Restoration of Exotic Annual Grass-Invaded Rangelands: Importance of Seed Mix Composition

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Restoration of exotic annual grass-invaded rangelands is needed to improve ecosystem function and services. Increasing plant species richness is generally believed to increase resistance to invasion and increase desired vegetation. However, the effects of species richness and individual plant life forms in seed mixes used to restore rangelands invaded by exotic annual grasses have not been investigated. We evaluated the effects of seeding different life forms and increasing species richness in seed mixes seeded after exotic annual grass control to restore desirable vegetation (perennial herbaceous vegetation) and limit exotic annual grasses at two sites in southeastern Oregon. We also investigated the effects of seeding two commonly used perennial grasses individually and together on plant community characteristics. Large perennial grasses, the dominant herbaceous plant life form, were the most important group to seed for increasing perennial herbaceous vegetation cover and density. We did not find evidence that greater seed mix species richness increased perennial herbaceous vegetation or decreased exotic annual grass dominance more than seeding only the dominant species. None of the seed mixes had a significant effect on exotic annual grass cover or density, but the lack of a measured effect may have been caused by low annual grass propagule pressure in the first couple of years after annual grass control and an unusually wet-cool spring in the third year post-seeding. Although our results suggest that seeding only the dominant plant life form will likely maximize plant community productivity and resistance to invasion in exotic annual grass-invaded northern Great Basin arid rangelands, seeding a species rich seed mix may have benefits to higher tropic levels and community stability. Clearly the dominant species are the most prudent to include in seed mixes to restore exotic annual grass-invaded plant communities, especially with finite resources and an increasingly large area in need of restoration.

Nomenclature: Imazapic; medusahead, *Taeniatherum caput-medusae* (L.) Nevski.

Key words: Bunchgrass, crested wheatgrass, diversity, dominant species, medusahead, seeding, species richness.

Exotic annual grasses are serious threat to biodiversity, ecosystem function, wildlife habitat, and livestock production in western North America, Africa, Asia, and Australia (Brooks et al. 2004; D'Antonio and Vitousek 1992; Davies 2011; Hobbs and Atkins 1988, 1990; Liu et al. 2006; Mack 1981; Milton 2004; Purdie and Slatyer 1976; Young 1992). Invasion by exotic annual grasses is especially devastating because they often increase the fire frequency and promote large catastrophic wildfires (Brooks et al. 2004; D'Antonio and Vitousek 1992; Davies and Nafus 2013; Hughes et al.

1991; Torell et al. 1961). This change in the fire cycle is an ecosystem level change that promotes the continued dominance by exotic annual grasses and facilitates invasion of adjacent noninvaded lands (D'Antonio and Vitousek 1992). Medusahead [*Taeniatherum caput-medusae* (L.) Nevski] is a problematic exotic annual grass that is rapidly spreading (Duncan et al. 2004) and causing substantial ecological damage to North American rangelands (Davies 2011; Davies and Svejcar 2008). It is highly competitive with native plants (Goebel et al. 1988; Hironaka and Sindelar 1975; Young and Mangold 2008). Control and restoration of medusahead-invaded rangelands is needed to maintain and improve ecosystem services as well as to reduce the threat of frequent, large, catastrophic wildfires.

Medusahead and other annual grasses can be controlled with pre-emergent herbicides (Davies 2010; Davies and Sheley 2011; Monaco et al. 2005; Musil et al. 2005). The effectiveness of pre-emergent herbicides have been improved by prescribed burning exotic annual grass-invaded

Management Implications

The minimal to no effect of seeding species, other than large perennial grasses, on total perennial herbaceous vegetation suggests that including them in restoration seed mixes will have limited impact on plant community resistance to exotic annual grass invasion in Wyoming big sagebrush rangelands. Our results suggest that seeding the dominant species is more critical to restoration success than seeding a mixture of species. In the Wyoming big sagebrush ecosystem, the most important herbaceous species to seed after disturbance is the large perennial grass group. These results probably do not apply to ecosystems with larger windows of time when conditions are adequate for plant growth. In these ecosystems, a more species rich seed mix containing species with varying temporal resource acquisition patterns is probably needed to effectively use available resources to limit invasibility. We recognize that seeding a mixture of species may have implications to productivity and invasibility over time because of species complementarity and that establishing a diverse community potentially has benefits to higher tropic levels and community stability. A mixture of species may also be more important in ecosystems with multiple invasive species. Species richness is important, but its importance may have been overly stated in some ecosystems. We suggest restoration practitioners can use the information in this study to help weight the cost-benefits of including additional plant species in restoration efforts.

rangelands to remove litter prior to herbicide application (Davies 2010; Davies and Sheley 2011; Kyser et al. 2007; Sheley et al. 2012). After successful control of exotic annual grasses, desirable, competitive vegetation must be established or exotic annual grasses will rapidly regain dominance of the plant community (Monaco et al. 2005; Sheley et al. 2007; Young 1992). Restoring desirable vegetation after exotic annual grass control has largely focused on perennial grasses (e.g. Davies 2010; Monaco et al. 2005; Sheley et al. 2012), because they compete heavily with and limit the establishment of exotic annual grasses (Davies 2008; James et al. 2008). Perennial grasses are also widely available and less expensive than other plant functional groups and often the dominant herbaceous vegetation in noninvaded steppe plant communities (Chambers et al. 2007; D'Antonio and Vitousek 1992; Davies 2011). Crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] and squirreltail [*Elymus elymoides* (Raf.) Swezey] are two large perennial bunchgrasses that have been shown to be competitive with medusahead (Davies 2010; Davies et al. 2010; Hironaka and Sindelar 1973, 1975). Thus, these two species are logical choices for seeding after medusahead control, but which species better suppresses medusahead or if seeding both species together conveys more benefits is unknown.

