

Resistance of Native Plant Functional Groups to Invasion by Medusahead (*Taeniatherum caput-medusae*)

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Understanding the relative importance of various functional groups in minimizing invasion by medusahead is central to increasing the resistance of native plant communities. The objective of this study was to determine the relative importance of key functional groups within an intact Wyoming big sagebrush–bluebunch wheatgrass community type on minimizing medusahead invasion. Treatments consisted of removal of seven functional groups at each of two sites, one with shrubs and one without shrubs. Removal treatments included (1) everything, (2) shrubs, (3) perennial grasses, (4) taprooted forbs, (5) rhizomatous forbs, (6) annual forbs, and (7) mosses. A control where nothing was removed was also established. Plots were arranged in a randomized complete block with 4 replications (blocks) at each site. Functional groups were removed beginning in the spring of 2004 and maintained monthly throughout each growing season through 2009. Medusahead was seeded at a rate of 2,000 seeds m^{-2} (186 seeds ft^{-2}) in fall 2005. Removing perennial grasses nearly doubled medusahead density and biomass compared with any other removal treatment. The second highest density and biomass of medusahead occurred from removing rhizomatous forbs (phlox). We found perennial grasses played a relatively more significant role than other species in minimizing invasion by medusahead. We suggest that the most effective basis for establishing medusahead-resistant plant communities is to establish 2 or 3 highly productive grasses that are complementary in niche and that overlap that of the invading species.

Nomenclature: Medusahead, *Taeniatherum caput-medusae* (L.) Nevski TACA8; bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* PSSPS; longleaf phlox, *Phlox longifolia* Nutt. PHLO2; Wyoming big sagebrush, *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young ARTRW8.

Key words: Weed management, invasive plant, weed ecology, prevention, restoration.

Throughout the western United States, a major factor affecting rangeland resources, fires, and watershed functioning is invasion by the winter-annual grass, medusahead [*Taeniatherum caput-medusae* (L.) Nevski ssp. *asperum* (Simk.) Melderis] (Miller et al. 1999). This invasive species was introduced in southeastern Oregon in 1884 (Turner et al. 1963). It currently infests several million hectares throughout the Pacific Northwest, California, and Nevada (Miller et al. 1999). Medusahead occurs in areas receiving 250 to 1,000 mm (10 to 39 in) of annual precipitation (Major et al. 1960). This weedy grass has invaded more than 2.5 million ha (6.178 million acres) throughout the western United States and continues to spread at a rapid rate (Miller 1996).

Medusahead aggressively displaces perennial grasses within the sagebrush steppe by preempting resources, and frequent fires destroy the shrub portion of the plant community (Young 1992). Thus, fire facilitates the conversion of rangeland from a perennial-dominated to an annual-dominated system. Medusahead-dominated sites have 50 to 80% less grazing capacity than the original native plant community (Hironaka 1961). Most ecologists believe that medusahead reduces plant and animal diversity and species richness, reduces suitable habitat for wildlife, accelerates erosion, and alters nutrient cycles, hydrologic cycles, and energy flow (Olson 1999).

Preventing the encroachment of medusahead onto non-infested areas and restoring those dominated by it are desired goals for managing this invasive weed (Peterson and Vieglais 2001; Sheley et al. 2007, 2008; Simberloff 2003; Zavaleta 2000). Therefore, establishing and maintaining a healthy plant community that resists initial invasion or reinvasion is central to implementing effective prevention and restoration programs (Sheley et al. 1996, 2009).

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Interpretive Summary

Ecologically based, invasive, annual grass management requires the implementation of effective prevention and restoration strategies (Masters and Sheley 2001). Identifying functional groups of species that hinder invasion or reinvasion by medusahead provides managers direction for focusing efforts on maintaining and promoting the highest priority plants within the community. As we anticipated, perennial grasses play a critically important role in minimizing invasion by medusahead, but it is unlikely that a single native-grass species provides enough niche overlap with this annual grass to prevent invasion because resistance probably requires the sequestration of nutrients from all nutrient pools within the soil profile, which may maximize biomass production (James et al. 2008; Rinella et al. 2007). Because removing shrubs, mosses, and most forbs had limited effect on medusahead, it appears that randomly maximizing species richness or diversity will not convey resistance as well as carefully chosen functional groups does. We suggest that carefully selecting two or three highly productive grasses that are similar in niche to the invading species provides a basis for designing medusahead-resistant plant communities.

