A MODEL EXPLAINING MEDUSAHEAD INVASION AND NOVEL TARGETED GRAZING APPROACHES OF CONTROL

by

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ABSTRACT

A Model Explaining Medusahead Invasion and Novel Targeted Grazing Approaches

by

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Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is a problematic invasive annual grass and its invasion superiority can be partially attributed to high tissue silica concentrations. I developed a model to explain the silica positive feedback cycle of invasion (Chapter 1) and attempted to interrupt the cycle through novel grazing approaches and reseeding efforts. Experiments were conducted to determine whether (1) grazing rotations between improved pastures and medusahead-infested rangeland would provide supplemental nutrients to increase consumption and digestion of the weed by cattle (Chapter 2), and (2) spraying medusahead with a glyphosate herbicide at different rates would increase intake and preference for the medusahead by sheep and cattle (Chapter 3). Additional experiments were aimed at (3) separating the influence of glyphosate from other chemicals added to the formulation (i.e., salt, other adjuvants) on medusahead use by cattle (Chapters 3 and 4), and (4) assessing the nutritional value and digestibility kinetics of medusahead treated with glyphosate at different rates and at different plant particle sizes in an *in vitro* fermentation study (Chapter 5). Finally, I determined if a combination of cattle grazing, trampling, and reseeding would represent a viable tool for revegetation efforts on medusahead-invaded rangelands (Chapter 6). Rotational grazing from supplemental pastures to medusahead-invaded rangeland positively influenced consumption of medusahead. Sheep in confinement preferred glyphosate-treated over non-treated medusahead in a two-way choice test, and cattle utilized glyphosate-treated medusahead more than non-treated plants while avoiding salt or adjuvants treatments. The *in vitro* study revealed that when medusahead is ground to 1 mm, or treated with glyphosate, are digested to a greater extent than larger particles (20 to 40 mm), or substrates not treated with the herbicide. Nevertheless, particle size had a greater influence on digestion than the glyphosate treatments. Finally, targeted cattle grazing and trampling had only a minor influence on perennial revegetation, with only small burnet (*Sanguisorba minor* Scop.) establishing. In summary, rotational grazing between improved pastures and medusahead-invaded pastures as well as glyphosate application increased consumption of medusahead by livestock and provided an opportunity for revegetation.

(255 pages)

PUBLIC ABSTRACT

A Model Explaining Medusahead Invasion and Novel Targeted Grazing Approaches

Casey N. Spackman

Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is currently one of the biggest threats to rangelands and livestock operations in the Western US. High silica concentrations in medusahead contribute to its invasiveness. I developed a model to explain how silica is involved in the invasion process, and attempted to manipulate silica to increase use of the grass by livestock. Experiments were conducted to determine: 1) whether rotational grazing on established forages of improved nutritional quality would provide supplemental nutrients to increase cattle use of medusahead; 2) evaluate intake of and preference for medusahead treated with a glyphosate herbicide at different rates by sheep; and 3) evaluate intake and selection of medusahead by cattle by separating the effects of a glyphosate herbicide (Roundup®) from other chemicals in the formulation (salt, adjuvant). Additionally, experiments were conducted to 4) determine the nutritional value and digestibility of medusahead treated with Roundup® at different rates and at different plant particle sizes; and 5) determine if cattle grazing with trampling can increase seeding success on medusahead-invaded rangelands. Rotational grazing from supplemental pastures to medusahead-invaded pastures increased medusahead use by cattle during the second year of the study. Furthermore, glyphosate did not increase medusahead consumption in a choice between three glyphosate treatments, but did in a two-way choice test. Cattle grazed glyphosate-treated medusahead more than that of the non-treated grass and completely avoided the salt-treated grass. The active ingredient in a glyphosate herbicide increased consumption of medusahead while other ingredients in the herbicide (i.e., salt and adjuvant) had no influence on this choice. A smaller particle size increased the digestibility of medusahead compared to larger particle sizes. Glyphosate also increases digestibility, but not as much as particle size. Finally, cattle trampling did not help establish seeded plant species, and the seeding attempt was unsuccessful. Thus, grazing rotations between improved pastures and medusahead-infested rangeland, and the combined glyphosate application-grazing are new approaches for medusahead control, as they prepare a seed bed for revegetation and increase the nutritional quality of the grass for improved livestock nutrition.

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CHAPTER 1

INTRODUCTION: A POTENTIAL MODEL OF MEDUSAHEAD INVASION AND ASSOCIATED RESEARCH NEEDS[1]

ABSTRACT

Medusahead (Taeniatherum caput-medusae (L.) Nevski) is currently one of the most detrimental invasive plants impacting United States rangeland sustainability and livestock operations; it decreases wildlife habitat, plant diversity, and increases the frequency of fires. These impacts are further compounded by the fact that traditional control techniques (i.e., mechanical, cultural, and chemical) are often unsuccessful. Consequently, there is a critical need to assess the underlying causes for medusahead invasion and potential obstacles to its control in an ongoing effort to better understand its ecology and develop improved, mechanistic, conceptual approaches for effective management. Here, we propose that this challenge can be partially mediated through considering how tissue Si concentrations influences three key processes associated with medusahead dominance within plant communities (i.e., plant productivity, litter decomposition, and herbivory), but have not previously been synthesized into a comprehensive conceptual model. This conceptual model illustrates a central role of Si and develops linkages between plant fitness, litter decomposition, and herbivory. However, despite the connectivity between plant characteristics and ecological processes associated with medusahead abundance, close examination of the current knowledge base suggests that considerable uncertainty exists in how control strategies impact tissue Si

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[1] Co-authored with Clint Stonecipher

concentrations. Thus, this article will first expose these knowledge gaps, then provide a comprehensive synthesis of medusahead invasion and the self-reinforcing feedback model, and finally suggest numerous essential research avenues and forge a path to developing more effective control strategies.

INTRODUCTION

Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is currently one of the most detrimental invasive plants impacting rangeland sustainability and livestock operations (Davies and Johnson, 2008; Miller et al., 1999; Young, 1992); it decreases wildlife habitat, plant diversity, and increases the frequency of fires (Davies and Johnson, 2008). These impacts are further compounded by the fact that traditional control techniques (i.e., mechanical, cultural, and chemical) are often unsuccessful. Consequently, there is a critical need to assess the underlying causes for medusahead invasion and potential obstacles to its control in an ongoing effort to better understand its ecology and develop improved, mechanistic, conceptual approaches for effective management. Here, I propose that this challenge can be partially mediated through considering how tissue silicon concentration influences three key processes associated with medusahead dominance within plant communities (i.e., plant productivity, litter decomposition, and herbivory), but have not previously been synthesized into a comprehensive conceptual model. This conceptual model illustrates a central role of Si and develops linkages between plant fitness, litter decomposition, and herbivory.

High tissue Si concentration is a key attribute of medusahead as it forms mineral silica complexes within stems, and forms an epidermal silica varnish on leaves, awns, and glumes (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964). The varnish hinders digestive processes within the rumen of herbivores and contributes to animal avoidance of medusahead (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017). The same varnish also limits leaf-litter decomposition, causing a persistent litter or thatch layer to develop (Torell et al., 1961; Young, 1992). Accumulated medusahead litter smothers other less adapted seedling species and increases herbivore pressure on established, co-occurring desirable plant species (Davies and Svejcar, 2008; Evans and Young, 1970; Pyke, 2000). Lastly, high tissue Si concentrations enhances medusahead fitness as accumulated litter improves germination and root development (Evans and Young, 1970). Consequently, Si concentrations are likely linked to increasing both the relative and overall abundance of medusahead in plant communities, decreasing native species diversity, reducing net primary productivity, and a contributor to the development of a positive feedback cycle that favor exotic species persistence at the expense of native species (Elgersma et al., 2012; Inderjit and Cahill, 2015; Suding et al., 2013).

A conceptual model portraying a linkage between tissue Si concentrations and the self-reinforcing positive cycle feedback of medusahead invasion will enhance a more mechanistic understanding of the ecological processes and potentially help refine grass control and restoration effort opportunities (Fig. 1.1). My model illustrates how tissue Si concentrations directly influences critical plant characteristics (i.e., fitness, structure, and chemical composition), which subsequently impact fundamental ecological processes (i.e., plant productivity, litter decomposition, and herbivory). However, despite the connectivity between plant characteristics and ecological processes associated with medusahead abundance, close examination of the current knowledge base suggests that considerable uncertainty exists in how control strategies impact tissue Si concentrations.

While several categories of medusahead control have been applied to reduce and/or suppress invasion (i.e., mechanical, cultural, and chemical), sustained control is rarely achieved. Thus, this article will first expose these knowledge gaps, then suggest numerous essential research avenues to reduce uncertainties and forge a path to developing more effective control strategies.

TRADITIONAL CONTROL METHODS

Mechanical

Mechanical control includes mowing and tilling, which have the potential to impact plant fitness by reducing medusahead seed production, the number of viable seeds dispersed within a plant community, and altering plant structure by removing or integrating the plant material into the soil organic mixture, respectively.

Mowing

A window of opportunity for mowing medusahead was proposed, which was ~35 d from late vegetative to early reproductive phenological stage (Brownsey et al., 2017). The same study estimated that mowing prior to seed head emergence decreased medusahead seed production by ~50%. However, early spring mowing may miss younger plants and allow recovery of damaged plants thus enabling medusahead to produce seeds and only temporarily reduce its abundance. The optimal timing of mowing and control should coincide with the period when the majority of plants have germinated, thus limiting plant propagation and production. However, because mowing removes and mulches standing biomass, its dispersal on the soil surface may exacerbate litter abundance. Increased litter abundance creates optimal seedbed conditions (i.e., microsites) for medusahead seedlings (Evans and Young, 1970) and may perpetuate its dominance in the plant community. Medusahead seeds also remain viable for up to three years (Nelson and Wilson, 1969), thus repeated mowing treatments must be applied, which may lead to detrimental impacts to native plant species (i.e., reduced abundance) (Davies et al., 2012). Furthermore, the short window of opportunity for mowing may be impractical for large scale infestations and over multiple years. In addition, medusahead infestations often occur on landscapes that are inaccessible to machinery due to slope and terrain, as well as being on poor rocky soils that can damage equipment (Young, 1992). Overall, mowing only targets one characteristic of medusahead fitness (abundance of germinable seeds), while potentially exacerbating another such as increasing litter and creating favorable seedbed conditions for medusahead germination (Evans and Young, 1970; Mariotte et al., 2017). Consequently, this method alone does not adequately alter feedback mechanisms responsible for medusahead persistence and dominance within plant communities.

Tillage

Tilling can disrupt the litter layer, incorporate it into the soil, and create favorable seedbed conditions for revegetation efforts. In addition, tilling can damage medusahead roots, bury germinable seeds, and reduce medusahead cover by ~50% (Kyser et al., 2007). It has been shown that medusahead seeds emerge poorly at depths greater than 5 cm (Young et al., 1969). However, tillage may also increase the potential for soil erosion, facilitate soil moisture and organic matter losses, and disturb biological crusts (Young, 1992). Moreover, soil disturbance has been shown to favor the production of medusahead biomass and seed production (Miller, 1996), which exacerbate its abundance in plant communities. As with mowing, tillage may not be feasible due to landscape factors that could damage equipment. In addition, tillage may damage fragile biological crusts, interrupt nutrient cycling, and remove desired native species, thus, providing a disturbance regime that favors additional undesirable exotic plant species (Kaltenecker, 1997; Locke and Bryson, 1997; Young, 1992).

Cultural

Cultural methods include prescribed fire and livestock grazing, which, similar to mechanical control, have the potential to impact plant fitness and plant structure through removal of the standing biomass and litter (Fig. 1.1).

Prescribed Fire

Prescribed fire can consume medusahead litter (Kyser et al., 2008) and possibly improve seedbed conditions for native species. In addition, medusahead matures 2-4 weeks later than other annual grasses, including cheatgrass (*Bromus tectorum* L.) (Dahl and Tisdale, 1975; Hironaka, 1961; Young, 1992), and retains its seeds within inflorescences until August (Davies, 2008). Thus, timing a prescribed fire to coincide with viable seed retention can destroy these seeds. Timing and temperature of a prescribed fire may be difficult as cold-winter areas of the Intermountain West constrain the effectiveness of prescribed fire to spring and early summer due to limited amounts of combustible biomass (Kyser et al., 2008). Furthermore, prescribed fires in the late summer early autumn have a higher escape risk. In addition, in order to consume seeds located on the soil surface, fires must reach temperatures greater than 250 ºC (DiTomaso et al., 1999; Sweet et al., 2008). Slow burning, high temperature fires may also be difficult to achieve and result in unintended damage to seeds of desirable plant species. Despite the potential for using prescribed fire to control medusahead seed production and emergence from seed banks, one study showed that repeated annual prescribed fire actually increased medusahead abundance even though litter and seed production were removed (Young et al., 1972). In general, wildfires can damage native vegetation and create opportunities for exotic plant establishment, as well as contribute to air pollution and atmospheric CO_2 climate change (Campbell and Cahill, 1996; D'Antonio and Vitousek, 1992; Peters and Bunting, 1994; Young, 1992). Furthermore, fire alters soil infiltration rates, porosity, conductivity, and storage capacity (Neary et al., 1999) and damages native vegetation that may then be replaced by fire-adapted invasive annual grasses (Billings, 1994; Whisenant, 1990).

Grazing

Livestock grazing has been shown to be the preferred method of medusahead control due to low-cost and practicality (Hamilton et al., 2015; James et al., 2015), positive effects on nutrient cycling (Davies et al., 2010; Hobbs, 1996), and limited disturbance compared to other control methods (e.g., mowing, tillage, and fire). For instance, livestock grazing removes standing vegetation and litter, and the animal waste (e.g., feces and urine) is high in nitrogen (N) directly influence soil N mineralization (Davies et al., 2010; Hobbs, 1996). However, livestock tend to avoid medusahead due to the its high tissue Si concentration, which limits rumen digestibility (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017) and provides an undesirable oral texture

(McNaughton et al., 1985). For this reason, herbivory of medusahead may be reduced due to its structural and chemical composition, which leads to medusahead avoidance and increased grazing pressure and repeated defoliation of more palatable perennial grasses (Belsky and Gelbard, 2000; Heady, 1961; Mueggler, 1972). Furthermore, the benefits of livestock grazing, including reductions in medusahead litter, are likely negligible as utilization is often minimal after seed head emergence (Davy et al., 2009; Lusk et al., 1961). Thus, livestock contributes little to interrupting of medusahead dominance, and may actually exacerbate its persistence.

Chemical

Herbicides are a primary form of medusahead control. There are many herbicides labeled for medusahead control, including pre-emergent, post-emergent, broad-spectrum, grass-selective, and growth regulator herbicides. For example, pre-emergence herbicides containing imazapic and rimsulfuron have been used in to control medusahead, but their efficacy has been highly variable (Davies, 2010; Davies and Sheley, 2011; Kyser et al., 2007, 2012b; Monaco et al., 2005; Sheley et al., 2007). This may be in part due to the accumulated litter inhibiting penetration to the soil surface (Kyser et al., 2007) or rapid degradation in warmer soils (Kyser et al., 2012b). In contrast, a relatively newer herbicide containing indazaflam has been shown to effectively control annual grasses by providing more consistent, prolonged (i.e. residual) pre-emergence control (Sebastian et al., 2017a, 2017b, 2016b, 2016a), although this herbicide has not yet been approved for areas grazed by livestock. This poses a problem, as most areas heavily infested with medusahead is also used for livestock production.

In contrast to pre-emergence herbicides, products containing glyphosate, a broad-spectrum post-emergent chemical, has been used at low rates to decrease medusahead abundance during tillering in a big sagebrush scrub ecosystem (Kyser et al., 2012a). By using low rates of glyphosate, medusahead abundance was reduced by ~95% with limited damage to shrubs and other native vegetation. Furthermore, if applied prior to seed set, glyphosate may temporary reduce seed production and viability. However, multiple applications are needed because glyphosate does not impact new seedlings emerging from the soil seed bank (Kyser et al., 2012a). Despite the potential of chemical control of medusahead, there are risks associated with herbicides. For instance, spray drift, volatilization, and different herbicide formulations may result in non-uniform applications and potentially injure non-targeted species (DiTomaso, 1997). Furthermore, repetitive herbicide application can favor the development of herbicide resistance in weeds (DiTomaso, 1997). Thus, herbicide application only offers a temporary medusahead control and will require with multiple applications, making it an unsustainable solution to medusahead persistence and dominance.

TISSUE SILICON CONCENTRATIONS

Form and Concentration

Silicon (Si) is the second most abundant element found within the earth's crust (Epstein, 1999), and the majority of biologically-derived terrestrial Si exists as amorphous silica (i.e., phytoliths), which are insoluble in water. In contrast, its soluble form, orthosilicic acid or simply silicic acid (Ma and Yamaji, 2006), is the form taken up by plant roots and deposited as insoluble amorphous silica within plant tissues (Currie and Perry, 2007; Epstein, 1999, 1994). For clarity, tissue Si concentration, is predominantly referring to deposited, insoluble, amorphous silica. Tissue silica varies widely amongst plant species (Hodson et al., 2005) and plants are generally classified as accumulators (1-10% silica on a dry matter (DM) basis) or non-accumulators (<1%). Some monocots such as rice (*Oryza sativa*), sugarcane (*Saccharum officinarum* L.), and members of the Cyperaceae family (sedges) are considered hyper-accumulators having greater than 10% silica in their tissues (Handreck and Jones, 1967; Ma and Takahashi, 2002; Neumann, 2003). Consequently, many grasses are considered accumulators, but tissue silica varies widely depending on geographical location, phenological stage, and environmental conditions (McNaughton et al., 1985). For instance, tissue silica ranges between 1 and 4% in alpine tundra grasses, whereas African savanna grasses contain up to 20% (Johnston et al., 1968; McNaughton et al., 1985). Furthermore, semiarid rangeland grasses are considered intermediate accumulators, with tissue silica ranging between 3 and 9% (Shewmaker et al., 1989), but the invasive annual grass, medusahead, stands out as a hyper-accumulator with values ranging between 10 and 19% (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964).

Transport and Deposition

The uptake of soluble Si varies between species, genotype, and root structure and its transport occurs via the transpiration stream (Ma and Yamaji, 2006). Transport can be active, passive, and/or rejective (Ma et al., 2004; Mitani and Ma, 2005; Takahashi et al., 1990). For example, accumulation in grasses is believed to be passive, wherein these plants often display tissue silica concentrations reflective of soil Si concentrations (Handreck and Jones, 1967; Ma et al., 2001). In contrast, some dicots exhibit a rejective transport mechanism associated with a physical barrier in roots allowing water and nutrient passage but limit soluble Si uptake (Jones and Handreck, 1969). Furthermore, hyper-accumulators such as rice (Feng et al., 2011; Ma et al., 2007), barley (Chiba et al., 2009), maize (Mitani et al., 2008), wheat (Casey et al., 2004; Rains et al., 2006), and cucumber (Liang et al., 2005) display an active transport mechanism facilitating soluble Si uptake into the transpiration stream (Chiba et al., 2009; Ma et al., 2007, 2006). Medusahead has similar tissue silica to that of rice, although it is unknown whether it uses an active or passive transport mechanism. As a semiarid species, it likely uses active transporters due to limited soil moisture, which might restrain a passive transport mechanism (Bloom et al., 1985; Hu and Schmidhalter, 2005).

As soluble Si is transported to various parts of the plant, it is dehydrated and polymerized into a di- or poly-silicic acid which then can be further polymerized within cellular structures to amorphous Si (Casey et al., 2004; Ma and Yamaji, 2006; Mitani and Ma, 2005). Cellular constituents such as hemicellulose, callose, pectin, and lignin have been shown to provide a framework for deposition (Guerriero et al., 2016). Tissue silica can also take on various forms, depending on deposition location, cell shape, plant species, and environmental conditions (Blackman, 1971; Li et al., 2014). The location for silica deposition also varies greatly among plant species (Lewin and Reimann, 1969; Lux et al., 2003). Moreover, tissue silica bodies have been observed in all major above ground plant parts of medusahead, including sausage-shaped bodies beneath the epidermis of culms and varnish-like structures on the awns as silified barbs (Swenson et al., 1964).

TISSUE SILICON AND MEDUSAHEAD PLANT CHARACTERISTICS

Plant Fitness

High tissue Si concentrations in medusahead influences numerous factors associated with plant fitness that can be linked to plant productivity (Fig. 1.1). For instance, tissue Si may contribute to the stratification period for optimal germination timing and root development. Furthermore, tissue Si negatively impacts litter decomposition, which contributes to seedbed conditions that favor germination and alterations in soil conditions. Overall, high tissue Si has a cascade of net positive effects on medusahead productivity, abundance, and persistence within plant communities.

Germination

Seed dormancy, after-ripening, and timing of germination are key processes involved in medusahead's ability to withstand environmental fluctuations and produce viable seedlings. Medusahead requires a cold-temperature stratification period (i.e., ~ 120 d below 5º C) to readily germinate when soil temperatures reach 10 and 15 ºC (McKell et al., 1962; Young et al., 1968). The awns contain inhibitory factors that facilitate delayed germination (Nelson and Wilson, 1969). Amorphous Si within the cellular endodermis, has been found to increase plant tissue rigidity (Ma et al., 2006; Namaganda et al., 2009; Raven, 1983) and prevent decomposition in the environment (Torell et al., 1961; Young, 1992). High tissue Si in the awns (Swenson et al., 1964) may contribute to the delayed degradation of these inhibitory factors thus facilitating optimal timing of germination. Alteration to tissue Si may concurrently alter the efficacy of the after-ripening period potentially causing premature germination. For instance, cheatgrass lacks inhibitory factors of germination and an instance was observed of untimely germination and death (Mack and Pyke, 1983). However, literature on the Si-stratification relationship of medusahead is absent and needs further investigation.

Seed Bed Conditions

Successful seedling establishment of plants is often determined by the number of safe sites provided by the soil surface (Evans and Young, 1970; Harper et al., 1965). Litter can create similar microsites to that of the soil, which benefit medusahead seeds (Young et al., 1971). For instance, as a consequence of high tissue Si concentrations, medusahead litter is slow to decompose (Fig. 1.1), thus contributing to years of persistent decadent plant material (Bovey et al., 1961; Young, 1992). Other plant components such as lignin (Aerts, 1997; Laishram and Yadava, 1988; Stott et al., 1983), tannin-protein complexes (Palm, 1988), and abundant C:N and C:P ratios (Goldman et al., 1987) reduce litter decomposition rates; however, Si is thought to be the primary contributor to slowed decay rates in medusahead (Torell et al., 1961; Young, 1992). Persistent medusahead litter reduces seasonal and daily temperature fluctuations, reduces water evaporation, and increases humidity, which altogether contribute to a more conducive growth and reproductive environment (Evans and Young 1970). Furthermore, the medusahead awns get caught within the litter, thus, limiting seed burial and intimate contact with the soil surface (Evans and Young, 1970). For other plant species, this may pose a dire problem as they require direct contact with a moisture-supplying substrate such as the soil, but medusahead seeds absorb moisture from the litter environment (i.e., hygroscopic) (Young, 1992). In support of the favorable, self-induced seedbed conditions, medusahead was found to produce 47 times more seedlings within its litter environment than on bare ground conditions (Evans and Young, 1970). This is not to say that medusahead cannot germinate without the presence of litter, but rather the accumulation of litter is a critical component of medusahead persistence.