Seeding a mixture of plant species or different life forms after medusahead control may increase resistance to re-invasion by increasing niche occupation. Diverse plant communities are generally expected to be more resistant to exotic plant invasion and produce more vegetation cover and biomass because of increased niche occupation (Cardinale et al. 2007; Dukes 2001; Knops et al. 1999; Pokorny et al. 2005). For example, Sheley and Carpinelli (2005) reported that increasing niche occupation during rehabilitation efforts decreased exotic plant establishment and dominance. However, disagreement exists as to whether species richness or dominant species maximize resistance to exotic plant invasion. Smith et al. (2004) reported that dominance was more important than species richness in determining resistance to invasion in a tallgrass prairie plant community. Similarly, Jiang et al. (2007) also reported that dominant species composition plays a critical role in determining resistance to invasion. These previous studies, excluding Sheley and Carpinelli (2005) did not evaluate the importance of species richness in a restoration setting. Thus, the relative benefits of seeding a mixture of species compared to focusing revegetation efforts on establishment of the dominant life form (i.e., large perennial grasses) remains relatively unknown in terms of maximizing productivity and resistance to re-invasion following medusahead control.

The objective of this study was to determine the influence of different seed mixes on medusahead and perennial herbaceous vegetation after application of control treatments in medusahead-invaded Wyoming big sagebrush plant communities in the northern Great Basin. Specifically, we evaluated the effects of seeding crested wheatgrass and squirreltail individually and together and increasing seed mix species richness on the cover and density of exotic annual grass and other plant functional groups. We also investigated the relative importance of different plant life forms for limiting reestablishment of exotic annual grass and increasing perennial herbaceous plant cover and density following annual grass control. We hypothesized that (1) seeding crested wheatgrass and squirreltail together compared to individually would result in a greater decrease in annual grass cover and density and a greater increase in perennial herbaceous vegetation, (2) that seeding large perennial grasses would be more effective than seeding Sandberg bluegrass (*Poa secunda* J. Presl) or forbs at limiting annual grass cover and density and increasing perennial herbaceous cover and density and (3) increasing species richness in the seed mix will increase perennial herbaceous cover and density and decrease exotic annual grass cover and density.

Materials and Methods

Study Area. The study was conducted in southeastern Oregon approximately 15 km (9 miles) south of Drewsey, OR (43°40′10.05″N, 118°25′51.54″W). Climate is typical of the northern Great Basin with cool, wet winters and hot, dry summers. Elevation was about 1,270 m (4166 ft) above

sea level. Our study occurred on two ecological sites: SR Clayey 9-12PZ and SR Cool 9-12PZ. Long-term average annual precipitation was 300 mm (11.8 in). Crop year (October 1 to September 30) was 99, 100, and 150% of the long-term average in 2008 to 2009, 2009 to 2010, and 2010 to 2011 at the Burns, OR Airport (Western Regional Climate Center 2012), approximately 41 km west of the study sites. All the plant communities were near mono-cultures of medusahead prior to treatment. Historic plant communities would have been Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) with either bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] or Idaho fescue (*Festuca idahoensis* Elmer) as the dominant large perennial grass interspersed with perennial and annual forbs and large patches of bare ground.

Experimental Design. We used a randomized complete block design at two sites to evaluate vegetation response to seeding different species combinations after exotic annual grass control. One year prior to seeding, all treatment plots were burned to remove exotic annual grass litter and then treated with imazapic (Plateau®) herbicide to control exotic annual grasses. The prescribed burn was applied in late October of 2007 as strip-head fires ignited with handheld drip torches. Air temperatures ranged between 16 and 20 C, humidity was 30 to 40%, and wind speeds were 6 to 8 km hr^{-1} during the burns. Fires consumed all fuels in study plots. Imazapic was applied at a rate of 87.5 g ai ha^{-1} (1.25 oz ai ac^{-1}) one week after prescribed burning the study sites. At each site, seeding treatments were applied in October of 2008 to 4 m^2 (43 ft^2) plots with a 0.5 m buffer between treatments and replicated four times. Treatments were: (1) crested wheatgrass, (2) bottlebrush squirreltail, (3) large perennial grass (LP), (4) Sandberg bluegrass (SB), (5) forbs (F), (6) LP-F, (7) LP-F-SB, and (8) a nonseeded control. Crested wheatgrass and bottlebrush squirreltail were seeded at 10 kg PLS ha^{-1} (8.9 lbs PLS ac^{-1}) The LP seed mixed consisted of crested wheatgrass and bottlebrush squirreltail both seeded at 5 kg PLS ha^{-1}. The SB and F treatments were seeded at 4 kg PLS ha^{-1}. Seeding rates were selected to be similar to rates used by local land management agencies. The F seed mix consisted of Ladak alfalfa (*Medicago sativa* L.), Indian paintbrush (*Castilleja applegatei* Fernald), western yarrow (*Achillea millefolium* L.) and cornflower (*Centaurea cyanus* L.) seeded at 1, 0.5, 0.3, and 2.2 kg PLS ha^{-1}, respectively. Crested wheatgrass, alfalfa, and cornflower are introduced species and the other seeded species are native. When seed treatments were combinations of life form groups the seed rates were the same as when the life form groups were seeded individually. Large perennial grasses were hand seeded in shallow linear furrows in the soil that traversed the length of the plot and were 20 cm (7.9 in) apart. Seeds were placed in the furrows

and covered with 1 to 2 cm of soil. Other species were broadcast seeded by hand and then covered with ~ 0.5 cm of soil. Seed methods were selected that would best meet the planting requirements of the species and simulate how the different species would be planted in a restoration seeding project.

Measurements. Vegetation cover and density was measured in June of 2009, 2010, and 2011. Twelve 0.2 m^2 quadrats were used to sample each treatment plot. The 0.2 m^2 quadrats were located at 0.5 m intervals along three 2-m transects. Transects were placed 0.5 m from the edge to the plot and from each other. Vegetation foliar cover was visually estimated by species in the 0.2 m^2 quadrats. Vegetation density was measured by counting by species all individuals rooted in the 0.2 m^2 quadrats. Rhizomatous species were counted by considering plants individuals if separated by > 10 cm. Plant life form group cover and density was calculated by summing individual species cover and density for each group. Total perennial herbaceous cover and density was determined by summing all perennial herbaceous groups together. Bare ground and litter cover were also visually estimated in the 0.2 m^2 quadrats in each plot.