Susceptibility of grasslands to invasion by medusahead may be influenced by plant community structure (Orians 1984), resource availability (Burke and Grime 1996; Elton 1958; Stohlgren et al. 1999; Tilman 1996), the temporal and spatial ability of competing species to capture resources (Brown 1998; Carpinelli 2001), and invader life history traits (Davis and Pelsor 2001). It has been proposed that functionally diverse plant assemblages resist invasion (Burke and Grime 1996; Levine and D'Antonio 1999; Sheley et al. 1996) through resource preemption (Davis and Pelsor 2001; Dukes 2001; Symstad 2000; Tilman 1999). Niche differentiation has been suggested as the mechanism for resource depletion (Hooper and Vitousek 1997; Hooper and Vitousek 1998), and maximizing niche occupation has been shown to decrease plant community invasibility (Brown 1998; Carpinelli 2001).

Increasing evidence suggests that plant functional traits are more important to ecological integrity and invasion resistance than plant species diversity or richness (Diaz and Marcelo 2001; Mack and D'Antonio 1998). Members of the same functional group share similar physiological and morphological traits, which are intimately linked to their strategies for performance and dominance (Chapin 1993; Lauenroth et al. 1978). The greater the functional trait differences, the less redundancy in plant community functions. Increasing functional diversity has been shown to decrease invasion by nonindigenous invaders through maximizing niche occupation and preempting resource use by invaders (Brown 1998; Carpinelli 2001; Dukes 2001). Additionally, a particular functional group may possess traits critical for minimizing the invasion by a particular species. With respect to medusahead, the key mechanism of invasion resistance within a system may depend on trait

variation among coexisting species and on how species abundance is distributed in the system (James et al. 2009).

Understanding the relative importance of various functional groups in minimizing invasion by medusahead is central to increasing the resistance of native plant communities. This knowledge provides the information necessary to optimize prevention and restoration programs by focusing efforts on those species with the highest probability of resisting invasion. The objective of this study was to determine the relative importance of key functional groups within an intact Wyoming big sagebrush–bluebunch wheatgrass community type on minimizing invasion. Because niche overlap and relative abundance are critical vegetation characteristics conveying resistance, we hypothesized that (1) plant communities with the highest functional group diversity would yield the lowest medusahead density and biomass, and (2) based on perceived niche overlap and relative abundance, the order of importance among functional groups for reducing medusahead density and biomass would be perennial grasses, annual forbs, perennial forbs, rhizomatous forbs, and shrubs.

Materials and Methods

Study Sites. This study was conducted on two intact sites within the Wyoming big sagebrush–bluebunch wheatgrass habitat type (Daubenmire 1980). This habitat type lies on the warm–dry end of grassland habitat types. The sites (43°22'N, 118°22'W, 1,300 m [4,265 ft] elevation) were within 0.01 km (10 m [0.006 mi, 33 ft]) of one another and were considered comparable, except for the shrub component. This habitat burns periodically (30 to 90 yr), which usually eliminates the shrub component of the system. One site had shrubs in the overstory, whereas the other site lacked a shrub component. Various perennial grasses and forbs were growing in association with the two dominant species (Table 1). There were more perennial forbs ($P = 0.02$) and mosses ($P = 0.03$) on the site with shrubs than on the site where shrubs were lacking. Long-term, annual precipitation at Drewsey, OR, 16 km north of the site, is 340 mm. Soil at both sites is a fine, montmorillonitic, mesic Xeric Haplargid with total nitrogen ranging between 0.03 and 0.08%.

Experimental Design. This study was conducted between 2004 and 2009. Individual species were assigned to specific functional groups based on morphology and rooting structure. Groups included shrubs, perennial grasses, perennial taprooted forbs, rhizomatous forbs, annual forbs, and mosses (Table 1). Annual grasses occurred on and adjacent to the sites, but not in the plots. Seven removal treatments were applied to 2 by 2-m plots. Plots were arranged in a randomized complete-block design with 4 replications (blocks) at each site. Removal treatments

Table 1. Means and P values generated from independent *t* tests for species biomass at two sites south of Drewsey, OR.