Root Development

Medusahead root development is similar to other annual grasses, although there are many unique traits that make it more competitive than neighboring plants. One similarity between cheatgrass and medusahead is that their roots develop at comparable rates, with root depths of both species being observed up to 100 cm (Hironaka, 1961). In addition, both annual grasses primarily germinate in the fall, continue their slow root growth through the winter, and have greater root elongation through spring and summer than newly established native perennial grass species (Harris, 1977; Hironaka, 1961). Collectively, these unique root development traits enable medusahead to gain a competitive advantage over perennial plant species and achieve greater resource acquisition (Harris, 1977; Harris and Goebel, 1976; James et al., 2010). However, medusahead diverges from other invasive species when it comes to root cell size and structure. For instance, Harris (1977) compared root cellular composition of medusahead, cheatgrass, and a perennial grass through photomicrographs and showed that medusahead had thicker cell walls and an overall larger root diameter than cheatgrass, but lower values than in the perennial grass species. It was proposed that the thicker cellular root endodermis may allow for transpiration to occur even if the surrounding soil environment is drier, particularly in the upper soil horizons. Similarly, when a Si-based fertilizer was applied to a variety of plant species (e.g., sorghum, rice, wheat, and potatoes), the endodermis root tissues were found to be more rigid and more efficient in water transpiration under droughty conditions (Chen et al., 2011; Crusciol et al., 2009; Gong et al., 2005; Hattori et al., 2003). Furthermore, Si has been associated with increased plant tissue rigidity (Ma et al., 2006; Namaganda et al., 2009; Raven, 1983). Despite considerable information on Si and its role in other plants, there is very limited information pertaining to medusahead roots and how it influences medusahead plant fitness.

Soil Properties

Medusahead can be found on a variety of soil types but more frequently in clayey soils as opposed to coarse textured, sandy soils (Dahl and Tisdale, 1975). Clayey soils are known for their high-water holding capacity, but shrink when they dry, creating large soil fissures. As cracks develop, plant seedlings and their roots can experience increased desiccation (Young et al., 1999). However, medusahead roots are well-adapted to this potential threat. For instance, if the primary root of medusahead dries out, an adventitious root emerges to replace the primary root (Young, 1992). Furthermore, vascular tissues are strengthened by Si accumulation and as a consequence they are able to withstand the shrinkage-induced tissue stress from the drying of clay soils (Hattori et al., 2003). It is of no surprise with these adaptive traits that medusahead responded more favorably (i.e., greater shoot and root growth) on clay soils compared to other invasive annual grasses such as cheatgrass and ventenata (*Ventenata dubia)* (Bansal et al., 2014).

Additionally, nutrient uptake and availability may also be related to medusahead invasion. For instance, a reciprocal transplant study between medusahead seeds of California and France showed that California soils produced larger plants than those from France (Blank and Sforza, 2007). It was proposed that California soils have greater nutrient content than those from France. In a comparative growth study, nitrogen and phosphorus additions increased biomass production of cheatgrass compared to medusahead (Dakheel et al., 1993). In the same study, when soils were deficient, cheatgrass again out-produced medusahead. When nitrogen was examined by itself, cheatgrass again produced more shoot and root mass than medusahead (MacKown et al., 2009). However, with each of these studies, soil or plant Si concentrations were not reported, likely due to the fact that Si was not being considered as an essential element of plant nutrition (Arnon and Stout, 1939; Epstein, 1972). Therefore, medusahead tissue Si concentration may play a larger role in nutrient use and growth than previously thought. For instance, medusahead is a hyper-Si accumulator (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964), and therefore possesses Si-associated growth and stress tolerance characteristics. Silica has been shown to increase root and leaf elongation in sorghum and rice plants (Hattori et al., 2003; Hossain et al., 2002). Silica soil concentrations and uptake by medusahead may facilitate increased growth and off-set the competitive superiority of cheatgrass described in the aforementioned studies. In addition, the rapid growth of medusahead roots, particularly in early spring, provides an opportunity to extract nutrients more quickly compared to slower growing perennial grasses, thus contributing to the superiority of the plant as an invader (Harris, 1977; Harris and Goebel, 1976; James et al., 2010). Furthermore, Si has been shown to enhance the efficiency of water and soil nutrient use, as well as to increase photosynthesis (Chen et al., 2011). Overall, Si may play a large role in clayey soil stress tolerance, geographic growth location, and nutrient acquisition of medusahead, thus contributing to the plants' abundance in the community.

Plant Structure

Tissue Si influences numerous structural factors of medusahead, which directly influence litter decomposition and herbivory and indirectly influence plant fitness (Fig. 1.1). In addition, the structural aspects of medusahead may influence plant production. Ultimately, Si-associated factors such as toxicity resistance, a photosynthetic barrier, culm rigidity, upregulation of the immune system, and plant texture contribute to the overall abundance of medusahead in a plant community.

Toxicity Resistance

The accumulation toxic metals can negatively impact a plant's fitness (Nagajyoti et al., 2010), and evidence suggests that tissue Si mitigates this toxicity through structural adaptations within the plants (Ma, 2004). For example, plant roots are the first line of defense against metal toxicity, which contain an apoplastic membrane and regulates the translocation of metals through cell walls (Emamverdian et al., 2018). Deposition of silica in the apoplastic membrane is thought to decrease the porosity of cell walls, thus reducing the movement of toxic metals and salts (Coskun et al., 2019; Gong et al., 2006; Wu et al., 2013). Similarly, some toxic metals may form Si-complexes within the cell walls of roots, increasing adsorption and reducing their mobility (Keller et al., 2015; Wang et al., 2004; Ye et al., 2012). However, Adrees et al. (2015) suggested that changes in root structure was not the only mechanism of decreased toxic metal uptake occurring. Modulation of the influx transporters by Si may also decrease toxic metal uptake. Consequently, these mechanisms could reduce potential metal toxicity in medusahead, but such studies have not addressed this possibility.

Photosynthetic Barrier

Reductions in the atmospheric ozone layer has resulted in increased ultraviolet-B (UV-B) radiation reaching the earth's surface (Madronich et al., 1998). Increased UV-B radiation can damage leaves and reduce the photosynthetic capacity of plants (Kakani et al., 2003). Interestingly, such damage was alleviated by supplementing rice with soluble Si, that increased leaf rigidity and the production of phenolic compounds (Li et al., 2004; Tamai and Ma, 2008). The presence of tissue Si within the cellular membranes also mitigated UV-B-induced reactive oxygen species, which are known to cause membrane damage, decreased enzyme activity, electrolyte leakage, and changes in gene expression (Coskun et al., 2019; Shen et al., 2010). Despite these studies, the relationship between photosynthesis and tissue Si in medusahead has not been evaluated.

Culm Rigidity

Medusahead plants can reach a height of over 600 cm tall, which is impressive given that its culms are typically thin (e.g., <1 mm diameter) and inflorescences are relatively large and 'wispy' (McKell et al., 1962), making them susceptible to lodging and breakage (Savant et al., 1996). Culm integrity of medusahead is potentially enhanced due to the accumulation of silica, which increases the rigidity of the stem and leaves of certain plants (Ma et al., 2006; Namaganda et al., 2009). High tissue Si in rice has been shown to prevent plant lodging (Lee et al., 1990; Savant et al., 1996). However, no studies have examined the associations between medusahead, tissue Si, and lodging.

Immune System Regulation

Wagner (1940) was the first to suggest that tissue Si increases plant defenses against stem boring pathogens; known as the mechanical barrier hypothesis. However, studies in rice (Rodrigues et al., 2004, 2003) and wheat (Bélanger et al., 2003; Rémus-Borel et al., 2009) have shown that there is an upregulation of the innate immune system (e.g. chitinases, peroxidase, polyphenol oxidases, phytoalexins, and phenolic compounds) following predation. Tissue Si is known to act as a modulator of these plant defenses. For instance, these tissue Si associated defenses increase the binding affinity of plant proteins within the defense signaling pathway, thus preventing these pathogenic enzymes from reaching their target (Datnoff et al., 2007; Fauteux et al., 2005). Furthermore, recent work on pathogens and stem boring insects demonstrated that these predators release effector proteins that interfere with the defense signaling pathway (Giraldo and Valent, 2013; Mugford et al., 2016). Soluble Si deposition strengthens the apoplastic membrane and prevents the effector proteins from reaching their target (Holub and Cooper, 2004; Nuernberger and Lipka, 2005). Another postulation is that tissue Si allows for the redistribution of energy stores to upregulate these defense responses. For instance, Si-accumulating plants may replace energy-dependent processes involved in building structural carbohydrates for non-energy-dependent ones (McNaughton et al., 1985; Van Soest, 2006). Energy stores that would otherwise be used for growth and development of plant structural components, are redistributed to the innate immune system (Coskun et al., 2019). Overall, the redistribution of energy stores and production of a tissue Si physical barrier allows for a stronger defense response upon predation. However, these theories on tissue Si and the upregulation of the innate immune response have not been explored in medusahead.

Plant Texture

Invertebrate insects (Massey et al., 2006), voles (Massey and Hartley, 2006), rabbits (Cotterill et al., 2007), livestock (Massey et al., 2009; Shewmaker et al., 1989), small granivores and birds (Longland, 1994; Savage et al., 1969) all show decreased preference for Si-rich grasses. This avoidance may be a consequence an undesirable oral texture. For instance, medusahead inflorescences have a large vertical awn attached to the seed with shorter lateral spiked glumes (Miller et al., 1999). Microscopic examination of long medusahead awns revealed that they contain Si-rich barbs (Swenson et al., 1964) which may cause irritation to mouthparts (Massey and Hartley, 2009). Disarticulation of seeds from the seed head occurs from July to October with the majority being dropped in August (Davies, 2008), thus providing an opportunity for herbivory without the consequence of irritation. However, Si bodies are still present in the stem (Swenson et al., 1964) and possibly the spiked glume, which may continue to provide an undesirable oral texture similar to the long seed awns. Other grasses such as cheatgrass lack these short spiked glumes, which in the absence of the long seed awn, become susceptible to herbivory (Vallentine and Stevens, 1994). In addition, tissue Si in grasses has been associated with increased tooth wear (Baker et al., 1959), gastrointestinal urolithiasis (Bailey, 1981), and esophageal tumors (O’Neill et al., 1982, 1980), possibly causing further medusahead avoidance. Overall, the texture caused by tissue Si may deter herbivory of medusahead facilitating a self-reinforcing Si positive feedback cycle.

Chemical Composition

Nutritive Quality

Tissue nutrient concentrations and their association to toxins largely influence the likelihood of a plant being consumed by an herbivore (Provenza et al., 2002). Bovey et al. (1961) showed that medusahead contains 10.4% crude protein (CP), 2.6% fat, 26.8% crude fiber, 6.1% lignin, and 13.9% ash during the vegetative stage prior to flowering. Subsequently, as the plant matures, CP and fat content rapidly decline while fiber, lignin, and ash concentrations increase (Bovey et al., 1961). Other more recent studies show similar trends for the nutritional composition of medusahead across time (Montes-Sánchez and Villalba, 2017; Villalba and Burritt, 2015). Plant ash is an indicator of tissue silica content, and silica of ash comprises values greater than 90% in rice plants (Yalçin and Sevinç, 2001). However, these values can be lower depending on plant species and tissue location (Lanning et al., 1980; Lanning and Eleuterius, 1983). Medusahead ash comprises over 70% tissue silica, whereas cheatgrass is 47% (Bovey et al., 1961). Even if medusahead was palatable after seed drop, the nutritional quality of the plant is inadequate to sustain grazers. Ungulates require a minimum of ~7.5% crude protein for body maintenance (National Research Council, 2007a, 2007b, 2000), and thus supplementation is required for animals grazing medusahead at later phenological stages. Chemical composition alone cannot explain the low intake and palatability of medusahead as it has similar nutritional value to that of other more preferred grass species (Montes-Sánchez et al., 2017; Stonecipher et al., 2016).

Digestibility

Tissue Si within plants has been proposed as a defense mechanism against herbivory (Hunt et al., 2008), similar to those induced by plant secondary compounds or toxins (Provenza et al., 2002). An epidermal tissue silica varnish in medusahead acts as a physical barrier limiting the degradation of the cell-wall by rumen microorganisms (Hunt et al., 2008). This barrier prevents utilization of the organic constituents beneath such a layer (Mayland and Shewmaker, 2001; Van Soest, 1994; Van Soest and Jones, 1968). Support for this reduced digestion mechanism was shown by Montes-Sánchez and Villalba (2017), who reported declines in digestibility of medusahead with increased increments of the plant's particle size; with larger particles conserving the tissue Si barrier to a greater extent than particles of a smaller size. Furthermore, difference in digestion rates were not influenced by lignin content, as alfalfa and fescue hay had similar lignin concentrations to those present in medusahead. In addition, soluble Si limits enzymatic activity (Kind et al., 1954), thus decreasing plant digestibility in the rumen (Smith et al., 1971). Finally, for every percentile unit increase in tissue silica there are between one and three percentile units of reduction in forage digestibility (Smith et al., 1971; Van Soest and Jones, 1968). In avian species, such as chukar partridges, cheatgrass seeds were preferred over medusahead seeds (Savage et al., 1969), likely due to high tissue Si in medusahead and a concomitant lower digestibility.

Animal supplementation of nutrient rich forages in combination with medusahead were shown to increase consumption of the troublesome grass (Hamilton et al., 2015; Montes-Sánchez et al., 2017; Stonecipher et al., 2016). However, in these studies, medusahead consumption was low and would likely not provide adequate control.

Furthermore, the tissue Si was unaltered when fed, and thus the defense mechanism of the plant still existed.

RESEARCH NEEDS

Although we know orthosilicic acid is the soluble Si form taken up by plants (Ma and Yamaji, 2006) and that Si is deposited as amorphous mineral silica in medusahead tissues (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964), critical knowledge gaps exist in understanding how Si is transported through the soil to the root, how roots respond to available Si, what mechanisms within the root are responsible for uptake, and how the Si is transported through the plant. In addition, addressing ways to constrain tissue Si deposition within medusahead is key to interrupting the positive feedback cycle and thus make control of medusahead more successful. However, the association between Si and medusahead has largely been unexplored, thus there are critical research needs that may lead to alternative methods of control and more successful management strategies. The following paragraphs outline the most prominent knowledge gaps and research needs of this Si relationship.

The Soil

The normal range of soluble Si in soil is between 0.6 to 1.0 mM but can be higher or lower depending on soil weathering processes (Epstein, 1994). Furthermore, when Si concentrations exceed 2 mM, it begins to polymerize into a gel and becomes unavailable for plant uptake (Ma et al., 2001). When rice and an *Equisetum* species were grown in deficient soluble Si conditions, plant leaves became necrotic and the whole plant began to wilt (Chen and Lewin, 1969; Yoshida et al., 1962). Reduced growth and production yields were also reduced in *Gramineae* species when grown in soluble Si deficient conditions (Vlamis and Williams, 1967). Thus, soil concentrations of soluble Si play a major role in plant uptake as well as the plants fitness.

Understanding the role of soil soluble Si in medusahead-invaded landscapes could improve and/or develop better control strategies. For instance, if hyper-silicon accumulating species such as rice and *Equisetum* species become less fit (i.e., leaf necrosis and wilting) in soluble Si deficient soils, medusahead too may have reduced fitness. However, it is unknown how low values of soil soluble Si impact medusahead. If the aforementioned deficiency does reduce medusahead fitness, further studies could develop control strategies that decrease soil Si. Because soluble Si polymerizes at concentrations greater than 2 mM (Ma et al., 2001), future studies could develop strategies such as chemical application or soil amendments, that would decrease the soluble Si in the soil.

The Root

Fitness of rice plants has been associated with its ability to uptake soluble Si through the root (Takahashi et al., 1990) and its regulation by the *Ls1* gene (Ma et al., 2004), which has been modified to increase plant production and disease resistance (Ma et al., 2006). If increased plant fitness can be achieved by identifying the uptake mechanism of soluble Si in rice, it is not unreasonable to conclude that identifying the transport mechanism in medusahead could also provide a means to reduce medusahead fitness through genetic manipulation, and indirectly interrupting the positive feedback cycle of invasion. However, genetic manipulation of invasive plants like medusahead on non-agronomical landscapes may prove difficult because introduction of an already invasive plant, whether genetically modified or not, is not looked upon as favorable.

Chemical application may provide a more viable means of interrupting an uptake mechanism rather than genetic modification. For instance, in a laboratory setting, the active transporter in rice was inhibited through the use of chemical metabolic inhibitors such as NaCN and 2, 4-dinitrophenol at low temperatures. These chemical inhibitors may be unfeasible in a landscape setting, but it sets the stage for exploring environmentally friendly chemicals that could have similar results. If a passive transport mechanism exists, competitive adsorption through addition of soil minerals may reduce the transport of soluble Si into the plant. However, identifying the uptake mechanism is critical before exploring soluble Si inhibition techniques.

Root cellular structure of medusahead was compared with other grasses and was found to have thicker cell walls and an overall larger root diameter than an annual grass, but less than in a perennial grass species (Harris, 1977). The thicker cellular root endodermis may allow for transpiration to occur even if the surrounding soil environment is drier, particularly in the upper soil horizons. However, root Si concentrations were not reported and are unknown. Evaluating root Si concentrations may give insight into why medusahead is superior in acquiring soil resources and tolerating soil environment fluctuations (e.g., drought, temperature). If root Si plays a role in medusahead fitness, opportunities for research become available for discovering how deposition of soluble Si in the roots occur. This may lead to control strategies that manipulate the soluble Si deposition processes within the root and as a consequence decrease medusahead fitness and invasion superiority. Overall, little is known about medusahead roots in relation to Si uptake and tissue silica concentrations.

The Shoot

Little is known about soluble Si transport and deposition as amorphous silica within tissues. As stated previously, livestock tend to avoid medusahead due to its high Si concentrations (Hunt et al., 2008; McNaughton et al., 1985; Montes-Sánchez and Villalba, 2017) and attempts to control medusahead through grazing have failed to address the constraints associated with this mineral. Understanding Si transport and deposition may give insight into Si manipulation and reduction, consequently increasing livestock grazing selection of medusahead through increased digestibility, nutritional value, and reduced abrasiveness for grazing animals. For instance, sub-lethal dose of a glyphosate containing herbicide were shown to reduce tissue silica concentrations and increase tillering in quackgrass (Coupland and Caseley, 1975). Similarly, low-rates of glyphosate application increased the nutritional quality of annual ryegrass (Armstrong et al., 1992; Gatford et al., 1999), and increased cattle preference for fescue treated pastures (Kisseberth et al., 1986). Nevertheless, tissue Si concentrations were not reported in the latter studies. Understanding how glyphosate alters the soluble Si deposition process and increases the nutritional composition of these plants may give insight into other chemical treatments that may have similar results for medusahead.

Aspects of plant structure (metal toxicity resistance, photosynthetic barrier, culm rigidity, immune system response) are possibly linked to medusahead tissue Si but these aspects need further study. For instance, toxic metal accumulations in plants can effect plant productivity (Adrees et al., 2015; Nagajyoti et al., 2010), increased UV-B radiation can damage leaves and reduce the photosynthetic capacity of plants (Kakani et al., 2003), low tissue Si can increase susceptibility of culms to breakage in rice plants (Lee et al., 1990; Savant et al., 1996), and a weak immune system response to predation can have detrimental consequences (Holub and Cooper, 2004; Nuernberger and Lipka, 2005), whereas tissue Si mitigates these issues. These processes are known in agronomical crops; however, it is unknown for medusahead. Elucidation of these topics could possibly lead to reduction in Si deposition, consequently reducing medusahead fitness and its structural integrity.

CONCLUSION

In summary, high tissue Si in medusahead may play a central role in affecting plant characteristics (i.e., plant fitness and structure, chemical composition) and processes (i.e., plant production, litter decomposition, and herbivory) that favor medusahead abundance and continued dominance within ecosystems. Overall, high Si likely plays a central role in the self-reinforcing positive feedback cycle, yet there are many research needs. In order to adequately address the Si positive feedback these gaps in knowledge need to be explored. Livestock grazing is the preferred method of medusahead control by land managers (James et al., 2015; Young et al., 1972) and thus manipulation of tissue Si concentrations within the shoots of medusahead will be the focus of this section.

I hypothesize that the addition of supplementary nutrients may enhance utilization of low-quality feeds, such as medusahead, by these animals, thus potentially increasing selection for and digestibility of the grass. Furthermore, I will explore how a glyphosate containing herbicide effects medusahead tissue Si concentrations and its nutritional quality, consequently determining the effects of selection by livestock for the unpalatable forage. These discoveries will hopefully create a method of control that constrains the self-reinforcing feedback cycle triggered by high tissue Si in medusahead through reduced plant productivity, decreased litter abundance, and increased herbivory. Here I propose the use of two strategies to determine if increased digestibility and reduced tissue Si concentration can interrupt the positive feedback cycle of medusahead invasion: (1) Provision of nutrients that potentially aid in the ruminal fermentation of forages with high concentration of antinutritional factors such as tissue Si, and (2) the use of an herbicide (glyphosate) that will potentially reduce tissue Si in medusahead while preserving its nutritional quality. Collectively, these two strategies will increase use of medusahead by livestock, which will reduce biomass of standing material and the environmental conditions created by medusahead litter. In turn, disturbance produced during the grazing process (e.g., trampling, litter and standing plant material elimination) will prepare a seedbed for seeding perennials which will further reduce the competitive ability of medusahead and provide nutritious forage for livestock. In order to test the aforementioned strategies, I provided the appropriate nutritional context through established stands of a cool-season perennial grass (*Agropyron fragile* (Roth) P. Candargy) and forage kochia (*Bassia prostrata* (L.) A.J. Scott) to enhance the use of medusahead by cattle (Objective 1). I then tested in sheep, preferences for glyphosate-treated medusahead at different rates to explore the potential beneficial effects of glyphosate on medusahead palatability (Objective 2). Subsequently, I tested preferences for glyphosate-treated medusahead by cattle, where I separated the specific effects of glyphosate from the effects of salt (Objective 3) and the adjuvant (Objective 4) present in the herbicide. I then tried to understand the impacts glyphosate has on the nutritional quality of medusahead by measuring the fermentation kinetics of the grass by using an *in vitro* gas production method where I incubated medusahead treated with a glyphosate at different particle lengths and from two locations (Objective 5) I finally tried determined the effects of trampling during the process of grazing medusahead as the preparation of a seedbed for reseeding perennials (Objective 6).

