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Invasion is Contingent on Species Assemblage and Invasive Species Identity in Experimental Rehabilitation Plots

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Abstract

Ecological studies often suggest that diverse communities are most resistant to invasion by exotic plants, but relatively few local species may be available to a rehabilitation practitioner. We examine the ability of monocultures and diverse assemblages to resist invasion by an exotic annual grass (cheatgrass) and an exotic biennial forb (dyer's woad) in experimental rehabilitation plots. We constructed seven assemblages that included three monocultures of grass, forb, or shrub; three four-species mixtures of grasses, forbs, or shrubs; and a three-species mixture of one species from each growth form in an experimental field setting to test resistance to invasion. Assemblages were seeded with cheatgrass and dyer's woad for two consecutive years and quantified as biomass and density of individuals from each exotic species. Soil NO_3^- and leaf-area index were examined as predictors of invasive plant abundance. Cheatgrass invasion was greatest in forb and shrub assemblages, and least in mixed grass or grass monoculture; dyer's woad invasion was greatest into mixed grass or grass monoculture, but least into monoculture or mixed-species assemblages composed of forbs or shrubs. The community composed of grasses, forbs, and shrubs suppressed invasion by both species. Consequently, assemblages were most resistant to invasion by species of the same growth form. Moreover, these monocultures and mixtures were generally similar in conferring resistance to invasion, but a monoculture of big sagebrush was more resistant than a mixture of shrubs. Soil NO_3^- was correlated with invasion by cheatgrass, whereas LAI was correlated with invasion by dyer's woad, suggesting these species were more limited by belowground and aboveground resources, respectively. Overall, increasing diversity with limited species did not necessarily enhance resistance to invasion.

Key Words: cheatgrass, dyer's woad, growth form, invasion resistance, species assemblage

INTRODUCTION

Seedings and plantings in rangelands throughout western North America are used to rehabilitate degraded pastures, provide forage for livestock and wildlife, and secure other ecosystem services. One such critical service is resistance to invasion by exotic plant species (Bakker and Wilson 2004; Pokorny et al. 2005; Funk et al. 2008; Benayas et al. 2009). Exotic plants are one of the most important threats to rangelands today, costing land managers in excess of \$5 billion per year in control and lost productivity (Pimental et al. 2005). Consequently, there is direct value in restoring productivity and preventing future invasion. An objective of many rehabilitation efforts is to establish a plant community on degraded land that will resist future invasion.

Although unassisted recovery of a plant community is constrained by the regional species pool and dispersal, rehabilitation following severe degradation is constrained by availability of species to practitioners (Burton and Burton 2002; Hufford and Mazer 2003; Bakker and Wilson 2004). High-diversity communities can be more resistant to invasion than lower-diversity communities because they may fully exploit above- and belowground resources (Elton 1958; Tilman 1997; Levine and D'Antonio 1999) or be more likely to contain a native species that preempts the niche (i.e., the sampling effect, Huston 1997; Fargione and Tilman 2005). These hypotheses have been supported in several studies (Naeem et al. 2000; Fargione and Tilman 2005; Pokorny et al. 2005; Hooper and Dukes 2010) with the specific finding that exotic species are suppressed by native species of similar growth form (Fargione et al. 2003). This relationship applies at the small scale (i.e., plot studies), but not necessarily at larger ones (Stohlgren et al. 1999; Fargione and Tilman 2005). For rehabilitation, however, only a subset of local species may be available for any activity, reducing the potential benefit of a diverse community. For example, Bakker and Wilson (2004) used five species in their experimental restoration of a northern Great Plains grassland, and only 11–12 species were used in an experimental restoration of a disturbance caused by oil shale extraction (Hoelzle et al. 2012). Although the US Bureau of Land Management stocks dozens of species (Shaw et al. 2005), the agency recommends fewer than 10 species for projects (Thompson et al. 2006). Rehabilitating a community that is

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resistant to invasion from a limited species pool can be challenging if invasion resistance is dependent on a nonrandom selection of species (Zavaleta and Hulvey 2004; Selmants et al. 2012).

Great Basin plant communities in the western United States are excellent model systems for examining the dependence of invasion resistance on community composition. Great Basin communities have experienced one of the most profound plant invasions in North America (Chambers et al. 2007). Following over 100 yr of livestock grazing and increased wildfire frequency, intensity, and scale, millions of hectares of historically perennial communities have been converted to near monocultures of exotic annual grasses (Knapp 1996; Pellant et al. 2004; Mensing et al. 2006), including *Bromus tectorum* L. (cheatgrass). More recently, secondary exotic forbs such as *Isatis tinctoria* L. (dyer's woad) and *Centaurea maculosa* (spotted knapweed) have invaded (Farah et al. 1988; Prév y et al. 2010). Although reestablishing perennial vegetation to reduce fire frequency and increase forage for wildlife and domestic livestock is critical in these landscapes (Pellant et al. 2004), the ability of rehabilitated landscapes to resist future invasion by these or other species is unclear.

