

First-Year Establishment, Biomass and Seed Production of Early vs. Late Seral Natives in Two Medusahead (*Taeniatherum caput-medusae*) Invaded Soils

Shauna M. Uselman, Keirith A. Snyder, Elizabeth A. Leger, and Sara E. Duke*

Re-seeding efforts to restore or rehabilitate Great Basin rangelands invaded by exotic annual grasses are expensive and have generally achieved limited success. There is a need to identify new strategies to improve restoration outcomes. We tested the performance of a native early seral seed mix (annual forbs, early seral grasses and shrubs) with that of a native late seral mix representative of species commonly used in restoration when growing with medusahead in soils of contrasting texture (sandy loam and clay loam) through the first growing season after seeding. Natives were also seeded without medusahead. We found that the grasses and forbs in the early seral mix established significantly better than those in the late seral mix, and the early seral mix significantly reduced aboveground biomass and seed production of medusahead by 16 and 17% respectively, likely because of competition with the early seral native forb, bristly fiddleneck. Medusahead performance was reduced in both soil types, suggesting utility of bristly fiddleneck in restoration is not limited to only one soil type. In contrast, the late seral mix did not suppress medusahead establishment, aboveground biomass or seed production. Although the native perennial grasses, particularly early seral species, were able to establish with medusahead, these grasses did not appear to have a suppressive effect on medusahead during the first growing season. Medusahead was able to establish and produce seeds on both soil types, demonstrating an ability to expand its current range in the Intermountain West, though aboveground biomass and seed production was higher in the clay loam. Our results suggest that certain species may play a key role in restoration, and that targeting early seral species in particular to find additional native species with the ability to suppress exotic annual grasses is an important next step in improving restoration outcomes in desert ecosystems.

Nomenclature: Medusahead (*Taeniatherum caput-medusae* (L.) Nevski); bristly fiddleneck (*Amsinckia tessellata* A. Gray).

Key words: Exotic annual grass, first-year establishment, functional traits, native plants, restoration, plant-soil relationships.

Exotic annual grasses have invaded the Great Basin of the western U.S. and altered the fire regime across millions of hectares of rangeland ecosystems (D'Antonio and

Vitousek 1992; Pellant and Hall 1994). As a result, extensive areas of sagebrush steppe, once dominated by shrubs and perennial grass, have been converted or are at risk to conversion to exotic annual grasslands (Bradley and Mustard 2005). Restoration or rehabilitation to a more diverse native plant community is desirable to improve wildlife and livestock habitat and forage quality, increase native species biodiversity, and reduce soil erosion and fire risk, but efforts to re-seed burned and otherwise degraded rangeland ecosystems often have only limited success (Eiswerth and Shonkwiler 2006; Epanchin-Niell et al. 2009). The propagules of exotic annual grasses are introduced by dispersal from nearby invaded sites and/or remain sufficiently present in the seedbank to permit reestablishment after fire (West and Young 2000), and it is

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* First and second authors: Postdoctoral Research Associate and Research Ecologist, USDA-Agricultural Research Service, Great Basin Rangeland Research Unit, Reno, NV 89512; third author: Associate Professor, Department of Natural Resources and Environmental Science, University of Nevada-Reno, Reno, NV 89557; fourth author: Statistician, USDA-Agricultural Research Service, Southern Plains Area Office, College Station, Texas 77845. Current address of first author: Department of Natural Resources and Environmental Science, University of Nevada-Reno, Reno, NV 89557. Corresponding author's E-mail: s.uselman@sbcglobal.net

Management Implications

Medusahead is an exotic annual grass that has invaded into the Intermountain West of the U.S., reducing native species biodiversity and increasing fire frequency. In a study of native and medusahead performance, we found that the early seral native annual forb, bristly fiddleneck, was an effective competitor with medusahead in two soil types, significantly reducing biomass and seed production by 16 to 17%. Given that this effect was relatively small, further research to examine whether the use of increased seeding density of bristly fiddleneck and/or whether greater diversity of species in the seeding mix would enhance exotic suppression is warranted. Native perennial grasses, particularly early seral grasses, established in higher numbers than native forbs and shrubs, demonstrating their importance in restoration seedings. Although they did not appear to have a suppressive effect on medusahead during their first growing season, perennial grasses have been found to be effective competitors with exotic annual grasses once mature. Our findings suggest that efforts to find additional novel candidate species for seed mixtures may be best focused on early successional species, similar to bristly fiddleneck, to improve restoration/rehabilitation outcomes in disturbed rangeland ecosystems.

thought that competition with exotics is a major barrier to the re-establishment of natives during restoration efforts (Brown et al. 2008).

Most seed mixtures used in rangeland re-seeding efforts have traditionally relied on mid- to late-seral species (Brown et al. 2008; Eiswerth and Shonkwiler 2006). Early seral species and exotic annual grasses like medusahead (*Taeniatherum caput-medusae* (L.) Nevski) are adapted to post-disturbance conditions and share many similarities in functional traits such as growth and resource acquisition strategies. Research done in Idaho found that the early seral native species squirreltail (*Elymus elymoides* (Raf.) Swezey) is capable of invading and persisting in sites dominated by exotic annual grasses (Hironaka and Sindelar 1973; Hironaka and Tisdale 1963). Similar to exotic annual grasses, early seral native species may be fast growing and/or they may complete their growth cycle and reproduce earlier in the growing season. Because of this greater niche overlap, early seral species may compete more strongly against exotic annual grasses than do later seral species (Funk et al. 2008). As a result, seeding early seral species may improve restoration success (Abella et al. 2012; Leger et al. 2014).

In particular, differences in functional traits of early vs. late seral species, such as accelerated growth phenologies, may confer advantages to native early seral species during the establishment phase when growing in the presence of exotic annual grasses like medusahead. Although studies have found that mature adults of some perennial plant species can effectively compete with and may even suppress exotic annual grasses (Blank and Morgan 2012; Booth et al. 2003; Borman et al. 1991; Chambers et al. 2007; Davies

2008; Humphrey and Schupp 2004), natives should have the ability to perform well in the first year after seeding for improved restoration outcomes. In this study, we compare the performance of early seral natives with that of late seral natives to examine whether early serals are able to establish and perform better than late serals in the presence of medusahead in the first year after seeding.