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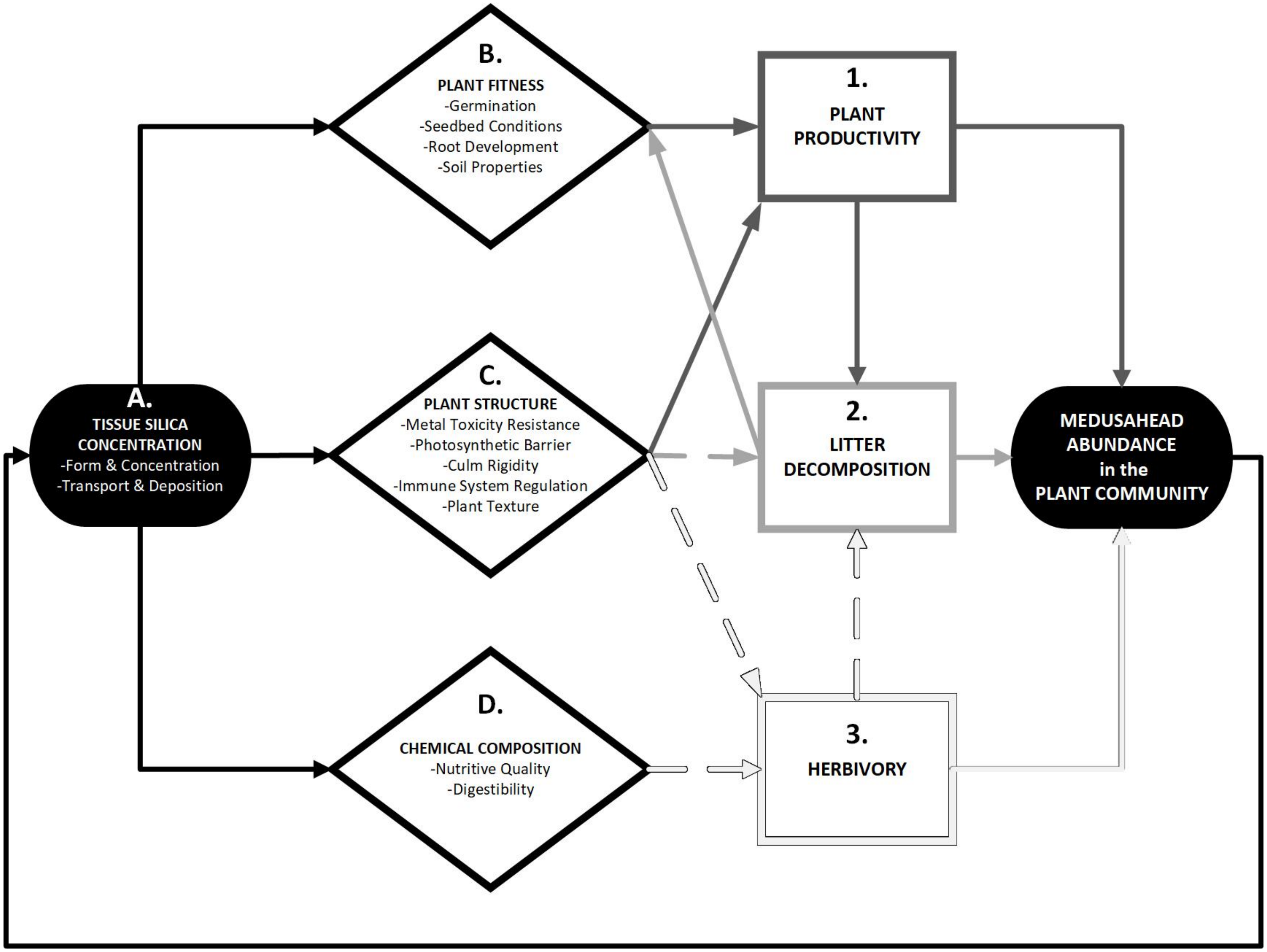
B.
PLANT FITNESS
-Germination
-Seedbed Conditions
-Root Development
-Soil Properties
1.
PLANT PRODUCTIVITY
A.
TISSUE SILICA CONCENTRATION
-Form & Concentration
-Transport & Deposition
C.
PLANT STRUCTURE
-Metal Toxicity Resistance
-Photosynthetic Barrier
-Culm Rigidity
-Immune System Regulation
-Plant Texture
2.
LITTER DECOMPOSITION
MEDUSAHEAD ABUNDANCE in the PLANT COMMUNITY
D.
CHEMICAL COMPOSITION
-Nutritive Quality
-Digestibility
3.
HERBIVORY

Figure. 1. A model explaining the self-reinforcing positive cycle feedback of medusahead invasion in relation to silicon (Si). High concentration of amorphous Si within medusahead tissue facilitates invasion through its direct impact on specific plant *characteristics* (represented by rhomboid shapes) and their consequential *processes* (represented by rectangles). Three *invasion pathways* (indicated by arrows and their associated color) link the characteristics and processes facilitating medusahead abundance in the plant community. High tissue Si concentrations (Characteristic A.) within the plant contribute to plant fitness (Characteristic B.) through favorable germination and seedbed conditions, increased root development, and better soil properties. Moreover, plant structure (Characteristic C.) such as increased toxicity resistance, presence of a photosynthetic barrier, increased culm rigidity, better immune system regulation, as well as an undesirable plant texture are all enhanced by Si. Furthermore, an epidermal silica varnish enhances the chemical composition of the plant (Characteristic D.) by preserving the nutritive quality and decreasing digestibility when consumed by herbivores. The characteristics of medusahead contribute to three key processes commonly associated with medusahead invasion which are increased plant productivity (Process 1.), decreased litter decomposition (Process 2.), and decreased herbivory (Process 3.). Each of these characteristics and processes contribute to the difficulties associated with medusahead control. The linkages between Si associated plant characteristics and processes gives insight into potential research needs that may help to develop improved mechanistic, conceptual approaches for effective medusahead management. These potential research needs may change the *net positive* (solid arrows) or *net negative* (dashed arrows) effects between plant characteristics and associated processes, reducing the overall abundance of medusahead in the plant community, ultimately interrupting the Si positive feedback cycle of invasion.

CHAPTER 2

GRAZING ROTATION ON RESTORED LAND AS A NEW TOOL FOR MEDUSAHEAD CONTROL[2]

ABSTRACT

Although livestock avoid unpalatable weeds, grazing represents a feasible control option for invasive species like medusahead (*Taeniantherum caput-medusae* (L.) Nevski) as suppling supplemental nutrients that provide a positive experience while grazing may increase consumption of medusahead. We hypothesized that rotational grazing which allows accessibility to established cool season grasses and forbs may provide livestock with the nutritional context necessary to increase utilization of medusahead. In a pilot study conducted in 2015 and an experiment 2016, beef cows (12) were randomly assigned to two treatments in 6 plots (2 animals/plot) in eastern Washington: 1) Supplemented animals grazed improved rangeland (IMP) for 45 min/d and then they grazed medusahead-infested rangeland (SUP; n=3 plots); and 2) Control animals grazed medusahead-infested rangeland only (NSUP; n=3 plots). The availability and quality of different forage types in the plant community, grazing events on these forage types, and animal behavior (movement and posture) using an ankle pedometer were assessed. In the pilot study, animals grazed annual grasses other than medusahead and green forbs during the experiment to a greater extent than all other forage types in IMP. During the pilot study, no differences were observed between treatments in the forage types selected (*P* > 0.05), however, biomass availability of perennial grasses declined in NSUP plots,

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[2] Co-authored with Clint Stonecipher

whereas it increased in SUP plots from the beginning to the end of the grazing period (*P* = 0.0382). During the experiment, SUP animals grazed medusahead to a greater extent (*P* = 0.003), and took fewer daily steps than NSUP animals (*P* = 0.022). Green forb cover was greater in SUP than in NSUP plots (P = 0.045). Thus, grazing improved pastures may represent a management tool that contributes to enhance medusahead use by cattle, which aids in restoration efforts aimed at reducing the abundance of the grass in medusahead-invaded rangelands.

INTRODUCTION

Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is currently one of the most detrimental invasive plants impacting western rangeland sustainability and livestock operations (Davies and Johnson, 2008; Miller et al., 1999; Young, 1992); it decreases the abundance and quality of forage available to livestock and wildlife, negatively impacts plant diversity, and increases the frequency of fires (Davies and Johnson, 2008). These impacts are further compounded by the fact that traditional control techniques (i.e., mechanical, cultural, and chemical) are often unsuccessful. Consequently, there is a critical need to assess the underlying causes for medusahead invasion and potential obstacles to its control in an ongoing effort to better understand and develop practical approaches for effective management strategies.

Livestock grazing has been shown to be the preferred method of medusahead management and control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015). However, utilization of standing medusahead vegetation and litter by livestock is generally low, as grazing animals tend to avoid this grass (Davies and

Svejcar, 2008; Hironaka, 1961). Livestock's aversive behavior for medusahead has been associated with high amorphous silicon (i.e., silica) concentrations within the plant, which forms an undigestible varnish, retarding microbial digestion in the rumen (Hunt et al., 2008) and constraining the availability of nutrients to the animal (Montes-Sánchez et al., 2017). New paradigms on foraging behavior such as the importance of positive experiences with the appropriate supply of nutrients are critical for increasing consumption of less palatable plant species such as medusahead. For instance, the provision of supplemental nutrients (i.e., carbohydrates, protein, and minerals) has been shown to alter the typical selection of low-quality feeds by livestock, since they provide the appropriate positive experiences necessary to increase consumption of unpalatable forages (Pérez et al., 1996; Villalba and Provenza, 1999). In addition, when protein concentrates are made available to livestock, the increase in nitrogen inputs to the rumen increases microbial recruitment and facilitates the digestion of forages that are low in protein and high in fiber (Griswold et al., 2003; Russell et al., 1992; Van Soest, 1994), possibly overcoming the medusahead-silica associated barrier of digestion. In support of this, protein concentrates have been shown to increase consumption of medusahead by sheep and cattle (Montes-Sánchez et al., 2017; Stonecipher et al., 2016; Hamilton et al., 2015). Nevertheless, concentrates can be costly and impractical to supply in medusahead-infested landscapes. Improved pastures of established cool season grasses and forbs may provide the appropriate nutrient supply required for increased consumption of medusahead by livestock when used in a rotational grazing strategy. Grazed areas could be then seeded with more desirable plant species, creating a positive feedback cycle of grazing-restoration which would expand the abundance of nutritious forages in medusahead-infested landscapes. Furthermore, creating a positive feedback cycle reduces the cost as well the need for continual concentrate supplementation to control medusahead infestations. Thus, the objective of this study was to determine whether improved pastures would provide the appropriate nutritional context to enhance consumption of medusahead by livestock and overcome the constraints on forage digestion impinged by the presence of the medusahead-silica barrier.

METHODS

All animal procedures were approved by the Utah State University Institute of Animal Care and Use Committee (#2117) and were conducted under veterinary supervision.

Study Site

The study was conducted on privately-owned land in the Channeled Scablands region of eastern Washington about 26 km south east of Ritzville, Adams County, WA (47º 03.62'N, 118º02.62'W; 544 m). Potential natural vegetation of the study area was predominantly sagebrush steppe (Daubenmire, 1970), however, invasive annual grasses have become the dominant species. Medusahead and downy brome (*Bromus tectorum* L.) constitute the majority of vegetation across this landscape but other weedy forbs such as bird vetch (*Vicia cracca* L.), fiddleneck (*Amsinckia intermedia* Fish. & Mey), tansy mustard [*Descurainia pinnata* (Walt.) Britt.], rush skeleton (*Chondrilla juncea L.*), black mustard [*Brassica nigra* (L.) Koch in Rochl], redstem filaree [Erodium cicutarium (L.) L'Hér.], prickly lettuce (*Latuca serriola* L.), wooly plantain (Plantago Patagonica Jacq.), western salsify (*Tragopogon dubius* Scop.), and western yarrow (*Achillea millefolium* L.

var. *occidentalis* DC.) are also present. Native perennial grasses were sparse with bulbous bluegrass (*Poa bulbosa* L.) being the only perennial grass present at the study site, which also has the potential to be invasive similar to that of the aforementioned annual grasses. Furthermore, remnants of bluebunch wheatgrass [*Pseudoroegneria spicataI* (Pursh) Á. Löve] and Sandberg bluegrass (*Poa Secunda* J. Presl) could be found in the surrounding landscape, but were also sparse.

A plot of 0.9 ha (219.6 x 41.0 m) was disked (McCormick International 480, Duluth, GA) by the land owner with four passes prior to planting. Plots were planted with Vavilov II Siberian wheatgrass (*Agropyron fragile* [Roth] P. Candargy) using a Gandy drop seeder (Anertec and Gandy Co., Owatonna, MN, USA) at a rate of 11.2 pure live seed kg · ha^{-1} in November 2010. One pass with a harrow was made after planting to cover the seed. Forage kochia (*Bassia prostrata* [L.] A.J. Scott) seed was broadcast with a Herd Sure-Feed Broadcaster (Herd Seeder Company, Inc., Logansport, IN, USA) in January 2011 at a rate of 2.2 kg · ha^{-1}. This plot constituted the improved pasture (IMP).

The soil typification was coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic typic hapoxeroll (Benge gravelly silt loam). The measured 30 year mean annual precipitation is 349.3 mm with 21% occurring in October-November (PRISM Climate Group, Oregon State University). Average October precipitation is 23.4 mm while in 2016 totals were well above normal at 123.4 mm with 61.5 mm of the precipitation occurring during the study. With adequate moisture, medusahead seeds began to germinate in thatch and by day 5 of the study, seedlings were abundantly present at approximately 3 mm of height.

Experimental Design

Plot Description

Three medusahead-invaded pastures of 0.4 ha (67.0 x 61 m) each were fenced using solar-powered electric fences, arranged side-by-side adjacent to the improved pasture (IMP), delimited by a barbed wire fence. Each of the three medusahead-invaded pastures were randomly assigned to two treatments: (1) supplementation (SUP), and (2) no supplementation (NSUP), forming paired plots of 0.2 ha (67.0 x 30.5 m) in each pasture. The IMP pasture was subdivided into three separate plots of 0.3 ha (73.2 by 41.0 m) delineated by electric fences, adjacent to the spatial replications of the SUP plots for access of the supplemented animals to established and improved forages in the rotational grazing strategy. The pilot study was conducted from October 30 to November 7, 2015.

The same treatment plots used in the pilot study were used during the following years experiment, from October 7 to 15, 2016. However, each medusahead-invaded plot was reduced to 0.186 ha (76.2 by 24.4 m), in order to increase the stock density and achieve a greater utilization of medusahead. Three additional ungrazed plots (UNGR) of the same dimensions were also fenced during 2016, adjacent to the treatment plots.

Animals

Twelve three-year-old Angus cross-breed heifers (569.6 ± 17.8 kg) were used in a pilot study, conducted during 2015, and a new group of twelve heifers (511.4 ± 9.5 kg) were used during the experiment in 2016. For both years, heifers were randomly paired, and then randomly allocated to SUP and NSUP treatments. Animals assigned to SUP were allowed to graze IMP for nutritional supplementation prior to grazing their respective medusahead-infested treatment. In contrast, NSUP animals were only allowed to graze their respective medusahead-infested plots without improved forage supplementation. Animals had free access to fresh water and trace mineral salt blocks throughout the study. The mineral composition of the blocks was: minimum 96% NaCl, 320 mg · kg Zn, 380 mg · kg Cu, 2,400mg · kg Mn, 2,400 mg · kg Fe, 70 mg · kg I, and 40 mg · kg Co.

Vegetation Assessment

At the beginning of the pilot study and the 2016 experiment, medusahead had completely senesced with most seeds being lost from the seed head. All other vegetation was completely senesced except for rush skeleton, western yarrow and some late germinated bird vetch, which was still green and in the reproductive phenological stage.

Biomass Availability

Above ground vegetation biomass was determined by hand clipping vegetation to a 1 cm stubble height within a 0.0985 m^2 square frame for both the pilot study and the 2016 experiment. In the pilot study, biomass in IMP was only taken prior to grazing at five random locations, while ten random locations were selected in SUP and NSUP plots, and all biomass was collected prior to and after grazing.

For the 2016 experiment, three 76.2 m transects were placed parallel to each other every 6.1 m through UNGR, SUP, and NSUP plots. Clipped samples were taken every 12.7 m excluding one sample at 38.1 m along each transect for a total of 4 samples per transect (n=12 per treatment). Three additional 73.2 m transects were placed every 10.3 m through each IMP replicated plot and 4 biomass samples were taken every 14.6 m along each transect (n=12). Clipped samples from the UNGR plot were only taken at the beginning of the experiment, whereas samples for the remaining plots were taken prior to and after grazing. Clipped vegetation samples were separated and then composited into the forage types: medusahead, other annual grasses, perennial grasses, and forbs (pilot study) and medusahead, other annual grasses, perennial grasses, green forbs, dry forbs, and thatch (experiment). Forage kochia was composited with all other forbs in the pilot study and with the rest of the collected green forbs in the 2016 experiment. Seeded perennial grasses in IMP were also composited with all other perennial grasses for both the pilot study and the 2016 experiment. All collected samples were dried using a forced-air oven at 60° C until constant weight and individually weighed for dry matter (DM) content.

Foliar Cover

During the experiment, foliar cover was estimated using the line-point intercept method (Herrick et al., 2005) prior to the beginning of the experiment in UNGR plots and both prior to and after grazing in SUP and NSUP plots. Plant foliar cover readings were taken along the same transects described for biomass collections every 1.5 m, excluding one point at 38.1 m for a total of 48 readings per transect (n=144 per treatment plot). Individual plant counts (i.e., to assess the proportion of foliar cover) along the transect were typified according to the same vegetation types in the biomass section with the addition of bare ground. Cover was not assessed in the IMP plots.

Chemical Analyses

Individual dried samples were composited by forage type across clips and treatment plot within each replicated pasture, and subsequently ground using a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 1 mm screen. Ground vegetation was then analyzed for crude protein (CP; AOAC, 2000; Method 990.03), acid detergent fiber (ADF; AOAC, 2000; Method 973.18), and neutral detergent fiber (NDF; Van Soest et al. 1991). Medusahead was additionally analyzed for acid insoluble ash (AIA; AOAC, 2000; Method 920.08) as an indicator of amorphous silicon content (also referred to as silica).

Animal Assessment

Scan Sampling

Daily scan sampling (Lehner, 1987) was used in the pilot study to determine selection of the different vegetation types (medusahead, other annual grasses, perennial grasses, and forbs). Foraging events in the IMP plots were categorized with other similar vegetation types (i.e., Siberian wheatgrass as a perennial grass and forage kochia as forb). SUP heifers were allowed to graze from 0800 to 0845 h in the IMP plot and then pairs of heifers in both treatments were released into their respective medusahead-invaded plots (SUP and NSUP) and allowed to graze from 0845 to 1100 h, and again from 1600 to 1700. Three observers (each assigned to one replicated pasture) focally sampled each animal for all grazing periods (IMP and medusahead-infested plots) at 2 min. intervals and recorded incidence of foraging events on the different vegetation types. Percentage of daily foraging events on each vegetation type within the diet was calculated based on the total number of daily foraging events. Animals were subsequently penned when not grazing in a 3.7 x 3.7 m pen built from corral cattle panels.

Bite Counts

To better capture grazing events on the different forage types, the assessment of vegetation use by cattle was changed from scans in the 2015 pilot study to bite counts in the 2016 experiment. Daily bite counts (Ortega et al. 1995) were used to determine cattle selection of the different vegetation types (medusahead, other annual grasses, perennial grasses, green forbs, dry forbs, and thatch). As described in the vegetation assessment section, Siberian wheatgrass was combined with other perennial grasses and forage kochia was combined with other green forbs within the IMP plot.

Heifers in the SUP treatment were allowed to graze from 0800 to 0845 h in the IMP plot and then both treatments were released into their respective treatment plots and allowed to graze medusahead-infested rangeland from 0845 to 1700 h. Three observers (each assigned to one replicated pasture) focally sampled each animal at 5 min. intervals and recorded incidence of bites for 45 min. in the IMP plot (4 observations per animal) and for 2.5 h in the morning and 1 h in the evening in the treatment plots (7 observation periods per animal in SUP and 7 for NSUP) to determine cattle selection of the different vegetation types. Percentage of daily bites on each forage type in the diet was calculated based on the total number of daily bites. As in the pilot study, animals were subsequently penned when not grazing in a 3.7 x 3.7 m pen.

Behavioral Activity

Prior to the beginning grazing for both the pilot study and the 2016 experiment, individual heifers across all treatment plots and spatially replicated pastures were isolated in a large animal squeeze chute and fitted with a pedometer (IceTags, Ice Robotics, UK) on the left hind leg for the duration of both study years. Second-to-second readings of activity levels (steps) and posture (lying and standing time, lying bouts) were measured with the use of these devices. IceManager software was used to extract data from the pedometer for analysis.

Statistical Analyses

The available aboveground biomass in both the pilot study and the 2016 experiment and foliar cover in the 2016 experiment were analyzed using a two-way factorial in a randomized block design. Block was the random effect with treatment plot (SUP and NSUP) and sampling time (prior to and after grazing) as the fixed factors. Biomass in IMP plots (pilot study) and UNGR plots (experiment) were not included in the analysis since sampling only took place prior to grazing. However, means are reported with their respective standard errors.

Individual nutritional content (CP, ADF, and NDF) before grazing of the different forage types in both the pilot study and the 2016 experiment were analyzed using a two-way factorial in a randomized block design. Block was the random effect, and treatment plot (SUP and NSUP) and forage type as the fixed factors. Annual grasses other than medusahead, and perennial grasses in the 2016 experiment had to be composited across blocks in order to have enough quantities of each of these forage types to run the nutritional analyses. Thus, these forage types were excluded from the statistical analysis due to lack of replication (means only reported).

The proportion of grazing events in IMP for both the pilot study and the 2016 experiment were analyzed in a two-way factorial in a randomized block design. Block was the random effect, with forage type and day of sampling as the fixed factors. Individual forage types in SUP and NSUP were also analyzed using the same model with the exception of treatment plot, and day of sampling as the fixed factors.

Prior to analysis of animal movement and posture in both the pilot study and the 2016 experiment, data was filtered for erroneous data which allowed for deletion of anomalies in irregular movements. Irregular movements (i.e., head scratching or fighting) for lying bouts were adjusted so that one lying bout occurred when the animals lying time exceeded one minute and no steps were taken. Similarly, lying and standing time were adjusted to reflect these lying bout changes. Filtered data was then analyzed for the IMP treatment plot using a one-way factorial in a randomized block design. Block was the random effect with treatment (IMP) as the fixed factor. The medusahead-ingested treatment plots (SUP and NSUP) were analyzed using a two-way factorial in a randomized block design. Block was the random effect with treatment (SUP and NSUP) and day of sampling as fixed factors.

Analyses were computed using the GLIMMIX procedure in SAS (SAS Inst., Inc. Cary, NC; Version 9.4 for Windows). The covariance matrix structure used was the one that yielded the lowest Bayesian information criterion. The model diagnostics included testing for a normal distribution and homoscedasticity. Data was transformed when needed according to the Box-Cox method but non-transformed data is reported (mean ±

standard error of mean). Means were analyzed using Tukey's multiple comparison test when F-ratios were significant ($P < 0.05$). A trend was considered when $0.05 < P < 0.10$.

RESULTS

Pilot Study

Biomass Availability

As expected, the biomass of perennial grasses and forbs in the improved pasture (IMP) was high (1026 and 601 $kg \cdot ha^{-1}$, respectively), whereas the abundance of medusahead and other annual grasses was relatively low (121 and 236 $kg \cdot ha^{-1}$, respectively). No differences were detected in biomass of medusahead, other annual grasses, and forbs between treatment plots, sampling times, and no interaction of treatment plot by sampling time was detected ($P > 0.05$). Biomass availability of perennial grasses declined in NSUP plots from the beginning to the end of the grazing period (154 to 82 $kg \cdot ha^{-1}$, respectively), whereas biomass of perennial grasses in SUP plots increased during the same period (90 to 167 $kg \cdot ha^{-1}$, respectively; treatment plot by sampling time interaction; $P = 0.038$). Nevertheless, there were no differences between treatment plots ($P = 0.959$), or across sampling times ($P = 0.216$) for this forage type.