Functional group	Site	Biomass g m ²	P value
Shrubs	No shrub	0	0.10
Wyoming big sage (<i>Artemisia tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & Young)	Shrub	304.79	
Annual forbs	No shrub	16.22	0.25
Maiden blue-eyed Mary (<i>Collinsia parviflora</i> Lindl.)	Shrub	13.47	
Bur buttercup (<i>Ceratocephala testiculatus</i> (Crantz) Bess)			
Tall annual willowherb (<i>Epilobium brachycarpum</i> K. Presl)			
Taproot forbs	No shrub	6.56	0.02
Giant lomatium [<i>Lomatium dissectum</i> (Nutt.) Mathias & Constance]	Shrub	23.01	
Largeflower hawksbeard (<i>Crepis occidentalis</i> Nutt.)			
Pale agoseris [<i>Agoseris glauca</i> (Pursh) Raf.]			
Rhizomatous forbs	No shrub	1.75	0.05
Longleaf phlox (<i>Phlox longifolia</i> Nutt.)	Shrub	3.09	
Perennial grass	No shrub	113.82	0.66
Bluebunch wheatgrass [<i>Pseudoroegneria spicata</i> (Pursh) A. Löve]	Shrub	75.18	
Bottlebrush squirreltail [<i>Elymus elymoides</i> (Rafin.) Swezey]			
Sandberg bluegrass (<i>Poa sandbergii</i> J. Presl)			
Moss	No shrub	1.04	0.03
Tortula moss [<i>Tortula ruralis</i> (Hedw.) G. Gaertn., B. Mey. & Scherb.]	Shrub	127.89	

included (1) everything, (2) shrubs, (3) perennial grasses, (4) taprooted forbs, (5) rhizomatous forbs, (6) annual forbs, and (7) mosses. A control where nothing was removed was also established. Functional-group removal was initiated in spring 2004 and was maintained monthly throughout each growing season through 2009. Removal involved wiping a 50% glyphosate [*N*-(phosphonomethyl) glycine] solution on the foliage of each species. Once the aboveground plant material had desiccated, it was clipped at the soil surface and maintained to determine biomass. Medusahead was broadcast-seeded in the fall of 2005 at a rate of 2,000 seeds m⁻² (186 seeds ft⁻²). We waited two growing seasons to seed medusahead to allow remaining species to adjust to the removal treatments. Seeds were collected in 2004 from nearby areas and stored in a cool-dry environment.

Sampling. Density of medusahead was measured in the spring of 2006 through 2009 in three randomly placed 0.2 by 0.5-m Daubenmire frames in each plot (Daubenmire 1980). In 2009, medusahead biomass was harvested in a single randomly located 0.5-m² (5.4 ft²) frame after the plants had senesced. Plants were harvested at ground level, dried at 60 C (140 F) for 48 h, and weighed. Weather conditions were monitored about 16 km northeast of the study sites.

Analysis. *Biomass Removed.* ANOVA¹ was used to assess the significance of treatment effects. Biomass collected each

year was summed to provide data representing the entire amount removed for each plot from 2004 to 2009. Sites were analyzed separately because the variances were not homogeneous. Mean separations were achieved using Fishers Protected LSD test comparisons at $\alpha = 0.05$ level of significance.

Removal Treatments. ANOVA was conducted as a split-plot using Proc Mixed software.¹ The ANOVA model analyzed medusahead density between sites and among years. In these models, rep (site or year) was used as the error term for site or year depending on the comparison. Removal treatment by rep (site or year) was used as the error term for testing the effects of removal treatment on medusahead density. Because medusahead biomass was only collected in 2009, year was not included in the ANOVA model for biomass. Means and standard errors are presented. In addition, Honestly Significant Differences (HSDs) are provided for comparing multiple means. Data presented are averaged over factors that were not significant or did not interact.