Statistical Analysis. Repeated measures ANOVAs using the PROC MIXED method is SAS v.9.1 (SAS Institute Inc., Cary, NC) were used to compare vegetation characteristics among seed mix treatments used after annual grass control. Individual analyses were conducted to determine the influence of seeding bottlebrush squirrel-tail and crested wheatgrass individually and together, the response of increasing diversity in the seed mix (more life forms), and the influence of seeding individual life from groups. Covariance structures used in the models were selected using the Akaike's Information Criterion (Littell et al. 1996). Treatment effects were also analyzed in each year. Means were separated with the LS MEANS procedure in SAS v. 9.1 (Littell et al. 1996). Significance level was set at P ≤ 0.05. For analyses, vegetation was separated into five life form groups: Sandberg bluegrass, large perennial grasses, annual grasses, perennial forbs, and annual forbs. Sandberg bluegrass was treated as separate life from group from the other perennial grasses because it is much smaller in stature and phenologically develops much earlier (James et al. 2008). Data that did not meet assumptions of normality were log-transformed. All figures and numbers reported are original, nontransformed data.

Results

Large Perennial Grasses. Total perennial herbaceous and perennial grass (Figure 1A) cover varied by the interaction between treatment and year (P = 0.03 and 0.03, respectively). Total perennial herbaceous response was the
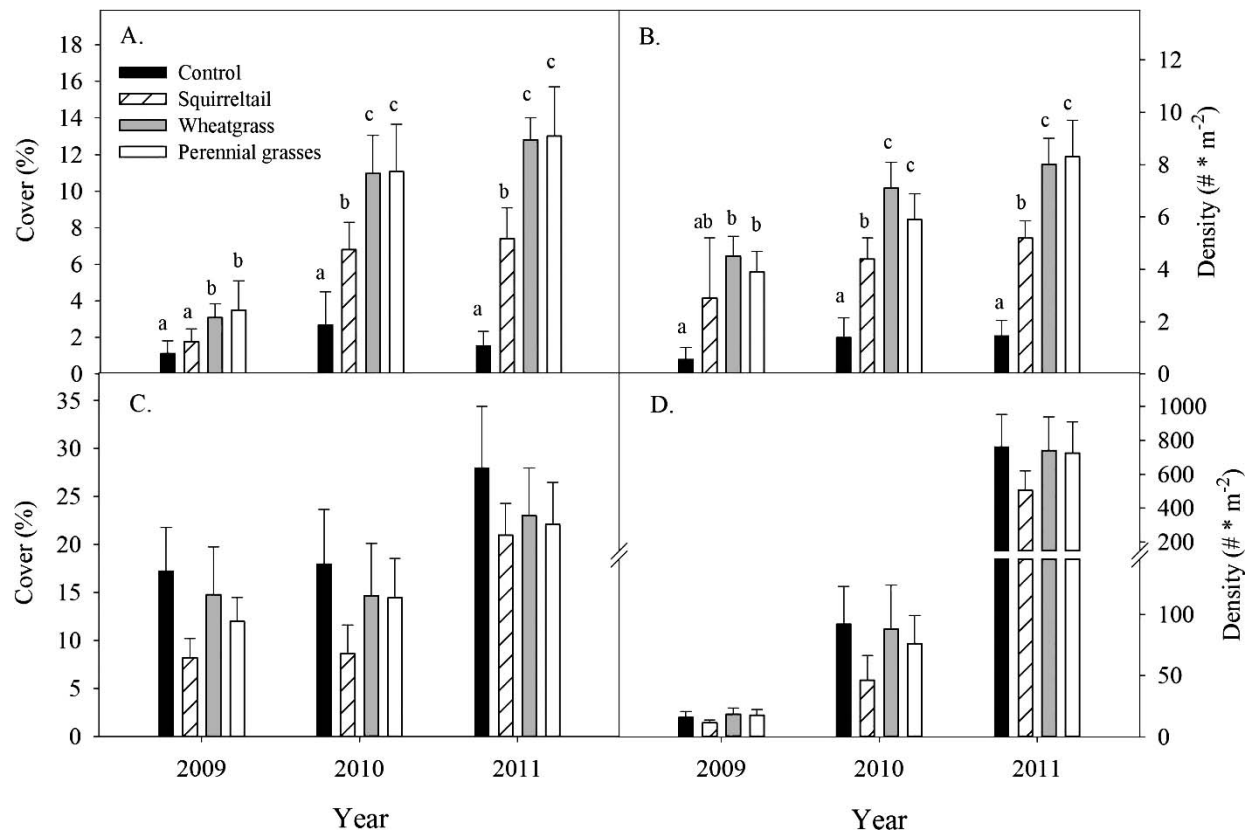
Figure 1. Large perennial bunchgrass cover (A) and density (B) and exotic annual grass cover (C) and density (D) in areas where medusahead was controlled and then seeded with nothing (control), bottlebrush squirreltail (squirreltail), crested wheatgrass (wheatgrass), and bottlebrush squirreltail and crested wheatgrass (perennial grasses). Lower case letters used to indicate significant (P ≤ 0.05) differences between treatments in that year.

