

Comparison of Medusahead-Invaded and Noninvaded Wyoming Big Sagebrush Steppe in Southeastern Oregon

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Abstract

Medusahead (*Taeniatherum caput-medusae* [L.] Nevski) is an exotic, annual grass invading sagebrush steppe rangelands in the western United States. Medusahead invasion has been demonstrated to reduce livestock forage, but otherwise information comparing vegetation characteristics of medusahead-invaded to noninvaded sagebrush steppe communities is limited. This lack of knowledge makes it difficult to determine the cost–benefit ratio of controlling and preventing medusahead invasion. To estimate the impact of medusahead invasion, vegetation characteristics were compared between invaded and noninvaded Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S. L. Welsh) steppe communities that had similar soils, topography, climate, and management. Noninvaded plant communities had greater cover and density of all native herbaceous functional groups compared to medusahead-invaded communities ($P < 0.01$). Large perennial grass cover was 15-fold greater in the noninvaded compared to invaded plant communities. Sagebrush cover and density were greater in the noninvaded compared to the medusahead-invaded communities ($P < 0.01$). Biomass production of all native herbaceous functional groups was higher in noninvaded compared to invaded plant communities ($P < 0.02$). Perennial and annual forb biomass production was 1.9- and 45-fold more, respectively, in the noninvaded than invaded communities. Species richness and diversity were greater in the noninvaded than invaded plant communities ($P < 0.01$). The results of this study suggest that medusahead invasion substantially alters vegetation characteristics of sagebrush steppe plant communities, and thereby diminishes wildlife habitat, forage production, and ecosystem functions. Because of the broad negative influence of medusahead invasion, greater efforts should be directed at preventing its continued expansion.

Resumen

La cabeza de medusa (*Taeniatherum caput-medusae* [L.] Nevski) es una grama anual exótica que invade los pastizales de trigüillo crestado en el oeste de los Estados Unidos. Se ha demostrado que la invasión de la cabeza de medusa reduce el forraje para el ganado, sin embargo otra información sobre las estepas de trigüillo crestado invadida y no invadida por la cabeza de medusa es limitada. Esta ausencia de conocimiento hace difícil determinar la relación costo–beneficio para controlar y prevenir la invasión de la cabeza de medusa. Para estimar el impacto de la invasión de cabeza de medusa, se compararon las características vegetativas entre las comunidades de estepas de trigüillo crestado grande de Wyoming (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S. L. Welsh) invadida y no invadida con suelos, topografía, clima, y manejo similares. Las comunidades de plantas no invadidas tuvieron la mayor cobertura y densidad de todos los grupos funcionales de las herbáceas nativas comparadas a las comunidades de cabeza de medusa invadida ($P < 0.01$). La cobertura grande de grama perene fue 15 veces mayor en las comunidades no invadidas comparada con las comunidades de plantas invadidas. La cobertura del trigüillo crestado fue mayor en las comunidades no invadidas comparada con las comunidades de cabeza de medusa invadidas ($P < 0.01$). La producción de biomasa de todos los grupos funcionales de herbáceas nativas fueron mayor en las no invadidas comparadas con las comunidades de plantas invadidas ($P < 0.02$). La producción de biomasa de la hierba anual y perene fue de 1.9 y 45 veces más, respectivamente, en las comunidades no invadidas que en las comunidades invadidas. La diversidad y la riqueza de especies fueron mayor en las comunidades no invadidas que en las comunidades de planta invadidas ($P < 0.01$). Los resultados de este estudio sugieren que la invasión de la cabeza de medusa altera sustancialmente las características vegetativas de las comunidades de estepas de trigüillo crestado; y de ese modo, disminuye el hábitat de vida silvestre, la producción de forraje y las funciones del ecosistema. Debido a la amplia influencia negativa en la invasión de la cabeza de medusa mayores esfuerzos deben ser dirigidos para prevenir su continua expansión.

Key Words: annual grass, *Artemisia tridentata*, diversity, invasive plants, production, *Taeniatherum caput-medusae*, weeds

INTRODUCTION

Invasive grasses are a serious problem around the world, with exotic annual grass invasions being most severe in the arid and semiarid regions of western North America (D’Antonio and Vitousek 1992). Invasion by exotic plant species has been speculated to negatively impact rangelands by decreasing productivity, reducing habitat, displacing native species, and

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altering ecosystem functions (DiTomaso 2000; Masters and Sheely 2001). However, there has been a general tendency to study control treatments rather than ecological impacts of invasive plants in rangelands (Olson 1999). Thus, information is limited detailing differences in vegetation characteristics between annual grass invaded and noninvaded native plant communities. The impacts of invasive plants on the environment, other plants, and wildlife habitat need to be quantified to provide information to improve and prioritize management (Lacey and Olson 1991).