Rehabilitations in the Great Basin historically involved establishing monocultures of exotic perennial grasses, but multispecies seedings are now more common. For example, *Agropyron cristatum* (L.) Gaertner (crested wheatgrass) was planted on millions of hectares in the western United States, despite it being an exotic species (Rogler and Lorenz 1983). Crested wheatgrass is an effective competitor with cheatgrass, because of its high relative growth rate and rapid uptake of soil nitrogen (Aguirre and Johnson 1991; Bilbrough and Caldwell 1997; Leffler et al. 2011). Seeding crested wheatgrass has been extensive (Rogler and Lorenz 1983), but doing so simply replaces a potential monoculture of cheatgrass with a potential monoculture of an exotic perennial grass. Stabilizing degraded sites with additional species might provide resistance to a broader suite of potential invaders because diverse communities more completely use above- and belowground resources (Hooper and Vitousek 1998; Mack et al. 2000; Spehn et al. 2000; Fargione and Tilman 2005). Additionally, diverse communities may be more suitable to native species establishment and provide greater value to wildlife (Pendery and Provenza 1987; Cox and Anderson 2004). Recent studies suggest communities of multiple functional groups, particularly those with forbs present, promote resistance to spotted knapweed invasion (Pokorny et al. 2005; Sheley and Carpinelli 2005).

We evaluate resistance to invasion of assembled communities composed of readily available species representative of the three dominant perennial growth forms (grasses, forbs, and shrubs) in shrub-steppe ecosystems. Assemblages were composed of single monoculture and four-species mixes of each growth form, and a three-species mix of one species from each of the three growth forms. Seeds of cheatgrass and dyer's woad were introduced into plots of species assemblages for 2 consecutive years, and resistance to invasion was determined by quantifying seedling density and shoot dry mass during two summers. We tested the following hypotheses: 1) within a growth form, diverse assemblages will be more resistant to invasion than a monoculture; 2) resistance to invasion is

proportionally greater in assemblages that contain species of the same growth form as the invader; and 3) the multiple growth form assemblage will be equally resistant to both species. In addition, we hypothesize that 4) aboveground and belowground resource availability will be positively correlated with plant invasion. We specifically examine leaf-area index (LAI) as a proxy for light availability, and soil NO_3^- during the autumn before invasive-species density and dry mass were sampled.

MATERIALS AND METHODS

Study Site

The experiment was conducted at Millville, Utah, USA (41°39.44'N, 111°48.88'W, 1402 m). Millville is a typical Intermountain West cold desert ecosystem (Caldwell 1985). Approximately 75% of total annual precipitation occurs as winter snowfall or spring and autumn rains when plants are not active. Consequently, this winter pulse of water provides essentially all the soil moisture for the growing season (Huxman et al. 2004) and plant growth is typically confined to April through June. During this time, much of the available soil N is depleted in perennial communities, but invasive annual-grass-dominated communities typically show higher soil $[\text{NO}_3^-]$ because they senesce early in the summer, allowing NO_3^- to accumulate because little leaching can occur (Booth et al. 2003; Hooker et al. 2008). Soil $[\text{NH}_4^+]$ remains low in Great Basin soils during late summer (Booth et al. 2003; Hooker et al. 2008). In this system, invasive annual grasses such as cheatgrass often germinate in the autumn and overwinter as a seedling, completing their life cycle the following spring (Knapp 1996). Deeper-rooted invasive plants such as dyer's woad germinate in the spring or autumn (Farah et al. 1988).

The study site was dominated by *Artemisia tridentata* spp. Nutt. (big sagebrush) and other native steppe species prior to settlement in the 1850s (Hull and Hull 1974). Most recently, the site was used for corn and alfalfa production, but was fallow from fall 2002 to spring 2003. Soils are a Ricks gravelly loam (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Calcic Haploxerolls). The 30-yr-average annual precipitation is 457 mm and was 690 mm and 535 mm in 2005 and 2006, respectively.

Plants for this experiment were initiated from seed in December 2002 in small containers (22 cm deep, 4-cm diameter), reared in a greenhouse until plants were ca. 15 cm in height, and transplanted to 1.5 × 1.5 m plots in May 2003. Each plot consisted of 24 plants in a 5 × 5 square arrangement equally spaced (30 cm apart) with the center plant missing to accommodate plot access by researchers, and 1-m-wide aisles separating plots. Seven species assemblages, each replicated 15 times, were randomly assigned to plots (Table 1). These assemblages consisted of three monocultures (grass [G-Mono], forb [F-Mono], or shrub [S-Mono]), three four-species mixtures of three growth forms (i.e., grass [G-Mix], forb [F-Mix], or shrub [S-Mix]), and a three-species mixed-growth-form assemblage composed of one species from each of the three growth forms (GFS-Mix). Assemblages were constructed with native and nonnative sagebrush-steppe species (Table 1)

Table 1. Assemblage name/code and nomenclature of species used to construct species assemblages in this study. Nomenclature follows Welsh et al. (1993), except for crested wheatgrass, which is a release by US Department of Agriculture–Agricultural Research Service, Logan, UT, USA. Status is either (N) indicating a native species, or (E) indicating an exotic species.