same as perennial grass response; therefore, we did not display total perennial herbaceous response in Figure 1. In 2009, 2010, and 2011 crested wheatgrass and the perennial grass (crested wheatgrass and bottlebrush squirreltail combined) treatment had greater total perennial herbaceous and perennial grass cover than the control and bottlebrush squirreltail treatments (P < 0.05). Total perennial herbaceous and perennial grass cover did not differ between the crested wheatgrass and perennial grass treatment in any year of the study (P > 0.05). In 2010 and 2011, the bottlebrush squirreltail treatment had greater total perennial herbaceous and perennial grass cover than the control (P < 0.05). Total perennial herbaceous and perennial grass (Figure 1B) density varied by treatment (P < 0.01), but the interaction between treatment and year were not significant (P = 0.38 and 0.40). In 2009, total perennial herbaceous and perennial grass density was not different between the control and bottlebrush squirreltail treatments or among the bottlebrush squirreltail, crested wheatgrass, and perennial grass treatments (P > 0.05). Total perennial herbaceous and perennial grass density was greater in the created wheatgrass and perennial grass

treatments than the control treatment (P < 0.05). In 2010 and 2011, total perennial herbaceous and perennial grass density was greater in the bottlebrush squirreltail treatment than the control (P < 0.05). In 2010 and 2011, total perennial herbaceous and perennial grass density were also greater in the crested wheatgrass and perennial grass treatments compared to the bottlebrush squirreltail and control treatments (P < 0.05). Annual grass (Figure 1C and 1D), Sandberg bluegrass, perennial forb, and annual forb cover and density did not differ by treatment or the interaction between treatment and year (P > 0.05). Bare ground and litter did not vary by treatment when all years were analyzed together or when years were analyzed separated or by the interaction between treatment and year (P > 0.05).

Individual Life Form Groups. Total perennial herbaceous cover varied by the interaction between treatment and year (P = 0.04; Figure 2A). In 2009, treatments did not differ in total perennial herbaceous cover (P > 0.05). In 2010 and 2011, the large perennial grass treatment had more total perennial herbaceous cover than the other treatments
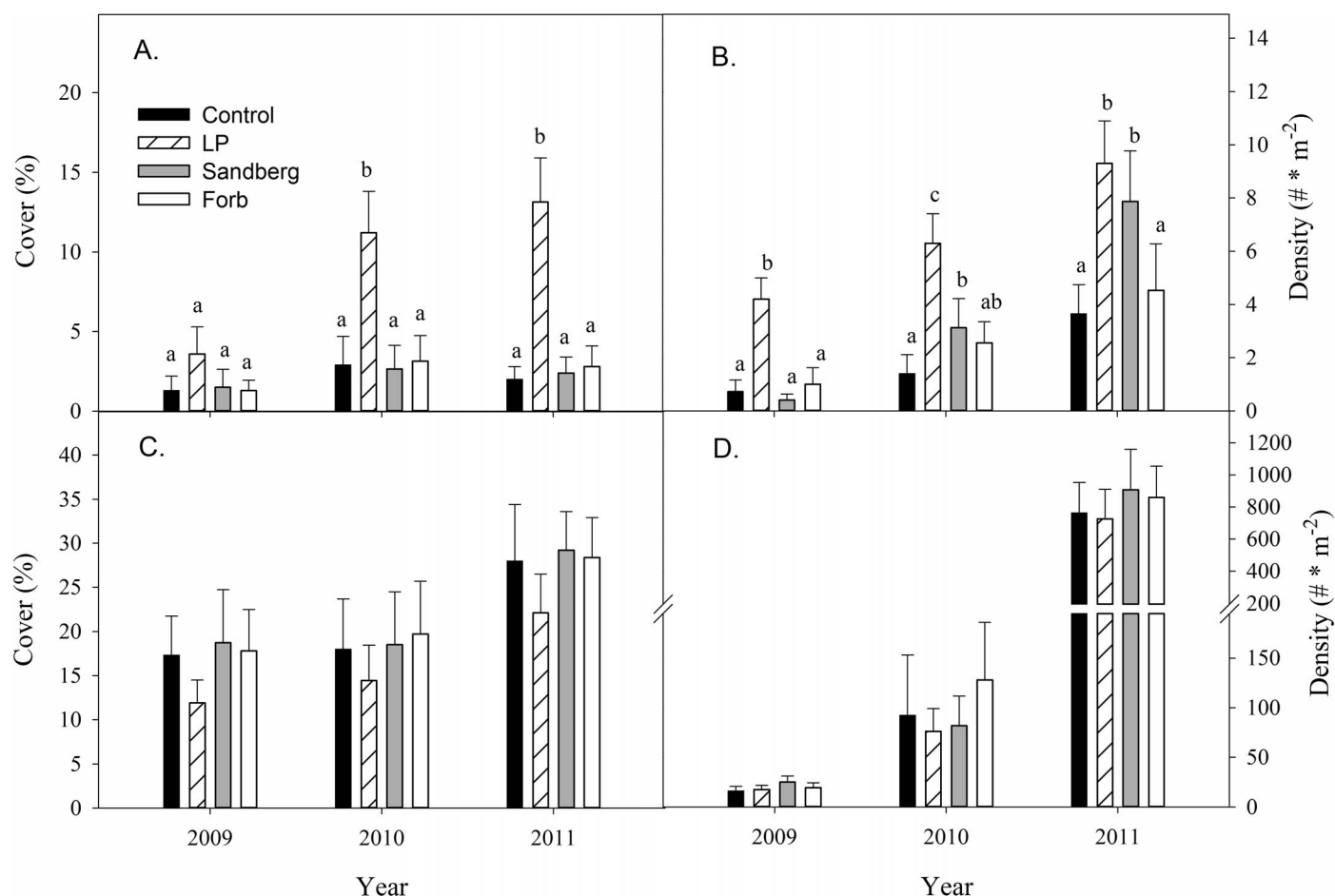
Figure 2. Total perennial herbaceous cover (A) and density (B) and exotic annual grass cover (C) and density (D) in areas where medusahead was controlled and then seeded with nothing (control), large perennial grasses (LP), Sandberg bluegrass (Sandberg), and forbs (forb). Lower case letters used to indicate significant (P ≤ 0.05) differences between treatments in that year.