The impacts of annual grass invasions in the western United States are recognized as a serious problem (Dahl and Tisdale 1975; Mack 1981; D'Antonio and Vitousek 1992; Young 1992; Young et al. 1999; Brooks et al. 2004), but information quantifying their impacts is limited. For example, medusahead (*Taeniatherum caput-medusae* [L.] Nevski) is an aggressive, exotic, annual grass invading rangelands in the western United States (Young 1992), but information detailing the negative impacts of medusahead has generally been limited to evaluations of livestock forage production after invasion. Thus, little is known about the impacts medusahead invasion has on plant diversity and wildlife habitat. This is a serious concern because large expanses of sagebrush (*Artemisia*) steppe in the Intermountain West have been invaded by medusahead or are threatened by its invasion. The rapid spread of medusahead is a serious management concern (Dahl and Tisdale 1975; Monaco et al. 2005), especially because most revegetation efforts in the Intermountain West fail (Young 1992; Young et al. 1999).

The invasion of medusahead can reduce grazing capacity by 50% to 80% (Hironaka 1961) and often results in near monocultures of medusahead (George 1992). Medusahead alters the plant communities it invades by competition, suppression, and increasing fire frequency. Medusahead can effectively compete with desirable vegetation (Hironaka and Sindelar 1975; Goebel et al. 1988; George 1992; Young and Mangold 2008). Medusahead litter has a slow decomposition rate, allowing it to accumulate over time and suppress desirable plants (Bovey et al. 1961; Harris 1965). Accumulation of medusahead litter also increases the quantity and continuity of fine fuel, which can increase fire frequency to the detriment of desirable vegetation (Torell et al. 1961; Young 1992; Young et al. 1999). Young (1992) considered medusahead to be the greatest threat to biodiversity of native plant communities in the Great Basin. However, impacts of medusahead invasion on many of the plant functional groups common to sagebrush steppe communities have not been evaluated.

Specifically, information is lacking regarding impacts of medusahead invasion on important sagebrush steppe habitat characteristics, including species richness and diversity and cover, density and production of native perennial and annual forbs, perennial bunchgrasses, and sagebrush. Davies (2008) reported that the density of large native perennial bunchgrasses was negatively correlated with medusahead invasion, but sagebrush, perennial forbs, and annual forbs were not associated with the ability of medusahead to invade sagebrush-bunchgrass communities. This suggests that forbs and sagebrush either do not compete effectively with medusahead or that they use resources temporally or spatially dissimilar to medusahead. However, the response of sagebrush and forbs to medusahead invasion is largely unknown. Understanding the

influence of medusahead invasion on forbs is important because forbs are a critical food source for many sagebrush obligate and facultative wildlife species. For example, forbs are an important component of sage-grouse (*Centrocercus urophasianus*) diets (Klebonow and Gray 1968; Wallestad et al. 1975; Drut et al. 1994). Similarly, sagebrush is a critical component of these ecosystems. Sagebrush is an important food source for many wildlife including sage-grouse (Patterson 1952; Wallestad et al. 1975), pygmy rabbits (Green and Flinders 1980; Shipley et al. 2006), deer (MacCracken and Hansen 1981; Austin and Urness 1983), and elk (MacCracken and Hansen 1981). Sagebrush also creates microsites and heterogeneity in herbaceous vegetation characteristics (Davies et al. 2007a). The impact of medusahead invasion on species diversity is also important because of its role in ecosystem functions. Plant diversity is important for preventing ecosystem nutrient loss and promoting nutrient cycling, carbon storing, and community productivity (Tilman et al. 1997; Hooper and Vitousek 1998).

A more thorough evaluation of the influence of medusahead invasion on Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S. L. Welsh) steppe plant communities is needed to better understand the impacts of medusahead invasion on diversity, wildlife habitat, and livestock forage production. This information is critical to improving estimates of the benefits of controlling and preventing medusahead invasion and determining the cost-benefit ratio of managing medusahead. Allocations of resources and legislation for invasive plant management will continue to be based upon inadequate information until the impact of these plants on ecosystem structure, composition, and function are quantified (Lacey and Olson 1991). The purpose of this study is to quantify the vegetation differences between medusahead-invaded and noninvaded Wyoming big sagebrush steppe. Because of the potential for medusahead to decrease native plants with increased fire frequency (Torell et al. 1961; Young 1992; Young et al. 1999), competition (Hironaka and Sindelar 1975; Goebel et al. 1988; George 1992; Young and Mangold 2008), and suppression from litter accumulation (Bovey et al. 1961; Harris 1965), we hypothesize that all native plant functional groups will have less cover, density, and biomass production in invaded than noninvaded communities. We also hypothesize that medusahead-invaded compared to noninvaded Wyoming big sagebrush steppe would have lower species richness and diversity.

