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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; Prevéy 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, 1 402 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 [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 [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)