(P < 0.01). The other treatments did not differ in total perennial herbaceous cover in 2010 and 2011 (P > 0.05). Total perennial herbaceous density varied by treatment (P = 0.03; Figure 2B), but not by the interaction between treatment and year (P = 0.51). Averaged across all sample years, total perennial herbaceous density was 1.7 to 3.5-fold greater in the perennial grass treatment compared to the other treatments (P < 0.05). Total perennial herbaceous density was generally highest in the perennial grass treatment, but was not different from the Sandberg bluegrass treatment in 2011 and the forb and control treatment did not differ from each other in any year (P > 0.05). Perennial grass cover varied by the interaction between treatment and year (P = 0.03). Perennial grass cover was greater in the perennial grass treatment than the forb, Sandberg bluegrass, and control treatments in each year of the study and when the years were analyzed together (P < 0.01). From 2009 to 2011, perennial grass cover in the perennial grass treatment increased from 3.5 ± 1.6% to 13.0 ± 2.7% (P < 0.01). Perennial grass cover did not

differ among the other treatments (P > 0.05). Perennial grass density varied by treatment (P < 0.01), but not the interaction between treatment and year (P = 0.69). The perennial grass treatment had about 2-fold more perennial grass individuals than the other treatments (P < 0.01). The other treatments did not differ in perennial grass densities (P > 0.05). Exotic annual grass cover and density did not differ by treatment or the interaction between treatment and year (P > 0.05; Figures 2C and 2D). Bare ground, litter, and perennial forb, annual forb, and Sandberg bluegrass cover and density did not vary by treatment when all years were analyzed together or separately or by the interaction between treatment and year (P > 0.05).

Species Richness. Increasing the seed mix species richness after large perennial grasses were seeded did not alter vegetation response. Total perennial herbaceous and perennial grass cover did not vary by treatment when all years were analyzed together (P = 0.10 and 0.09, respectively) or by the interaction between treatment and
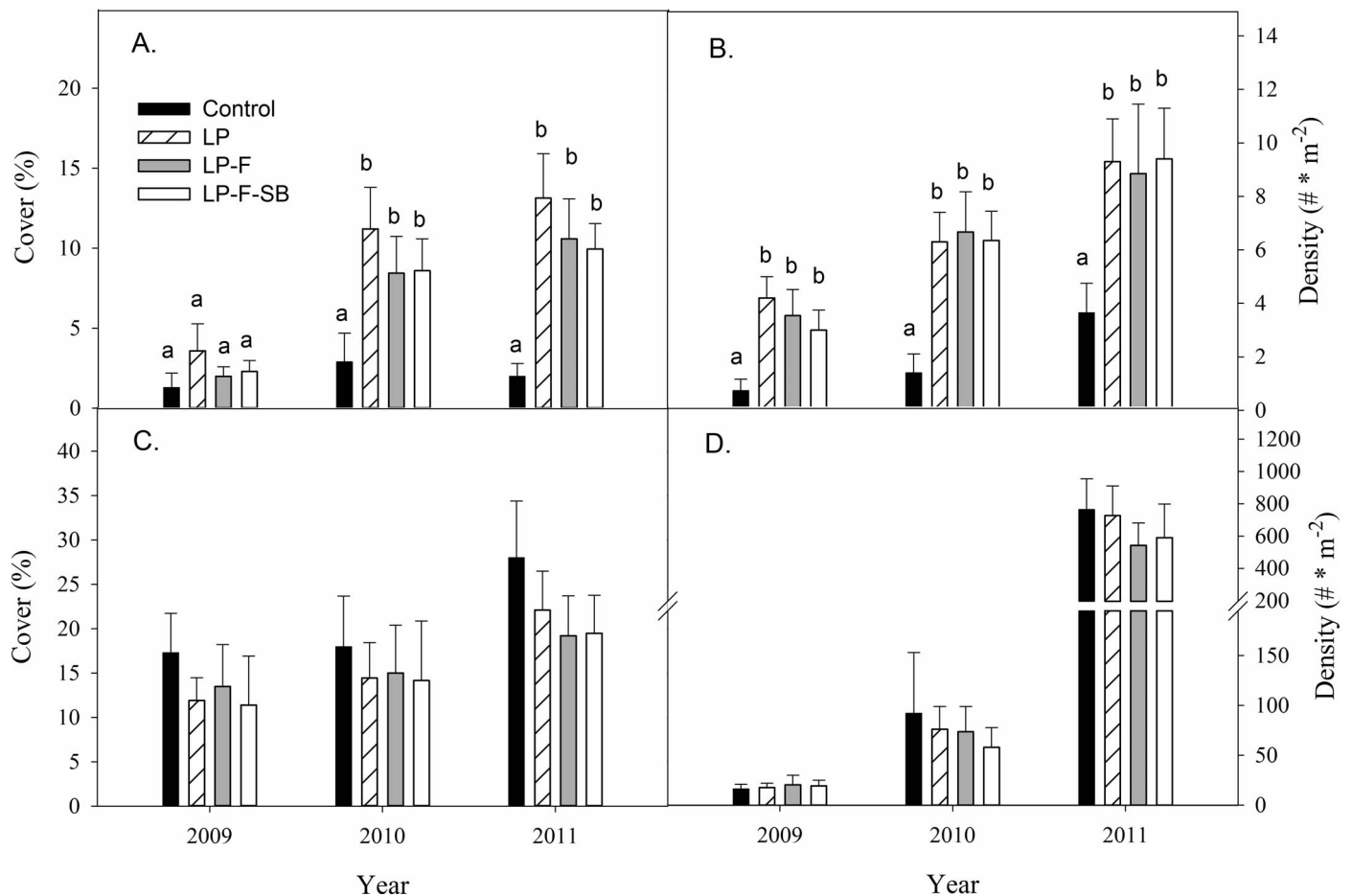
Figure 3. Total perennial herbaceous cover (A) and density (B) and exotic annual grass cover (C) and density (D) in areas where medusahead was controlled and then seeded with nothing (control), large perennial grasses (LP), large perennial grasses and forbs (LP-F), and large perennial grasses, forbs, and Sandberg bluegrass (LP-F-SB). Lower case letters used to indicate significant ($P \leq 0.05$) differences between treatments in that year.