METHODS

Study Area Description

The study was conducted in southeastern Oregon in Wyoming big sagebrush steppe rangeland between Buchanan, Princeton, Juntura, and Burns Junction, Oregon. The study area encompasses 160 000 ha of the western edge of the Snake River Ecological Province and eastern edge of the High Desert Ecological Province (Anderson et al. 1998). Climate is characteristic of the northern Great Basin with hot dry summers and cool wet winters. Average annual precipitation across the study sites ranges from 250 to 300 mm and mainly occurs in the fall, winter, and spring (Oregon Climatic Service 2007). Regional precipitation for the 2006–2007 crop year

(1 October to 30 September) was approximately 90% of the 30-year average. Elevation of study sites ranges from 960 to 1300 m above sea level. Light to moderate utilization by domestic livestock has occurred across the study area; however, livestock were excluded during the study. Noninvaded plant communities had an overstory dominated by Wyoming big sagebrush and a herbaceous understory dominated by bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), bluebunch wheatgrass-Idaho fescue (*Festuca idahoensis* Elmer), or bluebunch wheatgrass-Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), depending on site. Invaded sites had a herbaceous vegetation understory dominated by medusahead. Common forbs included hawkbeard (*Crepis* sp.), basalt milkvetch (*Astragalus filipes* Torr. ex Gray), woolly pod milkvetch (*Astragalus purshii* Dougl. ex Hook.), long-leafed phlox (*Phlox longifolia* Nutt.), desert parsley (*Lomatium* sp.), tailcup lupine (*Lupinus caudatus* Kellogg), and little blue-eyed Mary (*Collinsia parviflora* Lindl.). Whitetop (*Cardaria draba* [L.] Desv.) and field bindweed (*Convolvulus arvensis* L.) were common exotic perennial forbs in some of the medusahead infestations.

Experimental Design

To quantify the differences between medusahead-invaded and noninvaded Wyoming big sagebrush steppe plant communities, vegetation characteristics of medusahead-invaded plant communities (sites) were compared to those of noninvaded Wyoming big sagebrush steppe plant communities (sites). Invaded and noninvaded sites were blocked together by similar location, topography, soils, and management. Each block consisted of one medusahead-invaded and one noninvaded site. For invaded and noninvaded sites to be blocked they had to meet the following criteria: 1) located in the same land management unit (field, pasture, allotment, etc.) to ensure the same grazing history and <1 km apart; 2) soils in the same series (Natural Resource Conservation Service 2007); 3) elevation differences of <75 m; 4) similar slope and aspect; and 5) ecological site type and potential native vegetation had to be the same (Natural Resource Conservation Service 1997; Pellant et al. 2005; Davies et al. 2006). Nineteen invaded sites were located that could be blocked according to the above criteria with a noninvaded site. This resulted in 19 invaded and 19 noninvaded sites. Sites were considered noninvaded if no medusahead was growing in them. Invaded sites were selected if their understory was dominated by medusahead and were located at least 50 m inside of the edge of the infestation. Medusahead infestation at the invaded sites had been recorded >10 years prior to our study.

One representative, but randomly located 80 × 50 m plot (0.4 ha) plot was used to sample each site. Five 50-m transects, spaced at 20-m intervals, were deployed along the 80-m transect. Sampling of vegetation occurred from late May to mid-June in 2007. Shrub canopy cover by species was measured by line intercept (Canfield 1941). Canopy gaps less than 15 cm were included in the canopy cover measurements. Shrub density was determined by counting all rooted individuals in five 2 × 50 m belt transects at each site.

Herbaceous canopy cover and density were measured by species inside 40 × 50 cm frames (0.2 m²) located at 3-m

intervals on each transect line (starting at 3 m and ending at 45 m), resulting in 15 frames per transect and 75 frames per site. Herbaceous cover was estimated to a percent. Functional group and total cover was determined by adding individual species measurements together. Herbaceous biomass production by functional group was measured by clipping all standing vegetation in 15 randomly located 1-m² frames per site. Samples were oven dried, and then the current year's growth was separated from the previous year's growth and weighed. Species richness was determined by counting all species found in the 40 × 50 cm frames at each site. Herbaceous vegetation diversity was calculated from species density measurements using the Shannon diversity index (Krebs 1998).

Statistical Analysis

An analysis of variance (ANOVA) was used to test for vegetation differences between medusahead-invaded and intact Wyoming big sagebrush steppe plant communities (S-Plus 2000). Block and treatment (invaded or noninvaded) were used as explanatory factors. Fisher's Protected LSD was used to test for differences between means. Differences between means were considered significant if *P* values were ≤ 0.05 ($\alpha = 0.05$). Means are reported with standard errors (mean ± SE). For some analyses, herbaceous species were classified into functional groups based on phenology and morphology. The purpose of using functional groups is to combine species that respond similarly to environmental perturbation and to reduce data to a simpler form for analysis and presentation (Boyd and Bidwell 2002). Functional groups also permit comparisons among sites with different species composition (Davies et al. 2007b).