Results

Weather. During the past 30 yr, the average annual precipitation in the area was about 340 mm, arriving primarily in winter and spring (Figure 1a and 1b). Throughout the study period, annual precipitation was

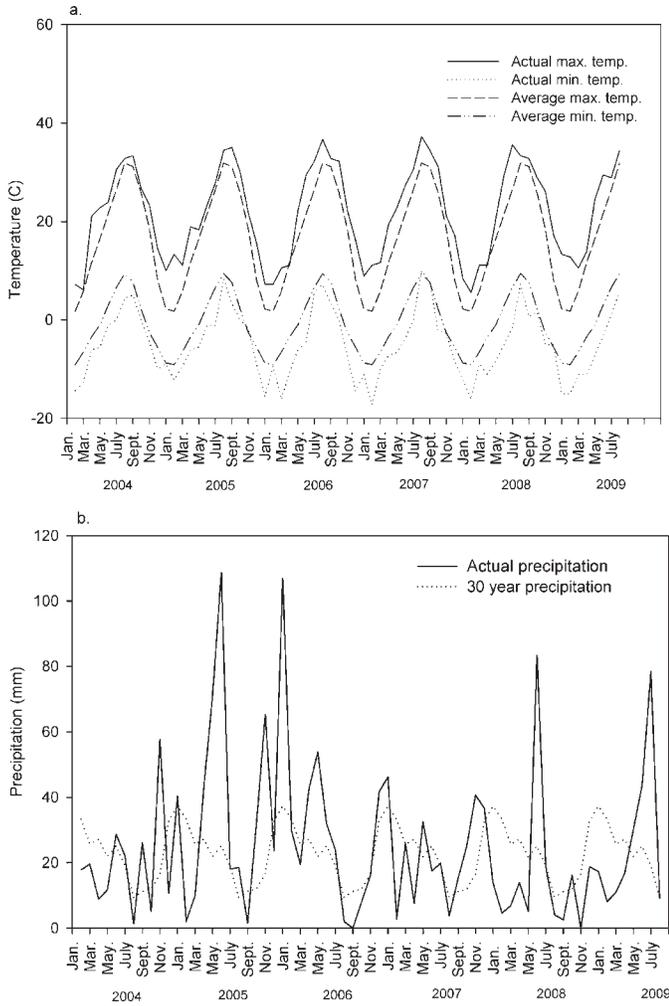


Figure 1. (a) Long-term (30 yr) temperature and actual temperature, and (b) precipitation and actual precipitation during the experiment at both sites.

close to average, but monthly precipitation was highly variable. Overall, summer temperatures were higher and winter temperatures were lower during the study than during the 30-yr averages.

Biomass Removed. No Shrubs. On the site with no shrubs, the most biomass removed was that of perennial grasses, which made up about one-third of the entire plant material on the plot (Figure 2a). Annual forb biomass removed was less than one-half that of the perennial grass, but it was not significantly different. All other functional groups produced less biomass than that of perennial grasses. The functional group with the most biomass removed on the shrub site was shrubs, but the amount of moss biomass removed was similar among plots (Figure 2b). The biomass of perennial grasses removed on this site was similar to all other functional groups, except shrubs.

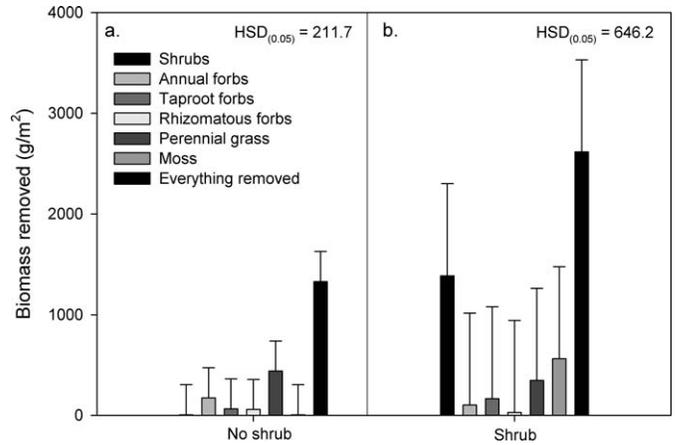


Figure 2. Amount of biomass removed from plots summed across years for the site (a) without shrubs and (b) with shrubs.

Year. Medusahead density varied among years, regardless of functional group removal treatments ($P = 0.0001$; $HSD_{(0.05)} = 26.9$). In 2006, there were about 165 medusahead plants m^{-2} averaged across removal treatments. The density of this invasive grass decreased to about 100 plants m^{-2} in 2007 and to about 40 plants m^{-2} in 2008. In 2009, medusahead density increased to about 90 plants m^{-2} .

