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Author(s): K.W. Davies and C.S. Boyd

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Original Research

Longer-Term Evaluation of Revegetation of Medusahead-Invaded Sagebrush Steppe☆

K.W. Davies [a],*, C.S. Boyd [b]

[a] Rangeland Scientist, US Department of Agriculture*–Agricultural Research Service.
[b] Research Leader, US Department of Agriculture*–Agricultural Research Service.

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ABSTRACT

Medusahead (*Taeniatherum caput-medusae* [L.] Nevski) and other exotic annual grasses have invaded millions of hectares of sagebrush (*Artemisia* L.) steppe. Revegetation of medusahead-invaded sagebrush steppe with perennial vegetation is critically needed to restore productivity and decrease the risk of frequent wildfires. However, it is unclear if revegetation efforts provide long-term benefits (fewer exotic annuals and more perennials). The limited literature available on the topic questions whether revegetation efforts reduce medusahead abundance beyond 2 or 3 yr. We evaluated revegetation of medusahead-invaded rangelands for 5 yr after seeding introduced perennial bunchgrasses at five locations. We compared areas that were fall-prescribed burned immediately followed by an imazapic herbicide treatment and then seeded with bunchgrasses 1 yr later (imazapic-seed) with untreated controls (control). The imazapic-seed treatment decreased exotic annual grass cover and density. At the end of the study, exotic annual grass cover and density were 2-fold greater in the control compared with the imazapic-seed treatment. The imazapic-seed treatment had greater large perennial bunchgrass cover and density and less annual forb (predominately exotic annuals) cover and density than the untreated control for the duration of the study. At the end of the study, large perennial bunchgrass density average 10 plant·m^{-2} in the imazapic-seed treatment, which is comparable with intact sagebrush steppe communities. Plant available soil nitrogen was also greater in the imazapic-seed treatment compared with the untreated control for the duration of the study. The results of this study suggest that revegetation of medusahead-invaded sagebrush steppe can provide lasting benefits, including limiting exotic annual grasses.

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Introduction

Exotic annual grass invasion is a serious threat to the historically perennial-dominated sagebrush (*Artemisia* L.) steppe ecosystem and fauna dependent on it (Davies et al., 2011). Exotic annual grass-invaded communities may burn more frequently than native dominated communities because of decreased fuel moisture, increased fine fuels, and fuel continuity (Brooks et al., 2004; Davies and Nafus, 2013). Exotic annual grasses can develop a grass-fire cycle, which can be particularly devastating to native plants that are not adapted to frequent fire (D'Antonio and Vitousek, 1992). One of the most problematic exotic annual grasses invading sagebrush steppe communities is medusahead (*Taeniatherum caput-medusae* [L.] Nevski) (Young, 1992; Nafus and Davies, 2014). Medusahead is rapidly spreading across the western United States (Duncan and Jachetta, 2005). Medusahead has high silica content and sharp awns that greatly limit its forage value to livestock (Hironaka, 1961; Torell et al., 1961). Invasion by medusahead results in the formation of a thick, persistent thatch layer that decreases native plant establishment and increases dry fine fuel amounts (Torell et al., 1961; Young et al., 1972; Young, 1992). Medusahead is also highly competitive with native vegetation (Hironaka and Sindelar, 1975; Goebel et al., 1988; Young and Mangold, 2008), leading to decreases in biodiversity and native plant abundance as medusahead density increases (Davies, 2011). Medusahead-invaded sagebrush steppe also does not provide quality habitat for a sagebrush obligate wildlife (Davies and Svejcar, 2008; USFWS, 2013).

Revegetation of medusahead-invaded rangeland is needed to restore ecosystem productivity and decrease the frequency of wildfires. Most successful efforts to revegetate medusahead-invaded sagebrush rangelands first control annual species with prescribed burning followed by a preemergent herbicide application, such as imazapic (Nafus and Davies, 2014). Burning is often applied before imazapic application to improve soil-herbicide contact and prepare the seedbed for planting (Davies, 2010; Davies and Sheley, 2011). Seeding perennial vegetation is usually postponed until 1 yr after preemergent herbicide application

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* Correspondence: K. W. Davies, Eastern Oregon Agricultural Research Center, 67826-A Hwy 205, Burns, OR 97720, USA. Tel.: +1-541-573-4074.
E-mail address: kirk.davies@usda.ars.gov (K.W. Davies).