Assemblage	Scientific name	Common name (status)
Grass monoculture (G-Mono)	<i>Agropyron cristatum</i> (L.) Gaertner × <i>Agropyron desertorum</i> (Fisch. ex Link) Schultes	Crested wheatgrass ‘CD II’ (E)
Forb monoculture (F-Mono)	<i>Achillea millefolium</i> ssp. <i>lanulosa</i> (Nutt.) Piper	Western yarrow (N)
Shrub monoculture (S-Mono)	<i>Artemisia tridentata</i> ssp. <i>tridentata</i> Nutt.	Basin big sagebrush (N)
Grass forb shrub (GFS-Mix)	<i>Agropyron cristatum</i> (L.) Gaertner × <i>A. desertorum</i> (Fisch. ex Link) Schultes	Crested wheatgrass ‘CD II’ (E)
	<i>Achillea millefolium</i> ssp. <i>lanulosa</i> (Nutt.) Piper	Western yarrow (N)
	<i>Artemisia tridentata</i> ssp. <i>tridentata</i> Nutt.	Basin big sagebrush (N)
Grass mix (G-Mix)	<i>Agropyron cristatum</i> (L.) Gaertner × <i>A. desertorum</i> (Fisch. ex Link) Schultes	Crested wheatgrass ‘CD II’ (E)
	<i>Poa secunda</i> Presl.	Sandberg bluegrass (N)
	<i>Elymus multisetus</i> (J.G. Smith) M.E. Jones	Big squirreltail ‘Sand Hollow’ (N)
	<i>Elymus spicatus</i> (Pursh) Gould	Bluebunch wheatgrass (N)
Forb mix (F-Mix)	<i>Achillea millefolium</i> ssp. <i>lanulosa</i> (Nutt.) Piper	Western yarrow (N)
	<i>Sanquisorba minor</i> Scop.	Small burnet (E)
	<i>Sphaeralcea munroana</i> (Dougl.) Spach in Gray	Munro’s globemallow (N)
	<i>Hedysarum boreale</i> Nutt.	Utah sweetvetch (N)
Shrub mix (S-Mix)	<i>Artemisia tridentata</i> ssp. <i>tridentata</i> Nutt.	Big sagebrush (N)
	<i>Purshia tridentata</i> (Pursh) DC.	Bitterbrush (N)
	<i>Kochia prostrata</i> (L.) Schrader	Prostrate kochia (E)
	<i>Chrysothamnus nauseosus</i> (Pallas) Britt.	Rubber rabbitbrush (N)

commonly used for rehabilitation (Richards et al. 1998; Thompson et al. 2006; Bernstein et al. 2013).

Invasive Species

The experimental plots were seeded with two exotic invasive species: the annual grass *Bromus tectorum* L. (cheatgrass) and the biennial forb *Isatis tinctoria* L. (dyer’s woad) in mid-November 2004 and late October 2005, approximately 18 mo following the initial construction of the plots, and after individual plants in the assemblages more fully occupied the available space (Fig. S1, available at <http://dx.doi.org/10.2111/REM-D-13-00140.s1>). Seed of both invasive species was collected within 1 km of the research area. A total of 400 viable seeds of both species were combined and broadcasted over the central 1 m² of plots in each year. Seed viability was 87% and 43% in 2004, and 91% and 28% in 2005 for cheatgrass and dyer’s woad, respectively; we accounted for fraction of germination to attain the desired viable seeding rate. Prior to seeding exotic species, the central 1-m² area of the soil surface in each plot was lightly scarified with a small garden rake to a depth of about 1 cm, to improve seed catchment and decrease movement of seed outside the plots.

Plot Measurements

We quantified invasion by both species by counting and harvesting seedlings of invasive species in the central 1-m² area of each plot to determine density and shoot dry mass in July 2005 and late June 2006. All seedlings were between 2 and 10 cm tall at the time of harvest and harvest caused negligible disturbance to the plots. Although these seedlings were small, they were harvested after the majority of growth for that season had occurred. The removal of seedlings each summer allowed us to replicate invasive species establishment in 2 consecutive yr in this experiment.

Aboveground shoot biomass was dried for 48 h at 60°C and weighed to determine dry mass. Leaf-area index (LAI) was measured in each plot with the use of a ceptometer (Accupar LP-80, Decagon Devices, Inc., Pullman, WA, USA) to document vegetation density of the assemblages and to use as a predictor of invasion. The ceptometer was placed in four regular locations in the center 1 m² of each plot, on the ground surface, and measured the interception of photosynthetically active radiation (400–700 nm) by the canopy. An above-canopy measurement was also necessary to calculate LAI integrated over the 80-cm linear sensor. We made measurements between 1 100 and 1 300 hours on cloudless days in autumn 2004 and 2005.

Soil nitrate was measured in autumn 2004 and 2005 by taking four 2-cm-diameter by 15-cm-deep soil cores ($n = 6$) in the center 1 m² of each plot to obtain soil samples, which were thoroughly mixed and extracted with 2-M KCl within 2 h of collection. The KCl solutions were filtered through preleached filter paper and frozen until analyzed colorimetrically with a flow injection autoanalyzer (Lachat Instruments, Milwaukee, WI) to determine combined concentrations of NO₂⁻ and NO₃⁻. Soil water content (for accurate NO₃⁻ measurement) was determined gravimetrically on these soil samples by weighing a subsample of the freshly collected soils, drying for 48 h at 105°C, and reweighing.