year ($P = 0.19$ and 0.16, respectively). In 2009, there was no difference among treatments in total perennial herbaceous (Figure 3A) and perennial grass cover among treatments ($P > 0.05$). In 2010 and 2011, the control treatment had less perennial grass and total perennial herbaceous cover than the other treatments ($P < 0.05$). Perennial grass and total perennial herbaceous vegetation (Figure 3B) density varied by treatment ($P < 0.01$), but not by the interaction between treatment and year ($P = 0.43$ and 0.87). In all years of the study, the control treatment had lower perennial grass and total perennial herbaceous vegetation density than the other treatments ($P < 0.01$). The LP, LP-F, and LP-F-SB treatments did not differ in perennial grass and total perennial herbaceous density ($P > 0.05$). Exotic annual grass cover and density did not differ between treatment when all years were analyzed together and when years were analyzed separately or by the interaction between treatment and year ($P > 0.05$). All other plant life form groups cover and density

and bare ground and litter did not differ among treatments or by the interaction between treatment and year ($P > 0.05$).

Discussion

Perennial Grass. Increasing large perennial grass species seeded did not appear to increase invasion resistance or increase total herbaceous cover and density. Seeding bottle squirreltail with crested wheatgrass did not increase perennial grass or total perennial herbaceous vegetation cover and density compared to seeding only crested wheatgrass. Areas seeded with crested wheatgrass had greater perennial grass cover and density compared to areas seeded with bottlebrush squirreltail suggesting that dominant species composition is important in restoration efforts. Similarly, Jiang et al. (2007) and Smith et al. (2004) reported that dominant composition was critical to plant community function. Sheley and James (2010)

suggested that the most effective basis for establishing plant communities resistant to invasion by exotic annual grasses is to establish two or three perennial grass species, whereas our results suggest seeding a single, highly competitive perennial grass may convey the same results. However, through time species complementarity may increase overall production and invasion resistance when several species are seeded compared to only the most dominant species (Cardinale et al. 2007). In addition, we only evaluated seeding two large perennial grasses and testing additions of other large perennial grasses over longer periods of time is warranted.

The lack of significant differences in exotic annual grass cover and density between the control and perennial grass treatment was surprising, especially with the relatively high establishment of perennial grasses (~ 8 individuals m^{-2}). Previous research has demonstrated that increases in perennial grass density reduce the abundance and cover of exotic annual grasses through competition for limited resources (Davies 2008; James et al. 2008). We speculate that we found no evidence of differences in exotic annual grass cover and density the first few years after successful control because annual grass propagule pressure was substantially reduced (i.e. seed limited). Additionally, the third year post-seeding had an unusually wet spring that may have negated the influence of perennial grasses on exotic annual grasses. Exotic annual grasses are favored by wet springs that lengthen their growing season (Knapp 1995) and other increases in resources (Vasquez et al. 2008). Thus, favorable growing conditions in 2011 may have limited competition for resources between perennial grasses and exotic annual grasses.

Further evaluation of seeding bottlebrush squirreltail and crested wheatgrass to limit medusahead are needed because of the short-term nature of this study. Previous research has shown that bottlebrush squirreltail can be competitive with medusahead (Hironaka and Sindelar 1973, 1975). Bottle-brush squirreltail's traits make it a promising candidate for restoration of medusahead and other exotic annual grass invaded rangelands (Jones 1998). Similarly, Davies et al. (2010) demonstrated the seeding crested wheatgrass could limit medusahead establishment and spread.

Life Form Groups. Large perennial grasses increased total perennial herbaceous vegetation cover more than the other seeded plant life forms suggesting that they are the most critical group to seed. Perennial grasses use a dispropor-tionate amount of resources and dominate the herbaceous understory in noninvaded plant communities in this system (Davies et al. 2006; James et al. 2008). Although no differences in exotic annual grass cover and density were detected between the perennial grass seeded and nonseeded treatments in the first three years after seeding, we expect that over time the increase in total perennial vegetation,

especially large perennial grasses and possibly Sandberg bluegrass, will reduce exotic annual grass dominance. Perennial grasses may need to grow for several years after achieving desired densities before they are large enough to effectively reduce exotic annual grasses (Bates et al. 2005). Davies et al. (2010) demonstrated that successfully establishing crested wheatgrass limited exotic annual grass establishment and Davies (2008) reported that exotic annual grass establishment decreased as large native perennial grass density increased. Bottlebrush squirreltail has also been demonstrated to be competitive with medusahead (Hironaka and Sindelar 1973, 1975). Simi-larly demonstrating that perennial grass is critical to exotic annual grass invasion resistance, Sheley and James (2010) reported that removing perennial grasses increased exotic annual grasses more than removing other plant functional groups.

Although seeding Sandberg bluegrass did increase the density of total perennial herbaceous vegetation, it did not influence total perennial herbaceous vegetation cover, probably because of its relatively small size. Seeded forbs rarely established and thus had no measured effect on any plant functional group. The limited to no effect of seeding Sandberg bluegrass and forbs suggest that it is highly improbable that either seeded group will have an impact on exotic annual grass dominance. Similarly, Davies (2008) reported that Sandberg bluegrass, annual forb, and perennial forb cover and density were not correlated with the establishment of medusahead. Sheley and James (2010) found that removing forbs had minimal impact on the susceptibility of plant communities to medusahead inva-sion. In addition, compared to large perennial grasses, Sandberg bluegrass and forbs make up a relatively small portion of intact plant communities in this system (Davies et al. 2006; Davies and Bates 2010). However, if Sandberg bluegrass increases in density and/or established individual grow larger they may suppress medusahead.