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to allow herbicide toxicity to subside (Davies, 2010; Davies et al., 2015). Short-term revegetation success has been variable (Monaco et al., 2005; Davies, 2010; Davies et al., 2014b), but successfully established perennial vegetation generally limits medusahead and other exotic annuals (Davies, 2010; Davies et al., 2015; Davies and Johnson, 2017). Longer-term evaluations of medusahead control are limited, especially evaluating revegetation success (James et al. 2015). Particularly important is determining if seeded perennial vegetation limits medusahead and other exotic annuals expression over extended time frames.

A critical component of a successful revegetation program is to establish enough plants to use soil nutrients to reduce their availability to exotic annual species. Though exotic annual grasses are more competitive for soil nutrients than perennial species (James, 2008; Leffler et al., 2011), exotic annual grasses are even more favored with greater nutrient availability, particularly nitrogen (Vasquez et al., 2009). Seeding competitive perennial vegetation can reduce soil nutrient availability, thereby increasing biotic resistance to exotic annual grass invasion (Davies et al., 2010). However, the effect of revegetating medusahead-invaded rangeland on soil nutrient availability is relatively unknown.

The purpose of this study was to investigate the longer (5-yr) effects of revegetation of medusahead-invaded sagebrush rangeland on perennial vegetation and exotic annuals, as well as soil nutrient availability. We hypothesized that areas prescribed burned followed by a fall imazapic application and then seeded with bunchgrasses 1 yr later (imazapic-seed) would have greater large perennial bunchgrass abundance and cover and reduced exotic annual grasses compared with untreated controls. We also expected that soil nutrient availability would be greater in the imazapic-seed treatment compared with the untreated controls because of reduced exotic annual species but would decrease over time with increases in perennial vegetation.

Methods

Study Area

The study was located in southeastern Oregon in the northwestern Great Basin. Five study sites were between Crane and Juntura, Oregon in medusahead-invaded sagebrush plant communities and were separated by up to 30 km. Elevation at study sites ranged from 972 to 1 052 m above sea level. Slopes were from 0° to 12° with varying aspects (northeast, southwest, and west aspects) depending on study site. Climate is representative of the northwestern Great Basin with most precipitation occurring in the winter and spring and with hot and dry summers. Long-term (1981 – 2010) average annual precipitation was between 249 and 258 mm (PRISM Climate Group, 2017). Annual crop-year (October – September) precipitation at the study sites varied from <75% to slightly > 100% of the long-term average during the study (PRISM Climate Group, 2017). Seeding crop-year precipitation (2011 – 2012) averaged 75% of the long-term average. The spring of 2015 and 2016 received more precipitation than average. Soil texture varied from loam to clay loam among study sites. Before medusahead invasion, the natural vegetation of study sites was Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S. L. Welsh)—bunchgrass steppe. Before treatments, vegetation at study sites was a near monoculture of medusahead with some cheatgrass (*Bromus tectorum* L.), a few (<0.4 plants·m^{-2}) residual native bunchgrass plants, and no sagebrush or other shrubs. Domestic livestock, but not wildlife, were excluded from study sites for the duration of the study with barbwire fences. Two of the imazapic-seeded plots had heavy and moderate winter – early spring use by elk in 2015 and 2016, respectively, based on density of dung pellet piles.