Forage Quality

There were no differences between SUP and NSUP plots in the contents of CP or NDF across all the forage types assayed (treatment plot effect: $P > 0.05$), and no treatment plot by forage type interaction was detected ($P = 0.105$). Crude Protein content was greater for forbs (78.1 g · kg DM) and lower for perennial grasses (46.2 g · kg DM), with medusahead and other annual grasses presenting intermediate values (52.7 and 49.8 g · kg DM, respectively; forage type effect: $P < 0.001$).

Concentrations of ADF were in general high and similar across forage types (ranging from 485.6 to 499.9 g · kg DM), except for the lower concentrations observed in forbs (153.2 g · kg DM; forage type effect: $P < 0.001$). Likewise, the concentration of ADF was the lowest for forbs in IMP (381.7 g · kg DM; treatment plot by forage type interaction: $P < 0.001$). There was a tendency for the concentration of ADF across all forage types to be lower in IMP (453.2 g · kg DM) than in SUP and NSUP plots (489.4 and 492.2 g · kg DM, respectively; treatment plot effect: $P = 0.062$). Perennial grasses had the greatest (708.3 g · kg DM), while forbs showed the lowest NDF concentrations (569.6 g · kg DM) out of all the forage types assayed (forage type effect: $P < 0.001$), and the same pattern was observed for perennial grasses in SUP plots and for forbs in IMP plots (treatment plot by forage type interaction: $P =0.006$). There were no observable differences between SUP and NSUP plots for the concentration of AIA in medusahead (treatment plot effect: $P = 0.857$).

Scan Sampling

Improved Plot Grazing. There were no differences in the proportion of grazing events for SUP animals in the improved pasture across days ($P > 0.05$), and there was no forage type by sampling day interaction ($P = 0.176$). However, SUP animals grazing in IMP displayed the greatest number of foraging events on annual grasses other than medusahead (71.5%), with intermediate grazing events on perennial grasses (11.8%), and even lower grazing events on forbs and medusahead (8.4 and 8.3%, respectively; forage type effect; $P < 0.001$).

Treatment Plot Grazing. The proportion of foraging events on all of the forage types assayed did not differ between treatments (treatment effect: $P > 0.05$), and no treatment by day interaction was detected ($P > 0.05$). However, the proportion of foraging events on medusahead by all animals increased across days (day effect: $P = 0.001$), with the lowest values occurring initially (14.6%) and the highest values recorded towards the end of the experiment (48.0%). Foraging events on annual grasses other than medusahead decreased over the duration of the experiment (77.4 to 48.7%, respectively; day effect: $P = 0.004$). The foraging events on perennial grasses was low at the beginning of the experiment (1.6%), and then it declined even further towards zero for the remainder of the experiment (day effect: $P < 0.001$). The proportion of foraging events on forbs were cyclical across the duration of the study with daily alternations between peaks and nadirs (ranging between 48.0 and 0.5%, respectively; day effect: $P = 0.002$).

Behavioral Activity

Improved Plot Grazing. There were no observable differences in animal steps across days in IMP (ranging between 333.8 and 140.8 steps, respectively; day of observation effect: $P = 0.834$). Animals remained standing for the entirety of the time (45 min) they spent daily on the improved pasture. Thus, no lying time or lying bouts were detected.

Treatment Plot Grazing. No differences were detected in animal movement (number of steps) between SUP and NSUP plots (528.9 and 462.9 steps, respectively; treatment effect: $P = 0.570$), and across days (ranging between 650.6 and 404.6 steps, respectively; day of observation effect: *P* =0.311), without a treatment by day interaction (*P* = 0.913). Animals grazed for the entirety of the time they spent on medusahead-infested plots, evidenced by the high standing time values and the lack of recordings of lying time and lying bouts.

Experiment

Biomass Availability

The biomass availability for the different forage types for the 2016 experiment is reported in Table 2.1. There was no observable difference in biomass availability between IMP, SUP, and NSUP plots (treatment plot effect) for medusahead, other annual grasses, or green forbs (*P* > 0.05). Likewise, no differences were detected across sampling times (before and after grazing) for the same forage types (*P* > 0.05), with no treatment plot by sampling time interaction (*P* > 0.05). However, biomass availability of perennial grasses in IMP was greater than in SUP or NSUP plots (treatment effect: *P* < 0.001), with no differences in sampling time (*P* = 0.141), and no treatment plot by sampling time interaction (*P* = 0.764). Biomass of dry forbs was greatest in NSUP plots with the lowest biomass occurring in IMP plots (treatment effect: *P* = 0.047). However, there were no differences in sampling time (*P* = 0.780), and no treatment plot by sampling time interaction (*P* = 0.4086). Biomass availability in UNGR plots displayed high numerical values for dry forbs, intermediate numerical values for medusahead, and low numerical values for perennial grasses, annual grasses other than medusahead, and green forbs.

Foliar Cover

The foliar cover for the different forage types across treatment plots in the 2016 experiment is reported in Table 2.1. There were no observable differences in perennial grass cover between SUP and NSUP plots (treatment plot effect: $P = 0.408$), before and after grazing (sampling time effect: $P = 0.845$), without a treatment plot by sampling time interaction ($P = 0.325$). Likewise, there were no differences in foliar cover for medusahead, other annual grasses, dry forbs, or for bare ground between SUP and NSUP plots (treatment plot effect: $P > 0.05$), and no treatment plot by sampling time interaction ($P > 0.05$). However, and as expected, cover declined from before to after grazing (sampling time effect) for medusahead, other annual grasses, green forbs, and dry forbs ($P < 0.05$), whereas cover increased for thatch and for bare ground ($P < 0.05$) during the same time frame. Furthermore, green forb cover was greater in SUP than in NSUP plots (treatment effect: $P = 0.045$), but no treatment plot by sampling time interaction was detected ($P = 0.674$). Thatch cover was highest in SUP plots after grazing and lowest in NSUP plots before grazing (treatment plot by sampling time interaction: $P = 0.019$), but no differences were detected in thatch cover between SUP and NSUP plots (treatment plot effect: $P = 0.618$).

Forage Quality

Nutritional quality for the different forage types and treatment plots for the 2016 experiment is reported in Table 2.3. There were no differences in CP, ADF, or NDF concentrations for the forage types assayed across treatment plots (treatment plot effect: $P > 0.05$). The concentration of CP was greater for green forbs than for medusahead (forage effect: $\mathrm{P} < 0.001$), and there was no treatment plot by forage type interaction ($P =$

0.175). The concentration of ADF was in general high and similar among all forage types, except for lower values observed in green forbs (forage type effect: $P < 0.001$). In addition, the concentration of ADF in dry forbs was high but similar between treatments, whereas green forbs in IMP displayed the lowest ADF values out of all the other forages assayed (treatment plot by forage type interaction; $P = 0.018$). The concentration of NDF was high and similar among forage types, except for dry forbs which presented even greater concentrations (forage type effect: $P = 0.001$). Furthermore, NDF concentrations were similar for dry forbs in IMP and NSUP plots, as well as for green forbs in SUP plots ($P > 0.05$). In contrast, the concentration of NDF in medusahead for the NSUP plot was the lowest among all forage types and plots assayed (treatment plot by forage type effect: $P = 0.029$). As with the pilot study, no differences were detected between SUP and NSUP plots regarding the concentration of AIA in medusahead (treatment plot effect: $P = 0.192$).

Bite Counts

Improved Plot Grazing. The proportion of daily foraging events (bite counts) on different forage types and treatment plots in the 2016 experiment is reported in Figure 2.1. There were no observable differences in the proportion of daily bite counts by SUP animals grazing in IMP (day effect: $P > 0.05$), and no forage type by day interaction was detected ($P = 0.115$). SUP animals grazing IMP displayed the highest proportion of bites on green forbs, intermediate for medusahead, perennial grasses and dry forbs, and the lowest proportions for annual grasses other than medusahead (forage type effect; $P < 0.001$). No bites on thatch were observed in the IMP plots.

Treatment Plot Grazing. The proportion of bites on the different forage types assessed did not differ between SUP and NSUP treatments (treatment plot effect: $P > 0.05$; Fig. 2.1), except for medusahead where SUP animals displayed a greater proportion of bites on this grass than NSUP animals (treatment plot effect: $P = 0.003$; treatment plot by day; $P > 0.05$; Fig. 2.1A). The proportion of bites on medusahead was low on day 1, and then it increased for days 2, 3 and 4, with an ensuing decline towards the last day of the experiment (day effect: $P = 0.007$). No bites on thatch were observed at the beginning of the experiment; however, the proportion of bites on this forage type increased exponentially as the experiment progressed, reaching its maximum on the last day of the experiment (day effect: $P < 0.001$; Fig 2.1B).

The proportion of bites on annual grasses other than medusahead declined over the duration of the experiment, with a maximum on day 2 and a minimum occurring on day 7 (day effect: $P = 0.003$; Fig 2.1C). Likewise, there was a decline in the proportion of bites on perennial grasses from the beginning to the end of the experiment, with a maximum occurring on day 3 and a minimum occurring on the last day of the experiment (day effect: $P = 0.010$; Fig 2.1D). There was also a decline in the proportion of bites on green forbs over the duration of the experiment, with a maximum occurring on the first day, a second peak occurring on day 5, and nadirs occurring on days 3 and 7 (day effect: $P = 0.002$; Fig 2.1E). No differences were detected for the proportion of bites on dry forbs across the duration of the experiment, although a declining trend was observed for the proportion of bites on this forage type with a high on the first day and a low on last day of the experiment (day effect: $P = 0.063$; Fig 2.1F).

Behavioral Activity

Improved Plot Grazing. Average daily steps taken by SUP animals over the duration of the experiment in the IMP plot are reported in Table 2.4. There was a tendency for SUP animals to take a greater number of steps at the beginning than at the end of the study (day effect: $P = 0.080$). Animals remained standing for the entirety of the time (45 min) they spent daily on the improved pasture. Thus, no lying time or lying bouts were detected.

Treatment Plot Grazing. No differences were detected between SUP and NSUP treatments regrading individual animal postures (standing time, lying time, and lying bouts) (treatment effect: $P > 0.05$; Table 2.4), and no treatment by day interaction was observed ($P > 0.05$). However, animals in SUP plots took fewer steps than animals in the NSUP plots over the duration of the experiment (treatment effect: $P = 0.022$: Fig. 2.2A). Daily steps were high on the first day of the experiment before declining to a minimum on day 4, with a small increase observed towards the end of the experiment (day effect: $P < 0.001$). No treatment by day interaction was detected for the number of steps taken by the animals ($P = 0.813$). The time heifers spent standing during the experiment fluctuated across days with a minimum on day 4 and a maximum on day 7 (day effect: $P < 0.001$; Fig 2.2B). Lying time was inversely related to standing time with a maximum on day 4 and a minimum on day 7 (day effect: $P < 0.001$; Fig. 2.2C). Similarly, lying bouts fluctuated across days with peaks on days 1, 4 and 8, and nadirs on days 3 and 7 (day effect: $P < 0.001$; Fig. 2.2D).

DISCUSSION

Nutritional Context

We determined whether establishing cool-season perennial grasses and selected forbs (forage kochia) provides the appropriate nutritional context to enhance use of medusahead. Medusahead contains high concentrations of undigestible amorphous silicon (i.e., silica), which forms a varnish on the epidermis of awns, culm, leaves and glumes (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964) that reduces digestion by rumen microbes (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017). In support of this, the concentration of acid insoluble ash, an indicator of silica content in forages (Charca et al., 2007), was high (between 6.0 and 8.6%, respectively) during both the pilot study and the experiment. Protein supplementation may increase microbial recruitment in the rumen, facilitating the digestion of plant fiber (Griswold et al., 2003; Russell et al., 1992) and possibly overcoming the medusahead-silica associated barrier, as it was shown in a previous medusahead supplementation study using canola meal (Stonecipher et al., 2016).

Consumption of unpalatable forages are not only determined by their biochemical properties but also by the sequence in which other more palatable forages are consumed (Flaherty, 1999; Freidin et al., 2012). For instance, intake induction or facilitation results when animals repeatedly ingest a less preferred food in association with a highly preferred food. The intake induction effect consists of increased consumption of the low-valued meal relative to controls where animals do not have access to the preferred food (Flaherty and Grigson, 1988; Freidin et al., 2011). This induction may be a consequence of animals partially attributing the post-ingestive effects of the preferred food to the low-palatable food because of the close temporal proximity between both ingestive events (Yearsley et al., 2006). Thus, we expected that more nutritious forages in the improved pastures ingested in a rotational sequence with the unpalatable grass medusahead may elicit an induction or facilitation effect, which in addition to the positive effects of protein on forage digestion, would promote increments in the ingestion of medusahead.

Nutritional analyses of the perennial grasses in the improved (IMP) plot during both the pilot study and the 2016 experiment showed that the protein levels were low to induce a positive effect on forage intake (ranging between 3.9 and 5.2%, respectively). In fact, the crude protein (CP) contents in perennial grasses were lower than those observed in medusahead and other annual grasses within the IMP plot. This may be a consequence of grass maturation; as grasses mature, protein levels decline while the structural components (e.g., lignified fiber) increase (Van Soest, 1994). During this study all grasses were completely senesced, which explains the low protein and high fiber content of these forages.

Forbs in the pilot study (represented primarily by forage kochia) presented greater concentrations of CP (~8%, respectively), although the levels of ingestion of this forage type were too low to induce a positive effect on grazing the medusahead-infested plots. During the experiment, the concentration of CP in green forbs was in the 6% range with ~40% acid detergent fiber (ADF), and heifers displayed a greater utilization of this forage type in IMP (Fig. 2.1E). Despite this low concentration of CP, which was below the 7 to 8 percent requirement to sustain the heifers (National Research Council, 2000), the greater consumption of green forbs (mainly forage kochia) and thus of CP by heifers in supplemented (SUP) plots likely favored the increase in the use of medusahead by this treatment relative to non-supplemented (NSUP) plots, where heifers lacked this additional protein input. In addition, it is also likely that these positive nutritional inputs experienced while grazing green forbs in IMP by SUP heifers and before grazing the treatment plots promoted an induction effect that enhanced selection of medusahead relative to NSUP animals (Flaherty and Grigson, 1988; Freidin et al., 2011).

Animal selection of different foods not only depends on the nutritional quality and relative abundance of a plant within a community but also on an animal's previous experiences with food (Villalba et al., 2015). The influence of prior experience was observed in the pattern of forage use by SUP animals in the improved pasture. Supplemented animals in the IMP plot during the pilot study selected annual grasses other than medusahead in high proportions (~70%, respectively), whereas this pattern changed during the experiment. Supplemented animals grazing the IMP plots showed a low proportion of bites on medusahead and other annual grasses, with a high proportion on perennial grasses and green forbs. This difference in selection patterns between study years may be explained by the contrasting exposure to forage types heifers experienced prior to testing. Animals in the pilot study were unfamiliar with the improved forages (i.e., Siberian wheatgrass and forage kochia) as these are forages not common in the landscapes were animals typically graze and were reared. In contrast, animals in the experiment were familiar with the improved forages, as portions of their grazing allotments had been rehabilitated with a similar mix of improved perennial grasses and forbs. Thus, heifers in the experiment may have taken advantage of the forages available in the improved pasture and thus displayed a greater utilization of medusahead in the medusahead-infested plots.

Forage Quality and Availability

Herbivores' forage selection are not only based on the biochemical characteristics of the forages on offer (i.e., quality), but also on the relative abundance of these forages within the plant community (Stephens and Krebs, 1986). The channeled scablands of eastern Washington is a 'hot spot' of invasion as previous mismanagement of grazing removed the perennial grass component in the plant community (Noss et al., 1995), thus opening a niche for invasive grasses. Currently, medusahead is replacing other invasive annual grasses and was the dominant species on the study site. This was evident in the medusahead-infested treatment plots by the low biomass availability and foliar cover of perennial grasses and high medusahead availability (Table 2.1 and 2.2).

The interplay between forage abundance and quality was evident by the pattern of medusahead use by cattle in this study. Animals initially avoided medusahead, explained by the presence of high contents of silica in the plant. Nevertheless, as perennial grasses, other annual grasses and forbs became depleted in response to selective grazing on these species of greater nutritional value, grazing events (pilot study) or number of bites (experiment) on medusahead increased, given its relative increase in abundance and thus in the relative likelihood of encounter rate of this species. In addition, as all other forage types decreased in their abundance, the relative abundance of thatch in the plots increased, which also led to increments in encounter rate and thus increased utilization of this less desirable forage type.

The selection of less abundant forages other than medusahead in the medusahead-infested plots may in part be explained by the greater CP and lower fiber contents of the former. However, these less abundant forages were lower in CP and greater in fiber contents than medusahead, and yet animals still sought out these forages over the weed. The silica varnish has been considered as a plant defense mechanism similar to the protection induced by plant secondary compounds or antinutritional factors (McNaughton et al., 1985), which constraints intake and preference for the grass. Several studies have shown evidence of weed avoidance and low intake patterns when animals are offered alternative forage options (Hamilton et al., 2015; Montes-Sánchez et al., 2017; Villalba et al., 2019). The perennial grasses in the plant community lacked this defense mechanism, and thus could explain why animals selected these forages over a defended plant like medusahead.

Medusahead and Grazing Selection

Interpretation of grazing selection in this study could be summated by the influence of forage quality, relative abundance, and prior grazing experiences. Grazing animals select for forages that meet their dietary needs particularly when balancing their energy to protein needs (Atwood et al., 2001). For instance, cattle supplemented with protein-rich feeds increased their selection of high-fiber grasses (Odadi et al., 2013), whereas sheep supplemented with energy selected for a protein-based diet (Montes-Sánchez, 2016). In addition, cows supplemented with canola meal (a protein source) took more bites on annual grasses than did non-supplemented animals, in pastures where medusahead constituted approximately 80 percent of the annual grass forage type (Stonecipher et al., 2016).

Consistent with our hypothesis, SUP animals took more bites on medusahead in the first four days of the experiment than did NSUP animals. Furthermore, during the same period, SUP animals took less bites on perennial grasses than that NSUP animals.

As discussed before, the increased ingestion of available protein from green forbs (i.e., forage kochia) may have promoted an induction effect or facilitated the digestion of medusahead, which explains the pattern of forage selection by SUP animals. In addition, the reduction in the use of perennial grasses by the SUP treatment may be due to the fact that heifers had this forage category available in the improved pasture. Animals satiate on the taste of foods consumed too frequently or in high amounts (Provenza, 1996), and thus it is likely that exposure to a high proportion of perennials in IMP reduced the drive to utilize this forage type in the medusahead-infested plots. This pattern of selection by cattle may contribute to the maintenance of perennials and reduction in the abundance of medusahead in landscapes invaded by this grass. This selective grazing may alleviate the problem observed in these landscapes, where there is a sustained grazing pressure on perennials, which enhances the competitive ability of medusahead.

On day 4, an anomaly of ~25 mm of precipitation occurred in the experiment. The combination of reduced plant abundance and the increase in moisture supplied to the thatch material, possibly decreasing thatch tissue rigidity, may have triggered the observed increase in consumption of the thatch by cattle. In addition, following day four, medusahead seedlings began to emerge from the thatch which may also have contributed to the large increases in thatch consumption. Medusahead seedlings are high in protein and low in fiber, compared to other more mature plants (Bovey et al., 1961; Lusk et al., 1961; Swenson et al., 1964), thus animals more readily consume the grass in the early phenological stages over that of later stages (DiTomaso et al., 2008). Consuming thatch in close temporal proximity to high-quality seedlings may have prompted positive post-ingestive experiences, which compounded with a reduction in forages alternatives and the close spatial association between thatch and emerging seedlings, enhanced the ingestion of thatch by heifers. Furthermore, after the anomaly of precipitation, there were no observable differences between treatment groups on the proportion of bites on medusahead and this might have been a consequence of increased nutrient availability due to the presence of seedlings for both treatment groups, diluting the initial differences observed between the two groups of heifers.

Behavior Levels of Activity

Cattle develop preferences for vegetation patches in a heterogenous landscape, particularly when that vegetation is of greater nutritional quality and bulk density (i.e., quantity of forage) (Bailey, 1995). In addition, when physiological needs are not met animals tend to search for patches that will satisfy these demands compared to when these needs are met (Egea et al., 2014; Provenza et al., 1998).

Heifers in the NSUP treatment displayed greater levels of locomotion (i.e., steps) than SUP animals in the medusahead-infested treatment plots during the experiment. Nevertheless, the total number of daily steps (i.e., steps taken in IMP and treatment plots) was greater for SUP than for NSUP animals (1398 vs 1287 steps, respectively), a consequence of the additional amount of time (45min) SUP animals spent in IMP. It is likely that SUP animals satiated on perennial grasses during this additional time and thus they spent less time searching for this forage type in the medusahead-infested plot. This was evident by the increased number of bites on medusahead and decreased number of bites on perennial grass relative to NSUP animals in the experiment. Furthermore, cattle spend 9 to 16 kcal · 100 kg BW to travel 1 km on level ground and these values may be greater depending on forage quality and distance between patches of palatable plants within the community (Di Marco and Aello, 1998). The combination of a poor nutritional environment exacerbated by the extra energy required in searching activities has negative consequences on animal fitness and wellbeing.

In this study, NSUP animals were expected to increase the number of steps and standing time relative to SUP animals, as a consequence of searching out patches that would meet their greater physiological needs. Additionally, it was expected that SUP animals would harvest a proportion of their required nutrients in the improved pasture, thus reducing their subsequent forage selectivity and searching time in the medusahead-infested plots. Nevertheless, heifers during the pilot study selected a greater proportion of low-quality annual grasses other than medusahead in IMP, which likely did not contribute to satisfy their physiological needs. This may explain why no behavioral differences were observed between SUP and NSUP animals grazing the medusahead-infested plots (Table 2.4). Alternatively, the restricted time available to graze the treatment plots in the pilot study likely contributed to reduce differences among treatments, since animals grazed steadily during all the time they had available at their respective plots. In contrast, SUP heifers during the experiment selected a greater proportion of green forbs in IMP, and the greater levels of protein and lower levels of ADF ingested (i.e., greater levels of non-structural carbohydrates) may have partially satisfied their physiological needs, reducing their searching time and thus the number of steps taken in the treatment plots relative to NSUP animals. Additionally, the selection of forages of greater quality in IMP in the experiment likely allowed SUP animals to take additional steps in IMP with lower negative consequences to their fitness than when they grazed lower-quality forages in the pilot study.

MANAGEMENT IMPLICATIONS

A rotational grazing approach with established cool-season perennial grasses and forbs may provide a means to reduce medusahead abundance in the plant community and provide a positive feedback cycle of grazing-restoration which could expand the abundance of nutritious forages in medusahead-infested landscapes. Medusahead is a superior invader as it is avoided by livestock, increasing the grazing pressure on other desirable species in the plant community. Supplementation with an improved pasture reduced the incidence of grazing on perennial grasses and increased medusahead consumption, reflected in greater biomass of perennials and greater cover of green forbs in plots grazed by supplemented animals.

Heifers selected perennial grasses and forbs to a high extent, even after improved pasture supplementation. Thus, caution is recommended when grazing medusahead-infested landscapes, even with improved pasture supplementation, in order to avoid overgrazing desirable forage species. Furthermore, we used a time intensive rotational grazing strategy that allowed animals to graze an improved pasture for a short duration in the morning before allowing them to graze on the medusahead-infested pasture. The time commitment to rotate animals to and from pastures may not be practical for some livestock operations, although rotations are essential, even when supplementation is not implemented, for landscapes invaded by medusahead in order to prevent further declines in desirable species abundance and land degradation. Rotations between improved pasture and medusahead-infested areas may entail larger temporal scales than those assessed in the present study (i.e., days instead of minutes grazing the improved pasture), particularly at large spatial scales where animals are spread out over large distances. At smaller spatial scales, rotations may entail movements at smaller temporal scales, creating short-duration and intensive treatment programs aimed at reducing the abundance of medusahead followed by revegetation efforts, which can be repeated across years, expanding the abundance of beneficial species throughout the invaded landscape. In addition, the low-cost of grazing treatments and utilization of the grass as a forage may offset input costs and time required for the implementation of sustainable programs of medusahead control.