Species Richness. We found no evidence that following large perennial grass seedings with forb or forb plus Sandburg bluegrass seedings on medusahead-invaded rangelands increased perennial herbaceous vegetation or decreased exotic annual grasses in the three years following seeding. Seeding additional plant species did not improve restoration success beyond seeding only perennial grasses. We expected that increasing species richness in the seed mix would increase niche differentiation and decrease plant community invasibility (Sheley and Carpinelli 2005); however, we did not measure a significant decrease in exotic annual grass density or cover with any of the treatments. Once large perennial grasses were included in the seed mix, no measured increases in perennial herbaceous vegetation occurred with the inclusion of additional plant functional groups. This may be in part

because of competition from the seeded perennial grasses. Crested wheatgrass is well known to be an effective competitor with other vegetation (Asay et al. 2001; Gunnell et al. 2010; Hendersen and Naeth 2005).

Our results may appear to be contrary to the idea that increasing diversity increases niche occupation and thereby decreases plant community invasibility (Dukes 2001; Hooper and Dukes 2010; Knops et al. 1999; Pokorny et al. 2005). However, in the Wyoming big sagebrush ecosystem in the northern Great Basin, large perennial grasses dominate the understory and other herbaceous vegetation generally represents only a small portion of the total herbaceous vegetation (Davies et al. 2006; Davies and Bates 2010). In contrast, other ecosystems may have a more even distribution of several plant life forms (e.g. Pokorny et al. 2005). The most productive species or plant group is probably most critical to seed after disturbance regardless of inherent levels of ecosystem diversity, but the relative importance of other species to productivity and invasibility may vary by ecosystem. In a summary of 44 experiments, Cardinale et al. (2007) found that diverse polycultures produced more biomass than their single most productive species in only 12% of the studies. However, diverse communities may be able to better capture resources, maintain high productivity, and reduce invasibility when resources fluctuate over time (Cardinale et al. 2007; Dukes 2001; Tilman et al. 1997). Thus, our result apply to ecosystems that have a single very dominant herbaceous plant functional group similar to the Wyoming big sagebrush ecosystem and probably not ecosystems that have a less pronounced dominant herbaceous functional group. Our results are also constrained by a relatively short temporal view of plant community dynamics after seeding and the limited number of species and functional group combinations we evaluated.

Increasing species richness is seed mixes may have limited impact in these ecosystems because of a relatively short period of time when resources are adequate for plant growth. Wyoming big sagebrush plant communities in the northern Great Basin only have adequate soil moisture and soil temperatures for plant growth for short period (3 to 4 months) in the spring and early summer compared to ecosystems that either have summer precipitation or winters warm enough for plant growth. Infrequently, fall precipitation occurs when plant growth can occur in this ecosystem. The growth of cool-season large perennial bunchgrasses essentially spans the entire period of time when plant growth can occur; the spring-early summer and, infrequently, the early fall. Ecosystems with large windows of opportunity for plant growth need plant species that differ in temporal resource acquisition to limit resource availability to invaders and maintain plant community productivity (Davies et al. 2007; Hooper and Dukes 2010). In addition, our results are short-term and longer term evaluations are needed to full understand the interactions between seed mix species richness and plant community resistance to invasion in northern Great Basin Wyoming big sagebrush plant communities.

Although we found no evidence that including additional herbaceous species (when additional life forms were seeded) increased cover and density of perennial herbaceous vegetation or increased invasion resistance when restoring exotic annual grass-invaded rangelands, restoration practitioners may still want to include a diversity of plant species in seed mixes. Plant community diversity is important to the diversity and productivity of higher tropic levels (Haddad et al. 2001; Knops et al. 1999). Plant species other than the dominant species may also be important for wildlife. For example, forbs in sagebrush ecosystem are a critical food source for sage-grouse (Barnett and Crawford 1994; Gregg et al. 2008; Johnson and Boyce 1990). Establishing a diverse plant community may also increase community stability (Hooper and Vitousek 1998; Tilman 1999; Tilman et al. 1997). In addition, better establishment of seeded forbs or seeding different species may have altered the plant community responses.

Acknowledgments

Literature Cited

Asay KH, Horton WH, Jensen KB, Palazzo AJ (2001) Merits of native and introduced Triticeae grasses on semiarid rangelands. Can J Plant Sci 81:45–52

Barnett JK, Crawford JA (1994) Pre-laying nutrition of sage grouse hens in Oregon. J Range Manage 47:114–118

Bates JD, Miller RF, Svejcar T (2005) Long-term successional trends following western juniper cutting. Rangeland Ecol Manag 58:533–541

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effect of invasive alien plants on fire regimes. BioScience 54:677–688

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. P Natl Acad Sci 104:18123–18128

Chambers JC, Roundy RA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77:117–145

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Ann Rev Ecol Syst 23: 63–87

Davies KW (2008) Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecol Manag 61: 110–115

Davies KW (2010) Revegetation of medusahead-invaded sagebrush steppe. Rangeland Ecol Manag 63:564–571

Davies KW (2011) Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. Oecologia 167:481–491

Davies KW, Bates JD (2010) Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. Rangeland Ecol Manag 63:461–466

Davies KW, Bates JD, Miller RF (2006) Vegetation characteristics across part of the Wyoming big sagebrush alliance. Rangeland Ecol Manag 59:567–575

Davies KW, Nafus AM (2013) Exotic annual grass invasion alters fuel amounts, continuity, and moisture content. Int J Wildland Fire 22: 353–358

Davies KW, Nafus AM, Sheley RL (2010) Non-native competitive perennial grass impedes the spread of an invasive annual grass. Biol Invas 12:3187–3194

Davies KW, Pokorny ML, Sheley RL, James JJ (2007) Influence of plant functional group removal on soil inorganic nitrogen concentrations in native grasslands. Rangeland Ecol Manag 60:304–310

Davies KW, Sheley RL (2011) Promoting native vegetation and diversity in exotic annual grass infestations. Restor Ecol 19:159–165