Experimental Design and Measurements

We used a randomized complete block design with five study sites (blocks) to compare treatments. Treatments were 1) medusahead controlled with a fall-prescribed fire followed with an imazapic application and then seeding 1 yr later with perennial bunchgrasses (imazapic-seed) and 2) untreated and unseeded control (control). Each treatment was applied to one of two 30 × 50 m plots separated by a 2-m buffer within each block. Prescribed burning occurred in late September 2010 using strip-head fires. During prescribed burns wind speed varied from 0 to 6 km·hr^{-1}, air temperature varied from 14°C to 29°C, and relative humidity ranged from 21% to 48%. Burns were nearly complete across plots with 95% of the medusahead litter and other fuels being consumed. Imazapic was applied within 10 d of burning at 87.5 g ai·ha^{-1} using a UTV-mounted 7-nozzle boom spray with a nozzle height of 0.6 m from the ground and a tank pressure of 207 kPa. During imazapic application air temperature ranged from 7°C to 16°C, and wind speed varied from 0 to 5 km·hr^{-1}. In early October 2011, one yr after imazapic application, treatment plots were seeded with crested wheatgrass (variety Hycrest) and Siberian wheatgrass (variety Vavilov) at 21.6 kg·ha^{-1} pure live seed with equal proportions by weight of each bunchgrass species. Crested and Siberian wheatgrass seeds were mixed together before being drill seeded using a Versa-Drill (Kasco, Inc., Shelbyville, IN) with drill rows spaced 23 cm apart.

Herbaceous cover and density were measured in mid-June in 2012 through 2016 along four parallel 45-m transects spaced 5 m apart in each treatment plot. Herbaceous canopy cover was estimated by species in 0.2-m^2 quadrats located at 3-m intervals on each 45-m transect, resulting in 60 quadrats per treatment plot. Quadrats were divided into 1%, 5%, 10%, 25%, and 50% sections to increase the accuracy of cover estimates. Bare ground, litter, and soil biological crust cover were also visually estimated in these quadrats. Herbaceous density was measured by species by counting individuals rooted inside of the 0.2-m^2 quadrats. No shrubs occurred in any of the imazapic-seeded or untreated control plots.

Plant available soil nutrient concentrations of total nitrogen (NO_3^- and NH_4^+), potassium, and phosphorus were estimated using four pairs of cation and anion ion exchange membrane probes (PRS-probes, Western Ag Innovations, Saskatoon, Saskatchewan, Canada) randomly placed in each treatment plot in each block. PRS-probes use an ion exchange membrane buried in the soil to attract and absorb ions to estimate the availability of soil nutrients to plants (Jowkin and Schoenau, 1998). PRS-probes were buried vertically in the upper 20 cm of the soil profile from 1 April through 30 July in 2012 – 2016. PRS-probes were extracted with 0.5 N HCl and analyzed colorimetrically with an autoanalyzer to determine nutrient concentrations.

Statistical Analysis

Treatment effects were estimated using repeated measures analyses of variances (ANOVAs) with years as the repeated factor in PROC MIXED SAS v. 9.4 (SAS Institute Inc., Cary, NC). Treatment was considered a fixed variable, and random variables were site and site-by-treatment interactions. Covariance structure for each repeated measures ANOVA was selected using Akaike's Information Criterion (Littell et al., 1996). Data were square root transformed when assumptions of ANOVA were not met. Figures and text report nontransformed (i.e., original) data. Herbaceous cover and density were grouped into five groups for analyses: large perennial bunchgrasses, Sandberg bluegrass (*Poa secunda* J. Presl), perennial forbs, exotic annual grasses, and annual forbs. Sandberg bluegrass was treated as a separate group because it is much smaller in stature, matures earlier, and responds differently to disturbance than other perennial bunchgrasses in the sagebrush ecosystem. The exotic annual grass group was predominately composed of medusahead with some cheatgrass. The annual forb group was largely composed of exotic annual species (94% cover and 96% density). Treatment means were considered different at $P \le 0.05$ and reported with standard errors in the text and figures.