Soil type appears to be important in the invasion success of medusahead, and may thus affect interactions between medusahead and native species. It appears that medusahead invasion is most closely associated with fine-textured to moderately fine-textured soils, including clays and clay loams (Dahl and Tisdale 1975; Young and Evans 1970), which may be related to differences in water holding capacity. However, limited observations have suggested that medusahead is capable of expanding its current range into more coarse-textured soils (Dahl and Tisdale 1975; Young 1992), demonstrating the need for restoration studies that compare plant performance in different soil types.

Our overall goal was to evaluate the performance (i.e., establishment, aboveground biomass production, and seed production) of the exotic annual grass medusahead and native species mixtures, each composed of grass, forb, and shrub functional groups, during first-year plant growth in a common garden with two different soil types (a clay loam and a sandy loam). Our first objective in this study was to assess the potential suppressive effect of two native seed mixes, one composed of early seral species versus a representative traditional seed mix composed of late seral species. We hypothesized that the early seral seed mix would have a greater suppressive effect on medusahead relative to the late seral seed mix, and that this effect would be strongest in a sandy loam where medusahead is presumed to be least well adapted based on anecdotal observations. Our second objective was to compare the relative performance of the two seed mixes when growing in the presence of medusahead. We hypothesized that the early seral seed mix would be more successful when growing in the presence of medusahead. Our third objective was to examine differences in medusahead performance in the two soil types. We hypothesized that medusahead would be most successful on a clay loam where it is presumed to be most well adapted.

Materials and Methods

Selection of Species for Seed Mixes. Each seed mix was composed of two species of perennial grasses, two forbs, and one shrub. For the traditional seed mix, we chose species that are representative of seeding mixes that have been commonly used in past restoration seedings in the Great Basin. We have termed this seed mix the late seral seed mix because it is composed of species that are later

Table 1. Comparison of functional traits among species in the early vs. late seral seed mixes.

Species	Functional traits	Citations
<u>Early seral seed mix:</u>		
Bristly fiddleneck	Facultatively fall-emerging, annual, disturbance-oriented	Forbis 2010
Veatch's blazingstar	Spring emerging, annual, disturbance-oriented	Forbis 2010
Squirreltail	Facultatively fall-emerging, perennial, earlier maturing, disturbance-oriented	Hardegee et al. 2010; Hironaka and Tisdale 1972
Sandberg bluegrass	Facultatively fall-emerging, perennial, earlier maturing, disturbance-oriented	Blaisdell 1958; Hardegee et al. 2010
Rubber rabbitbrush	Spring emerging, perennial, disturbance-oriented, faster growing	Meyer et al. 1989
<u>Late seral seed mix:</u>		
Palmer's penstemon	Spring emerging, perennial	Meyer and Kitchen 1992
Gooseberryleaf globemallow	Spring emerging, perennial	Jorgensen and Stevens 2004
Snake River wheatgrass	Facultatively fall-emerging, perennial, later maturing	Ray-Mukherjee et al. 2011
Indian ricegrass	Facultatively fall-emerging/spring-emerging, perennial, later maturing	Jones 2009
Wyoming big sagebrush	Spring emerging, perennial, slower growing	Meyer et al. 1990

seral relative to the species in the early seral seed mix. The following species were included: Palmer's penstemon (*Penstemon palmeri* A. Gray), gooseberryleaf globemallow [*Sphaeralcea grossulariifolia* (Hook. & Arn.) Rydb.], Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth 'Secar'), Indian ricegrass [*Achnatherum hymenoides* (Roem. & Schult.) Barkworth 'Rimrock'], and Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young). The early seral seed mix was composed of the following species: bristly fiddleneck (*Amsinckia tessellata* A. Gray), Veatch's blazingstar (*Mentzelia veatchiana* Kellogg), squirreltail [*Elymus elymoides* (Raf.) Swezey], Sandberg bluegrass (*Poa secunda* J. Presl), and rubber rabbitbrush [*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird]. Table 1 shows a comparison of functional traits for the species in the early and late seral seed mixes.

Experimental Design and Implementation. Seeds of the early seral native species and medusahead were hand-collected from multiple wild populations in northern Nevada, USA in 2010. Seeds of the late seral seed mix were purchased from a commercial vendor (Comstock Seeds, Gardnerville, NV, USA), following the procedure for a typical restoration seeding. We tested seeds for viability using tetrazolium staining (Association of Official Seed Analysts 1988), as detailed in Forbis (2010).

Soils used for the experiments were collected from 0 to 15 cm (0 to 6 in) at multiple field locations in Wyoming big sagebrush communities in northern Nevada, and included a Wylo series (clayey, smectitic, mesic, Lithic Argixeroll; hereafter referred to as the "clay loam") and a Wedertz series (fine-loamy, mixed, superactive, mesic

Durinodic Xeric Haplargid; hereafter referred to as the "sandy loam") (Soil Survey Staff, NRCS). We collected the clay loam soil from three sites along a 3-km (2-mi) transect off Buffalo Meadows Road, north of the Smoke Creek Desert (approximately 130 km N of Reno, 40°43'N, 119°48'W; 1,435 to 1,465 m (approximately 4700 to 4800 feet) elevation, and we collected the sandy loam soil from three sites along a 5-km transect at Bedell Flat (approximately 35 km N of Reno, 39°51'N, 119°49'W; 1,525 to 1,585 m elevation). For each soil type, soil was collected from several locations at each of the three sites and coarse sieved (12.5 mm; 0.5 in) in the field. For each soil type, the soil collections were homogenized and filled into pots by weight to approximate field bulk density.