Statistical Analysis

Our first hypothesis, that diverse assemblages will be more resistant to invasion than monoculture, was tested with analysis of variance (ANOVA) as a factorial experiment with a completely randomized design. The statistical model analyzed the fixed main effects of year, assemblage, and their interaction on response variables of seedling density and shoot dry mass of both invasive species. The ANOVA was followed by a Tukey Honestly Significant Difference (HSD) comparison between

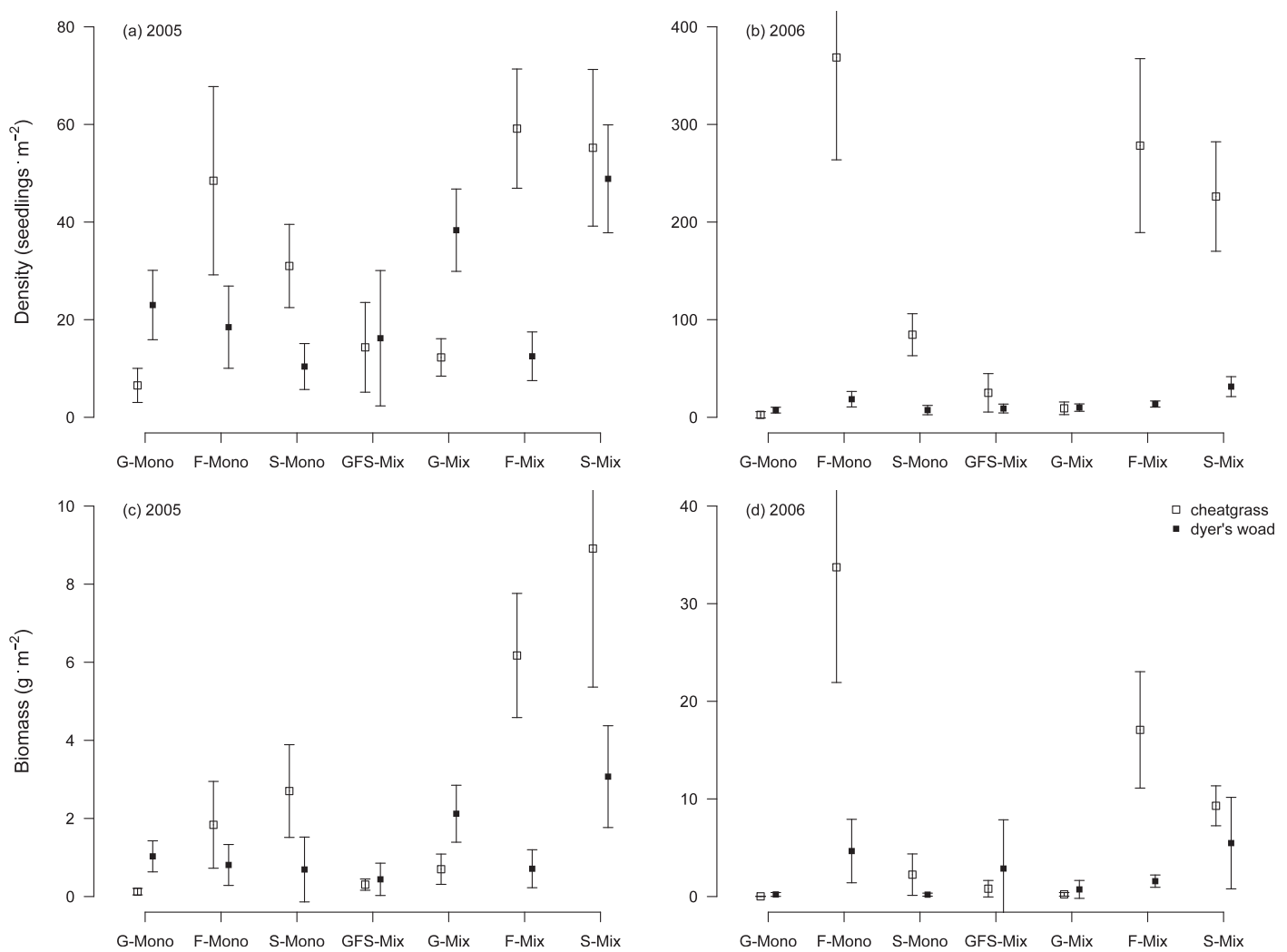


Figure 1. Mean (\pm 95% confidence interval) seedling density (**a** and **b**) and biomass (**c** and **d**) for cheatgrass and dyer's woad in 2005 (**a** and **c**) and 2006 (**b** and **d**) for seven experimental assemblages, $n=15$. Species identification as in Table 1: G-Mono indicates grass monoculture; F-Mono, forb monoculture; S-Mono, shrub monoculture; GFS-Mix, grass forb shrub mixture; G-Mix, grass mix; F-Mix, forb mix; and S-Mix, shrub mix. Some error bars extend beyond the y-axis to aid visualization. Note different y-axis scales among years.

monocultures and mixed-species assemblages within each growth form. The second and third hypotheses regarding susceptibility of different assemblages to invasion by cheatgrass or dyer's woad were examined with an ANOVA on proportional seedling density and shoot dry mass of cheatgrass. Proportional density and dry mass were calculated as the density or mass of cheatgrass normalized by the total density or mass of the sum of cheatgrass and dyer's woad. Proportional data were transformed with arcsine square root to normalize these data prior to analysis with the same ANOVA model as above. Proportional data are graphically presented as the median with an asymmetrical 95% confidence interval derived from a binomial (i.e., bounded 0–1) distribution. We examined the fourth hypothesis regarding resource availability and invasion with the use of Spearman rank correlation between soil NO_3^- or LAI and density or biomass of each invasive species in each of the 2 yr of study. All analyses were conducted with the use of the LM and TUKEYHSD functions (ANOVA)

or COR.TEST (correlation) within the statistical computing language R (R Core Team 2013) with $\alpha=0.05$.