Results

The interaction between year and treatment did not influence Sandberg bluegrass cover (P 0.463). Sandberg bluegrass cover did not differ between the imazapic-seed (0.39% ± 0.15%) and control (0.09% ± 0.02%) treatment ($P = 0.409$) or years ($P = 0.113$) and did not exceed 0.5% in either treatment in any year. Large perennial bunchgrass cover was influenced by the interaction between year and treatment (Fig. 1**A**; $P = 0.002$). Large perennial grass cover generally increased in the imazapic-seed treatment over time but remained largely the same in the untreated control. Large perennial bunchgrass cover was 17- to 59-fold greater in the imazapic-seed compared with the control treatment. Exotic annual grass cover was less in the imazapic-seed treatment compared with the untreated control (Fig. 1B; $P = 0.015$). In the last sampling year (fifth year post seeding), exotic annual grass cover was 2-fold greater in the untreated control compared with the imazapic-seed treatment. Exotic annual grass cover varied by year ($P = 0.004$) but was not influenced by the interaction between year and treatment ($P = 0.355$). Perennial forb cover was not influenced by the interaction between year and treatment ($P = 0.070$) and did not differ between the imazapic-seed (3.63% ± 0.71%) and control (2.29% ± 0.47%) treatment ($P = 0.201$) but did vary by year ($P = 0.007$). Annual forb cover was influenced by the interaction between year and treatment (Fig. 1C; $P < 0.001$). Annual forb cover increased in the untreated control treatment over time, but not the imazapic-seed treatment. By the final sampling, annual forb cover was 14-fold greater in the untreated control compared with the imazapic-seed treatment. Bare ground varied by the interaction between year and treatment (Fig. 1D; $P < 0.001$), with it decreasing over time in the imazapic-seed treatment but fluctuating in the untreated control. Bare ground was greater in imazapic-seed treatment than the untreated control. In the final sampling, bare ground was 3-fold greater in the imazapic-seed treatment compared with the untreated control. Litter varied by the interaction between treatment and year ($P < 0.001$). It generally followed an inverse pattern of bare ground; litter decreasing in the control and increasing in the imazapic-seed treatment over time. Litter was 2- to 10-fold greater in the untreated control compared with the imazapic-seed treatment, with it averaging 62.0% ± 4.48% and 12.4% ± 2.12% in the imazapic-seed and control treatment, respectively. Soil biological crust did not differ between treatments ($P = 0.501$), among years ($P = 0.657$), and was not influenced by the interaction between year and treatment ($P = 0.093$).

Sandberg bluegrass density was influenced by the interaction between year and treatment (Fig. 2A; $P < 0.001$). Sandberg bluegrass density varied from 3- to 5-fold greater in the imazapic-seed treatment compared with the untreated control. Perennial bunchgrass density varied by the interaction between year and treatment (Fig. 2B; $P = 0.045$). Large perennial bunchgrass density varied over time in the imazapic-seed treatment but remained largely unchanged in the untreated control. Large perennial bunchgrass density was 13- to 75-fold greater in the imazapic-seed treatment compared with the untreated control. Exotic annual grass density was influenced by the interaction between year and treatment (Fig. 2C; $P = 0.026$). Exotic annual grass density increased over time in the imazapic-seed treatment, but no apparent trend was observed in the untreated control. At the final sampling, exotic annual grass density was > 2-fold greater in the untreated control compared with the imazapic-seed treatment. Perennial forb density varied by year ($P = 0.002$), but it did not differ between the imazapic-seed (15.11 ± 3.2 plants·m^{-2}) and control (14.51 ± 2.76 plants·m^{-2}) treatment and was not influenced by the interaction between year and treatment ($P = 0.827$ and 0.172, respectively). Annual forb density was influenced by the interaction between year and treatment (Fig. 2D; $P < 0.001$). The difference between the control and imazapic-seed treatment varied over the 5 sampling yr. Annual forb density was on average 41-fold greater in the untreated control than the imazapic-seed treatment.

Plant available soil inorganic nitrogen varied by the interaction between year and treatment (Fig. 3A; $P < 0.001$). The difference between treatments became less over time. Nitrogen was 5- to 6-fold greater in the imazapic-seed compared with the untreated control in the first 3 yr after seeding.