A common garden approach was used to test exotic and native plant performance in the two different soil types while controlling for environmental conditions. Soil-filled treepots (41 cm deep, 15 cm by 15 cm surface area; TPOT2, Stuewe and Sons, Inc., Tangent, OR, USA) containing either of the two soil types were sunk into the ground at the University of Nevada Agricultural Experiment Station in Reno, NV, USA. The two soil types were randomly distributed across a 650 m² field, with a minimum distance of 45 cm between pots, and the study area was fenced to exclude small mammals. Two experiments were performed concurrently, using completely randomized designs. First, we designed a 2 by 3 factorial experiment to assess the performance of medusahead when growing with and without the early seral and late seral native seed mixes. This experiment was also designed to test the relative performance of the early seral versus the late seral seed mix when growing in the presence of the exotic. There were two levels of soil type (clay loam and sandy

loam) crossed with three levels of seed mix (early seral mix, late seral mix, and no mix). Treatments that were composed of only exotics were replicated 15 times (2 by 1 by 15 = 30), while treatments that were composed of exotics with natives were replicated 23 times (2 by 2 by 23 = 92), for a total of 122 experimental units. Because we anticipated greater variation in treatments composed of a combination of exotics and natives, we increased the replication for those treatments. We designed a second fully randomized 'No Exotic' experiment to evaluate the performance of the native seed mixes when growing in the absence of medusahead. Two levels of soil type (clay loam and sandy loam) were crossed with two levels of seed mix (early seral mix and late seral mix), and treatments were replicated 9 times (2 by 2 by 9) for a total of 36 experimental units. This experiment was seeded at the same time, and performed concurrently with the medusahead experiment.

In the medusahead experiment, 10 or 20 seeds were sown by hand into randomized locations within each pot using a 20-location fixed grid in October 2010. This experiment used an additive design because we were interested in testing the effect of the natives on medusahead. This is best achieved by maintaining a constant density of the target exotic and varying the presence/absence of the potential competitor, rather than using a replacement series, which can confound potential effects of intraspecific competition among medusahead seedlings with effects of interactions with native species (Snaydon 1991). We used three species combinations: (1) exotic only (10 seeds), (2) exotic (10 seeds) and early seral natives (10 seeds, consisting of two of each species), and (3) exotic (10 seeds) and late seral natives (10 seeds, consisting of two of each species). In the 'No Exotic' experiment, 10 native seeds were sown into randomized locations within each pot, using two species combinations: (1) early seral natives only (10 seeds, consisting of two of each species) and (2) late seral natives only (10 seeds, consisting of two of each species). For both experiments, we used seeding rates (i.e., 10 native seeds pot^{-1} , or 444 seeds m^{-2}) that were within the range of recommended seeding rates suggested for rangelands (Monsen and Stevens 2004). All species combinations were randomly assigned to pots containing each of the two soil types (i.e., clay loam or sandy loam, see above). Grasses were sown to a depth of 1.27 cm (0.5 in) to simulate the use of a rangeland drill with a 0.5 in. depth band. Forbs and shrubs were sown to a depth of 0.32 cm (0.125 in) to achieve surface to near-surface seeding and ensure seed-to-soil contact in seed placement, simulating usage of a surface seeder or seed dribbler in large-scale rangeland restoration/rehabilitation seedings (Stevens and Monsen 2004). Seeds were placed by hand at the specified depths and the soil surface was pressed closed.

Seeds were planted in October 2010 prior to significant precipitation inputs and the onset of freezing temperatures

which is commonly required for stratification and/or germination of cold desert plants, including species used in this study (Table 1 citations). Seed viability testing based on tetrazolium staining was completed after seedling (Supplemental Appendix 1; <http://dx.doi.org/10.1614/IPSM-D-13-00068.SA1>). Because of the low seed viability of the two shrubs (rubber rabbitbrush, 25%; Wyoming big sagebrush, 56%), we re-seeded both species in January of 2011. For rubber rabbitbrush, each grid location received an additional three seeds; and for Wyoming big sagebrush each grid location received an additional one seed, to bring the final addition of viable seed to approximately 100%.

Beginning in late spring/early summer 2011, we began intensively monitoring and collecting seeds once they matured, by species and by pot. This was done as often as daily during peak seed production. As an added precaution against seed loss, we placed mesh screening material (1.5 mm) around the pots as needed. This mesh size was adequate to trap seeds with their reproductive structures, as the species with the smallest seeds (Palmer's penstemon and Veatch's blazingstar) did not produce flowers during the study. At the termination of seed production, we counted the number of surviving individuals and collected aboveground biomass by species and by pot. Annuals were senescent at the time of biomass collection. Because of differences in growth and reproductive phenologies of the species, collections spanned through the end of fall (Dec. 2011). Biomass samples were oven-dried at 65 °C (149 °F) to constant mass, then weighed. Biomass of seeds produced during the experiment was separated from non-reproductive biomass for seed count.

Total precipitation was collected continuously using a tipping bucket rain gauge fitted with a precipitation adapter for snowfall in winter months. Air temperature data was collected adjacent to the study site (Western Regional Climate Center, DRI). We included several additional pots of each soil type with no plants (4 by 2) in order to evaluate the behavior of the two soil types under the same environmental conditions during the study period. One pot of each soil type was instrumented for continuous soil volumetric water content (VWC) using Campbell CS616 Water Content Reflectometer probes (Campbell Scientific, Inc., Logan, UT, US), installed vertically to integrate soil VWC (%) over a depth of 0 to 30 cm. In addition, we used a hand-held probe (CD620, CS620, Campbell Scientific, Inc.) to measure soil VWC every 1 to 3 wk in the other pots ($n = 3$ for each soil type). We took measurements integrating 0 to 12 cm (October 2010 to January 2012) and 0 to 20 cm (March 2011 to January 2012). Soil VWC data was summarized as daily averages or point measurements by depth increment. We determined the permanent wilting point (-1.5 MPa by convention) for both soil types ($n = 3$) using a WP4 Dewpoint Potentiometer (Decagon Devices, Inc.).