RESULTS

Plot assemblages of different growth forms and species composition differed in exotic annual grass and exotic biennial forb invasion (Fig. 1, Table 2). We observed a significant year \times assemblage interaction for density and biomass of cheatgrass, and for density of dyer's woad, indicating unique responses to assemblage in each year. For biomass of dyer's woad, assemblages differed in invasion, but we observed no significant "year" effect. The pattern was the same for the proportion of density and biomass represented by cheatgrass; for density, there was a significant year \times assemblage interaction, whereas for biomass, only assemblages differed in invasion.

Table 2. *F* values from type III ANOVA evaluating the effects of year (Y) and assemblage (A) on total invasion (density and shoot dry mass) and proportional invasion (density and shoot dry mass). Proportional density and dry mass is the fraction of total invasive individuals or biomass attributable to cheatgrass (or dyer's woad, because cheatgrass and dyer's woad sum to unity in this analysis).

Effect	df	Cheatgrass		Dyer's woad		Proportional invasion	
		Density	Dry mass	Density	Dry mass	Density	Dry mass
Y	1	91.2 ²	33.6 ²	23.8 ²	2.70	24.6 ²	2.74
A	6	31.7 ²	24.6 ²	14.3 ²	2.97 ¹	46.3 ²	44.0 ²
Y × A	6	18.5 ²	18.9 ²	3.91 ¹	1.67	3.02 ¹	1.28

¹*P* < 0.01.

²*P* < 0.001.

The greatest number of invasive individuals of both species was observed in the western yarrow monoculture (F-Mono) and the forb and shrub mixtures (F-Mix and S-Mix, respectively) in 2005 and 2006 (Figs. 1a and 1b). The three least invaded assemblages, as measured by seedling density, were the monoculture of crested wheatgrass (G-Mono), the grass mixture (G-Mix), and the multiple-growth-form mixture (GFS-Mix). In 2005, the most heavily invaded assemblages had between 30 and 60 cheatgrass and up to 50 dyer's woad seedlings · m⁻². In 2006, some assemblages were heavily invaded, including F-Mono, F-Mix, and S-Mix; e.g., over 200 cheatgrass seedlings · m⁻². Fewer dyer's woad individuals established in 2006 than in 2005.

A similar pattern emerged for biomass of each invasive species (Figs. 1c and 1d). The highest biomass was observed in F-Mix and S-Mix assemblages; the lowest invasive biomass was found in G-Mono, the grass mixture (G-Mix), and GFS-Mix. In 2005, the heavily invaded F-Mix and S-Mix assemblages had over 6 g · m⁻² of cheatgrass biomass. In 2006, F-Mono had nearly 35 g · m⁻² of cheatgrass biomass. The greatest biomass of dyer's woad (ca. 5 g · m⁻²) was observed in F-Mono and S-Mix in 2006. However, overall invasive biomass in 2005 was not different from 2006 for dyer's woad (Table 2). Regardless of the measure of invasion or the year, total invasion into the most susceptible assemblages was 10- to 20-fold greater than into the least susceptible assemblages.

Invasion into our mixtures was generally not lower than invasion into our monocultures. Invasion into G-Mono and G-Mix was similar regardless of metric (density or biomass), year, or species (Table 3). Invasion into F-Mono and F-Mix was similar except for biomass of cheatgrass in 2006; here F-Mono experienced greater invasion by cheatgrass than F-Mix. Invasion into S-Mix was generally greater than invasion into S-Mono (Table 3); this result is evident for cheatgrass density in

2006, dyer's woad density in 2005 and 2006, and dyer's woad biomass in 2006.

Assemblages were not susceptible to invasion by the same growth form. Despite lower total invasion, seedling density and shoot dry mass indicate that G-Mono and G-Mix were mostly invaded by dyer's woad, whereas F-Mono, S-Mono, and S-Mix were mostly invaded by cheatgrass (Fig. 2). In several cases, these differences were striking: cheatgrass represented 95% of the invasive seedlings in F-Mono in 2006 and dyer's woad represented 94% of the invasive seedlings in G-Mono across both years. The GFS-Mix assemblage was more equally invaded by both species, with cheatgrass representing between 44% and 62% of density and biomass in both years.

Above- and belowground resource availability varied among assemblages and years (Figs. S2 and S3, available at <http://dx.doi.org/10.2111/REM-D-13-00140.s1>). LAI in 2004 varied between 0.8 and 2.2 for S-Mix and S-Mono plots, respectively. In 2005, LAI varied between 1.5 for G-Mix and 4.1 for S-Mono. Soil NO₃⁻ was between 1.3 and 5.9 μg · g⁻¹ for G-Mono and G-Mix, respectively, in 2004. In 2005, Soil NO₃⁻ varied between 0.77 and 5.47 μg · g⁻¹ in GFS-Mix and F-Mono, respectively. These LAI and NO₃⁻ values indicate considerable production of planted individuals such that little bare ground was evident in the plots (Fig. S1, available at <http://dx.doi.org/10.2111/REM-D-13-00140.s1>). In 2004, soil NO₃⁻ exceeded 22 μg · g⁻¹ in plots with no individuals established.

Measures of resource availability were correlated with success of both invasive species (Table 4). Light availability in the assemblages, as measured by LAI, was a modest predictor of invasion by dyer's woad, but not by cheatgrass. For dyer's woad, high LAI was associated with low density and low biomass in 2005 and 2006. LAI explained ca. 10% of the variation in density or biomass of dyer's woad each year. Soil NO₃⁻ availability was more strongly correlated with density and biomass of cheatgrass than dyer's woad (Table 4). In 2005,

Table 3. *P* values for preplanned Tukey Honestly Significant Difference comparisons between monoculture and mixed-species assemblages within each growth form. Bold values are significant at *P* < 0.05.