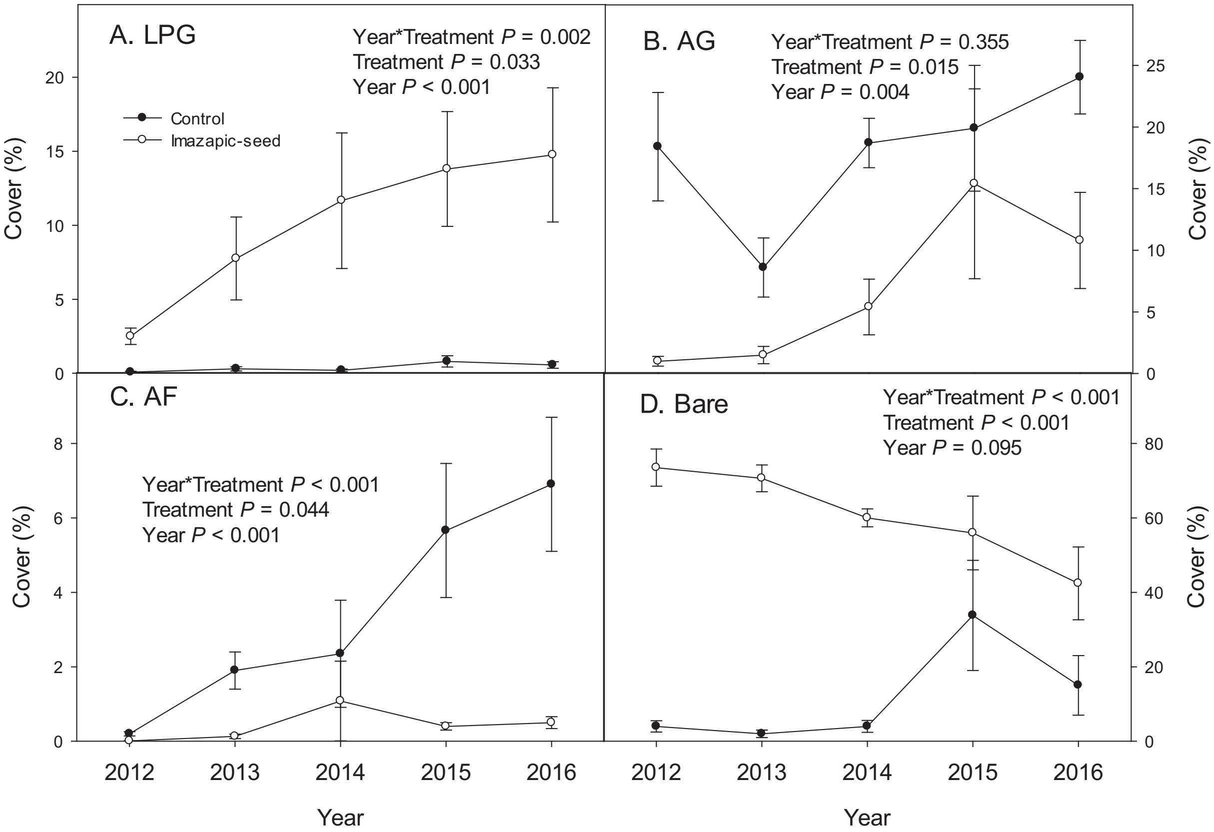

Figure 1. A, Large perennial bunchgrass. **B,** Exotic annual grass. **C,** Annual forb. **D,** Bare ground cover (mean ± S.E.) in the imazapic-seed treatment and untreated control from 2012 to 2016. LPG indicates large perennial bunchgrass; AG, exotic annual grass; AF, annual forb.