Data Analysis. ANOVA was used to assess differences among seed mix and soil type for establishment (plants pot^{-1}), aboveground biomass (g pot^{-1}) and seed production (seeds pot^{-1}). For medusahead, models included the following factors: seed mix (early mix, late mix, no seed mix) and soil type (clay loam, sandy loam). For natives, models included the following factors: seed mix (early mix, late mix), soil type (clay loam, sandy loam), and functional group (grass, forb, shrub). We did not directly compare native species in the context of our treatment structure, instead focusing on functional groups and the overall effects of the early/late seral mix. Tukey-Kramer HSD tests were performed to compare means when model effects were significant. Prior to statistical analysis, biomass and seed production of medusahead data and establishment of natives growing with medusahead data were log-transformed (i.e., $\log_{10}[X+1]$) to meet assumptions of homogeneity of variance and normal distribution of residuals. As expected, there was greater variation in native establishment among our replicates with both natives and medusahead. We initially considered the inclusion of natives data (e.g., native establishment) as covariates in the medusahead models, but this failed to improve model fits and did not change results. Repeated measures ANOVA was used to assess differences in point measurements of soil VWC between the two soil types for each depth increment. Differences between the moisture content of the two soil types were determined for each sampling date by testing the one degree of freedom hypothesis of difference between treatments (slice tests). Prior to analysis, VWC data was arcsine-transformed (i.e., transformed by the arcsine of the square root of the proportion) (Zar 1996). All data were analyzed using JMP 9.0 statistical analysis software (SAS Institute Inc., Cary, NC, USA), with $\alpha = 0.05$ set as the significance level. Figures and tables show mean ± 1 SE.

Results

Environmental Variables. Although the study site received somewhat regular inputs of precipitation during the winter and spring, there was an extended dry period after early June of 2011 (Figure 1a). For the 2011 water year, total precipitation (253 mm) was above average for Reno, NV (178 mm, Western Regional Climate Center, DRI), but it was within the average range for the Wyoming big sagebrush zone of sagebrush steppe in the Great Basin (Goodrich et al. 1999). Although soil moisture was relatively high during most of the cold wet season, the period of drought during the summer and fall resulted in an extended and severe dry down of soil moisture. This is reflected in very low soil VWC values by late summer that continued into the fall of 2011 (Figure 1b). Soil VWC differed significantly between the two soil types over the course of the study for the 0 to 12 cm ($F = 239.90_{1,5,776}$,

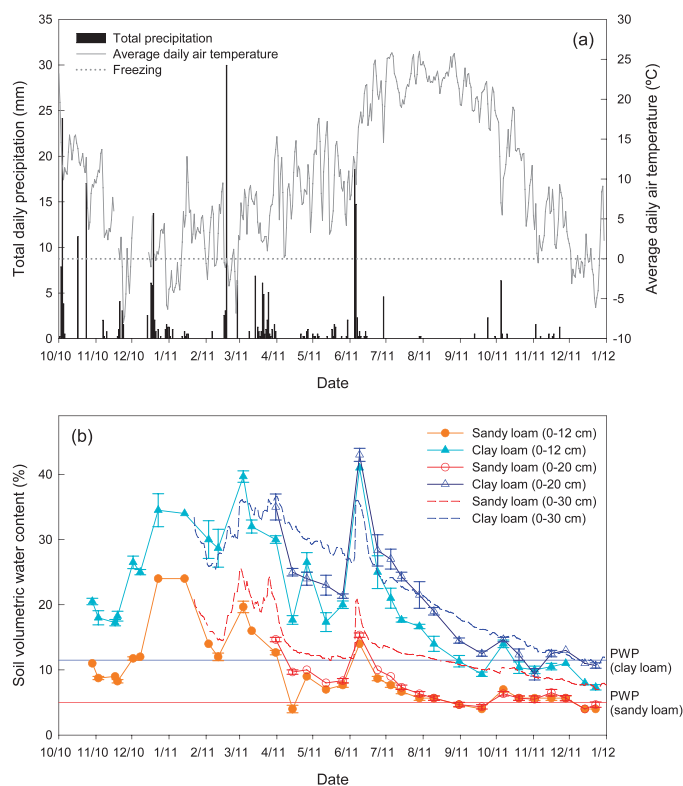


Figure 1. Environmental conditions at the study site from October 1, 2010 through January 1, 2012. In (a), total daily precipitation (mm) and average daily air temperature ($^{\circ}\text{C}$) are shown. In (b), soil volumetric water content (VWC, %) is shown for both soil types. Note that VWC was measured periodically using a handheld probe for the 0 to 12 cm and 0 to 20 cm depths ($n = 3$), while VWC was measured continuously for the 0 to 30 cm depth (daily average values shown, $n = 1$). The permanent wilting point (-1.5 MPa by convention; PWP) is indicated with a colored reference line (blue = clay loam and red = sandy loam). Below the PWP, soil water is unavailable for plant uptake. See text for methods details.

$P < 0.0001$) and for the 0 to 20 cm depth increments ($F = 315.05_{1,4,86}$, $P < 0.0001$), for all sampling dates ($P < 0.0001$, all dates, both depth increments). Both soil types began approaching critically low levels of soil moisture in July (sandy loam) or August (clay loam). For the sandy loam, the soil VWC did not differ between the 0 to 12 cm and 0 to 20 cm depth increments after mid-July onwards ($P > 0.05$, all dates). However, for the clay loam it was higher in the 0 to 20 cm vs. 0 to 12 cm depth increment from 24 June through 19 September ($P < 0.05$, all dates). Initially as the soils began to dry down in early summer, the clay loam maintained higher water availability longer than the sandy loam, particularly in the deeper depth increment.