	Cheatgrass				Dyer's woad			
	Density		Dry mass		Density		Dry mass	
	2005	2006	2005	2006	2005	2006	2005	2006
Grass	0.999	0.999	0.999	0.999	0.224	0.999	0.999	0.999
Forb	0.999	0.149	0.964	< 0.001	0.998	0.999	0.999	0.773
Shrub	0.999	< 0.001	0.626	0.446	< 0.001	0.002	0.960	0.049

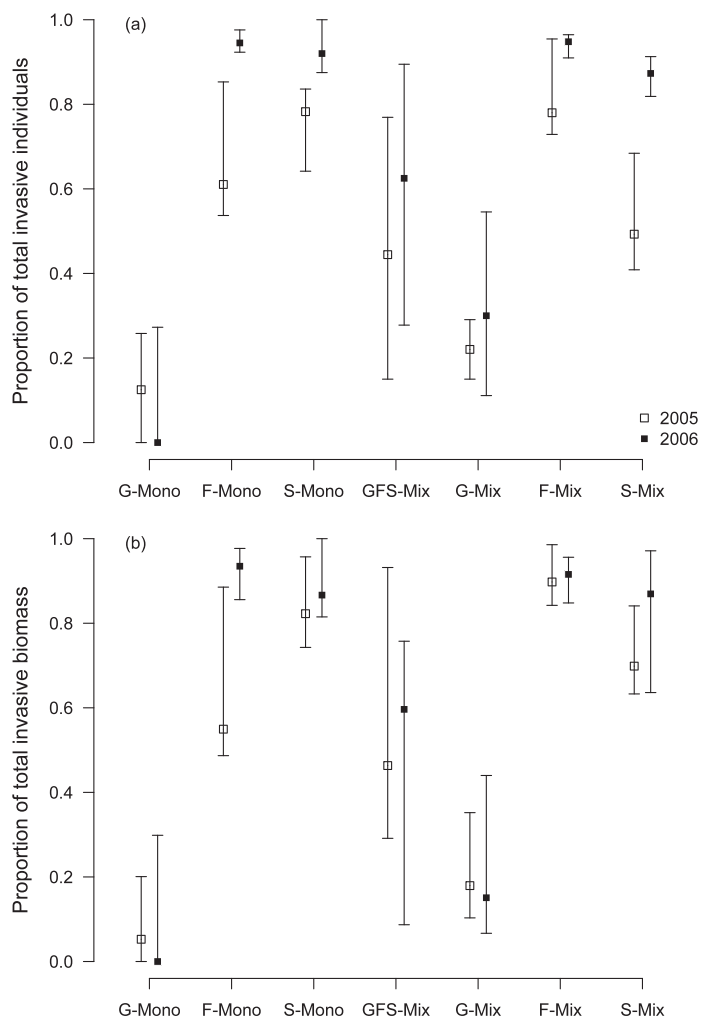


Figure 2. Median (\pm 95% confidence interval) proportion of total invasive species density (a) and biomass (b) as cheatgrass. A value close to 1 indicates nearly all the invasive individuals or biomass were cheatgrass; a value close to 0 indicates nearly all the invasive individuals or biomass were dyer's woad. The balance of individuals or biomass is dyer's woad, because cheatgrass and dyer's woad sum to unity. Species identification as in Table 1: G-Mono indicates grass monoculture; F-Mono, forb monoculture; S-Mono, shrub monoculture; GFS-Mix, grass forb shrub mixture; G-Mix, grass mix; F-Mix, forb mix; and S-Mix, shrub mix.

soil NO_3^- was only moderately correlated with biomass of cheatgrass, explaining ca. 8% of the variation among plots. In 2006, soil NO_3^- explained 21% of the variation among plots in cheatgrass density and biomass, and 10% of the variation

among plots in dyer's woad density and biomass. In all cases, high NO_3^- was associated with either higher density or biomass of the invasive species.

DISCUSSION

Data collected on seedling density and shoot biomass of two exotic invasive species from different growth forms indicate: 1) the mixtures of a single growth form were not more resistant to invasion than monocultures of crested wheatgrass, western yarrow, or big sagebrush; 2) mixtures and monocultures were most resistant to invasion by exotic species of the same growth form; 3) our assemblage of multiple growth forms (GFS-Mix) was equally resistant to both invasive species, whereas our assemblages of a single growth form (G-Mix, F-Mix, S-Mix) were susceptible to one invasive or the other; and 4) above- and belowground resource availability was correlated with invasion. These data partly support theory regarding diversity and resistance to invasion; the most diverse assemblage (GFS-Mix) was resistant to multiple species, but single-growth-form assemblages were not necessarily more resistant than the monocultures examined here.

The first hypothesis, which posited that our single-growth-form assemblages (G-Mix, F-Mix, S-Mix) would be more resistant to invasion than our monocultures (G-Mono, F-Mono, S-Mono), was not supported by these data; some of our monocultures were more resistant to invasion than mixtures. G-Mix was just as effective at resisting invasion as G-Mono, and S-Mono was more effective at conferring resistance than S-Mix. As predicted by theory, F-Mono was less effective at conferring resistance than F-Mix, but only against cheatgrass and only for biomass in 2006.