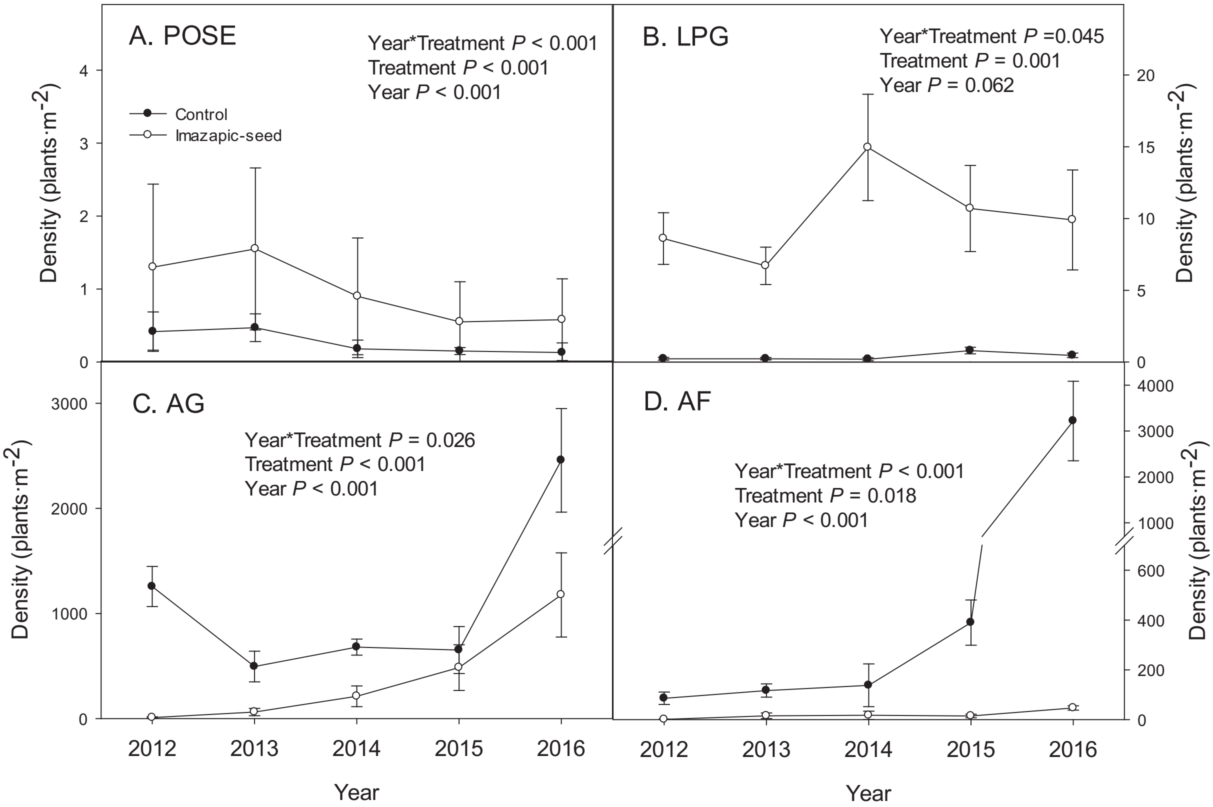

Figure 2. A, Sandberg bluegrass. **B,** Large perennial bunchgrass. **C,** Exotic annual grass. **D,** Annual forb density (mean ± S.E.) in the imazapic-seed treatment and the untreated control from 2012 to 2016. POSE indicates Sandberg bluegrass; LPG, large perennial bunchgrass; AG, exotic annual grass; AF, annual forb.

In the final 2 yr, nitrogen was only 2-fold greater in the imazapic-seed compared with the untreated control. Available potassium varied by the interaction between treatment and year (Fig. 3B; $P = 0.043$); however, no clear pattern emerged. Available phosphorus was not influenced by the interaction between treatment and year ($P = 0.116$) and did not differ between the imazapic-seed (10.67 ± 1.46 μg·10 cm^{-2}·2 $months^{-1}$) and control (9.32 ± 0.87 μg·10cm^{-2}·2 $months^{-1}$) treatment ($P = 0.559$). Available phosphorus varied among years ($P = 0.009$).

Discussion

In support of our hypothesis, the imazapic-seed treatment increased large perennial bunchgrass dominance and decreased the cover and density of exotic annual grasses and annual forbs. Our results are in contrast with the James et al. (2015) conclusion from a meta-analysis that by the second or third yr after seeding with combinations of burning and herbicide, medusahead abundance was similar between treated and untreated plots. Similar to our results, Monaco et al. (2017) found in a review of the literature that herbicide treatment and seeding decreased cheatgrass abundance over the long term. At the end of our study (5 and 6 yr after seeding and herbicide application, respectively), exotic annual grass density and cover was > 2-fold greater in the untreated control than in the imazapic-seed treatment. In addition, annual forb (predominately exotic species) cover and density were 14- and 69-fold greater in the untreated control compared with the imazapic-seed treatment. This suggests that seeding after treatments to control exotic