Establishment (plants pot^{-1}). Establishment of medusahead was not affected by seed mix ($F = 0.25_{2,115}$, $P =$

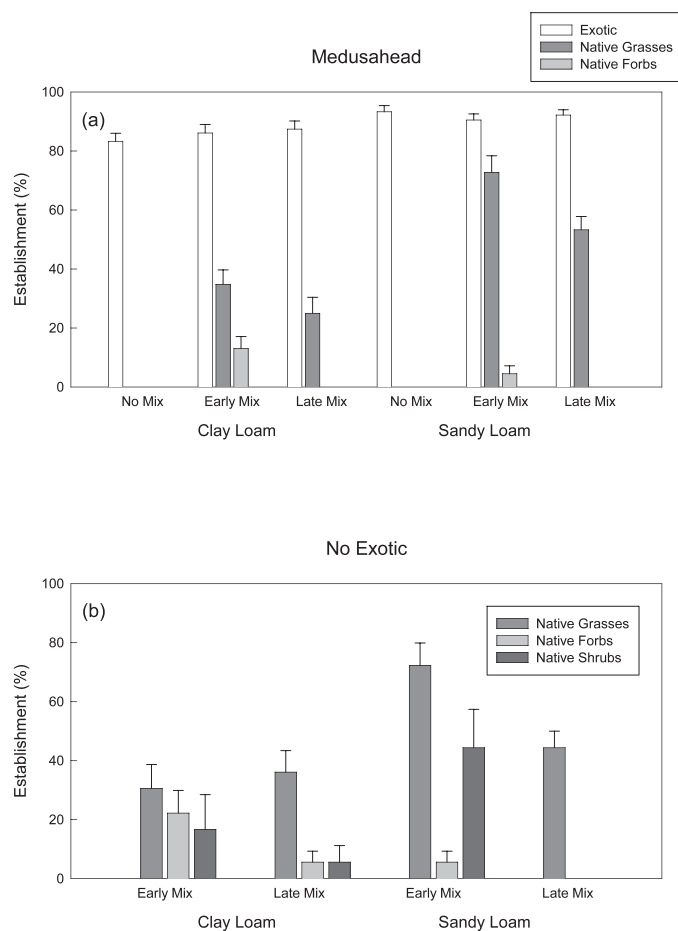


Figure 2. Establishment (% of seeded) of the exotic and natives for each functional group, shown by soil type and by seed mix for the (a) Medusahead experiment, and (b) 'No Exotic' experiment with only natives. Mean $\pm$ SE. Statistical analyses were performed on establishment as # plants pot^{-1} , but establishment is shown as % for ease of viewing.

0.78), but it was significantly higher in sandy loam than clay loam ($F = 9.38_{1,115}$, $P = 0.003$) (Figure 2a). However, establishment was overall very high in all treatments and ranged from 83 to 93%.

When growing with medusahead, establishment of early seral natives was higher than that of late seral natives for grasses and forbs but not for shrubs (seed mix by functional group interaction; $F = 4.04_{2,261}$, $P = 0.02$) (Figure 2a). Additionally, native grasses generally exhibited higher establishment than forbs and shrubs. Establishment of grasses was higher in sandy loam than clay loam, while establishment of forbs and shrubs was not significantly affected by soil type (soil type by functional group interaction; $F = 31.50_{2,261}$, $P < 0.0001$).

When growing alone, native establishment varied with seed mix, soil type, and functional group (seed mix by soil type by functional group interaction; $F = 3.96_{2,96}$, $P = 0.02$) (Figure 2b). Early seral grasses exhibited higher

establishment than late seral grasses in sandy loam but not in clay loam, while the other functional groups did not differ significantly by seed mix or soil type. Additionally, early seral grasses had higher establishment in sandy loam than clay loam, but late seral grasses were not affected by soil type. For the most part, establishment of native grasses was higher than forbs and shrubs, except for early seral grasses growing in clay loam.

Aboveground Biomass Production (g pot^{-1}) and Seed Production (seeds pot^{-1}). Aboveground biomass production and seed production of medusahead were significantly affected by seed mix ($F = 4.84_{2,115}$, $P = 0.01$ and $F = 3.69_{2,115}$, $P = 0.03$, respectively) and soil type ($F = 41.82_{1,115}$, $P < 0.0001$ and $F = 24.78_{1,115}$, $P < 0.0001$, respectively) (Figures 3a and 4a). Both biomass and seed production of medusahead were significantly suppressed by the early seral seed mix relative to when the exotic was growing alone, although this effect was relatively small. Averaged across both soil types, the reduction in exotic aboveground biomass and seed production was 16 and 17%, respectively. The exotic biomass and seed production were more strongly reduced in the sandy loam (21 and 22%, respectively) than in the clay loam (13 and 14%, respectively). In contrast, biomass and seed production of medusahead were not suppressed by the late seral seed mix. Additionally, biomass and seed production of the exotic were 66 and 59% higher in the clay loam than the sandy loam, respectively.

When growing with medusahead, native aboveground biomass production and seed production varied by seed mix, soil type, and functional group (seed mix by soil type by functional group interaction; $F = 3.83_{2,261}$, $P = 0.02$ and $F = 4.21_{2,261}$, $P = 0.02$, respectively) (Figures 3a and 4a). Both biomass and seed production of early native forbs was higher in clay loam than sandy loam: all other native treatment group means were zero or near zero.

When growing alone, native aboveground biomass and seed production varied by seed mix and functional group (seed mix by functional group interaction; $F = 7.55_{2,96}$, $P = 0.0009$ and $F = 6.04_{2,96}$, $P = 0.003$, respectively) (Figures 3b and 4b). Early seral native production was higher than late seral native production for forbs, but not for grasses and shrubs. In the early seral mix, production of native forbs exceeded that of the other functional groups. In addition, both biomass and seed production of natives were higher in clay loam relative to sandy loam ($F = 3.84_{1,96}$, $P = 0.05$ and $F = 4.29_{1,96}$, $P = 0.04$, respectively).