The pattern we observed suggests choice of species within a growth form is crucial to conferring resistance. For the forbs, F-Mono composed of only western yarrow was highly invaded; the addition of other forbs increased resistance of the assemblage through complementarities with other species in the mix (Hooper 1998; Fargione and Tilman 2005). For the shrubs, big sagebrush effectively resisted invasion, and adding other shrub species into the assemblage, which reduced the relative abundance of big sagebrush, reduced resistance. The enhancement or degradation of resistance by adding additional species to a monoculture may stem from different patterns of resource use among species (Spehn et al. 2000; Fargione and Tilman 2005). Conversely, crested wheatgrass provided strong resistance in monoculture, which was not reduced by the

Table 4. Spearman (rank) correlations coefficients (r) between dependent invasion variables (species density and shoot dry mass) measured in summer 2005 and 2006 and independent plot variables (leaf area index [LAI], soil NO_3^-) measured in autumn 2004 and 2005, respectively.

Year	Variable	Cheatgrass		Dyer's woad	
		Density	Shoot dry mass	Density	Shoot dry mass
2005	LAI	-0.056	-0.102	-0.354 ³	-0.307 ²
	Soil NO_3^-	0.189	0.280 ²	0.140	0.173
2006	LAI	0.055	-0.009	-0.269 ²	-0.275 ²
	Soil NO_3^-	0.441 ³	0.477 ³	0.236 ¹	0.392 ³

¹ $P < 0.05$.

² $P < 0.01$.

³ $P < 0.001$.

presence of other species. Crested wheatgrass is highly competitive and capable of resisting invasion by exotic annual grasses through rapid soil resource use (Rogler and Lorenz 1983; Aguirre and Johnson 1991; Bilbrough and Caldwell 1997; Whitson and Koch 1998, Leffler et al. 2011). These findings are consistent with studies suggesting species composition influences ecosystem processes such as resistance to invasion (Hooper and Vitousek 1998; Spehn et al. 2000; Fargione et al. 2003; Fargione and Tilman 2005), but also studies suggesting that nonrandom assemblages of species yield different resistance to invasion than random ones (Zavaleta and Hulvey 2004; Selmants et al. 2012). Consequently, choice of species is especially important when few species are used in a rehabilitation activity.

The second hypothesis was clearly supported because resistance to invasion was proportionally greater in our assemblages that contained species of the same growth form as the invader. The most effective invader into G-Mono and G-Mix plots was dyer's woad, and the most effective invader into our S-Mono, S-Mix, F-Mono, and F-Mix was cheatgrass. In experimental prairie assemblages, each of four growth forms (forbs, C₃ and C₄ grasses, and legumes) was most effective at resisting invasion by members of the same growth form (Fargione et al. 2003). In western Montana, spotted knapweed invasion was high when forbs were removed from the system, but lower when only grasses or shallow-rooted forbs were removed (Pokorny et al. 2005); forbs again suppressed an invasive forb. In California grasslands, early-season native species were most effective at resisting early-season invasive species; the same was true for late-season native and invasive species (Hooper and Dukes 2010). In each of these cases, resistance to invasion arises from high niche overlap within growth forms that created complementarity among species in resource use (Hooper 1998; Fargione et al. 2005). All grasses in this study, including cheatgrass, are cool season, which have rapid growth in early spring, early reproductive maturity, and little growth in late summer (Arredondo et al. 1998). Shrubs require deep soil water during the summer when precipitation is largely absent or ineffective (Ryel et al. 2010; Leffler and Ryel 2012). Biennial invaders such as dyer's woad access deep water to persist through summer. If native shrubs effectively use this water source, it is difficult for other species to invade the system (Ryel et al. 2010; Leffler and Ryel 2012) because resource availability is critical for invasion success (Davis et al. 2000; Davis and Pelsor 2001).

Forbs in this study were effective at excluding dyer's woad, but not cheatgrass. Consequently, species such as western yarrow likely were most competitive for deeper soil resources, consistent with its drought tolerance (Leonard et al. 2008). Western yarrow stands were resistant to invasion by *Centaurea maculosa* (spotted knapweed), another deep-rooted forb (Maron and Marler 2007). High forb diversity can provide resistance to invasive species (Pokorny et al. 2005; Sheley and Carpinelli 2005), but classifying species as "forb" alone can hide much functional variation. Although the forbs examined here were effective at excluding dyer's woad, other species, specifically winter annual forbs, may be more effective at suppressing cheatgrass (Forbis 2010) because they are phenologically more similar (Hooper and Dukes 2010) to this invasive.

The third hypothesis, which suggested that our GFS-Mix assemblage would be resistant to cheatgrass and dyer's woad, was supported. Although the GFS-Mix was not more effective at reducing overall invasion than G-Mono or G-Mix, it was equally invaded by cheatgrass and dyer's woad (Fig. 2). The combination of growth forms in the GFS-Mix may have depleted resources in the near-surface soil, which limited the success of cheatgrass (Beckstead and Augspurger 2004; Perry et al. 2010; Leffler and Ryel 2012), and depleted deeper soil water, which reduced the success of deep-rooted invasive forbs like dyer's woad (Prevéy et al. 2010; Leffler and Ryel 2012). Here, we observed an advantage to selecting species of multiple growth form for conferring resistance to two invaders.