RESULTS

Cover

Native herbaceous vegetation cover was less in medusahead-invaded compared to noninvaded sagebrush plant communities (Fig. 1). Sandberg bluegrass, large perennial bunchgrass, native perennial forb, and annual forb cover were higher in noninvaded than medusahead-invaded plant communities ($P < 0.01$). Differences were greatest in Sandberg bluegrass and large perennial bunchgrass cover, which were more than 24- and 15-fold greater, respectively, in the noninvaded than invaded plant communities. Total herbaceous (native and exotic combined) vegetation and sagebrush cover were 1.6- and 8.7-fold greater, respectively, in noninvaded compared to medusahead-invaded communities ($P < 0.01$). Bare ground and moss-crust cover were higher in noninvaded compared to medusahead-invaded communities ($P < 0.01$). Medusahead, exotic perennial forb, and litter cover were greater in medusahead infestations than noninvaded sagebrush plant communities ($P < 0.01$). Cheatgrass and other shrub cover did not differ between invaded and noninvaded plant communities ($P = 0.28$ and 0.30, respectively).

Density

Sandberg bluegrass, large perennial bunchgrass, native perennial forb, and annual forb densities were between 1.9- and 22-fold higher in the noninvaded compared to the medusahead-

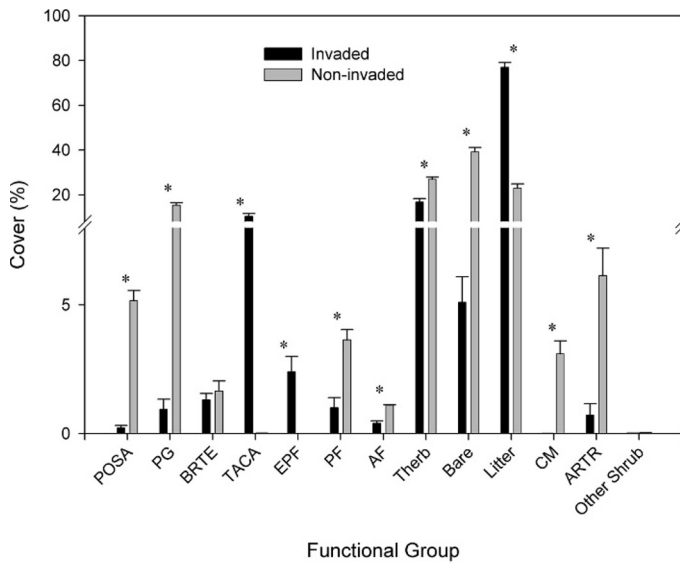


Figure 1. Cover (mean+SE) in medusahead-invaded and noninvaded Wyoming big sagebrush plant communities. POSA indicates Sandberg bluegrass; PG, large native perennial bunchgrass; B RTE, cheatgrass; TACA, medusahead; EPF, exotic perennial forbs; PF, native perennial forbs; AF, annual forbs; Therb, total (native and exotic) herbaceous; Bare, bare ground; Litter, litter; CM, crust and moss; ARTR, Wyoming big sagebrush; and Other shrub, other shrubs. Asterisk (*) indicates a significant difference ($P \leq 0.05$) in cover for that attribute between medusahead-invaded and noninvaded plant communities.

invaded communities ($P \leq 0.05$; Fig. 2). Sagebrush density was 3.5-fold greater in noninvaded compared to the invaded plant community ($P < 0.01$). Medusahead, total herbaceous (native and exotic combined), and exotic perennial forb densities were greater in the invaded than noninvaded plant communities ($P < 0.01$). Cheatgrass and other shrub densities did not differ between plant communities ($P = 0.20$ and 0.52 , respectively).

Production

Biomass production by native plant functional groups was greater in noninvaded than invaded plant communities (Fig. 3). Large perennial grass and Sandberg bluegrass production were 27- and 93-fold greater in noninvaded compared to invaded plant communities ($P < 0.01$). Perennial forb and annual forb production were 1.9- and 45-fold higher, respectively, in the noninvaded than invaded communities ($P < 0.02$ and < 0.01 , respectively). Total native herbaceous production was 7.8-fold greater in the noninvaded compared to the medusahead-invaded communities ($P < 0.01$). Annual grass production, mainly medusahead, was 42-fold greater in the invaded compared to the noninvaded plant communities ($P < 0.01$). Total herbaceous (native and exotic combined) production did not differ between plant communities ($P = 0.61$).

Species Richness and Diversity

Species richness was almost 2-fold greater in noninvaded compared to medusahead-invaded plant communities ($P < 0.01$). Medusahead-invaded communities averaged 12 ± 0.7 species compared to 21 ± 1.0 species in noninvaded communities. Medusahead-invaded plant communities also were less