Discussion

We found that the early seral seed mix had higher establishment than the late seral mix because of the

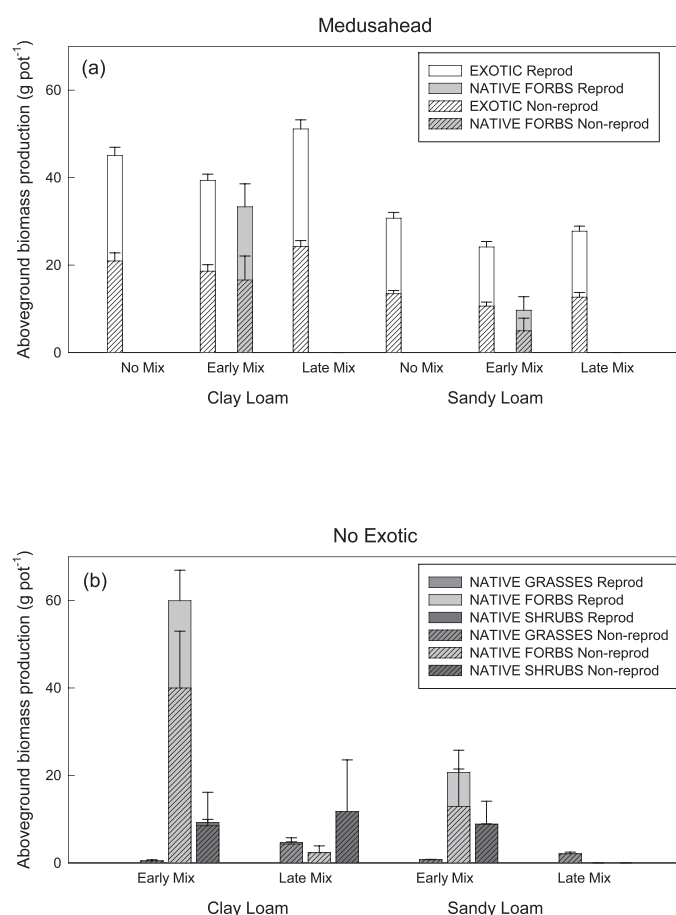


Figure 3. Aboveground biomass production (g pot^{-1}) of the exotic and natives for each functional group, shown by soil type and by seed mix for the (a) Medusahead experiment, and (b) 'No Exotic' experiment with only natives. Biomass is distinguished between reproductive (i.e., seeds; no hash marks) and non-reproductive biomass (hash marks). Mean $\pm$ SE. Note that native grasses do not appear in (a) because their biomass was $< 0.1 \text{ g pot}^{-1}$ in all treatment combinations.

performance of grasses and forbs, and that the early seral mix resulted in small but significant reductions in aboveground biomass and seed production of the exotic medusahead in both soil types. In contrast, the late seral seed mix did not suppress establishment, aboveground biomass or seed production of the exotic. Although native grasses established in the presence of medusahead, native grass aboveground biomass and seed production was negligible during the first year after seeding with the exotic. However, it should be noted that seed production of perennial grasses would not be expected to be high in the first year of growth. Only the native early seral forb functional group was able to produce any substantive aboveground biomass or seeds (Figures 3a and 4a). Because one of the early seral forbs (Veatch's blazingstar) had no establishment (Table 2), biomass and seed production of

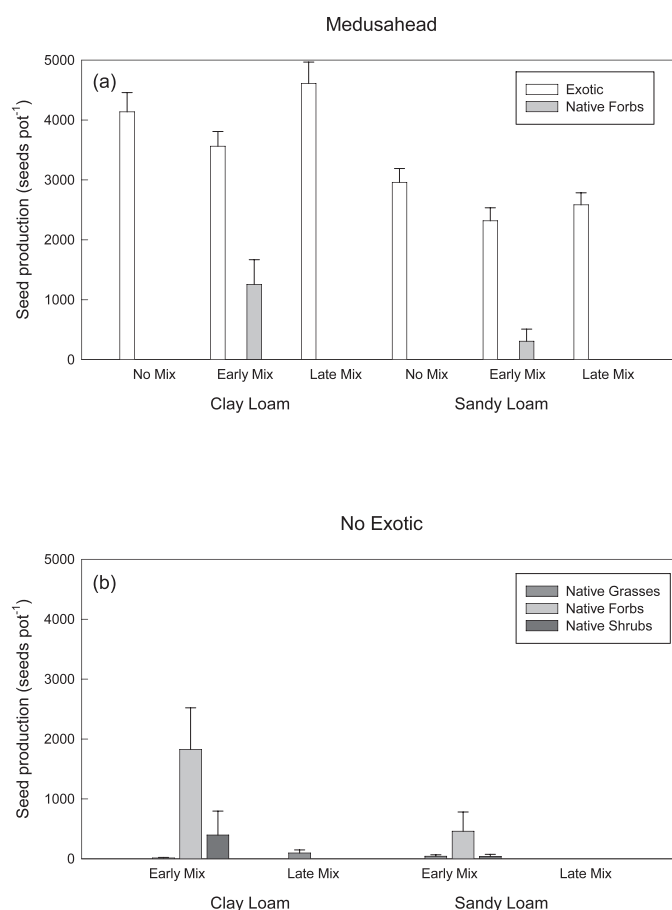


Figure 4. Seed production (seeds pot^{-1}) of the exotic and natives for each functional group, shown by soil type and by seed mix for the (a) Medusahead experiment, and (b) 'No Exotic' experiment with only natives. Mean $\pm$ SE.

the early seral forbs was due entirely to the other species, bristly fiddleneck. As the native grasses remained very small, using few resources for growth and reproduction during the first year of growth, it seems unlikely that they negatively impacted medusahead. Thus, our findings suggest that bristly fiddleneck was mostly responsible for the suppression of medusahead biomass and seed production during this first growing season.

Performance of invaders is reduced when resident communities include natives that overlap in resource-use functional traits (Brown and Rice 2010; Fargione et al. 2003; Young et al. 2009), and certain native species in particular may be especially effective competitors with exotics (Abella et al. 2012; Thomsen and D'Antonio 2007). Similar to medusahead, bristly fiddleneck is a fast-growing winter annual capable of establishing and thriving in post-disturbance conditions. Seedlings of bristly fiddleneck had an earlier emergence phenology than all other native species in this study, except grasses, and although they did emerge later than medusahead, bristly fiddleneck

Table 2. Establishment, shown as number of individuals (and as percentage of seeded^a), for each species by treatment (mean $\pm$ SE).