Removal Treatments. Density. The effects of removal treatments on medusahead density did not depend on year ($P = 0.62$) or site ($P = 0.06$) or their interactions ($P > 0.05$). Thus, only the main effect ($P < 0.0001$) of removing various functional groups significantly influenced medusahead density (Figure 3). The highest medusahead density resulted from removing perennial grasses, which was nearly double that of any other removal treatment. The second highest density of medusahead resulted from removing rhizomatous forbs (phlox), which produced

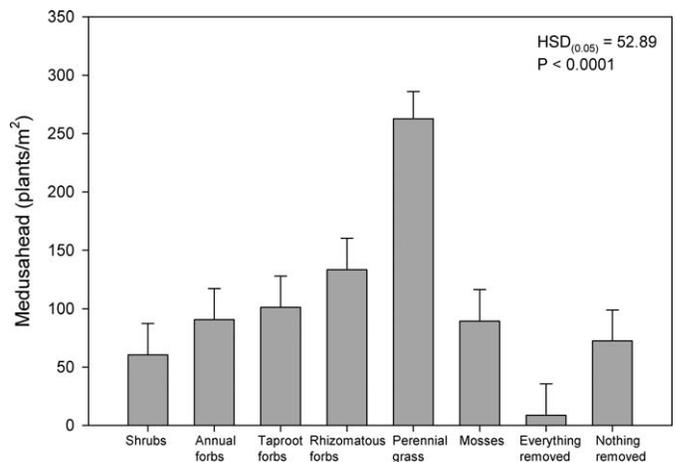


Figure 3. Effect of functional group removal on medusahead density averaged across years.

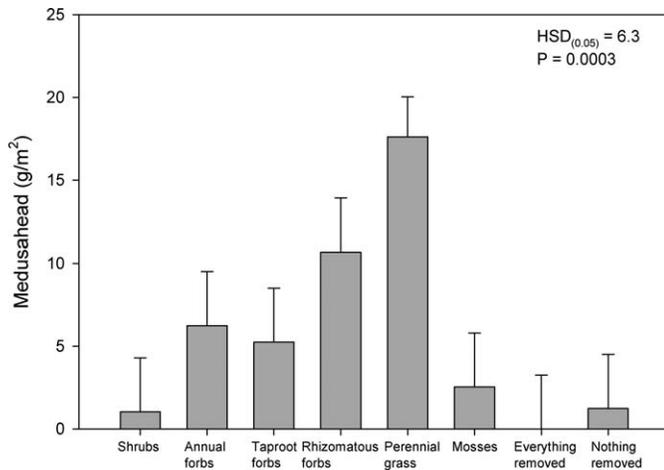


Figure 4. Effect of functional group removal on medusahead biomass in 2009.

about 125 plant m^{-2} of the invasive grass. These were the only two functional groups whose removal increased medusahead density over areas where nothing was removed. Removing everything produced the lowest medusahead density, which was about 8 plants m^{-2} averaged across all years and both sites.

Biomass. The main effect of removal treatment was the only significant factor to affect medusahead biomass (site, $P = 0.32$; site by treatment, $P = 0.57$; Figure 4). Removing perennial grasses yielded about 18 $g\ m^{-2}$ (0.53 $oz\ yd^{-2}$; 0.012 $lb\ ft^{-2}$) of medusahead biomass, which was higher than any other removal treatment. Removing rhizomatous forbs produced the second highest medusahead biomass (about 10 $g\ m^{-2}$), but this was not significantly different from the amount of biomass after removing annual forbs or taprooted forbs. Removing shrubs, mosses, everything, or nothing, all produced less than 2.5 $g\ m^{-2}$ of medusahead.

Discussion

Medusahead is an invasive annual grass that has invaded millions of hectares of rangeland and continues to rapidly spread. Effective medusahead prevention and native plant restoration strategies are essential to protecting and recovering the ecological goods and services garnered from these rangelands (Davies and Sheley 2007; Masters and Sheley 2001). Establishing and maintaining healthy plant communities that are resistant to invasion is important to enduring prevention and restoration programs (Pokorny et al. 2005; Sheley et al. 1996). Knowledge about plant community composition and functional groups that convey invasion resistance is central to developing enduring medusahead management programs.