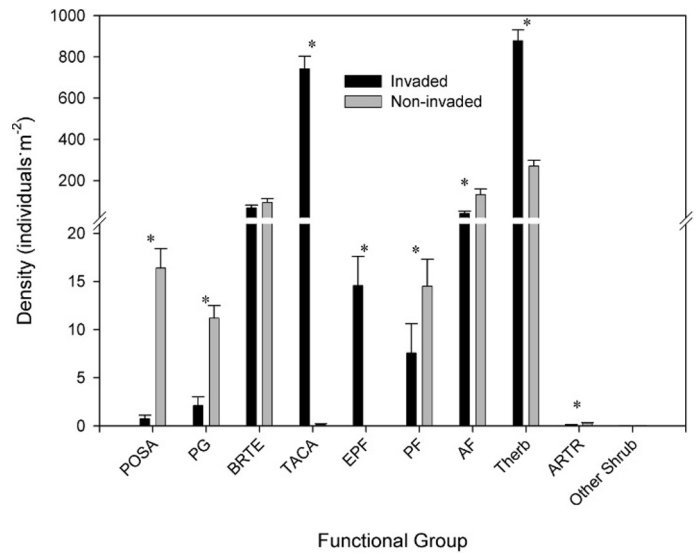


Figure 2. Functional group densities (mean+SE) in medusahead-invaded and noninvaded Wyoming big sagebrush plant communities. POSA indicates Sandberg bluegrass; PG, large native perennial bunchgrass; B RTE, cheatgrass; TACA, medusahead; EPF, exotic perennial forbs; PF, native perennial forbs; AF, annual forbs; Therb, total (native and exotic) herbaceous; ARTR, Wyoming big sagebrush; and Other shrub, other shrubs. Asterisk (*) indicates a significant difference ($P \leq 0.05$) in density for that functional group between medusahead-invaded and noninvaded plant communities.

diverse than noninvaded plant communities. Shannon diversity index was 2.6-fold greater in the noninvaded (1.5 ± 0.1) compared to the invaded (0.57 ± 0.1) plant communities ($P < 0.01$).

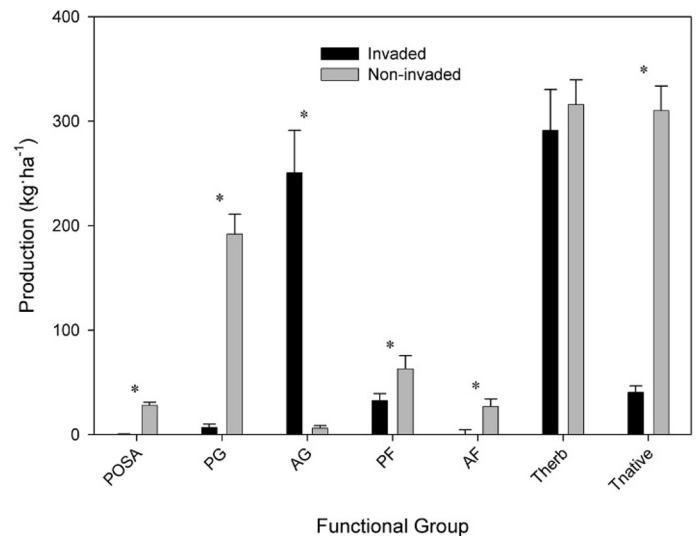


Figure 3. Functional group biomass production (mean+SE) in medusahead-invaded and noninvaded Wyoming big sagebrush plant communities. POSA indicates Sandberg bluegrass; PG, large native perennial bunchgrass; PF, native perennial forbs; AG, exotic annual grass (mainly composed of medusahead); AF, annual forbs; Therb, total (native and exotic) herbaceous; and Tnative, total native herbaceous. Asterisk (*) indicates a significant difference ($P \leq 0.05$) in production for that functional group between medusahead-invaded and noninvaded plant communities.

DISCUSSION

This study quantifies some of the differences between medusahead-invaded and noninvaded Wyoming big sagebrush plant communities. Information comparing exotic plant invasions to noninvaded plant communities has been identified by Lacey and Olson (1991) and Olson (1999) as greatly needed and generally lacking. Medusahead invasion of Wyoming big sagebrush plant communities appears to degrade wildlife habitat, reduce livestock forage, and negatively impact ecosystem function. The results of this study imply that the differences between invaded and noninvaded plant communities are the result of medusahead invasion decreasing native vegetation and plant diversity. Based on the results of this study, we also speculate that negative impacts of medusahead on invaded sites have not reached their potential. Further reductions in native vegetation and diversity are possible and potentially inevitable in already invaded communities. Other invasive plants, especially exotic annual grasses, probably are having a similar negative influence on other native rangelands.

Medusahead-invaded sagebrush steppe produces less desirable habitat for most Intermountain West wildlife species compared to noninvaded sagebrush steppe. Medusahead is contributing 62% and 85% of the herbaceous cover and density, respectively, in the invaded sites (Figs. 1 and 2). Fewer native perennial forbs and annual forbs in medusahead-invaded than noninvaded communities would negatively affect sagegrouse and other wildlife species (Klebenow and Gray 1968; Wallestad et al. 1975; Drut et al. 1994; Connelly et al. 2000). The loss of sagebrush with medusahead invasion would negatively affect sagegrouse (Patterson 1952; Wallestad et al. 1975; Connelly et al. 2000), other sagebrush obligates (Green and Flinders 1980; Shipley et al. 2006), and sagebrush-facultative wildlife species (MacCracken and Hansen 1981; Austin and Urness 1983).