Species ^b												
Treatment	Exotic	Native Grasses				Native Forbs				Native Shrubs		
	TACA	ELEL	POSE	ELWA	ACHY	AMTE	MEVE	PEPA	SPGR	ERNA	ARTR	
Establishment as no. individuals (and as % of seeded)												
Medusahead expt.												
Clay loam												
<i>No Mix</i>	8.3 ± 0.3 (83 ± 3)	—	—	—	—	—	—	—	—	—	—	
<i>Early Mix</i>	8.6 ± 0.3 (86 ± 3)	0.7 ± 0.2 (35 ± 8)	0.7 ± 0.1 (35 ± 7)	—	—	0.5 ± 0.2 (26 ± 8)	0 (0)	—	—	0 (0)	—	
<i>Late Mix</i>	8.7 ± 0.3 (87 ± 3)	—	—	0.7 ± 0.2 (33 ± 8)	0.3 ± 0.1 (17 ± 6)	—	—	0 (0)	0 (0)	—	0 (0)	
Sandy loam												
<i>No Mix</i>	9.3 ± 0.2 (93 ± 2)	—	—	—	—	—	—	—	—	—	—	
<i>Early Mix</i>	9.0 ± 0.2 (90 ± 2)	1.4 ± 0.2 (70 ± 8)	1.5 ± 0.1 (75 ± 6)	—	—	0.2 ± 0.1 (9 ± 5)	0 (0)	—	—	0 (0)	—	
<i>Late Mix</i>	9.2 ± 0.2 (92 ± 2)	—	—	1.5 ± 0.1 (76 ± 5)	0.6 ± 0.1 (30 ± 7)	—	—	0 (0)	0 (0)	—	0 (0)	
No Exotic expt.												
Clay loam												
<i>Early Mix</i>	0.9 ± 0.3 (44 ± 15)	0.9 ± 0.3 (44 ± 15)	0.3 ± 0.2 (17 ± 8)	—	—	0.9 ± 0.3 (44 ± 15)	0 (0)	—	—	0.3 ± 0.2 (17 ± 12)	—	
<i>Late Mix</i>	—	—	—	1.0 ± 0.3 (50 ± 14)	0.4 ± 0.2 (22 ± 9)	—	—	0.2 ± 0.1 (11 ± 7)	0 (0)	—	0.1 ± 0.1 (6 ± 6)	
Sandy loam												
<i>Early Mix</i>	1.4 ± 0.2 (72 ± 9)	1.4 ± 0.2 (72 ± 9)	1.4 ± 0.2 (72 ± 9)	—	—	0.2 ± 0.1 (11 ± 7)	0 (0)	—	—	0.9 ± 0.3 (44 ± 13)	—	
<i>Late Mix</i>	—	—	—	1.2 ± 0.2 (61 ± 11)	0.6 ± 0.2 (28 ± 9)	—	—	0 (0)	0 (0)	—	0 (0)	

^a 100% establishment of the exotic species is equivalent to 10 plants established (out of 10 seeded), while 100% establishment of native species is equivalent to 2 plants established (out of 2 seeded).

^b Species codes are as follows: TACA (*T. caput-medusae*; medusahead), ELEL (*E. elymoides*; squirreltail), POSE (*P. secunda*; Sandberg bluegrass), ELWA (*E. wawawaiensis*; Snake River wheatgrass), ACHY (*A. hymenoides*; Indian ricegrass), AMTE (*A. tessellata*; bristly fiddleneck), MEVE (*M. veatchiana*; Veatch's blazingstar), PEPA (*P. palmeri*; Palmer's penstemon), SPGR (*S. grossulariifolia*; gooseberryleaf globemallow), ERNA (*E. nauseosa*; rubber rabbitbrush), and ARTR (*A. tridentata* ssp. *wyomingensis*; Wyoming big sagebrush).

seedlings grew very quickly (Uselman et al., personal observation). In February, newly emerged seedlings were slightly smaller, if not already comparable in size to medusahead seedlings, and by mid-April they exceeded the size of medusahead seedlings. Bristly fiddleneck are tap-rooted plants that can ultimately achieve a larger stature than medusahead plants, and like medusahead, can produce a copious number of seeds. Both species actively grow during an overlapping time period and compete for limiting resources. These similarities in functional traits could explain why medusahead biomass and seed production was significantly lower when growing with bristly fiddleneck. Strong suppressive effects of bristly fiddleneck have been observed with the exotic annual grass downy brome (*Bromus tectorum* L.) when the forb was seeded at higher densities (Leger et al. 2014), indicating it may have potential as a restoration species in invaded habitats. Unexpectedly, we found similar responses in the two soil types; this is promising because it suggests that the use of this native species for restoration may be possible in a variety of sites.

Although the performance of medusahead was significantly reduced by the presence of bristly fiddleneck, the rates of medusahead seed production were high in all treatments (Figure 4), so the magnitude of this reduction would likely not result in a large biological effect. An increased seeding density of bristly fiddleneck or inclusion of different native species in the early seral seed mix may further reduce the performance of medusahead. In this study, we used a seeding rate of two seeds pot^{-1} for bristly fiddleneck because it was one of five native species included in the early seral seed mix. While the total native seeding rate (i.e., 10 native seeds pot^{-1} , or 444 seeds m^{-2}) was within the range of rates typically used in semiarid rangeland seedings, this rate was effectively lowered because some species had low or negligible establishment, including Veatch's blazingstar, gooseberryleaf globemallow, and Wyoming big sagebrush (Table 2). Higher native seeding rates may result in increased establishment for native species in general (Hardegree et al. 2011; Mazzola et al. 2011; Seabloom 2011), though it is important to consider the biology of specific species, forbs in particular, in order to minimize potential negative interactions between the desired seeded species when designing restoration seed mixtures (Parkinson et al. 2013). Greater diversity of native species, including native annuals, may also result in increased establishment in restoration seedings, especially given differences among species in environmental cues required for germination and other growth stages. For example, in an assessment of seven native annual forbs over the past > 100 yr in the Great Basin, Leger (2013) found that species performance differed with climate variables related to temperature and precipitation and suggested that this type of information could be used to design a native

species mix for restoration with species that would perform well in differing climate years. Thus, inclusion of a greater diversity of seeded native species as a form of community 'bet-hedging' against inter-annual climate variability, in addition to higher seeding rates of bristly fiddleneck, may result in better suppression of medusahead and improved restoration outcomes. Testing in multiple years would be informative.