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Table 2.1. Biomass availability by different forage types at the start and end of grazing periods in eastern Washington in 2016 of a grazing study (mean ± standard error of mean).

		Biomass (kg · ha^{-1} dry matter)				
Treatment	Time	Medusahead	Other Annual Grass	Perennial Grass	Green Forb	Dry Forb
IMP	Before Grazing	227.0 ± 80.4	33.9 ± 22.6	848.3 ± 142.5^{a}	451.8 ± 276.0	367.2 ± 256.3^{c}
	After Grazing	278.3 ± 80.4	85.4 ± 22.6	773.6 ± 142.5^{a}	630.3 ± 276.0	404.4 ± 256.3^{bc}
SUP	Before Grazing	162.2 ± 80.4	50.1 ± 22.6	25.1 ± 142.5^{b}	529.9 ± 276.0	954.3 ± 256.3^{ab}
	After Grazing	61.8 ± 80.4	23.2 ± 22.6	3.7 ± 142.5^{b}	480.0 ± 276.0	578.1 ± 256.3^{abc}
NSUP	Before Grazing	203.6 ± 80.7	51.3 ± 22.8	47.5 ± 143.9^{b}	363.2 ± 278.1	1504.0 ± 259.0^{a}
	After Grazing	71.9 ± 80.7	33.0 ± 22.6	4.2 ± 142.5^{b}	229.0 ± 276.0	715.2 ± 256.3^{abc}
UNGR[1]	Before Grazing	262.0 ± 62.8	52.2 ± 16.3	28.5 ± 15.4	51.9 ± 20.0	1243.4 ± 249.6

IMP= Improved pasture.

SUP= Supplemented animal pasture.

NSUP= Non-supplemented animal pasture.

UNGR= Ungrazed control pasture.

[a-c] Different superscript within a column by year are significantly different ($P < 0.05$).

[1] Excluded from statistical analysis due to only clipping prior to grazing.

Table 2.2. Proportion of foliar vegetation cover of different forage types within treatment plots in a 2016 grazing study in eastern Washington.

Day	Medusahead	Other Annual Grasses	Perennial Grasses	Green Forbs	Dry Forbs	Thatch	Bare Ground
Supplemented %							
Before Grazing	30.6 ± 3.4^{a}	2.5 ± 0.6^{ab}	2.9 ± 3.0	12.5 ± 2.0^{a}	20.3 ± 1.0^{a}	24.3 ± 1.1^{b}	7.0 ± 3.2^{b}
After Grazing	7.9 ± 3.4^{b}	1.1 ± 0.6^{b}	0.7 ± 3.0	5.0 ± 2.0^{ab}	6.8 ± 1.0^{b}	58.0 ± 1.1^{a}	20.6 ± 3.2^{a}
Non-supplemented %							
Before Grazing	28.0 ± 3.4^{a}	4.3 ± 0.6^{a}	3.9 ± 3.0	7.3 ± 2.0^{a}	22.7 ± 1.0^{a}	26.8 ± 1.1^{b}	7.1 ± 3.2^{b}
After Grazing	7.9 ± 3.4^{b}	0.9 ± 0.6^{b}	7.6 ± 3.0	1.6 ± 2.0^{b}	5.9 ± 1.0^{b}	53.9 ± 1.1^{a}	22.3 ± 3.2^{a}
Ungrazed[1] %							
Before Grazing [1]	32.5 ± 1.2	3.9 ± 1.1	3.9 ± 1.6	16.8 ± 1.1	5.9 ± 0.8	28.3 ± 2.9	8.7 ± 1.7

$^{a\text{-}b}$Different letters within a column are significantly different ($P < 0.05$).

[1] Excluded from statistical analysis due to measurements only being taken at the beginning of the study.

Table 2.3. Nutritional quality of different forage types within treatment plots prior to grazing conducted in eastern Washington in 2016 (mean ± standard error of mean).

	Content ($g \cdot kg^{-1}$ dry matter)			
Treatment	CP	ADF	NDF	AIA[1]
Medusahead				
IMP	52.0 ± 4.3^{b}	519.7 ± 25.1^{ab}	756.7 ± 18.5^{ab}	70.7 ± 5.4
SUP	48.3 ± 4.3^{b}	523.7 ± 25.1^{ab}	746.7 ± 18.5^{ab}	81.3 ± 5.4
NSUP	50.3 ± 4.3^{b}	514.3 ± 25.1^{ab}	724.7 ± 18.5^{b}	86.3 ± 5.4
Other Annual Grasses[2,3]				
IMP	54.8	553.0	739.1	
SUP	42.3	556.7	709.2	
NSUP	49.7	583.1	729.7	
Perennial Grasses[2,3]				
IMP	36.3	497.0	696.0	
SUP	46.3	548.7	711.2	
NSUP	50.7	522.1	675.7	
Green Forbs				
IMP	62.0 ± 4.3^{ab}	396.0 ± 25.1^{b}	754.7 ± 18.5^{ab}	
SUP	77.0 ± 4.3^{a}	482.0 ± 25.1^{ab}	841.0 ± 18.5^{a}	
NSUP	76.3 ± 4.3^{a}	464.7 ± 25.1^{ab}	783.0 ± 18.5^{ab}	
Dry Forbs				
IMP	60.7 ± 4.3^{ab}	555.6 ± 25.1^{a}	827.0 ± 18.5^{a}	
SUP	62.3 ± 4.3^{ab}	549.7 ± 25.1^{a}	785.7 ± 18.5^{ab}	
NSUP	70.0 ± 4.3^{ab}	548.0 ± 25.1^{a}	831.0 ± 18.5^{a}	

CP= crude protein; ADF= acid detergent fiber; NDF= neutral detergent fiber; AIA= acid insoluble ash (>90% is silica; Charca et al., 2007).

[1] Medusahead plant samples were the only forage type analyzed.

[2] Samples composited across replicates for sufficient quantity to analyze sample.

[3] Due to lack of replication, samples were excluded from the statistical analysis.

[a-d] Different superscript within column and year are significantly different ($P < 0.05$).

Table 2.4. Behavioral levels of activity of beef heifers (mean ± standard error of mean) in a grazing study during 2016 in eastern Washington.

	Treatment			
Parameter	SUP	NSUP	*P*-value	IMP[1,2]
Steps, number/d	1175.6 ± 21.6	1286.6 ± 21.6	0.022	222.8 ± 15.0
Standing Time, h/d	6.6 ± 0.1	6.7 ± 0.1	0.323	0.75
Lying Time, h	1.9 ± 0.1	1.8 ± 0.1	0.371	
Lying Bouts, d	1.8 ± 0.3	1.9 ± 0.3	0.833	

SUP = supplemented animals.

NSUP = non-supplemented animals.

IMP = improved pasture for supplemented animals.

[1] Animals were allowed to graze the improved pasture for 45 min.

[2] Lying time and lying bouts were zero

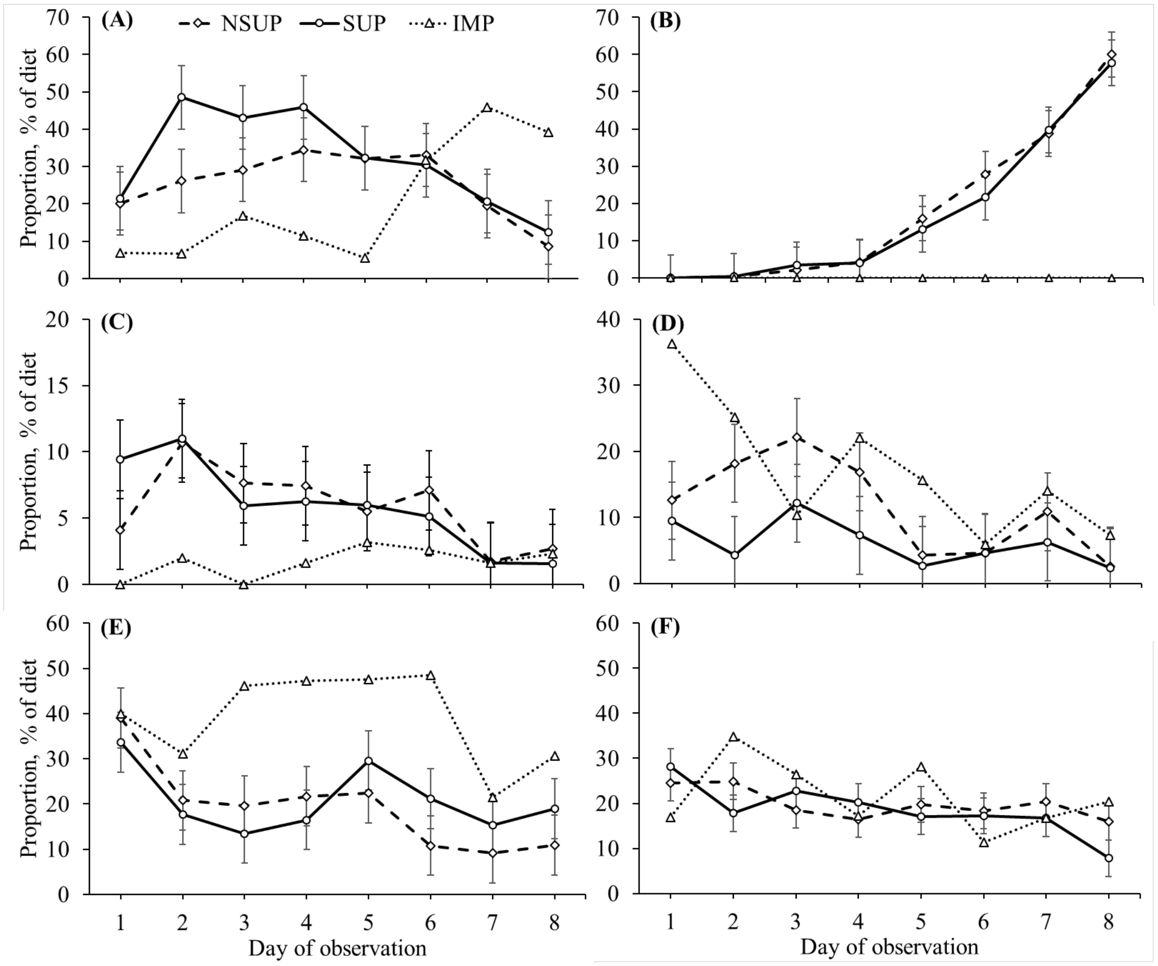

Figure 2.1. Proportion of bites during grazing events recorded by supplemented (SUP) and non-supplemented (NSUP) groups (n=2/treatment) of heifers and the average for both treatments in a 2016 grazing experiment. Heifers grazed on plots with high levels of medusahead infestation, bites during grazing events were recorded in treatment pastures for 8 h (0900 to 1700). Three groups of 2 heifers were allowed to graze in the improved pasture (IMP) from 0800 to 0845 in order to receive supplemental nutrition prior to grazing their respective plots (SUP), whereas three other groups (NSUP) were not allowed to graze during this time. Proportion of grazing events on (A), medusahead; (B), thatch; (C), annual grasses; (D), perennial grasses; (E), green forbs; (F), dry forbs. Vertical bars represent standard error of means.

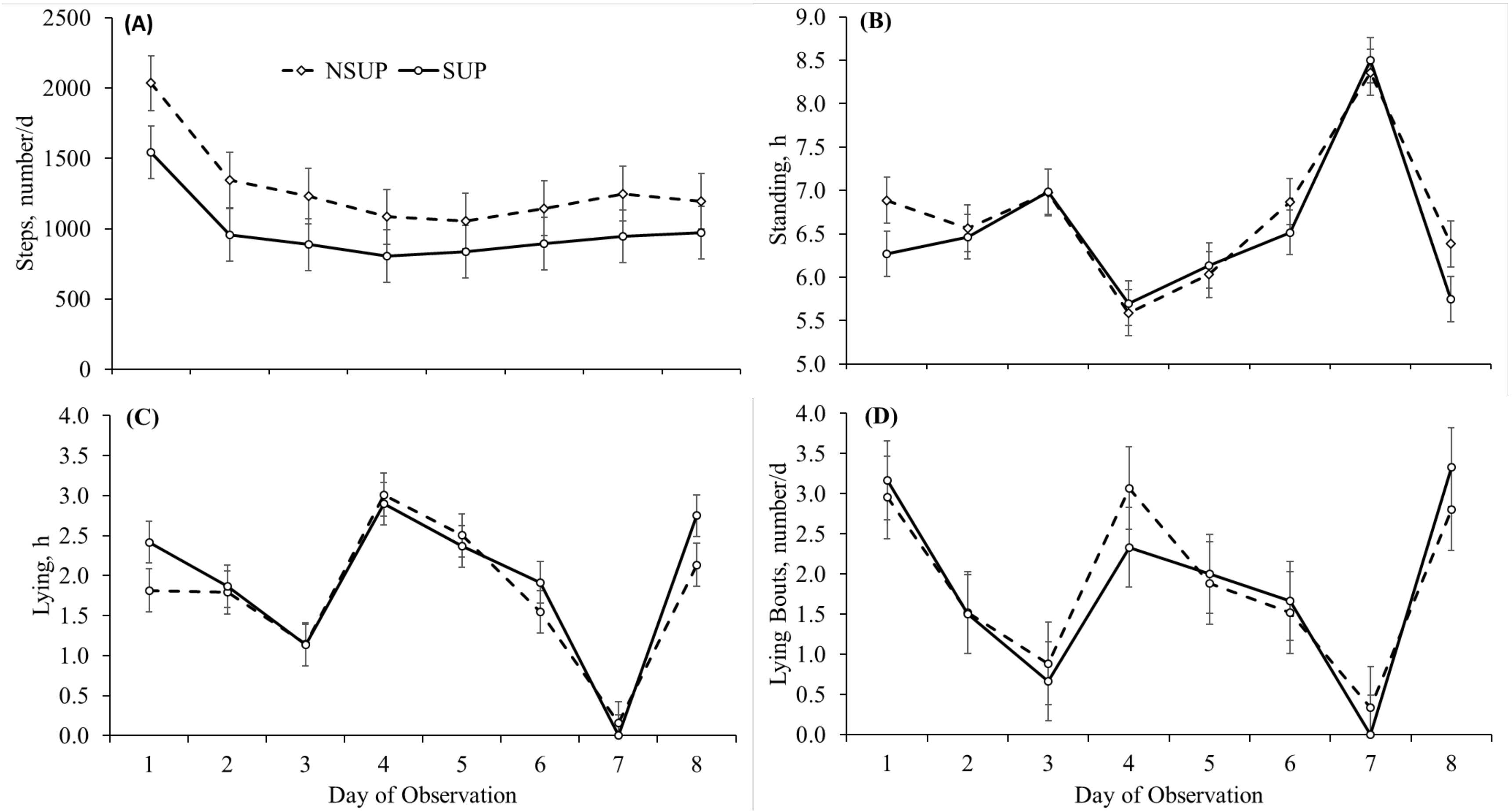

Figure 2.2. Behavioral levels of activity during an 8-day grazing study in 2016 of supplemented (SUP) and non-supplemented (NSUP) beef heifers. Number of daily steps taken (A), standing time (B), lying time (C), and lying bouts (D) are reported. Means were averaged over animal pairs and blocks according to treatment. Standard error of mean is indicated by vertical bars.

CHAPTER 3

HERBICIDE APPLICATION ON MEDUSAHEAD AND FORAGING BEHAVIOR BY LIVESTOCK: SEPARATING THE EFFECTS OF GLYPHOSATE AND POTASSIUM SALT[3]

ABSTRACT

Livestock tend to avoid grazing the invasive grass medusahead (*Taeniantherum caput-medusae* (L.) Nevski), and glyphosate applications have been shown to increase consumption of unpalatable plants. Thus, we evaluated intake of and preference for medusahead treated with glyphosate by livestock in two separate experiments, as well as the influence of the potassium salt present in glyphosate on selection of this grass. In 2015 (experiment 1), twenty-four lambs were randomly assigned to individual pens and grouped into three medusahead-glyphosate treatments (8 lambs/treatment), consisting of different herbicide rates: 1) 788 g ae $\cdot$ ha^{-1} (High); 2) 394 g ae $\cdot$ ha^{-1} (Low); and 3) no herbicide (CTRL). Lambs were conditioned to *ad libitum* amounts of their respective medusahead-glyphosate treatments and subsequently to three-way choice tests among medusahead treated at the three rates, as well as a two-way choice between medusahead treated at the high glyphosate rate and CTRL. During conditioning and three-way choice tests, non-treated medusahead was consumed to a greater extent than glyphosate-treated medusahead ($P < 0.05$). In the two-way choice, all groups of lambs tended to consume greater amounts of medusahead treated at a high rate of glyphosate ($P = 0.052$).

In 2016 (experiment 2), six medusahead-infested pastures were divided into three

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[3] Co-authored with Clint Stonecipher

treatment plots: 1) glyphosate applied at 394 g ae · ha^{-1}; 2) potassium chloride (KCl) in the herbicide, applied at 173 g · ha^{-1} (KCl); and 3) Control (CTRL, no chemical application). Twelve angus-cross steers were randomly paired and randomly assigned to graze one of the described plots. Medusahead defoliation declined to a greater extent in the glyphosate-treated plots than in the rest of the treatments ($P = 0.022$). Thus, these results suggest that an integrated approach of herbicide treatment and grazing is a viable tool to increase the forage value of medusahead and control its spread on rangelands.

1. Introduction

Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is currently one of the most detrimental invasive plants impacting rangeland sustainability and livestock operations in the western United States (Davies and Johnson, 2008; Miller et al., 1999; Young, 1992); it decreases the abundance and quality of forage available to livestock and wildlife, negatively impacts plant diversity, and increases the frequency of fires (Davies and Johnson, 2008).

Livestock grazing has been shown to be a preferred method of medusahead control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015). However, livestock utilization of standing medusahead vegetation and litter is often unsuccessful as grazing animals tend to avoid consuming the weed (Davies and Svejcar, 2008; Hironaka, 1961). This aversive behavior has been associated with high amorphous silicon contents in the plant (i.e., silica), which retards microbial digestion in the rumen (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017) and reduces the nutritional value of the ingested forage (Montes-Sánchez et al., 2017).

The herbicides 2, 4-D, tebuthiuron, picloram and glyphosate have been shown to temporarily increase grazing preference for treated plants (Kisseberth et al., 1986; Scifres et al., 1983), attributed to an increase in the nutritional quality of the sprayed forage (Siever-Kelly et al., 1999). For instance, glyphosate in the form of its isopropylamine salt was applied at low rates prior to anthesis of annual ryegrass (*Lolium rigidum* Graudin), which subsequently increased nitrogen concentrations, preserved soluble carbohydrates, and increased digestible dry matter compared to untreated plants (Armstrong et al., 1992; Gatford et al., 1999). Furthermore, low rates of glyphosate in the form of its isopropylamine salt applied prior to medusahead anthesis has been shown to be an effective control strategy without serious injury to shrubs and other perennial grass species in the plant community (Kyser et al., 2012).

Integrated approaches to medusahead control, such as livestock grazing in combination with low rates of glyphosate application, may address the low-nutritional quality of the grass increasing its forage value, which would reduce medusahead spread and aid habitat restoration. It is likely that the growth retardation imposed by the herbicide would inhibit the accumulation of silica in the grass, potentially increasing its palatability, although the effects of glyphosate on medusahead are largely unknown. Alternatively, the presence of a salt (KCl) in the glyphosate herbicide may contribute to increase palatability as livestock may display preferences for mineral sources (Schulkin and Schulkin, 1991). Thus, the objectives of this study were to (1) explore the influence of glyphosate on medusahead nutritional quality and on foraging behavior by sheep and (2) separate the influence of glyphosate on medusahead from that promoted by a salt

(KCl) present in the herbicide on foraging behavior by cattle.

2. Material and methods

2.1. Experimental Design: Experiment 1

All animal procedures were approved by the Utah State University Institute of Animal Care and Use Committee (#2619). Two separate experiments were conducted for exploring glyphosate-treated medusahead preferences by livestock. Experiment 1 occurred from June 25 to July 3, 2015 using individually penned sheep, whereas Experiment 2 occurred from June 11 to June 18, 2016 in grazing cattle. In both experiments, animals had no previous experience with consuming medusahead, and they had free access to water and trace mineral blocks (composition: minimum 96% NaCl, 320 mg/kg Zn, 380 mg/kg Cu, 2,400mg/kg Mn, 2,400 mg/kg Fe, 70 mg/kg I, and 40 mg/kg Co) throughout the duration of the studies.

2.1.1. Medusahead Treatments

Monoculture of medusahead (*T. caput-medusae* (L.) Nevski) on private land, located in Mantua, Box Elder County, Utah (41º 29′ 51″ N and -111º 56′ 32″ W) were treated with the herbicide *Hi-Yield*® Super Concentrate *Killzall II*® (glyphosate in the form of its isopropylamine salt; Voluntary Purchasing Group, Inc., Bonham, TX, USA) at three rates: 1) 788 g ae $\cdot$ ha^{-1}(High); 2) 394 g ae $\cdot$ ha^{-1} (Low); and 3) no herbicide treatment (CTRL). The herbicide treatment took place on June 15, 2015, in order to provide treated medusahead for a familiarization period (conditioning), and again on June 19, 2015, which provided treated medusahead for ensuing preference tests (see below).

Medusahead was in the mid-reproductive stage when herbicides were applied with the stems beginning to dry.

Treated plants were harvested daily using a lawnmower (Husqvarna HD800BBC with a bag catcher) to a particle length of approximately 5 cm and transported to the Green Canyon Ecology Center, located at Utah State University in Logan (41°45′59″ N, -111°47′14″ W) for fresh offerings (as fed basis) to animals.

Representative daily samples of medusahead samples offered and refused were placed in a forced-air drying oven (VWR 1350F, Sheldon Manufacturing, Cornelius, OR, USA) and dried at 60°C to constant weight in order to obtain the DM biomass weights and express intake by lambs on a DM basis per kg BW.

2.1.2. Animals and Medusahead Treatments

Twenty-four commercial Finn-Columbia-Polypay-Suffolk crossbred lambs of both sexes (4 months of age) with an average initial body weight (BW) of 25.4 ± 0.1 kg were individually penned outdoors, under a protective roof in individual, adjacent pens measuring 1.5 × 2.5 m. Ten days prior to the conditioning period, lambs were familiarized with pens and fed *ad libitum* amounts of alfalfa pellets. All lambs were vaccinated against *clostridium perfringens* types C & D and tetanus toxoid (2 mL/lamb), and they were dewormed with an oral drench of ivermectin (0.2 mg/kg BW).

The experiment was arranged as a randomized block design, where animals were blocked by BW and then randomly assigned to one of three medusahead treatment groups (8 lambs/treatment), where they received medusahead treated with glyphosate at the rates described above: (1) High (HG); (2) Low (LG), and (3) no herbicide treatment-CTRL (CG). All medusahead-treated and non-treated plants were in the late reproductive phenological stage upon feeding with prominent seed heads and awns, which remained intact after mowing.