Medusahead-invaded compared to noninvaded plant communities also produce less livestock forage. Medusahead-invaded communities produce only 13% of the native biomass production of the noninvaded plant communities. Most of the native herbaceous plants, especially the common species that contribute the majority of biomass production, provide palatable forage for livestock (Natural Resource Conservation Service 2008). Because of the low to non-existent value of medusahead for livestock forage (Bovey et al. 1961; George 1992), our results suggest that medusahead invasion can reduce livestock forage by nearly 90% when comparing the native plant biomass production between invaded and noninvaded sites. These results are greater than Hironaka's (1961) estimate of a 50% to 80% reduction in grazing capacity as a consequence of medusahead invasion in Idaho. Degree of medusahead dominance, site potential, and interannual climatic conditions probably influence the negative impacts of medusahead on forage production.

Our study supports the speculation of Young (1992) and George (1992) that medusahead invasion reduces diversity. Lower species richness and diversity in medusahead-invaded compared to noninvaded plant communities is a serious concern. Reduced diversity can result in ecosystem nutrient loss, altered nutrient cycling, long-term decreases in carbon stores, and reduced productivity (Tilman et al. 1997; Hooper

and Vitousek 1998). The loss of diversity also decreases the probability of fully restoring medusahead-invaded plant communities. Because commercial seed sources do not exist for many native forbs commonly found in Wyoming big sagebrush plant communities, restoration efforts would have to depend on natural dispersal or expensive hand-collected seeds. Neither option could be a reasonable method to restore large infestations either because of low probability of success and/or high expense. Restoration of invaded shrub-steppe systems can also be limited by invasion-induced changes in the spatial and temporal distribution of soil resources (Brooks et al. 2004).

The negative impact of medusahead invasion on native vegetation will continue to increase in severity, even on sites that are near-monocultures of medusahead. We observed substantially higher litter cover on the medusahead-invaded communities, suggesting that medusahead invasion has increased the fine fuel loads and continuity; this can potentially lead to an increase in fire frequencies, to the detriment of remaining native vegetation. In agreement with these results, Torell et al. (1961) and Young (1992) reported that medusahead invasion increases the continuity and amounts of fine fuels. Suppression by medusahead litter (Bovey et al. 1961; Harris 1965) coupled with medusahead's highly competitive nature (Hironaka and Sindelar 1975; Goebel et al. 1988; George 1992; Young and Mangold 2008) could also lead to further reductions in native plant cover, density, biomass production, and diversity. The greater cover and density of exotic perennial forbs in the medusahead-invaded compared to the noninvaded communities could also further negatively influence native plants. Dissimilar to native plants, the exotic perennial forbs might be more tolerant of more frequent fires (Sheley et al. 1999).

We were surprised that medusahead invasion appears to reduce the cover and density of Sandberg bluegrass as much as or more than the large perennial bunchgrasses (Figs. 1 and 2). Typically, Sandberg bluegrass is considered an early successional species that resists disturbance more than large perennial bunchgrasses (Anderson 1962; Robertson 1971; Bates et al. 2000). Relatively similar phenology and nutrient acquisition patterns could lead to more direct competition between medusahead and Sandberg bluegrass (James et al. 2008). Davies (2008) noted that differences in Sandberg bluegrass cover and density did not influence the ability of medusahead to invade sites. Davies' (2008) results could be due to either lack of competition between medusahead and Sandberg bluegrass or that medusahead is such an effective competitor with Sandberg bluegrass that medusahead is not noticeably affected by Sandberg bluegrass presence. Another possible contributing factor is that medusahead is indirectly suppressing Sandberg bluegrass. The accumulation of medusahead litter could be shading the photosynthetically active tissue of the relatively short-stature Sandberg bluegrass.

The differences in medusahead-invaded and noninvaded plant communities can probably be extrapolated to better understand possible implications of other exotic plant invasions. Other invasive species that similarly increase fire frequencies probably have substantial impacts on native plant and organism communities. The effects of invaders are probably particularly devastating when they alter disturbance regimes (Vitousek 1990; D'Antonio and Vitousek 1992). For

example, cheatgrass has been reported to increase the fire frequencies to the point that native plant communities cannot recover (Whisenant 1990). If the relationship between medusahead-invaded and noninvaded plant communities holds true for other invasive plants, areas invaded by these other invasive plants will have lower diversity, provide less suitable habitat for native plant community obligates, and produce less forage for livestock than noninvaded plant communities.