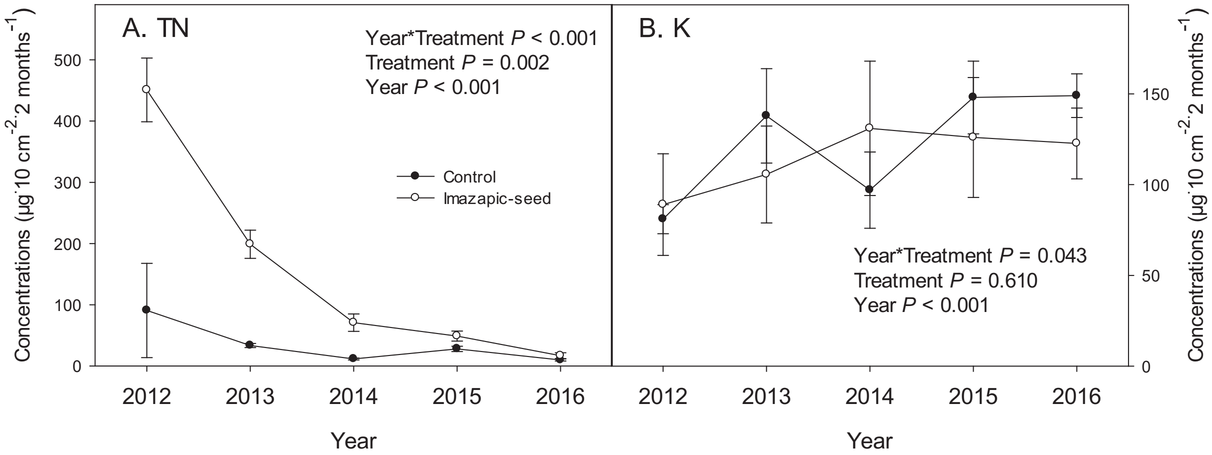

Figure 3. Plant available total inorganic nitrogen (**A**) and potassium (**B**) concentrations (mean ± S.E.) in the soil in the imazapic-seed treatment and the untreated control during the growing season in 2012 through 2016. TN indicates total inorganic nitrogen; K, potassium.

annual grasses can augment the seedbank with desired species to establish these species in sufficient numbers to significantly reduce exotic annual species. Prior, shorter-term research has shown results similar to our findings (e.g., Davies, 2010; Sheley et al., 2012; Davies et al., 2015). Our results likely contrast with the James et al. (2015) meta-analysis because seeded perennial vegetation may fail to establish. When seeded perennial vegetation does not establish, perennial vegetation dominance does not increase and exotic annuals redominate the plant community (Monaco et al., 2005; Davies et al., 2014b). However, if seeded vegetation does establish in significant abundance, exotic annuals will be suppressed. The key is establishing sufficient perennial vegetation. For example, planting seedlings of perennial bunchgrasses and combinations of perennial grasses and shrubs after annual grass control limited exotic annual grass cover to $<$ 2% five and 6 yr after planting compared with $>$ 25% annual grass cover in plots not planted with perennials (Davies and Johnson, 2017).

The imazapic-seed treatment appears to have changed the trajectory of the plant community from an exotic annual-dominated community to a perennial or perennial-annual dominated plant community. Large perennial grass cover continued to increase for 5 yr post seeding, which suggests a fundamental change in the plant community composition. This also implies that the effects of controlling exotic annual grasses and seeding perennial bunchgrasses may persist. The increase in exotic annual grasses in the final 2 yr (2015 and 2016) of the study in the imazapic-seed treatment is concerning; however, these were unusually favorable years for exotic annual grasses. For example, exotic annual grasses were found in intact plant communities where they were not found before 2015 (EOARC data file). Though we doubt that the increase in exotic annual grasses in the imazapic-seed treatment indicates a change away from a perennial-dominated community, especially since exotic annual grass cover was less in 2016 (11%) than 2015 (15%), it would be valuable to continue to monitor. In addition, exotic annual grass cover increased in the untreated control treatment from 20% in 2015 to 24% in 2016. Furthermore, annual forb cover and density were maintained at low levels in the imazapic-seed treatment but increased substantially in the untreated control. This suggests that competition from perennial vegetation was limiting annual species in the imazapic-seed treatment, which is critical for shifting the trajectory of the plant community away from annual dominated.