2.1.3. Conditioning

Every day from 0900 to 1600 lambs received 200 g of freshy harvested and chopped medusahead (as-fed basis) in wooden feeders (16.5 x 5.5 x 4.0 cm), HG, LG, or CG according to their respective medusahead treatments, and additional amounts of medusahead were added to the feeders when the amounts remaining were below 20% of the amounts offered initially. Medusahead intake for each animal was estimated by the difference between the amounts offered and refused. Conditioning occurred from June 25 to June 28, 2015.

After collection of medusahead refusals, all lambs received *ad libitum* amounts of alfalfa pellets until 1700, then pellet refusals were collected and no other feed was offered until the following day.

2.1.4. Preference Tests

Three-way choices. From June 29 to July 1, 2015, and from 0900 to 1600, all lambs received a simultaneous offer of treated (High, Low) and non-treated (CTRL) medusahead in three wooden boxes with 100 g (as-fed basis) of plant material in each box. Boxes were placed side-by-side, with a random distribution of medusahead treatments across boxes. After collection of refusals, lambs were fed alfalfa pellets as described for conditioning.

Two-way choices. From July 2 to July 3, all lambs received a simultaneous offer of treated medusahead at a high rate (High) and CTRL and fed as described for the three-way choice, except that 150 g (as-fed basis) of medusahead were presented initially in each box.

2.2. Experimental Design: Experiment 2

2.2.1. Site Description

This grazing experiment was conducted on a heavily invaded medusahead area, located on privately-owned land in southern Cache County, Utah (41º34’05.34” N, -111º53’53.89” W). The ecological site is Mountain Stony Loam (Wadman, 2012), which is located at 1682 m and has slopes between 5 and 13%. The soil is stony, cobbly, or gravelly loam textured and permeability is moderate slow to moderate. The mean annual precipitation is 457 mm and mean annual temperature between 3 and 7º C with 83 frost free days.

The plant community is Mountain Big Sagebrush (*Artemisia tridentata* Nutt.) with introduced non-native annual grass species (Wadman, 2012). The invasive annual grasses, medusahead and cheatgrass (*Bromus tectorum* [L.]) constituted the majority of the plant community in the experimental site. Perennial grasses such as kentucky bluegrass (*Poa* pratensis [L.]), Letterman’s needlegrass (*Achnatherum lettermanii)*, slender wheatgrass (*Elymus trachycaulus*), Sandberg bluegrass (*Poa secunda*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and intermediate wheatgrass (*Thinopyrum intermedium*) were also present but at lesser densities. Forbs such as common yarrow (*Achillea millefolium*), tapertip onion (*Allium acuminatum*), arrowleaf balsamroot

(*Balsamorhiza sagittate*), and field bindweed (*Convolvus arvensis*) were also present.

2.2.2. Medusahead and Treatment Plots

The experiment was arranged as a randomized block design consisting of six blocks (0.056 ha^{-1} each). Each block contained three treatment plots (6.1 x 30.5 m): 1) a plot sprayed with glyphosate in the form of its potassium salt (Roundup RT 3®; RT3) at a rate of 394 g ae · ha^{-1}; 2) a plot sprayed with potassium salt (KCl) at a rate of 173 g · ha^{-1}, representing the amount of KCl delivered with RT3 at a rate of 394 g ae · ha^{-1}, and 3) an untreated plot with no chemical application (CTRL). Chemicals were applied using a CO2-pressurized backpack sprayer at a rate of 153 L · ha^{-1} on June 1, 2016. Medusahead was in the late vegetative phenological stage prior to spraying and in the early reproductive stage at the beginning of the grazing period. Each block was fenced using solar-powered electric fences. Cattle panels were used to build six 3.7 x 3.7 m pens, which were adjacent to each of the fenced blocks.

2.2.3. Animals

Twelve Angus-cross steers (301.1 ± 13.1 kg of initial BW) were randomly paired and assigned to each experimental block. A familiarization period occurred from June 11 to June 14, 2016, where cattle were allowed to graze the treatment plots from 0800 to 1030 h and again from 1700 to 1800 h. From 1030 to 1700 h cattle were allowed to graze an established perennial grass pasture (bluebunch wheatgrass), which was also delineated with electric fence. A preference test period occurred from June 15 to June 18, 2016, where cattle were only allowed to graze the treatment plots from 0800 to 1700 h. Animals were subsequently penned in their respective pens, adjacent to each block.

2.2.4. Bite Counts

Three observers were assigned to 2 blocks (4 animals/observer) in order to focally sample steers during grazing times in the treatment plots (see above) using the bite count method (Ortega et al., 1995) at 5 min intervals on three different forage types, medusahead, other grasses, and forbs, to determine vegetation selection for 2.5 h in the morning and 1 h in the evening. The number of daily bites taken on individual forage types was calculated as a percentage of the total daily bites taken. Observers were randomly switched among blocks on a daily basis, such that different observers counted bites on different animals throughout the experiment.

2.2.5. Residence Time

Time spent grazing within each treatment plot (residence time) was timed and recorded using a stop watch during the bite count assessment. Daily residence time in each treatment plot was calculated as a percentage of the total daily observed time spent grazing.

2.2.6. Medusahead Defoliation

Twenty-one squares (90.2 cm^2) containing medusahead tillers were marked in a zig-zag formation off a center transect every 1.4 m across each treatment plot to measure daily defoliation. Flagging tape was used to delineate the perimeter of the square, which was anchored to the soil with nails at each corner. The height of the tallest tiller within the square was measured every other day of the grazing period in order to asses medusahead defoliation. This procedure was a modification of the technique originally described by O'Reagain and Grau (1995) to assess defoliation of bunchgrasses, and adapted for medusahead (Montes-Sánchez et al., 2017).

2.2.7. Biomass Availability

Above ground biomass availability was determined before grazing and after an 8-d grazing period (sampling time; n=2) by hand clipping all vegetation within a 0.0985 m^2 frame to a 1-cm stubble height. Five frames were randomly placed down the middle of each plot, separated by species, and composited into forage types of medusahead, other grasses (constituting annual grasses other than medusahead and perennial grasses), and forbs. All samples were placed in the forced-air drying oven and dried at 60°C to constant weight.

2.3. Forage Chemical Composition

Dried samples in both experiments were ground in a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 1-mm screen. Ground samples were analyzed for crude protein (CP; AOAC, 2000; Method 990.03), acid detergent fiber (ADF; AOAC, 2000; Method 973.18), and neutral detergent fiber (NDF; Van Soest et al., 1991). Acid insoluble ash (AIA; AOAC, 2000; Method 920.08) was analyzed for medusahead samples in both experiments as an indicator of amorphous silicon concentrations (Charca et al., 2007). Medusahead samples in Experiment 1 were also analyzed for water soluble carbohydrates (WSC; DuBois et al., 1956), NDF digestibility after 30 h (NDFd30; Goering, 1970), and ash free NDF (aNDFom; Van Soest et al., 1991). In addition, mineral concentration in medusahead samples of Experiment 1 were determined using inductively coupled plasma mass spectrometer (ICP-MS; Elan 6000, PerkinElmer, Shelton, CT, USA) by the Utah State Veterinary Diagnostics Laboratory (Logan, UT, USA).

2.4. Statistical Analyses

2.4.1. Experiment 1

Food intake (DM basis, g/kg BW) was analyzed using a mixed effects model in a split-plot design with lambs (random factor; experimental unit) nested within group. Group (HG, LG, and CG), day, and medusahead treatments (High, Low and CTRL in Choice tests) were the fixed factors in the analysis.

Each parameter of medusahead quality (CP, ADF, NDF, AIA, NDFom, dNDF30, and WSC) and individual macro and trace minerals were assessed using a mixed effects model in a one-way factorial with a repeated measures design. Medusahead treatment was the fixed factor with sampling time (beginning and end of conditioning and 3- and 2-way choice tests; n = 6) as the repeated measure in the analysis.

2.4.2. Experiment 2

The number of daily bites taken were averaged over animal pairs (experimental unit) within each treatment plot. The bites on individual forage types (medusahead, other grasses, and forbs) within each treatment plot was calculated as a percentage of the daily bites taken on each forage type. Daily residence time on each treatment plot was calculated as a percentage of the total daily time spent grazing. The proportion of medusahead tiller height removal (defoliation) was calculated by taking the initial tiller height (day 0) within each square, subtracting the tiller height of the same square on each subsequent day from the initial tiller height, divided by the initial tiller height. The proportion of defoliation was averaged across squares in each treatment plot and block for each sampling day.

Available aboveground biomass was assessed using a two-way factorial in a randomized block design. Block was the random effect with treatment plot (RT3, KCl, CTRL) and sampling time (before and after grazing) as the fixed factors in the analysis. Forage quality (CP, ADF, NDF) of the different forage types assayed was assessed using the same model as biomass availability with block as the random effect, treatment plot and forage type as the fixed factors. Medusahead defoliation and residence time in each treatment plot for each grazing period (familiarization and preference test) were analyzed using a two-way factorial in a randomized block design. Block was the random effect with treatment plot and day of observation as the fixed factors in the analysis. The proportion of animal bites were analyzed using the same model as medusahead defoliation and residence time with block as the random effect, with day of observation and forage types as the fixed factors in the analysis.

In both experiments, the variance-covariance structure used was the one that yielded the lowest Bayesian information criterion. The model diagnostic included testing for a normal distribution and homoscedasticity. Data was transformed when needed according to the Box-Cox method but back-transformed data is reported (mean ± standard error of mean). Means were analyzed using Tukey's multiple comparison test when F-ratios were significant ($P < 0.05$). A trend was considered when $0.05 < P < 0.10$. Data analyses was performed using the GLMMIX procedure in SAS (SAS Inst., Inc. Cary, NC; Version 9.4 for Windows).

3. Results

3.1. Experiment 1

3.1.1. Forage Quality

The chemical composition of medusahead treated with different rates of glyphosate in both experiments is reported in Table 3.1. Additional nutritional analyses (WSC; NDF digestibility after 30 h, and ash free NDF organic matter) of medusahead in Experimetn1 are reported in Fig 3.1. There were no differences in concentrations of CP, ADF, NDF, aNDFom, AIA, or WSC across medusahead treatments ($P > 0.05$). However, untreated medusahead (CTRL) tended to show lower digestibility of NDF after a 30 h incubation (aNDF30) than medusahead treated with high or low doses of herbicide (Treatment effect; $P = 0.080$; Fig 3.1B).

Concentration of minerals in medusahead (29 elements, including Si) were similar across the different medusahead treatments ($P > 0.05$; Table 3.2).

3.2. Experiment 2

3.2.1. Forage Quality

There were no differences among treatment plots across all forage types assayed for the concentrations of CP or NDF (P >0.05; Table 3.1), and there was no treatment plot by forage type interaction ($P > 0.05$) detected for the concentration of CP, ADF, and NDF ($P > 0.05$). The concentration of CP was low and similar for medusahead and other grasses, with forbs showing the greatest concentration of this parameter (forage type effect: $P < 0.001$). The concentration of ADF across all forage types assayed was highest in the CTRL plot and lowest in the RT3 plot (treatment plot effect: $P < 0.001$), while the contents of this parameter were high for medusahead, intermediate for other grasses, and low for forbs (forage type effect: $P < 0.001$). Concentration of NDF in medusahead and other grasses was similar and high, whereas forbs displayed even greater concentration of this parameter (forage type effect: $P < 0.001$). No differences were detected for AIA concentrations of medusahead across treatment plots ($P = 0.638$).

3.3. Experiment 1. Foraging behavior

3.3.1. Conditioning

Average dry matter intake (DMI) of herbicide-treated and non-treated (CTRL) medusahead by lambs during the conditioning and choice periods are reported in Fig. 3.2. No differences in DMI were detected among groups of lambs during the conditioning period ($P = 0.300$; Fig 3.2A). However, intakes initially increased to a maximum value on day 3, before declining to a minimum on the last day of conditioning (day effect: $P < 0.001$). On day 3, the group exposed to the non-treated medusahead (CG) showed the greatest intake values, whereas the group exposed to medusahead treated with a high dose of herbicide (HG) displayed the lowest intakes (day by group interaction: $P < 0.001$).

3.3.2. Three-way Choice Test

Average intake across all groups was greater for CTRL than for herbicide-treated medusahead (High and Low) (medusahead treatment effect; $P < 0.0001$; Fig 3.1B). There was a tendency for all groups to follow this pattern, with the exception of the HG group, which also consumed greater amounts of medusahead treated with the high dose of glyphosate, whereas the LG group consumed the lowest amounts of this medusahead treatment (group by forage interaction: $P = 0.090$). No differences in total DMI consumed during choice tests were observed among treatment groups during three-way choices, and medusahead intakes were in general low (Figure 3.1B). Medusahead intake remained fairly stable across days as no day effect or interactions with group or medusahead treatment were detected ($P > 0.05$).

3.3.3. Two-way Choice Test

The group exposed to medusahead treated with a high dose of glyphosate (HG) consumed the greatest amounts of medusahead, whereas the group exposed to medusahead treated with a low dose of herbicide (LG) consumed the lowest amounts of the grass (group effect: $P = 0.048$; Fig. 3.2C). There was a strong tendency for all groups of lambs to consume greater amounts of medusahead treated with a high dose of glyphosate (High) than non-treated medusahead (CTRL) (medusahead treatment effect: $P = 0.052$). Overall DMI during 2-way choice tests did not fluctuate across days (day effect; $P > 0.05$), and no interactions were detected for the main factors in the analyses ($P > 0.05$).

3.4. Experiment 2. Foraging Behavior

3.4.1. Proportion of Bites

Familiarization period: The proportion of daily bites taken on different forage types, daily residence time in treatment plots, and daily medusahead defoliation by grazing animals during the familiarization and preference test periods are reported in Fig. 3.3. The proportion of bites on medusahead across days of observation were low, while bites on forbs were also low but greater than on medusahead, with grasses other than medusahead showing the highest proportion of bites (forage type effect: $P < 0.001$; Fig. 3.3A). There were no observable differences in the total proportion of bites taken by animals across days of observation ($P = 0.780$). Grasses other than medusahead had the greatest proportion of bites across the duration of the familiarization period, with medusahead and forbs being similar and low except for the last day of observation where forbs had a greater proportion of bites than those observed for medusahead (forage type by day of observation interaction: $P = 0.002$).

Preference test period. The proportion of bites on forbs across days of observation were low, whereas the proportion of bites on medusahead were also low but greater than on forbs. Grasses other than medusahead showed the highest proportion of bites during the period (forage type effect: $P < 0.001$; Fig. 3.3B). There were no differences in the total proportion of bites taken by animals across days of observation ($P = 0.615$). Grasses other than medusahead had the greatest proportion of bites across the duration of the preference test period, with medusahead and forbs being similar and low except for the last day of observation where cattle took more bites on medusahead than on forbs (forage type by day of observation interaction: $P = 0.001$).

3.4.2. Residence time

Familiarization period. Animals spent the greatest proportion of time grazing on CTRL plots across days of observation, with KCl plots showing an intermediate residence time, and RT3 plots revealing the lowest values ($P = 0.049$; Fig. 3.3C). There were no differences across days of observation in the time spent grazing the treatment plots ($P = 0.915$). Animals spent the greatest proportion of time grazing the CTRL plot on day 3 of observation, whereas residence time in RT3 was the lowest for this day of observation (treatment plot by day of observation interaction: *P* = 0.018).

Preference test period. No differences were detected in residence time across treatment plots (*P* = 0.597; Fig. 3.3D), days of observation (*P* = 0.983), and no treatment plot by day of observation interaction was revealed (*P* = 0.212).

3.4.3. Medusahead defoliation

Familiarization period. The average proportion of tiller height removal (defoliation) of medusahead across days of observation was greater for the RT3 plot, whereas medusahead defoliation in the KCl and CTRL plots was absent, showing similar and positive values, indicative of plant growth (treatment plot effect: *P* = 0.022: Fig. 3.3E). Additionally, average defoliation of medusahead across all treatment plots was absent and increased across days of observation with the lowest tiller height occurring on day 0, while on day 2 and 4 tiller height was similar and greater than on day 0 (day of observation effect: *P* < 0.001). The same pattern was observed in the KCl and CTRL plots as on day 2 tiller height increased and remained similar on day 4, whereas in the RT3 plot, medusahead tillers were defoliated in incremental amounts across days of observation (treatment plot by day of observation interaction: *P* = 0.011).

Preference test period. There were no observable differences across days between treatment plots on medusahead defoliation (treatment plot effect: *P* = 0.101; Fig. 3.3F), and no treatment plot by day of observation interaction was detected (*P* = 0.326). There was a decline across treatments in average medusahead tiller height between days of observation with the greatest defoliation occurring on the last day of observation (day of observation effect: $P < 0.001$).

3.4.4. Biomass Availability

The biomass availability for the different forage types in experiment 2, prior to and after grazing, are reported in Table 3.3. There were no differences in biomass availability of forbs and grasses other than medusahead across treatments ($P > 0.05$), and no treatment plot by sampling time interaction was detected for all forage types assessed ($P > 0.05$). Medusahead biomass availability was high and similar for KCl and CTRL relative to RT3 plots, which showed the lowest biomass availability (treatment plot effect: $P = 0.001$). Biomass availability of medusahead across all treatments was greater during the pre-grazing than during the post-grazing sampling time (sampling time effect: $P = 0.037$). The same pattern was observed for forbs and grasses other than medusahead (sampling time effect: $P < 0.05$).

4. Discussion

4.1. Silica, Forage Quality, and Herbicide Effects

We determined whether the application of an herbicide (glyphosate) to the unpalatable grass medusahead would increase intake by sheep and cattle and we attempted to separate the influence of glyphosate from that promoted by the salt present in the herbicide (KCl) on foraging behavior by cattle. The unpalatability of medusahead is explained by the presence of high concentrations of undigestible amorphous silicon (i.e., silica), which forms a varnish on the epidermis of awns, culms, leaves and glumes (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964) that reduces digestibility (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017). In support of this, the concentration of acid insoluble ash (AIA), an indicator of silica content in forages (Charca et al., 2007), was high in medusahead (9.5 to 13.5%, range) during both experiments.

Sub-lethal doses of glyphosate have been shown to reduce silica concentrations in quackgrass (*Elymus repens*) (Coupland and Caseley, 1975), and similar results were predicted to occur for medusahead. Nevertheless, glyphosate application did not alter medusahead tissue silica concentration in both experiments, nor elemental silicon concentrations in Experiment 1. As medusahead matures, silica concentrations in the plant were reported to decrease by only 1 to 3 percentile units (Swenson et al., 1964), or increase by only 1 percentile unit (Bovey et al., 1961). The elapsed time between chemical application and forage sampling was small (10 d), which in addition to the small changes in silica content as the plant matures may explain the lack of differences in AIA (i.e., silica) content between treated and non-treated plants in this study.

Glyphosate is a non-selective herbicide that targets the shikimate pathway and inhibits enzyme production of plant growth (Franz et al., 1997). Thus, as non-treated medusahead plants continued to mature, glyphosate-treated plants ceased growth. When glyphosate is applied at different phenological stages, specifically before anthesis, the herbicide treatment preserves the plant nutritional composition at that stage of growth when the application occurred (Gatford et al., 1999). Contrary to these findings, no differences among treatments were observed for the concentration of crude protein in both experiments. Nevertheless, lower acid detergent fiber (ADF) contents were detected in medusahead treated with glyphosate during experiment 2. As grasses mature, protein levels often decline, while concentration of structural carbohydrates (e.g., fiber) increase (Buxton et al., 1995; Van Soest, 1994). In experiment 1, medusahead was in the mid-reproductive phenological stage when glyphosate was applied, and thus it is likely that such reductions in CP or increases in fiber contents already occurred. On the other hand, glyphosate was applied at the late vegetative phenological stage in experiment 2, which likely allowed for further medusahead maturation in the non-glyphosate treatments, and preserved the nutritional quality (i.e., lower ADF contents) of glyphosate-treated medusahead. Overall, different phenological stages at which medusahead was treated likely accounted for the differences in ADF contents observed in herbicide-treated medusahead across experiments. Furthermore, and as discussed with AIA concentrations, the short duration between chemical application and forage sampling likely accounted for the lack of significant differences in nutritional quality observed between glyphosate and control treatments.

Medusahead digestible neutral detergent fiber after 30 h of incubation (dNDF30) was greater for glyphosate-treated medusahead in experiment 1. Thus, even when the herbicide treatment did not influence neutral detergent fiber contents, likely due to the reasons described above; it improved fiber degradability. Consistent with this finding, treated plants were observed to be more brittle than untreated plants in this study. Fractures in the silica structure (e.g., from plant brittleness) may provide better access for microbes to degrade the cellular constituents of the plant (Buxton and Redfearn, 1997), evidenced by an increase in dNDF30 for the glyphosate-treated medusahead. Gatford et al., (1999) showed similar increases in digestibility of glyphosate-treated annual ryegrass and attributed these changes to the disruption or arrest of the lignification process. Alteration in the lignin structural complex may have weakened the fibrous bonds within the plant, thus allowing for increased digestibility.

4.2. Glyphosate Rate and Lamb Foraging Preferences

Diet selection in herbivores is determined by animal genetics and experiences with the environment (Provenza and Balph, 1988). Experience to the orosensorial and post-ingestive attributes of a specific food will ultimately determine if that food is preferred or avoided (Villalba et al., 2015). For instance, lambs that had positive experiences with grazing a deferred roughage (e.g. weeping lovegrass), consuming more of that forage than inexperienced animals (Distel et al., 1996). Nevertheless, too frequent of excessive exposure to the same feed leads to satiety (Provenza, 1996), which can be aversive if the feed is deficient in nutrients or contain plant defenses (Distel and Villalba, 2018; Provenza, 1996), or anti-nutritional factors such as silica (Bovey et al., 1961; McNaughton et al., 1985). Lambs in experiment 1 were conditioned to different "medusahead types" representing plants treated or not (CTRL) with glyphosate, prior to choice tests. Given the positive influence of experience on foraging selection (Burritt and Provenza, 1997; Distel et al., 1996), it was expected that the different treatment groups would select for familiar over unfamiliar foods. Contrary to this prediction, all groups of lambs in 3-way choice tests preferred non-treated over glyphosate-treated medusahead, except for lambs in the high glyphosate-treatment group, which also consumed similar amounts of the high rate of glyphosate treated medusahead to that of the non-treated medusahead. Animals may have satiated on the orosensorial or post-ingestive attributes of glyphosate-treated medusahead to a greater extent than on untreated medusahead during conditioning, which prompted lambs to show greater intakes on non-treated medusahead. In contrast, during the two-way choice, animals preferred glyphosate-treated medusahead over non-treated medusahead, likely explained by the greater fiber digestibility observed in the former. In fact, intakes of glyphosate-treated medusahead in the two-way choice were numerically similar to the combined intakes of medusahead treated at low and high rates in the three-way choice test. Thus, combining the amounts of medusahead treated at high and low doses during 3-way choice tests, reveals that lambs consumed more herbicide-treated medusahead than non-treated medusahead. Intakes between glyphosate treatments in the 3-way choice tests showed that lambs did not discriminate between medusahead treated at low or high doses and thus they consumed amounts that in combination reflected the amounts of glyphosate-treated medusahead consumed in 2-way choice tests. The nutritional quality of glyphosate-treated medusahead at the 2 rates was fairly similar, with a tendency for greater dNDF30 in both glyphosate treatments than in CTRL. In addition, the color of the glyphosate-treated grass at both rates contained predominately yellow-grey hues, which likely prevented discrimination, whereas the CTRL treatment was dominated by green hues and sheep can discriminate feeds based on color (Bazely and Ensor, 1989). Discrimination of the orosensorial characteristics of treated medusahead plants likely followed the same pattern described for color.