MANAGEMENT IMPLICATIONS

Medusahead invasion appears to greatly reduce wildlife habitat, livestock forage, and diversity. The potential of medusahead to escalate the plight of sagebrush obligate wildlife species by degrading habitat is a serious concern for rangeland and wildlife managers. Comparing the habitat needs of sage-grouse to the vegetation characteristics of medusahead-invaded sagebrush communities suggests that each hectare invaded by medusahead is a hectare of habitat lost. Lower diversity on medusahead-invaded plant communities also is a very serious concern because of its potential influence on ecosystem functions. The potential broad negative effects of medusahead invasion suggest that there are substantial benefits to preventing and revegetating medusahead invasions. However, revegetation of medusahead infestations is rarely successful in the Intermountain West (Young 1992; Young et al. 1999); thus, current management should focus on containment, prevention, and controlling infestations where revegetation will not be required. More attention and resources need to be directed towards protecting sagebrush steppe from medusahead invasion. Other invasive plant species are probably having similar potential impacts on native plant communities and the organisms that depend on them; thus, greater efforts to control and prevent the spread of invasive plants is warranted on rangelands and other wildlands around the world.

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LITERATURE CITED

- ANDERSON, E. W. 1962. Behavior of forage yields on some range sites in Oregon. *Journal of Range Management* 15:245–252.
- ANDERSON, E. W., M. M. BORMAN, AND W. C. KRUEGER. 1998. The ecological provinces of Oregon: a treatise on the basic ecological geography of the state. Corvallis, OR, USA: Oregon Agricultural Experiment Station. 138 p.
- AUSTIN, D. D., AND P. J. URNESS. 1983. Overwinter forage selection by mule deer on a seeded big sagebrush-grass range. *Journal of Wildlife Management* 47:1203–1207.
- BATES, J. D., R. F. MILLER, AND T. J. SVEJCAR. 2000. Understory dynamics in cut and uncut western juniper woodlands. *Journal of Range Management* 53:119–126.
- BOVEY, R. W., D. LE TOURNEAU, AND L. C. ERICKSON. 1961. The chemical composition of medusahead and downy brome. *Weeds* 9:307–311.
- BOYD, C. H., AND T. G. BIDWELL. 2002. Effects of prescribed fire on shinnery oak plant communities in western Oklahoma. *Restoration Ecology* 10:324–333.
- BROOKS, M. L., C. M. D'ANTONIO, D. M. RICHARDSON, J. B. GRACE, J. E. KEELEY, J. M. DITOMASO, R. J. HOBBS, M. PELLANT, AND D. PYKE. 2004. Effect of invasive alien plants on fire regimes. *BioScience* 54:677–688.
- CANFIELD, R. H. 1941. Application of the line interception methods in sampling range vegetation. *Journal of Forestry* 39:388–394.
- CONNELLY, J. W., M. A. SCHROEDER, A. R. SANDS, AND C. E. BRAUN. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967–985.
- DAHL, B. E., AND E. W. TISDALE. 1975. Environmental factors relating to medusahead distribution. *Journal of Range Management* 28:463–468.
- D'ANTONIO, C. M., AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Reviews in Ecology and Systematics* 23:63–87.
- DAVIES, K. W. 2008. Medusahead dispersal and establishment in sagebrush steppe plant communities. *Rangeland Ecology and Management* 61:110–115.
- DAVIES, K. W., J. D. BATES, AND R. F. MILLER. 2006. Vegetation characteristics across part of the Wyoming big sagebrush alliance. *Rangeland Ecology and Management* 59:567–575.
- DAVIES, K. W., J. D. BATES, AND R. F. MILLER. 2007a. The influence of *Artemisia tridentata* spp. *wyomingensis* on microsite and herbaceous vegetation heterogeneity. *Journal of Arid Environments* 69:441–457.
- DAVIES, K. W., M. L. POKORNY, R. L. SHELEY, AND J. J. JAMES. 2007b. Influence of plant functional group removal on soil inorganic nitrogen concentrations in native grasslands. *Rangeland Ecology and Management* 60:304–310.
- DITOMASO, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255–265.
- DRUT, M. S., W. H. PYLE, AND J. A. CRAWFORD. 1994. Technical note: diets and food selection of sage grouse chicks in Oregon. *Journal of Range Management* 47:90–93.
- GEORGE, M. R. 1992. Ecology and management of medusahead. *University of California Range Science Report* 23:1–3.
- GOEBEL, C. J., M. TAZL, AND G. A. HARRIS. 1988. Secar bluebunch wheatgrass as a competitor to medusahead. *Journal of Range Management* 41:88–89.
- GREEN, J. S., AND J. T. FLINDERS. 1980. Habitat and dietary relationships of pygmy rabbits. *Journal of Range Management* 33:136–142.
- HARRIS, G. A. 1965. Medusahead competition. In: Proceedings of the cheatgrass symposium, Vale, OR. Portland, OR, USA: Bureau of Land Management. p. 66–69.
- HIRONAKA, M. 1961. The relative rate of root development of cheatgrass and medusahead. *Journal of Range Management* 14:263–267.
- HIRONAKA, M., AND B. W. SINDELAR. 1975. Growth characteristics of squirreltail seedlings in competition with medusahead. *Journal of Range Management* 28:283–285.
- HOOPER, D. U., AND P. M. VITOUSEK. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* 68:121–149.
- JAMES, J. J., K. W. DAVIES, R. L. SHELEY, AND Z. T. AANDERUD. 2008. Linking resource partitioning and species abundance to invasion resistance. *Oecologia* 156:637–648.
- KLEBONOW, D. A., AND G. M. GRAY. 1968. Food habits of juvenile sage grouse. *Journal of Range Management* 21:80–83.
- KREBS, C. J. 1998. Ecological methodology. 2nd ed. Menlo Park, CA, USA: Benjamin Cummings. 624 p.
- LACEY, J. R., AND B. E. OLSON. 1991. Economic and resource impacts of noxious range weeds. In: L. F. James, J. O. Evans, M. H. Ralphs, and R. D. Child [Eds.]. Noxious range weeds. Boulder, CO, USA: Westview Press. p. 5–16.
- MACCRACKEN, J. G., AND R. M. HANSEN. 1981. Diets of domestic sheep and other large herbivores in southcentral Colorado. *Journal of Range Management* 34:242–243.
- MACK, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-ecosystems* 7:145–165.
- MASTERS, R. A., AND R. L. SHELEY. 2001. Principles and practices for managing rangeland invasive plants. *Journal of Range Management* 54:502–517.