Davies KW, Svejcar TJ (2008) Comparison of medusahead-invaded and noninvaded Wyoming big sagebrush steppe in southeastern Oregon. Rangeland Ecol Manag 61:623–629

Dukes JS (2001) Biodiversity and invasibility in grassland microcosms. Oecologia 126:563–568

Duncan CE, Jachetta JJ, Brown ML, Carrithers VF, Clark JK, DiTomaso JM, Lym RG, McDaniel KC, Renz MJ, Rice PM (2004) Assessing the economic, environmental, and societal losses from invasive plants on rangelands and wildlands. Weed Technol 18: 1411–1416

Goebel CJ, Tazi M, Harris GA (1988) Secar bluebunch wheatgrass as a competitor to medusahead. J Range Manage 41:88–89

Gregg MA, Barnett JK, Crawford JA (2008) Temporal variation in diet and nutrition of preincubating greater sage-grouse. Rangeland Ecol Manag 61:535–542

Gunnell KT, Monaco TA, Call CA, Ransom CV (2010) Seedling interference and niche differentiation between crested wheatgrass and contrasting native Great Basin species. Rangeland Ecol Manag 63: 443–449

Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops JMH (2001) Contrasting effects of plant richness and composition on insect communities: a field experiment. Am Nat 158:17–35

Henderson DC, Naeth MA (2005) Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. Biol Invas 7:639–650

Hironaka M, Sindelar BW (1973) Reproductive success of squirreltail in medusahead infested ranges. J Range Manage 26:219–221

Hironaka M, Sindelar BW (1975) Growth characteristics of squirreltail seedlings in competition with medusahead. J Range Manage 28: 283–285

Hobbs RJ, Atkins L (1988) Effect of disturbance and nutrient addition on communities in the Western Australian wheatbelt. Aust J Ecol 13: 171–179

Hobbs RJ, Atkins L (1990) Fire related dynamics of a *Banksia* woodland in south-western Australia. Aust J Bot 38:97–110

Hooper DU, Dukes JS (2010) Functional composition controls invasion success in a California serpentine grassland. J Ecol 98:764–777

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121–149

Hughes F, Vitousek PM, Tunison T (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawaii. Ecology 72:743–746

James JJ, Davies KW, Sheley RL, Aanerud ZT (2008) Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. Oecologia 156:637–648

Jiang XL, Zhang WG, Wang G (2007) Biodiversity effects on biomass production and invasion resistance in annual verse perennial plant communities. Biodivers Conserv 16:1983–1994

Johnson GD, Boyce MS (1990) Feeding trials with insects in the diet of sage grouse chicks. J Wildl Manage 54:89–91

Jones TA (1998) Viewpoint: the present status and future prospects of squirreltail research. J Range Manage 51:326–331

Knapp PA (1995) Intermountain West lightning-caused fires: climatic predictors of area burned. J Range Manage 48:85–91

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant richness on invasion dynamics, disease outbreaks, insects abundances, and diversity. Ecol Lett 2:286–293

Kyser GB, DiTomaso JM, Doran MP, Orloff SB, Wilson RG, Lancaster DL, Lile DF, Porath ML (2007) Control of medusahead (*Taeniatherum caput-medusae*) and other annual grasses with imazapic. Weed Technol 21:65–75

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS System for Mixed Models. SAS Institue Inc. Cary, North Carolina. 633 p

Liu J, Dong M, Miao SL, Li ZY, Song MH, Wang RQ (2006) Invasive alien plants in China: role of clonality and geographical origin. Biol Invasions 8:1461–1470

Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7:145–165

Milton S (2004) Grasses as invasive alien plants in South Africa. S Afr J Sci 100:69–75

Monaco TA, Osmond TM, Dewey SA (2005) Medusahead control with fall- and spring-applied herbicides in northern Utah foothills Weed Technol. 19:653–658

Musil CF, Milton SJ, Davis GW (2005) The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. S Afr J Sci 101:337–344

Pokorny ML, Sheley RL, Zabinski CA, Engel RE, Svejcar TJ, Borkowski JJ (2005) Plant functional group diversity as a mechanism for invasion resistance. Restor Ecol 13:448–459

Purdie RW, Slatyer RO (1976) Vegetation succession after fire in sclerophyll woodland communities in south-eastern Australia. Aust J Ecol 1:223–236

Sheley RL, Bingham BS, Davies KW (2012) Rehabilitating medusahead (*Taeniatherum caput-medusae*) infested rangelands using a single-entry approach. Weed Sci 60:612–617

Sheley RL, Carpinelli MF (2005) Creating weed-resistant plant communities using niche-differentiated nonnative species. Rangeland Ecol Manag 58:480–488

Sheley RL, Carpinelli MF, Morghan MJR (2007) Effects of imazapic on target and nontarget vegetation during revegetation. Weed Technol 21:1071–1081

Sheley RL, James J (2010) Resistance of native plant functional groups to invasion by medusahead (*Taeniatherum caput-medusae*). Invasive Plant Sci Manag 3:294–300

Smith MD, Wilcox JC, Kelly T, Knapp AK (2004) Dominance not richness determines invasibility of tallgrass prairie. Oikos 106:253–262

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. P Natl Acad Sci 94:1857–1861

Torell PJ, Erickson LC, Haas RH (1961) The medusahead problem in Idaho. Weeds 9:124–131

Vasquez E, Sheley R, Svejcar T (2008) Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. Invasive Plant Sci Manag 1:287–295

Western Regional Climate Center (2012) Cooperative climatological data summaries. (http://www.wrcc.dri.edu/climatedata/climsum/) Accessed on October 2, 2012

Young JA (1992) Ecology and management of medusahead (*Taeniatherum caput-medusae* ssp. *asperum* [SIMK.] Melderis). Great Basin Nat 52:245–252

Young K, Mangold J (2008) Medusahead outperforms squirreltail through interference and growth rate. Invasive Plant Sci Manag 1: 73–81