The combined intakes of medusahead across treatments in experiment 1 were low and only a fraction of the required DM intake to sustain the lambs. This result was similar to previous studies where penned lambs also showed low intakes of the grass (Hamilton et al., 2015; Villalba et al., 2019). Lusk et al., (1961) and DiTomaso et al., (2008) reported that livestock would consume medusahead prior to the emergence of seed heads. The long ‘wispy’ silicified awns can be abrasive to mouth parts, potentially causing injury, thus deterring consumption of the forage (Young, 1992). Awns were prominent in Experiment 1 and this may have been a contributing factor to explain why lambs evidenced low medusahead intakes despite herbicide application with a greater fiber degradability. However, the increase in glyphosate treated medusahead consumption in the two-way choice, similar to the combined intake of treated medusahead (high and low rates) in 3-way choice tests, shows promise that even at a later phenological stage, glyphosate may increase consumption of medusahead, despite having the awns present.

4.3. Glyphosate, Salt, and Cattle Grazing Selection

Grazing has been described as the preferred method for medusahead control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015). Confining sheep at high densities prior to the emergence of the medusahead seed head was shown to increase the consumption of medusahead (DiTomaso et al., 2008; Lusk et al., 1961). Nevertheless, utilization of standing medusahead vegetation and litter by livestock is often unsuccessful as grazing animals tend to avoid consuming the grass (Davies and Svejcar, 2008; Hironaka, 1961). As described for experiment 1, sub-lethal doses of glyphosate may increase medusahead preference due to improvements in nutritional quality caused by growth retardation, consistent with previous studies on other grasses (Gatford et al., 1999; Kisseberth et al., 1986). Alternatively, ruminants have evolved cravings and preferences for the taste of salt, in order to satiate their dietary needs for different minerals (Schulkin and Schulkin, 1991). Thus, it is also possible that cattle would prefer glyphosate-treated medusahead triggered by the presence of the salt (KCl) present in the glyphosate herbicide, providing a taste dimension animal typically seek to satisfy their mineral requirements during the foraging process. Thus, in experiment 2 we attempted to isolate the influence of the salt by applying a treatment that provided this chemical but not glyphosate. We predicted that if preferences for glyphosate-treated medusahead is triggered by salt, then preferences by cattle should be similar between KCl- and glyphosate-treated plots, but greater than untreated plots.

When cattle started to graze their respective paddocks, they initially avoided medusahead (Fig. 3.3), partially explained by the presence of the anti-nutritional factor silica, as explained before. However, as grasses other than medusahead and forbs, of greater nutritional value, became depleted in response to selective grazing, the number of bites on medusahead increased. This increase was evident through the increase in the relative abundance of medusahead and thus the greater likelihood of encounter rate for this species. Forage selection is determined both by the plants biochemical properties (quality) and its relative abundance within the plant community (quantity) (Stephens and Krebs, 1986).

Animals also spent a greater proportion of their grazing time in non-treated than in glyphosate-treated plots (Fig. 3.4). Cattle develop preferences for vegetation patches in a heterogenous landscape, particularly when that vegetation is of greater nutritional quality and bulk density (i.e., quantity of forage) (Bailey, 1995). In addition, when physiological needs are not met, animals tend to search for patches that will satisfy these demands compared to when these needs are met (Egea et al., 2014; Provenza et al., 1998). The difference in residence time across treatments may in part be explained by the increase in searching time for more palatable species in the non-treated plots which also presented a greater bulk density than glyphosate-treated plots.

Despite the low proportion of bites on medusahead and low residence time in the glyphosate-treated plot, medusahead tillers in the glyphosate-treated plot decreased to a greater extent (~ 50% more) than in the other treatments (Fig. 3.3F). In fact, tiller height in the non-glyphosate treated plots had a minimal decline (CTRL and KCl), suggesting very low use. Additionally, the biomass of medusahead declined in glyphosate-treated plots (~60% decline), whereas it increased in salt treated plots, and had a minimal decline in the non-treated plot (Table 3.3). The greater use of the glyphosate-treated medusahead than non-glyphosate treated medusahead may be partially explained by the lower contents of acid detergent fiber (ADF) and potential greater degradability of the forage in the rumen. The low use of medusahead in the salt-treated plot could potentially be explained by mineral satiety and thus reduced preference for salty tastes, as cattle had trace-mineral salt blocks available ad libitum in the study. Thus, cattle removed medusahead in the glyphosate-treated plots despite having to consume excess potassium salt in the process. Tradeoffs exist when animals graze diverse forages in order to satisfy their multiple and dynamic needs, evident when one nutrient is consumed in excess in order to meet the physiological need for another nutrient (Langhans, 1995). For instance, lambs deficient in energy supply show greater preferences for flavors associated with sodium propionate than for flavors associated with a vehicle (water), but they avoid flavors associated with sodium chloride, when their physiological need for sodium were already met (Villalba and Provenza, 1996). Thus, energy-deficient lambs prefer sodium propionate despite the fact that they would avoid sodium, if this element is not tied to calories that the animals need (i.e., NaCl). Similarly, requirements for potassium salt, or mineral requirements in general were likely met in our study, but cattle need to satisfy their daily needs of energy, which may explain, in part, why animals continued to consume the forages in the glyphosate-treated plot, despite having similar potassium salt concentrations to the KCl plot.

Finally, medusahead is highly competitive for resources, and likely contributes to the failure of establishing of more desirable species through reseeding efforts. For instance, revegetation efforts of desirable species on medusahead-invaded rangelands is often more successful when some type of medusahead control is used (Davies, 2010; Nafus and Davies, 2014). Increasing livestock consumption of medusahead through the use of a glyphosate containing herbicide may increase consumption of medusahead and therefore create more conducive conditions for revegetation.

5. Conclusions

Grazing represents a sustainable method of medusahead control and it aids in restoration efforts on medusahead-infested landscapes. However, ruminants tend to avoid medusahead, although glyphosate treatments may improve the nutritional composition of the grass. Only small improvements in nutritional composition (reduced fiber contents increased fiber digestibility) were observed in this study, likely due to a late phenological treatment that prevented further conservation of the nutritional composition of medusahead compared to earlier phenological stages. Despite these small responses, sheep and cattle showed increments in the use of this grass that coincided with small changes in nutritional quality, suggesting that a combined treatment herbicide-grazing is a viable option to reduce medusahead abundance within the plant community and ‘unlock’ the grass as a potential forage source.

A short “effective” period has been identified when grazing livestock consume medusahead, typically at early stages of development (Brownsey et al., 2017; DiTomaso et al., 2008; Lusk et al., 1961). Glyphosate could arrest grass growth and preserve the plant at the phenological stage at which it was applied. If glyphosate application coincides with when medusahead is palatable for livestock (i.e., prior to seed head emergence), the duration by which medusahead is palatable for livestock could be extended. Further research should explore the application of glyphosate at earlier stages of growth, which may enhance the benefits in nutritional quality and potentially the use by livestock. Nevertheless, an optimal application may also consider the trade-off quality-quantity as earlier applications mean lower biomass available to harvest. In addition, removal of standing medusahead vegetation and soil disturbance through livestock trampling prepares a site for revegetation of desirable plant species. Finally, glyphosate application prior to seed head emergence reduces the quantity of viable offspring in subsequent years, thus reducing the invasive grasses' abundance in the plant community. Overall, the integrated approach of glyphosate application and cattle grazing shows promise as a practical tool for management of medusahead and its reduction within the plant community.

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Tables and Figures

Table 3.1. Nutrient content medusahead (*Taeniantherum caput-medusae* (L.) Nevski) treated with glyphosate at 788 g ae · ha^{-1} (High), 394 g ae · ha^{-1} (Low), and no chemical treatment (CTRL) in a 2015 (experiment 1) penned sheep preference study and forage types treated with glyphosate at 394 g ae · ha^{-1} (RT3), potassium chloride of the glyphosate herbicide at 173 g · ha^{-1} (KCl), and no chemical treatment (CTRL) in a 2016 (experiment 2) cattle grazing study in northern Utah (mean ± standard error of mean).

	Content (% dry matter)			
Experiment 1	CP	ADF	NDF	AIA
	Medusahead			
CTRL	6.5 ± 0.4	41.4 ± 2.3	64.3 ± 1.4	13.4 ± 1.4
Low	6.8 ± 0.5	42.1 ± 2.9	64.1 ± 1.8	9.5 ± 1.7
High	7.5 ± 0.4	41.4 ± 2.3	65.8 ± 1.4	10.2 ± 1.4
	Content (% dry matter)			
Experiment 2	CP	ADF	NDF	AIA[1]
	Medusahead			
CTRL	7.5 ± 0.3^{c}	43.3 ± 0.6^{a}	64.9 ± 1.0^{b}	13.7 ± 0.3
KCl	8.4 ± 0.3^{bc}	43.1 ± 0.6^{a}	65.3 ± 1.0^{b}	13.5 ± 0.3
RT3	8.3 ± 0.3^{bc}	38.7 ± 0.6^{b}	63.8 ± 1.0^{b}	13.3 ± 0.3
	Other Grasses			
CTRL	7.7 ± 0.3^{bc}	41.2 ± 0.6^{ab}	65.5 ± 1.0^{b}	
KCl	8.1 ± 0.3^{bc}	40.5 ± 0.6^{ab}	64.8 ± 1.0^{b}	
RT3	7.4 ± 0.3^{c}	38.1 ± 0.6^{b}	66.1 ± 1.0^{b}	
	Forbs			
CTRL	10.8 ± 0.3^{a}	33.4 ± 0.6^{c}	90.6 ± 1.0^{a}	
KCl	11.0 ± 0.3^{a}	30.8 ± 0.6^{cd}	88.7 ± 1.0^{a}	
RT3	10.1 ± 0.3^{ab}	27.8 ± 0.6^{d}	89.6 ± 1.0^{a}	

CP = crude protein.
ADF = acid detergent fiber.
NDF = neutral detergent fiber.
AIA = acid insoluble ash.

[1] Medusahead was the only forage type analyzed.

[a-c] Same superscript within column and experiment are not significantly different ($P > 0.05$).

Table 3.2. Macro and trace mineral concentrations medusahead (*Taeniantherum caput-medusae* (L.) Nevski) treated with a glyphosate containing herbicide at: 788 g ae · ha^{-1} (High), 394 g ae · ha^{-1} (Low), and no chemical treatment (CTRL) in a 2015 (experiment 1) penned sheep study located in northern Utah (mean ± standard error of mean).

Mineral	*Treatment*			*P*-value
	High	Low	CTRL	
	Content (% dry matter)			
Phosphorus	18.1 ± 2.3	17.6 ± 2.9	16.7 ± 2.3	0.916
Calcium	53.8 ± 12.8	32.9 ± 15.7	38.2 ± 12.8	0.568
Sodium	0.90 ± 0.23	0.49 ± 0.29	0.57 ± 0.23	0.512
Potassium	94.0 ± 12.9	86.9 ± 15.8	86.5 ± 12.9	0.905
Magnesium	18.0 ± 6.1	7.7 ± 7.4	11.2 ± 6.1	0.571
Zinc	0.36 ± 0.05	0.27 ± 0.07	0.30 ± 0.05	0.544
Copper	0.05 ± 0.01	0.04 ± 0.01	0.05 ± 0.01	0.521
Iron	9.5 ± 3.8	4.5 ± 4.7	15.7 ± 3.8	0.259
Manganese	0.93 ± 0.26	0.56 ± 0.32	1.16 ± 0.26	0.404
Silicon	3.5 ± 0.4	3.8 ± 0.4	3.5 ± 0.4	0.820

Table 3.3. Biomass availability (mean ± standard error of mean) of associated forage types within chemical treatments of: a glyphosate herbicide in the form of its potassium salt applied at 394 g ae · ha^{-1} (RT3), potassium salt of the herbicide applied at 173 g · ha^{-1} (KCl), and no chemical treatment (CTRL), prior to (pre-graze) and after (post-graze) a 2016 cattle grazing study (experiment 2) located in northern Utah (means ± standard error of mean).

	Pre-graze	Post-graze
Treatments	Medusahead (kg/ha^{-1} dry matter)	
RT3	353.0 ± 107.8^{ab}	143.5 ± 107.8^{b}
KCl	700.9 ± 107.8^{a}	716.4 ± 107.8^{a}
CTRL	784.1 ± 107.8^{a}	450.8 ± 107.8^{ab}
	Other Grass (kg/ha^{-1} dry matter)	
RT3	705.3 ± 155.1^{ab}	311.0 ± 155.1^{b}
KCl	918.1 ± 155.1^{ab}	741.1 ± 155.1^{ab}
CTRL	924.2 ± 155.1^{a}	522.5 ± 155.1^{b}
	Forbs (kg/ha^{-1} dry matter)	
RT3	143.2 ± 104.8^{bc}	31.1 ± 104.8^{d}
KCl	332.3 ± 104.8^{ab}	105.9 ± 104.8^{cd}
CTRL	463.3 ± 104.8^{a}	124.9 ± 104.8^{bc}

$^{a-e}$ Means followed by the same superscript within plant type are not different at $P >$ 0.05.

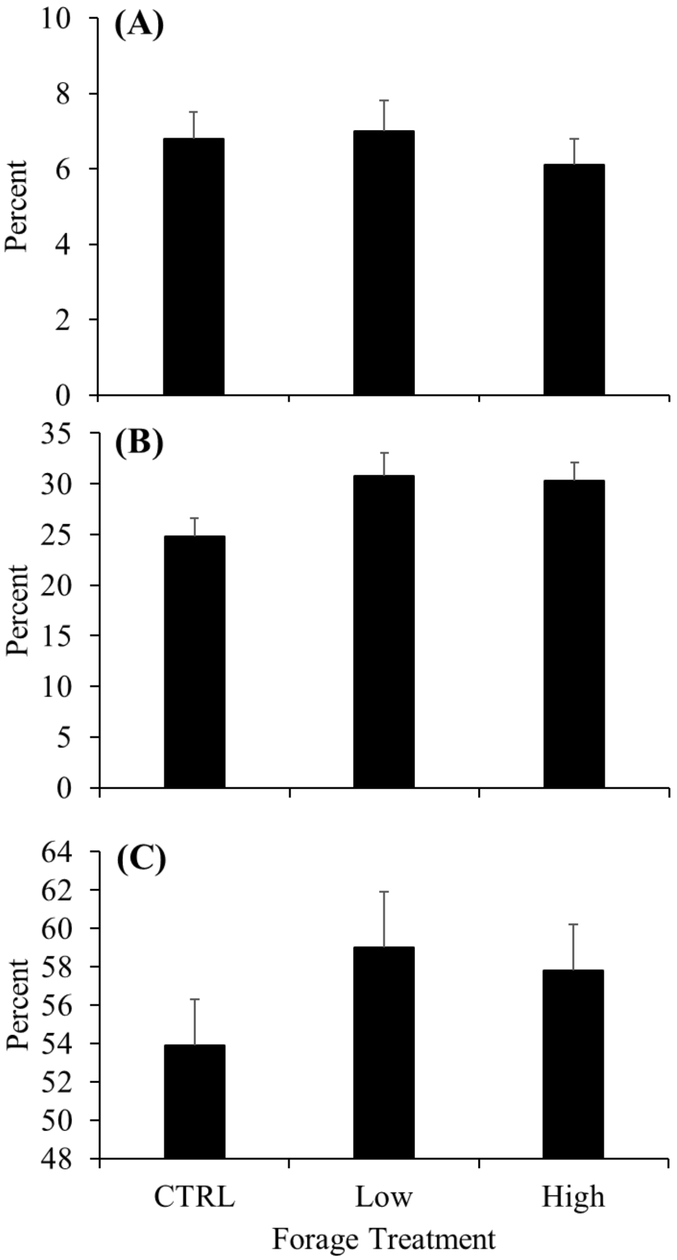

Fig. 3.1. Nutrient content (dry matter basis) of medusahead (*Taeniantherum caput-medusae* (L.) Nevski) treated with a glyphosate herbicide in the form of its isopropylamine salt at: 788 g ae · ha^{-1} (High), 394 g ae · ha^{-1} (Low), and no chemical treatment (CTRL) in a 2015 (experiment 1) penned sheep study located in northern Utah (mean ± standard error of mean). (A) Water Soluble Carbohydrates; (B) Neutral Detergent Fiber digestibility after 30 h; (C) ash free neutral detergent fiber organic matter.

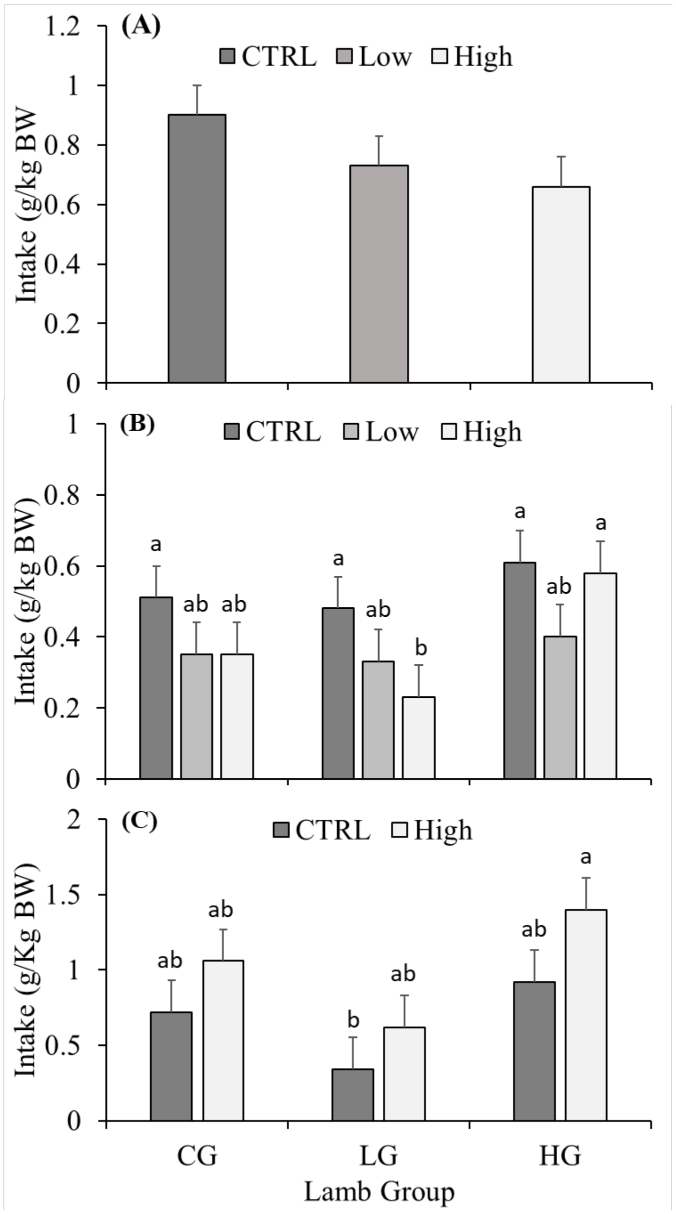

Fig. 3.2. Intake (dry matter basis) of medusahead (*Taeniantherum caput-medusae* (L.) Nevski) treated at different rates of glyphosate in its form of isopropylamine salt at: 788 g ae · ha^{-1} glyphosate rate (High); 394 g ae · ha^{-1} glyphosate rate (Low); and no chemical application (CTRL), by three groups of lambs: High treated medusahead group (HG); Low treated medusahead group (LG); and non-treated medusahead group (CG; 8 lambs/group). Lambs were randomly assigned one of the three herbicides treated medusahead forages in a conditioning period (A). A preference period enused by offering lambs a three-way choice between all herbicide treated forages (B), and a two-way choice between CTRL and High herbicide treated forages (C). Medusahead intake was averaged across days with mean and standard error of mean reported. Same letters (a-b) within figure are not significantly different ($P > 0.05$).

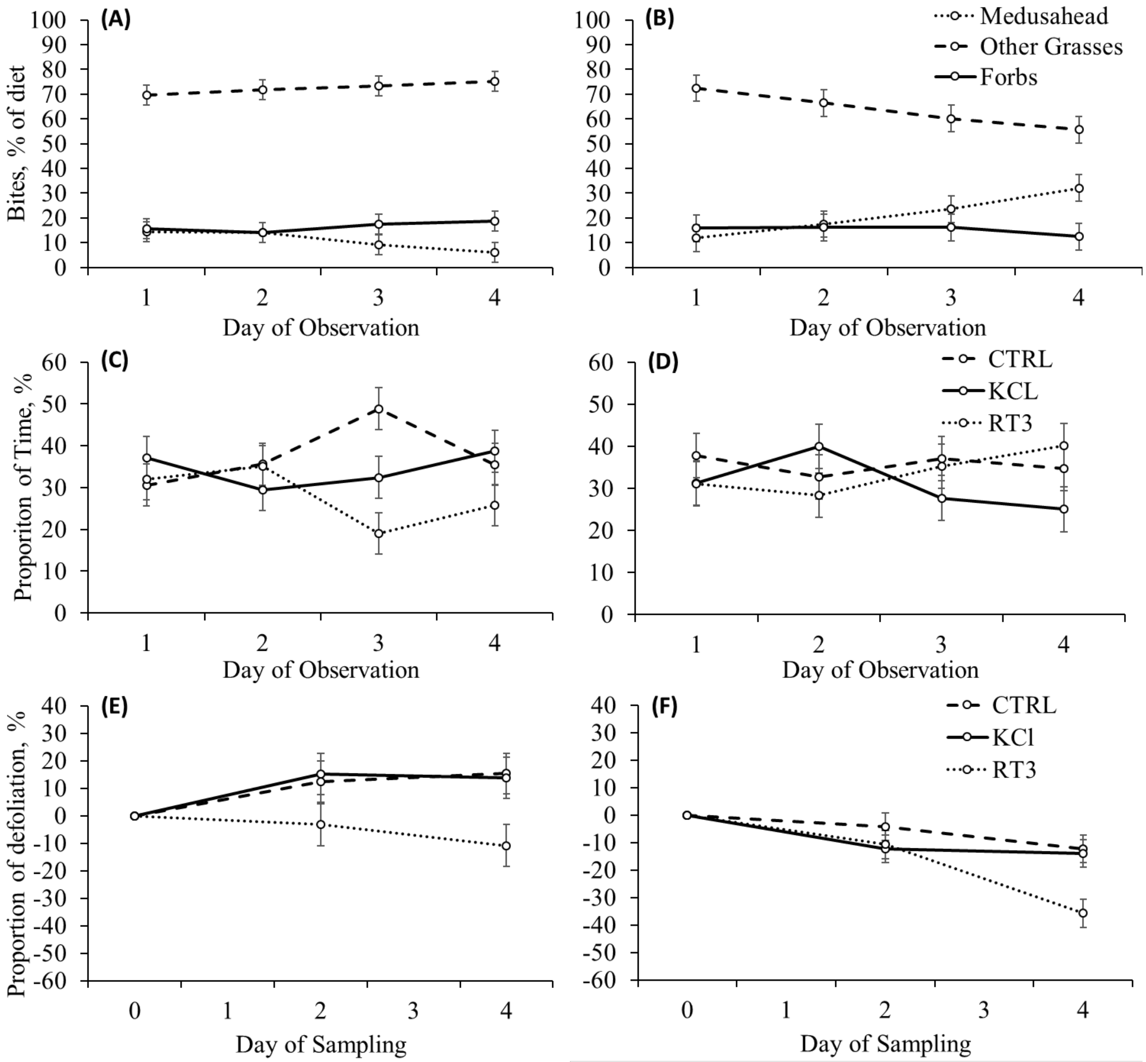

Fig. 3.3. Beef cattle foraging behavior during a 2016 grazing study (experiment 2) conducted in northern Utah. The proportion of daily bites by animals on different forage types during a familiarization (A) and a preference test period (B); the proportion of time spent grazing in different treatment plots (residence time) of: glyphosate in the form of its potassium salt applied at a rate of 395 g ae · ha^{-1} (RT3), potassium chloride, a constituent in the glyphosate herbicide applied at 173 g · ha^{-1} (KCl), and no chemical treatment (CTRL) during a familiarization (C) and a preference test period (D); and the proportion of medusahead tiller height removal (defoliation) by grazing animals in the same treatments during a familiarization (E) and a preference test period (F). Means of a percent are reported with the standard error of the mean represented by vertical bars.