Ecologically healthy, invasion-resistant plant communities can be achieved by maximizing niche occupation with

desired species (Pokorny et al. 2005; Sheley and Carrpinelli 2005; Symstad 2000). Establishing and maintaining species that have complementary niche requirements can help facilitate invasion resistance (Symstad 2000). For example, Sheley and Carrpinelli (2005) found that combining crested wheatgrass [*Agropyron cristatum* (L.) Gaertn. “hycrest”] and alfalfa (*Medicago sativa* L.) had lower spotted knapweed (*Centaurea stoebe* L.) density and biomass than monocultures or grass mixtures because the two species occupied complementary niches. In this study, it was hypothesized that plant communities with the highest functional group diversity would yield the lowest medusahead density and biomass because of the likelihood that niche occupation would be high. Among those treatments in which medusahead established, the community without plant removal was among those treatments with minimum medusahead density or biomass. This supports the contention that functional group diversity conveys some degree of invasion resistance.

Using the same theory, we also anticipated that removing all the desired plant material from the plots would yield the highest medusahead density and biomass. However, very few medusahead plants established in the first year, and they did not survive to the following years in plots where everything was removed. Mangla et al. (2009) found that density-independent factors play a major role in the establishment of medusahead in stressful environments that vary widely during the growing season during the establishment phase. We speculate that removing all plant material created microclimatic weather conditions that became too extreme for seedling survival. Thus, we believe medusahead establishment may be facilitated by plant or litter cover that provides a buffer from extreme conditions (Sheley et al. 2009).

In many management situations, maintaining and restoring the entire suite of species is impractical because of managerial and environmental constraints. Focusing efforts on those functional groups that most minimize invasion may be a more practical approach. It has been suggested that indigenous plants whose functional traits match that of an invader may be particularly important in invasion resistance (Pokorny et al. 2005). We failed to reject the hypothesis that removing perennial grasses would increase medusahead density and biomass more than removing other functional groups. Similarly, medusahead density was negatively correlated to preinvasion, perennial tussockgrass [*Poa flabellata* (Lam.) Hook. f. (excluded)] density (Davies 2008). Based on phenology and rooting depth, perennial grasses may provide substantial niche overlap with medusahead. Bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] and squirreltail [*Elymus elymoides* (Rafin.) Swezey] acquire nitrogen from relatively deep in the soil profile, whereas Sandberg bluegrass (*Poa secunda* J. Presl) acquires nitrogen mainly from shallow soil

layers (James et al. 2008). In addition, Sandberg bluegrass has the ability to maintain positive and stable growth rates at low and high temperatures (Monaco et al. 2005).

Although maximizing niche occupation through high functional group diversity can be an important mechanism for invasion resistance, the relative abundance of desired species may play a significant role in minimizing invasion (Kennedy et al. 2002; Wardle and Zackrisson 2005). For example, Rinella et al. (2007) found that on a per-gram of biomass basis, each resident plant group similarly suppressed invader growth. In our study, grasses comprised one-third of the total vegetation biomass on the site without shrubs. On the shrubby site, there was no difference in the biomass of understory vegetation removed, but the high variance associated with biomass removal probably accounted for the lack of detection of any differences on this site. In a study linking nitrogen partitioning and species abundance to annual grass invasion, dominant, perennial grasses acquired the most nitrogen from all nitrogen pools because of their abundance (James et al. 2008). Thus, the key mechanism of invasion resistance may depend on trait variation among species in an assemblage and their relative abundance. Collectively, a suite of species may be important to maximizing biomass production, usurping soil resources, and preempting resource acquisition by invading species (Naeem and Li 1997; Rinella et al. 2007; Robinson et al. 1995).

It is clear that annual forbs can affect the abundance and diversity of annual grasses (Polley et al. 2006). After perennial grasses, we anticipated that annual forbs, taprooted forbs, and rhizomatous forbs, in that order, would limit medusahead density and biomass. However, removing any of the three forb groups had the same effect on medusahead density and biomass, although removing rhizomatous forbs seemed to increase medusahead over that of other functional groups, other than perennial grasses. It was interesting because the amount of biomass of rhizomatous forbs removed was small compared with other functional groups, suggesting that the reproductive underground roots may extend and forage in the niche desired by medusahead.

Sources of Materials

¹ SAS 2009 statistical software, SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513.

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