Our fourth hypothesis, regarding the influence of above-ground and belowground resource availability on invasion, was also supported, although the influence of resource availability on invasion was small (Table 4). Soil NO₃⁻ availability in 2005 had a strong influence on cheatgrass invasion and a modest influence on dyer's woad invasion in 2006. Cheatgrass has a high N uptake capacity and responds to increased N availability to a greater extent than native species (James 2008; Leonard et al. 2008; Leffler et al. 2011). The generally stronger correlation between belowground resources and invasion by cheatgrass compared to dyer's woad further indicates the importance of shallow soil resources for cheatgrass. Canopy LAI played a role in invasion by dyer's woad in 2005 and 2006. Although light availability is not typically limiting in semiarid systems (Goldberg and Novoplansky 1997), a mature sagebrush canopy can provide considerable shade and possibly reduce germination or establishment by species requiring high light. Many of the experimental plots were considerably shaded (Fig. S2, available at <http://dx.doi.org/10.2111/REM-D-13-00140.s1>).

More cheatgrass individuals in forb and shrub plots largely drive the greater level of invasion in 2006 compared to 2005. The difference between years is not likely due to differences in LAI; establishment by cheatgrass was only weakly suppressed by LAI, which was higher in 2006 than 2005 (Fig. S1, available at <http://dx.doi.org/10.2111/REM-D-13-00140.s1>). The difference may be partly due to higher soil NO₃⁻ in 2006 than 2005 in the F-Mono assemblage (Fig. S3, available at <http://dx.doi.org/10.2111/REM-D-13-00140.s1>). Soil NO₃⁻, however, cannot explain greater invasion in F-Mix and S-Mix, because NO₃⁻ was lower in these plots in 2006 compared to 2005. These year-to-year differences illustrate that resistance to invasion is dynamic and does not depend on species composition alone (Heger and Trepl 2003; Daleo et al. 2009). For example, meteorological factors not examined here, such as temperature and the timing of precipitation, may influence germination by cheatgrass (Roundy et al. 2007). Furthermore, there was the potential for soil-plant feedbacks to influence invasion success (Kulmatiski et al. 2008) in the second year of the experiment; these factors would not have played a role in the first year.

Our study has several important aspects to consider when drawing broader conclusions from these findings. First, the study was conducted in a former agricultural field that was previously tilled and fertilized, thus, altering soils from more natural settings. However, soil NO₃⁻ data collected in unplanted plots randomly located within the study area

(median, 2.39 and 1.21 $\mu\text{g} \cdot \text{g}^{-1}$ in 2004 and 2005, respectively) were not different from other systems in the Intermountain West (Booth et al. 2003; Hooker et al. 2008) and many sites that appear natural were previously tilled (Morris et al. 2011). Second, our assemblages were established from planted individuals to ensure that mixtures were not dominated by a single species and remained equally diverse. Consequently, variation in diversity has been eliminated as an explanation for differences in resistance among mixtures, with the tradeoff that these plots are not representative of any particular natural system. Third, we removed invasive individuals in early summer rather than allowing them to establish further; consequently our findings are limited to the establishment phase of invasion (Theoharides and Dukes 2007), but we were able to replicate the initial invasion process in 2 different years. Finally, we did not examine monocultures of all the species included in our mixtures; doing so would have necessitated using fewer species or reducing replication considerably. There is precedent for nonrandom selection of species and studies suggest that random and nonrandom assemblages will yield different resistance to invasion (Zavaleta and Hulvey 2004; Selmants et al. 2012). Consequently, inference should be limited to the monocultures and mixtures we report here, rather than extended to assemblages in general. The general conclusion, that selection of species matters for resistance to invasion when few species are used, is robust.

MANAGEMENT IMPLICATIONS

The hypotheses posed here and our results have three important implications. First, the choice of rehabilitation species is important because not all assemblages confer the same level of resistance to invasion (Bakker and Wilson 2004; Zavaleta and Hulvey 2004; Selmants et al. 2012). Many rehabilitation efforts simply seed a mix of local species without considering ecosystem services of the potential assemblage (e.g., Kaplan and Hoeffner 2010). In an ideal rehabilitation effort with numerous species available seeding a diverse mixture may allow the restored community to develop in a manner akin to succession. Given practical limitations such as seed availability (Burton and Burton 2002; Hufford and Mazer 2003), however, selection of appropriate species assemblages is critical. Practitioners should consider growth form and life history when selecting species to promote invasion resistance to a known exotic plant (Heger and Trepl 2003; Cleland et al. 2013). Second, diverse assemblages derived from a limited species pool are not necessarily more resistant to invasion than the monocultures we examined because species such as crested wheatgrass are highly resistant to the most widespread invaders in the region (Rogler and Lorenz 1983; Whitson and Koch 1998; Davies et al. 2010). Encouragingly, a diverse mixture of grasses (many native) was not less resistant to invasion than a monoculture of crested wheatgrass. Diverse communities benefit native ungulates or birds of conservation concern (Pendery and Provenza 1987; Wilson et al. 2009) in the Great Basin, USA. We also caution against the use of monocultures, because restoring with a single species might provide resistance to one invader, but result in vulnerability to others. Diversification of crested wheatgrass monocultures should continue

(Gunnell et al. 2010). Thirdly, invasion did occur, albeit at low levels, in the most resistant assemblage constructed here; hence, resistance to exotic plant invasion is not complete (Levine et al. 2004). However, as minor components of communities, exotic species will likely have minimal impact on ecosystem functioning (Corbin and D'Antonio 2011). A general strategy, based on the tests of ecological theory presented here, should include selection of plant materials that are functionally unique and correspond to the growth form of various potential invasive species (Funk et al. 2008).

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