- MONACO, T. A., T. M. OSMOND, AND S. A. DEWEY. 2005. Medusahead control with fall- and spring-applied herbicides in northern Utah foothills. *Weed Technology* 19:653–658.
- NATURAL RESOURCE CONSERVATION SERVICE. 1997. National range and pasture handbook. Fort Worth, TX, USA: US Department of Agriculture, Natural Resource Conservation Service, Grazing Lands Technology Institute. 472 p.
- NATURAL RESOURCE CONSERVATION SERVICE. 2007. Soil survey. Available at: <http://soils.usda.gov/survey/s>. Accessed 10 April 2007.
- NATURAL RESOURCE CONSERVATION SERVICE. 2008. Plants database. Available at: <http://plans.usda.gov/>. Accessed 6 May 2008.
- OLSON, B. E. 1999. Impacts of noxious weeds on ecologic and economic systems. In: R. L. Sheley and J. K. Petroff [EDS.]. *Biology and management of noxious rangeland weeds*. Corvallis, OR, USA: Oregon State University Press. p. 4–18.
- OREGON CLIMATE SERVICE. 2007. OCS home page. Available at: <http://www.ocs.oregonstate.edu/index.html>. Accessed 25 July 2007.
- PATTERSON, R. L. 1952. *The sage grouse in Wyoming*. Denver, CO, USA: Sage Books. 341 p.
- PELLANT, M., P. SHAVER, D. A. PYKE, AND J. E. HERRICK. 2005. Interpreting indicators of rangeland health. Version 4. Denver, CO, USA: US Department of the Interior, Bureau of Land Management, National Science and Technology Center. Technical Reference 1734-6 BLM/WO/ST-00/001+1734/REV05. 122 p.
- ROBERTSON, J. H. 1971. Changes on a sagebrush–grass range in Nevada ungrazed for 30 years. *Journal of Range Management* 24:397–400.
- SHELEY, R., M. MANOUKIAN, AND G. MARKS. 1999. Preventing noxious weed invasion. In: R. L. Sheley and J. K. Petroff [EDS.]. *Biology and management of noxious rangeland weeds*. Corvallis, OR, USA: Oregon State University Press. p. 69–84.
- SHIPLEY, L. A., T. B. DAVILA, N. J. THINES, AND B. A. ELIAS. 2006. Nutritional requirements and diet choices of the pygmy rabbit (*Bachylagus idahoensis*): a sagebrush specialist. *Journal of Chemical Ecology* 32:2455–2474.
- S-PLUS. 2000. Version 7.0. Seattle, WA, USA: Mathsoft, Inc.
- TILMAN, D., C. L. LEHMAN, AND K. T. THOMSON. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Science* 94:1857–1861.
- TORELL, P. J., L. C. ERICKSON, AND R. H. HAAS. 1961. The medusahead problem in Idaho. *Weeds* 9:124–131.
- VITOUSEK, P. M. 1990. Biological invasions and ecosystem process: toward an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- WALLESTAD, R., J. G. PETERSON, AND R. L. ENG. 1975. Foods of adult sage grouse in central Montana. *Journal of Wildlife Management* 39:628–630.
- WHISENANT, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [COMPS.]. *Cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management*. Ogden, UT, USA: US Department of Agriculture, Forest Service, Intermountain Research Station. p. 4–10.
- YOUNG, J. A. 1992. Ecology and management of medusahead (*Taeniatherum caput-medusae* ssp. *asperum* [Simk.] Melderis). *Great Basin Naturalist* 52:245–252.
- YOUNG, J. A., C. D. CLEMENTS, AND G. NADER. 1999. Medusahead and clay: the rarity of perennial seedling establishment. *Rangelands* 21:19–23.
- YOUNG, K., AND J. MANGOLD. 2008. Medusahead outperforms squirreltail through interference and growth rate. *Invasive Plant Science and Management* 1:73–81.