Large perennial bunchgrass density peaked in the third year after seeding and then decreased in the following 2 yr. This may potentially be, in part, a response to increases in exotic annual grasses; however, it was likely the result of self-thinning. As plants grow larger, they may self-thin to the appropriate level for the site (Mueggler and Blaisdell, 1955). This likely occurred at our sites as large perennial bunchgrasses were increasing in size, as evident by cover increasing with time. The decrease in perennial bunchgrass density is probably not a concern, as there were still nearly 10 plants$\cdot$m^{-2} in the final sampling. This is approximately the density of intact Wyoming big sagebrush-bunchgrass communities in this ecoregion (Davies and Bates, 2010). However, it will be critical that bunchgrass recruitment offsets mortality over the long term to prevent redomination by exotic annuals. Decreases in perennial bunchgrasses in these sagebrush systems often result in increases in exotic annual grasses (Chambers et al., 2007; Hulet et al., 2010).

We speculate that, at least partially, sufficient perennial bunchgrass establishment was achieved because of successful control of exotic annual grasses with burning and imazapic application. Exotic annual grass cover was $<$ 2% in the imazapic-seed treatment in the first two growing seasons after seeding; therefore, resource use (i.e., to the exclusion of bunchgrass seedlings) was likely minimal. Successful, multiyear control of exotic annuals is likely necessary for bunchgrass establishment because exotic annuals are highly competitive with bunchgrass seedlings (Goebel et al., 1988; Young and Mangold, 2008; Vasquez et al., 2009). Exotic annual grasses can also deplete soil moisture earlier in the growing season (Melgoza et al., 1990), decreasing the probability of perennial seedling establishment. Precipitation was below average in the seeding year, further suggesting that successful annual grass control was a major factor contributing to bunchgrass establishment, especially since most successful rangeland seedings occur in average to above-average precipitation years (Hardegree et al., 2016).

Our hypothesis that the imazapic-seed treatment would increase available soil nutrients was only partially supported. Total plant available inorganic nitrogen was greater in the imazapic-seed treatment, but available potassium and phosphorus were similar between the control and imazapic-seed treatment. Nitrogen may be more responsive to treatments than other soil nutrients. In the first few years, inorganic nitrogen concentrations likely increased because sites were burned and vegetation was greatly reduced with the imazapic application. Nitrogen often increases after burning because nutrients that were tied up in plant materials are released (Davies et al., 2007; Rau et al., 2008). Dissimilar to our results, Rau et al. (2008) and Davies et al. (2014a) found other soil nutrients also increased with burning. Our results may have differed because communities burned in their studies were not heavily invaded with exotic annual grasses and were dominated by woody vegetation. Plant available inorganic nitrogen remained high for several years in the imazapic-seed treatment likely because imazapic limited exotic annual species and perennial bunchgrass seedlings were small, and then nitrogen probably decreased over time because herbaceous vegetation (especially perennial bunchgrasses) and litter increased. However, available inorganic nitrogen was still twofold greater in the imazapic-seed treatment 5 yr after seeding, suggesting that the increase in perennial species and decrease in exotic annual species was affecting ecological processes such as nutrient cycling.

Implications

Revegetating medusahead-invaded rangelands can be successful when medusahead is controlled by integrating prescribed burning and imazapic application followed 1 yr later with seeding perennial bunchgrasses. Our success was likely contingent upon successful control of exotic annuals, and, therefore, similar results should not necessarily be expected if the control is not as complete. Our results suggest that successful control of medusahead followed with seeding perennial vegetation can limit exotic annual grass and annual forbs for at least 5 yr after seeding. Most importantly, large perennial bunchgrass cover increased over time in the imazapic-seed treatment and at the end of the study was greater than the average found in intact Wyoming big sagebrush communities (Davies et al., 2006). However, other native functional group cover, particularly Sandberg bluegrass and sagebrush, was less than found in intact communities (Davies et al., 2006); thus, it may need to be reestablished to further suppress exotic species. The increase in exotic annual grasses in the imazapic-seed treatment in the last 2 yr of the study may suggest that a follow-up herbicide treatment will be needed in the future to facilitate further increases in perennial vegetation and limit exotic annuals; however, longer-term evaluation is needed to determine if further control will be necessary. Alternatively, fluctuations in annual grass cover and density may not be a concern when the plant community is dominated by perennial bunchgrasses.

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