The capacity of bristly fiddleneck to reduce aboveground biomass and seed production of medusahead suggest that it may play a role in facilitating succession to a more desirable late seral vegetation state, though bristly fiddleneck is not a forage species itself. In a greenhouse study, the inclusion of native annuals with desirable native perennial species reduced downy brome biomass without reducing the desired species biomass (Perry et al. 2009). Bristly fiddleneck has been found to facilitate the growth rate of the native grass squirreltail when growing in the presence of downy brome (Leger et al. 2014). In the Mojave Desert, Abella et al. (2012) found that early successional communities were more effective at limiting the establishment of exotic grasses. An early successional forb community (largely driven by a single forb species) substantially reduced biomass production of red brome (*Bromus rubens* L.) and was least invasible by this invasive annual grass (Abella et al. 2012). Taken together, our results and those of Abella et al. (2012) suggest that certain species may play a key role in restoration, and that identification of additional early seral native species with the ability to suppress exotic annual grasses is an important next step in improving restoration outcomes in desert ecosystems.

Native grasses had higher first-year establishment than either the native forb or shrub species in this study, and the early seral native grasses had higher establishment than late seral native grasses when seeded with medusahead (Figure 2a). Although the native grasses remained very small during the first growing season when seeded with medusahead, they may be capable of persisting within a mixed native-exotic community and may later become competitive with exotics in the second year of growth (e.g., Ferguson 2012; Humphrey and Schupp 2004). In comparison to exotic annual grasses, native perennial grasses have been found to be at a competitive disadvantage in the seedling stage (Aguirre and Johnson 1991; James et al. 2011) and juvenile mortality can be very high during the first growing season (Mazzola et al. 2011; Pyke 1990). During the early establishment of perennial seedlings that germinate and emerge in the fall, slowed root growth relative to exotics during cold winter months (i.e., winter dormancy) is thought to be an important reason for failure of some natives to establish in stands of exotic annual grasses (Harris 1977). Although native grasses demonstrated an ability to persist through the first year of growth, data from our study do not indicate whether native perennials will suppress medusahead in a second year of growth.

Notably though, bristly fiddleneck seed production was comparable to that of medusahead in the first year (in terms of seeds individual⁻¹, data not shown), and presence of this native annual in the second year may facilitate native grasses, as has been observed with downy brome (Leger et al. 2014). Additional study is needed to determine the longer term outcome.

Our data support observations and suggestions that medusahead is a highly competitive plant (Davies and Svejcar 2008; Young 1992; Young and Mangold 2008), capable of expanding its current range (Dahl and Tisdale 1975; Johnson and Davies 2012; Young 1992). Establishment of medusahead was slightly but significantly higher on the sandy loam, but it was high in all treatments (ranging from 83 to 93%; Figure 2a). Medusahead roots have a well-developed endodermis, protecting them against water loss during periods of very low soil moisture (Harris 1977; Hironaka 1961). This is an important adaptation that may help explain the very low rates of attrition for this species. Although medusahead was able to successfully establish in both soil types, the exotic's production of aboveground biomass and seeds were, as predicted, 66 and 59% higher on the clay loam, respectively (Figures 3a and 4a). In addition, the suppressive effect of the early seral mix on the exotic was weaker in the clay loam relative to the sandy loam, suggesting that medusahead is better adapted to the finer textured soil. The clay loam maintained higher water availability longer than the sandy loam, particularly in deeper depths, as the soils began to dry down in summer (Figure 1b). Medusahead was likely able to benefit from this greater availability of water for growth and reproduction during its maturation in July. Although differences in water holding capacity between the two soil types can help explain the observed differences in plant performance, we cannot rule out the possibility that other factors (e.g., pathogens) may have also affected performance. Medusahead average per capita seed production was 282 ± 14 seeds plant⁻¹ in the sandy loam compared to 477 ± 20 seeds plant⁻¹ in the clay loam, so although seed production was lower in the sandy loam it was still relatively high. It should be noted that medusahead-invaded sites that are severely degraded would likely require weed control prior to seeding natives (e.g., Kyser et al. 2013).

Our key findings were that early seral grasses and forbs were better at establishing with medusahead than were late seral species, and that the early seral native annual forb bristly fiddleneck was an effective competitor with the exotic annual grass medusahead, reducing biomass and seed production of the exotic by a small but significant amount. Results of our study point to a promising line of new potential studies. It would be informative to examine the response of medusahead to differing seeding densities of bristly fiddleneck to establish an optimal rate that would provide the greatest suppressive effect on medusahead biomass and seed production. Additionally, a greater

number of species in the seeding mix may enhance medusahead suppression and improve restoration success. Notably, native perennial grasses, especially early seral species, were able to establish in the presence of medusahead in higher numbers than native forbs or shrubs, demonstrating their importance in restoration, though they did not appear to have a suppressive effect on the exotic during the first growing season. Additional research is needed to assess the impact of native perennial grasses seeded with medusahead over a longer time frame to discover whether these species may suppress the exotic during later stages of community development. Of utmost importance, future research identifying novel candidate species for seed mixtures will be instrumental for improving the success of native plant community restoration in desert ecosystems. Results of this study and others (Abella et al. 2012; Leger et al. 2014) suggest that efforts focusing on early successional species in particular may be most likely to result in improved restoration outcomes in disturbed arid and semi-arid systems.

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