted knapweed (Tables 3 & 4). Ratios ranged from 5.3 to 75.8.

Discussion

Traditionally, species choice for seeding during revegetation has focused on establishing a single species, typically grasses for livestock production (Mueggler & Stewart 1980). Where mixtures are recommended they often only include grasses (Borman et al. 1991). Sustainable rehabilitation and restoration must include forbs because they play important roles in nutrient cycling and energy flow (Pokorny et al. 2004), and they provide resistance to invasion (Carpinelli 2001; Pokorny 2002). However, establishing forbs is very difficult because of their individual propagation characteristics (Rose 1998). We found evidence supporting our hypothesis that seeding a rich mixture of species would provide average, but consistent, seedling establishment. In our study, two species had lower establishment than the mixture, two species had similar density as the mixture, and two species had higher density than the mixture. Although some species had lower emergence in the driest regime, the establishment within the mixture was not influenced by watering. This suggests that without a priori knowledge of species germination and establishment characteristics, or stable weather patterns, a mixture may provide consistent forb establishment. Seeding success using a single species relies on the quality of the knowledge about the propagation of that species. A mixture may possess a variety of requirements for germination and emergence, so at least one or two species traits match current year conditions. In unpredictable environments common throughout the semiarid steppe of the western United States, restorationists may enhance the establishment of native forbs by seeding a rich mixture of species.

Increasing either water frequency or seed density increased establishment. Although their study only considered grasses, Sheley et al. (1999) found that increasing seed density resulted in greatly increased establishment after two years. Although seeding at 500 seeds/m² resulted in no establishment, seed densities of 2,500 and 12,500 seeds/m² resulted in tiller densities of 80 and 140 plants/m², respectively, at one site and 158 and 710 plants/m² at a second site. In our study, increasing the seed density about 2.5 times increased emergence of four species 3- to 4-fold. Increasing the seed density of the mixture doubled the density of forbs. It appears that increasing the seed density enhances the likelihood that a seed reaches a safe site for germination (Sheley et al. 2005). Restorationists may enhance native forb establishment by increasing the

Table 1. Multiple regression analysis for the prediction of biomass (g/plant) using their initial density.

Dependent Variable Biomass (g/plant)	Intercept (β_0)	Purple Coneflower (β_1)	Forb Mixture (β_2)	Spotted Knapweed (β_3)	r^2
Spotted knapweed	183.5	-0.0038	-0.0295	0.0118	0.38
SE	12.09	0.02	0.008	0.001	
Purple coneflower	12.20	0.0366	-0.0057	-0.0015	0.28
SE	3.47	0.005	0.002	0.0004	
Forb mixture	46.70	-0.0455	0.066	-0.005	0.48
SE	8.75	0.01	0.006	0.0009	

Table 2. Multiple regression analysis for the prediction of biomass (g/plant) using their final density.

Dependent Variable Biomass (g/plant)	Intercept (β_0)	Purple Coneflower (β_1)	Forb Mixture (β_2)	Spotted Knapweed (β_3)	r^2
Spotted knapweed	176.03	-0.06	-0.07	0.04	0.64
SE	10.58	0.02	0.01	0.003	
Purple coneflower	4.26	0.10	-0.004	-0.001	0.79
SE	2.15	0.004	0.002	0.0006	
Forb mixture	31.22	-0.06	0.14	-0.01	0.74
SE	7.11	0.01	0.007	0.002	

Table 3. Double ratio assessing niche differentiation.

Dependent Variable	Niche Differentiation
Purple coneflower versus forb mixture	-9.3
Forb mixture versus Spotted knapweed	5.3
Purple coneflower versus Spotted knapweed	75.8

The greater the distance from unity, the greater the differentiation.

Table 4. Double ratio assessing niche differentiation.

Dependent Variable	Niche Differentiation
Purple coneflower versus forb mixture	66.7
Forb mixture versus Spotted knapweed	8
Purple coneflower versus Spotted knapweed	58.1

The greater the distance from unity, the greater the differentiation.

seeding rate. Conversely, we believe that increasing watering frequency increased the availability of safe sites for germination and emergence.

Germination, dormancy, and viability are often provided to restorationists in hopes of allowing the prediction of emergence of each species (Sheley et al. 1993). However, other studies focusing on forbs have found little relationship between germination or viability of each species and their emergence (Wirth & Pyke 2003). In our study, low germination of Arrowleaf balsamroot and Sticky geranium indicated poor establishment, which occurred. Conversely, high germination and/or viability did not necessarily translate directly into higher establishment. Therefore, we believe that the ability to predict forb emergence from germination, dormancy, and viability data is unlikely (Rose 1998).

Comparison of survival rates of the mixture versus Purple coneflower revealed that seeding a mixture had substantial benefits for enhancing the final density of forbs, especially if high densities of invasive weeds are present in the seed bank (Davis 1990). We suggest that under increased competition, the wide range of forb species occupied more niches and facilitated greater overall survival (e.g., Carpinelli 2001).

Spotted knapweed, when sown with a diverse mixture of species that included alfalfa, was more competitive than the desired species during the first two years of establishment (Carpinelli et al. 2004). However, the desired mixture ultimately dominated the site seven years later (Sheley et al. 2005). We found partial evidence that a mixture of species would be more competitive with Spotted knapweed during establishment. When using initial density to predict biomass, the forb mixture had a 7-fold stronger influence on Spotted knapweed biomass than Purple coneflower alone. However, when using final density to predict biomass the two coefficients were nearly the same. In both analyses, the mixture had greater niche overlap than Purple coneflower alone, suggesting that the mixture was using resources more similarly to Spotted knapweed. Seeding a rich seed mixture may also provide greater resistance to reinvasion by exotic weeds.

It is critical that forbs are a part of the species mixtures if revegetation is to be sustainable (Pokorny 2002). However, despite this importance, forbs are often not included in seed mixtures because of their difficulty of establishment. We believe that using a mixture of forbs, rather than a single species, will enhance the likelihood of establishment in various and unpredictable environment. This is because the group possesses a variety of traits, some of which may match year-year and site-site environments. Furthermore, once a higher richness of forbs is established, they may be more competitive with invasive weeds and therefore, persist longer.

Implications for Practice

- Managing invasive forb weeds requires the establishment and maintenance of desired forb species, which has been very difficult.
- One problem is that weather conditions in any given year may not match the germination and emergence requirements of desired species.
- Using more than one species from the same functional group, such as forbs, may help overcome the year-year variation in weather because at least some species within the functional group may have traits allowing germination under the current year's weather conditions.
- Once a diverse group of species is established, the group can outcompete the weeds and will likely persist longer.

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