CHAPTER 4

PREFERENCE FOR ROUNDUP®-TREATED MEDUSAHEAD BY CATTLE: SEPARATING THE INFLUENCE OF THE HERBICIDE'S MAIN CONSTITUENTS[4]

ABSTRACT

Livestock tend to avoid grazing the invasive grass medusahead (*Taeniantherum caput-medusae* (L.) Nevski) due to its low nutritional value, although treatment with the herbicide glyphosate may preserve nutrient contents and increase digestibility, reversing this trend. We evaluated whether the chemical constituents within the herbicide Roundup RT 3® could improve the forage value of the grass and contribute to its control in medusahead-invaded landscapes. Four replicated pastures received five treatments: 1) Roundup RT 3® (RT3), 2) glyphosate in its potassium salt (GS), 3) glyphosate only (G) (all applied at 788 g ae · ha^{-1}), 4) the inert ingredients only (adjuvant; ADJ; 285.0 ml · ha^{-1}), and 5) no chemical application (CTRL). Eight steers were randomly paired and assigned to graze the medusahead-infested pastures for 10 h daily during 5 consecutive days. Plant biomass, bite counts, and nutritional composition of medusahead (MH), *Ventenata dubia* (Ve), other annual grasses (AG), perennial grasses (PG), annual forbs (AF), and perennial forbs (PF) were assessed. Application of chemicals containing glyphosate (RT3, GS, G), prevented large increases in MH biomass, relative to pre-chemical application values (chemical efficacy; $P = 0.048$). Furthermore, grazing cattle displayed greater utilization of the glyphosate containing treatments, reducing relative

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[4] Co-authored with Clint Stonecipher

biomass by 50 to 80%, respectively, relative to pre-grazing values (grazing efficacy; *P* = 0.044). However, bites on MH did not differ among treatments (*P* = 0.242), but they increased over the duration of the study (*P* = 0.012). No differences among treatments were observed for crude protein or silica content in MH ($P > 0.05$), although fiber content in MH, Ve, AG and AF were lower for the glyphosate-containing treatments than for ADJ or CTRL. The integrated approach of glyphosate application and cattle grazing reduces medusahead abundance, despite only small nutritional changes, providing an efficient and sustainable method of medusahead control.

INTRODUCTION

Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is currently one of the most detrimental invasive plants impacting rangeland sustainability and livestock operations in the western U.S. (Davies and Johnson, 2008; Miller et al., 1999; Young, 1992); it decreases the abundance and quality of forage available to livestock and wildlife, negatively impacts plant diversity, and increases the frequency of fires (Davies and Johnson, 2008). Livestock grazing has been shown to be a preferred method of medusahead control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015). However, livestock utilization of standing medusahead vegetation and litter is typically low as grazing animals tend to avoid consuming the grass (Davies and Svejcar, 2008; Hironaka, 1961). This aversive behavior has been associated with high silica contents in the plant, which retards microbial digestion in the rumen (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017) and reduces the nutritional value of the ingested forage (Montes-Sánchez et al., 2017).

The herbicides 2, 4-D, tebuthiuron, picloram and glyphosate have been shown to temporarily increase grazing selection of treated plants (Kisseberth et al., 1986; Scifres et al., 1983), attributed to preservation in the nutritional quality of the sprayed forage (Siever-Kelly et al., 1999). For instance, glyphosate in the form of its isopropylamine salt was applied at low rates prior to anthesis of annual ryegrass (*Lolium rigidum* Graudin), which subsequently preserved the concentrations of nitrogen and soluble carbohydrates, and increased dry matter digestibility relative to untreated plants (Armstrong et al., 1992; Gatford et al., 1999). Furthermore, low rates of the same glyphosate formulation applied prior to medusahead anthesis has been shown to be an effective control strategy without serious injury to shrubs and other perennial grass species in the plant community (Kyser et al., 2012).

Integrated approaches to medusahead control, such as livestock grazing in combination with low rates of glyphosate application, may improve the nutritional quality of the grass, which in turn would reduce medusahead spread and aid habitat restoration. It is likely that the growth retardation imposed by the herbicide would reduce the concentration of silica in the grass, thus increasing its palatability, although it is unknown whether glyphosate, the salt, and/or the inert ingredients are responsible for these changes. Alternatively, the presence of other chemicals in the herbicide (i.e., adjuvants) may increase the palatability of the grass, as sugars and salt represent rewards that may increase selection of forages and locations in livestock (Bailey and Welling, 1999; Burritt et al., 2005). Thus, the objectives of this study were to determine the influence of the herbicide Roundup RT 3® or its chemical constituents on medusahead control (chemical efficacy) when applied to the plant prior to seed head emergence, and whether these chemicals influence preference by cattle through changes in the plant's nutritional quality during an integrated herbicide-grazing approach to weed control.

MATERIAL AND METHODS

All procedures conducted with animals were approved by the Utah State University Institute of Animal Care and Use Committee (#2619).

Site Description

The study was conducted on privately-owned land in southern Cache County, Utah (41º34'15.6" N, -111º54'40.2" W). The ecological study site is Mountain Stony Loam (Wadman, 2012), which is located at 1646 m and has a slope of 5%. The soil is stony, cobbly, or gravelly loam textured and permeability is moderate slow to moderate. The mean annual precipitation is 457 mm and mean annual temperature between 3 and 7º C with 83 frost free days (Wadman, 2012). The invasive annual grasses, medusahead and cheat grass (*Bromus tectorum* [L.]) constituted the majority of the plant community within the study site with a recently identified introduced invasive annual grass ventenata (*Ventenata dubia* L.), which was also predominant. Perennial grasses such as kentucky bluegrass (*Poa pratensis* [L.]), Letterman's needlegrass (*Achnatherum lettermanii*), slender wheatgrass (Elymus trachycaulus), Sandberg bluegrass (Poa secunda), bluebunch wheatgrass (*Pseudoroegneria spicata*), and intermediate wheatgrass (*Thinopyrum intermedium*) were also present but at lesser densities. Forbs such as common yarrow (*Achillea millefolium*), tapertip onion (*Allium acuminatum*), arrowleaf balsamroot (*Balsamorhiza sagittate*), and field bindweed (*Convolvus arvensis*) were also present at low densities.

Experimental Design

Two prominently invaded medusahead patches of 0.15 ha each, approximately 500 m away from one another, were selected within a 250 ha rangeland livestock pasture. Two 0.058 ha (38.1 x 15.2 m) pastures (hereafter referred to as a blocks) were arranged side-by-side within each medusahead patch and fenced with a solar-powered electric fence. The four blocks were subdivided into five plots of 0.01 ha (38.1 x 3.0 m) each, and randomly assigned to five chemical treatments: 1) glyphosate in the form of its potassium salt with inert ingredients (RT3), 2) glyphosate in the form of its potassium salt without inert ingredients (GS), 3) glyphosate only (G), and 4) the inert ingredients contained in Roundup RT 3® (adjuvant; ADJ) (Bayer Co. North Carolina, USA), and 5) an untreated plot (CTRL). Glyphosate-containing chemicals (RT3, GS, and G) were applied at 788 g ae ha^{-1}, while ADJ was applied at 285.0 mL ha^{-1}, a rate that provided the same amount of adjuvant delivered with RT3. All chemicals were obtained with consent from Bayer Co. (North Carolina, USA). Chemicals were applied using a CO2-pressurized backpack sprayer at a rate of 153 L ha^{-1} on May 29, 2017. Medusahead was in the late vegetative phenological stage prior to chemical application.

Animals

Eight angus-cross beef steers (458.6 ± 12.6 kg BW) were randomly paired and pairs assigned to each of the four blocks. Steers were allowed to choose between the different chemically-treated plots and forage types to determine their foraging preferences from June 9 to June 13, 2016. Pairs were penned when not grazing in their respective 3.7 x 3.7 m pens, built from corral cattle panels adjacent to each block. During the study, animals had free access to water and trace mineral blocks (mineral composition: minimum 96% NaCl, 320 mg · kg Zn, 380 mg · kg Cu, 2,400mg · kg Mn, 2,400 mg · kg Fe, 70 mg · kg I, and 40 mg · kg Co).

Vegetation Assessment

Medusahead, ventenata, and other annual grasses treated with glyphosate-containing chemicals (RT3, GS, and G) remained in the late vegetative phenological stage after chemical application, whereas non-glyphosate containing chemicals (ADJ) and CTRL did not arrest growth, therefore maturation continued after chemical application for these treatments. Even with unaltered growth, emergence of a seed head (i.e., early reproductive stage) for ventenata did not occur until after the end of the study, whereas medusahead and other annual grasses had prominent seed heads throughout the grazing period. Perennial grasses were in the early to mid-vegetative stage for the entire duration of the study. The phenological stage of forbs varied depending on species from early vegetative to late reproductive phenological stage. As described for medusahead, glyphosate-containing herbicide treatments preserved the forbs at the phenological stage at which they were treated, whereas non-glyphosate containing chemicals allowed for further maturation.

Biomass Availability and Reduction

Aboveground vegetation biomass was determined prior to chemical application (pre-chemical), 10 d after chemical application (post-chemical), and after a 5-d grazing period (post-graze; sampling times) by hand clipping all vegetation within a 0.0985 m^2

frame to a 1-cm stubble height. Five frames were randomly placed down the middle of each plot, separated by species, and composited into 6 forage types: Medusahead, ventenata, other annual grasses, perennial grasses, annual forbs, and perennial forbs. Samples were subsequently dried in a forced air oven (VWR 1350F, Sheldon Manufacturing, Cornelius, OR, USA) at 60º C until constant weight for estimates of dry matter biomass availability. The effects of biomass reduction (relative values) after chemical application and grazing were calculated as a percentage of the initial biomass values.

Foliar Cover

Foliar cover was estimated with line-point intercept method (Herrick et al., 2005), prior to chemical application, every 30 cm along one transect (n=124) placed down the middle of each treatment plot. Individual plant species counts along the transect were classified according to the same vegetation types in the biomass availability section with the addition of thatch and bare ground. The proportion of cover of each forage type was calculated as a percentage of the total counts for individual transects, treatment plot and block.

Chemical Composition

Dried biomass samples were weighed and then ground in a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 1-mm screen. Individual dried samples were composited by forage type across clips and treatment plot within each block. Ground vegetation for the pre- and post-chemical application sampling times were subsequently analyzed for crude protein (CP; AOAC, 2000; Method 990.03), acid detergent fiber (ADF; AOAC, 2000; Method 973.18), and neutral detergent fiber (NDF; Van Soest et al. 1991). Medusahead and ventenata were additionally analyzed for acid insoluble ash (AIA; AOAC, 2000; Method 920.08) as an indicator of amorphous silicon content (i.e., silica).

Animal Assessment

Bite Counts

Daily bite counts (Ortega et al., 1995) were used to determine selection of the same vegetation types described in the biomass availability section. All steers were allowed to graze from 0800 to 1800 h starting June 9 and ending June 13, 2017 (days of observation). Two observers (each assigned to two blocks) focally sampled each animal, within the observers assigned blocks, at 5 min. intervals and recorded incidences of bites for 2.5 h in the morning (from 0900 to 1130) and 1 h in the evening (from 1700 to 1800) for each treatment plot (7 observation periods per animal). The number of daily bites taken within each treatment plot by individual forage types were calculated as a percentage of the total daily bites taken within each treatment plot.

Residence Time

Time spent grazing within each treatment plot (residence time) was timed and recorded using a stop watch during the bite count assessment. Daily residence time in each treatment plot was calculated as a percentage of the total daily time spent grazing.

Statistical Analyses

The absolute biomass availability, the proportion of bites on individual forage types, residence time, and the proportion of vegetation cover, were analyzed using a two-way factorial in a randomized block design. Block was the random effect for each analysis. Treatment plots (RT3, GS, G, ADJ, CTRL) and sampling times (pre- and post-chemical application, or pre- and post-grazing) were the fixed factors in the analysis for assessments of absolute biomass availability; treatment plots and days of observation (5 d) were the fixed factors for the analysis of the proportion of bites and residence time; and treatment plots and forage types were the fixed factors for the proportion of biomass removal in the vegetation cover analysis. Relative biomass reductions for chemical and grazing effects were each analyzed in a one-way factorial randomized block design, with block as the random effect and treatment plots as the fixed factor.

Forage types that yielded a small amount of sample during the collection period were composited across blocks within each treatment in order to have enough sample to conduct nutritional analyses. Due to the lack of replication, composited samples were excluded from statistical analyses (means only reported). In the rest of the cases, data was analyzed in a two-way factorial in a randomized block design, with block as the random effect and treatment plots and sampling times (pre- and post-chemical) as the fixed factors in the analysis.

The variance-covariance matrix structure used was the one that yielded the lowest Bayesian information criterion. The model diagnostics included testing for a normal distribution and homoscedasticity. Data was transformed when needed according to the

Box-Cox method but back-transformed data is reported (mean ± standard error of mean). Means were analyzed using Tukey's multiple comparison test when F-ratios were significant ($P < 0.05$). A trend was considered when $0.05 < P < 0.10$. Data analyses were performed using the GLIMMIX procedure in SAS (SAS Inst., Inc. Cary, NC; Version 9.4 for Windows).

RESULTS

Vegetation Assessment

Relative Biomass Reduction

The relative biomass reduction of medusahead and annual forbs in response to the chemical treatments and grazing preferences is reported in Fig. 4.1. No differences among treatments were detected for the chemical treatments and grazing effects on ventenata, perennial grasses, or perennial forbs ($P > 0.05$). The biomass of medusahead 10-d after chemical application increased for all treatments relative to pre-application values but it was greatest for CTRL, intermediate for ADJ, and lowest for all glyphosate-treated plots (treatment plot effect: $P = 0.048$; Fig. 4.1A). Furthermore, the biomass of medusahead 5-d after grazing (post-grazing) increased relative to pre-grazing values for the ADJ treatment and it decreased for all other treatments, with the greatest decline occurring for the G treatment (treatment plot effect: $P = 0.044$; Fig. 4.1B). No differences in relative biomass reduction post-grazing were detected across treatments for annual grasses other than ventenata or medusahead ($P = 0.318$), but there was a strong tendency for an increment in the biomass of this plant category post-grazing in GS and CTRL (Table 4.3), and reductions in biomass post-grazing for the rest of the treatments (treatment plot effect: *P* = 0.054). Biomass of annual forbs after 10-d of chemical application increased relative to initial values for ADJ and CTRL treatments, whereas it decreased for all other treatments, with the G plot displaying the greatest reduction (treatment effect: *P* = 0.012: Fig. 4.1C). Biomass of annual forbs declined post-grazing relative to pre-grazing recordings in all treatments, with CTRL showing the lowest reductions and RT3 displaying the greatest removal values (treatment effect: *P* = 0.017: Fig. 4.1D).

Biomass Availability

Biomass availability of the different forage types across treatment plots and sampling times are reported in Table 4.1. There were no differences across treatment plots regarding biomass availability of medusahead, ventenata, perennial grasses, or perennial forbs ($P > 0.05$), and no treatment plot by sampling time interaction was detected for these forage types ($P > 0.05$). Likewise, no differences were detected across treatment regarding sampling times (pre- and post-chemical application, or pre- and post-grazing) for medusahead biomass availability (*P* = 0.6384). Biomass availability of ventenata across all treatment plots declined from post-chemical to post-grazing sampling times (sampling time effect: *P* = 0.005). The same pattern was observed for annual grasses other than medusahead, perennial grasses, and annual forbs (sampling time effect: $P < 0.05$).

Annual forb biomass availability across sampling times was greatest in ADJ, intermediate in CTRL, and lowest in the RT3, GS and G treatment plots (treatment plot effect (*P* = 0.005). Furthermore, annual forb biomass availability was greatest in the G treatment plot during the pre-chemical sampling time and lowest during the post-graze sampling time (treatment plot by sampling time interaction: $P = 0.002$). The biomass availability of perennial forbs across treatments was greatest during the pre-chemical, intermediate during post-chemical, and lowest during the post-graze sampling times (sampling time effect: $P = 0.001$).

Foliar Cover

The proportion of vegetation foliar cover across treatment plots and different forage types is reported in Table 4.2. There were no differences in foliar cover among treatment plots across all forage types assayed ($P = 0.992$). Nevertheless, ventenata had the greatest foliar cover of all forage types assayed, with medusahead, other annual grasses, and annual forbs having high foliar cover but less than that observed for ventenata. Perennial grasses showed intermediate foliar cover, with perennial forbs, thatch and bare ground displaying the lowest cover values (forage type effect: $P < 0.001$) Additionally, annual grasses other than medusahead and ventenata displayed the greatest foliar cover values in the GS plot, while thatch displayed the lowest value in the CTRL plot (treatment plot by forage type interaction: $P < 0.001$).

Forage Quality

The nutritional content of the different forage types within treatment plots and sampling times (prior to and after chemical application) are reported in Table 4.3. There were no differences in CP, ADF, and AIA across treatment plots for medusahead samples ($P > 0.05$), but NDF content was lower for GS ($P < 0.05$) and tended ($P < 0.10$) to be lower for RT3 and G than for the CTRL or ADJ treatments (treatment plot effect: $P = 0.004$). Due to the lack of replication, RT3 and G samples were not analyzed statistically, although NDF contents were in the range of those lower values observed for GS.

There were no differences observed in CP, ADF, NDF, and AIA content for ventenata across treatment plots ($P > 0.05$). Nevertheless, CP content in ventenata was greater prior to than after chemical application (sampling time effect: $P = 0.018$), and lowest for the GS an ADJ treatments after chemical application (treatment plot by sampling time effect: $P = 0.024$). The ADF content of ventenata across treatment plots was greater after than before chemical application (sampling time effect: $P = 0.009$), but no treatment plot by sampling time interaction was detected ($P = 0.280$). The AIA content of ventenata across treatment plots tended to be greater prior to than after chemical application ($P = 0.087$), and no treatment plot by sampling time interaction was detected for this parameter ($P = 0.674$).

There were no differences among treatments for CP, ADF, and NDF content for annual grasses other than medusahead or ventenata across sampling times ($P > 0.05$). Nevertheless, CP content was greater prior to than after chemical application (sampling time effect: $P = 0.018$), and no treatment plot by sampling time interaction was detected ($P = 0.496$). Furthermore, ADF content was greater after than before chemical application (sampling time effect: $P = 0.009$), and there was a tendency for RT3, ADJ, and CTRL plots to show lower contents of ADF prior to than after chemical application ($P = 0.010$). The same pattern was observed for NDF contents ($P < 0.001$).

Perennial grasses did not show any differences in CP or ADF contents among treatment plots or sampling times, and no treatment plot by sampling time interaction was detected ($P > 0.05$). There was strong tendency for NDF to be greater after than before chemical application (sampling time effect: $P = 0.051$), and no treatment plot by sampling time interaction was detected (*P* = 0.241).

Annual forbs did not display any differences in CP concentration across sampling times or treatment plots (*P* = 0.197), and no treatment plot by sampling time interaction was detected (*P* > 0.05). The NDF (P=0.044) and ADF (P = 0.038) concentrations were greater for ADJ and CTRL than from glyphosate-treated plots.

Animal Assessment

Bites

The proportion of bites across treatment plots and days of observation on the different forage types are reported in Fig. 4.2. There were no differences across days of observation in the proportion of bites taken on medusahead, ventenata, or perennial forbs among all treatment plots (*P* > 0.05), and no treatment plot by day interaction was detected for all the forage types assayed (*P* > 0.05). Likewise, there were no differences in the proportion of bites on ventenata, annual grasses other than ventenata or medusahead, or perennial forbs across days of observation (*P* > 0.05). In contrast, the proportion of bites on medusahead were the lowest on day two with the greatest value occurring on the last day of the study (day effect: *P* = 0.012; Fig. 4.2A). Average number of bites on annual grasses other than ventenata or medusahead tended to be greater in the RT3 plot, intermediate in the GS, G, and CTRL plots, and lower in the ADJ plot (treatment plot effect: *P* =0.099; Fig. 4.2C).

Bites on perennial grasses were the greatest in the G plot, with the GS plot displaying the lowest values (treatment plot effect: *P* = 0.032; Fig. 4.2D). In addition, there was a decline in the proportion of bites on perennial grasses from the beginning to the end of the study (day effect: $P < 0.001$) and a strong tendency for a greater number of bites on annual forbs in the CTRL plot and lower number of bites on this forage type in the G plot (treatment plot effect: $P = 0.063$), with daily alternations between peaks and nadirs for this forage type (day effect: $P = 0.004$; Fig. 4.2E).

Residence Time

The proportion of time spent grazing by steers in the different chemical treatments (residence time) across days of observation are reported in Fig. 4.3. Residence time averaged across days of observation was greatest in the ADJ treatment plot and lowest in the G treatment plot (treatment plot effect: $P < 0.001$), but no changes in residence time across days of observation were detected ($P = 0.808$). Additionally, steers spent more time grazing in the CTRL plot, whereas they spent the least amount of time grazing in the G plot on the last day of the experiment (treatment plot by day of observation interaction: $P < 0.001$).

DISCUSSION

Chemical Efficacy

We determined the influence of the herbicide Roundup RT 3® as well as the effect of its chemical constituents on medusahead control (chemical efficacy) when applied prior to seed head emergence, and whether these chemicals influence the nutritional quality of medusahead and other forage types in the plant community, as well as foraging preferences by cattle. Glyphosate is a non-selective post-emergent herbicide that has been used in a variety of agricultural and non-agricultural settings to control undesirable plant species (Baylis, 2000). Different chemical formulations of this herbicide improve handling and storage (Franz et al., 1997). Furthermore, adjuvants within the different glyphosate formulations enhance the absorption and retention of the herbicide within the plant (Hartzler, 2001). Thus, it would be expected that applications of the chemical constituents of a glyphosate-containing herbicide would have varying efficacies on the different plant species within the plant community, particularly medusahead. As expected, chemicals with the active ingredient glyphosate (GS, G, and RT3) reduced the production of medusahead biomass 10 d after application by > 500%, relative to no chemical treatment (CTRL), and > 100%, relative to the inert chemical only (adjuvant; ADJ) treatment (Fig. 4.1A). Annual forbs were also affected by the glyphosate treatments as biomass production declined by > 50%, and > 130% relative to the CTRL and ADJ treatments, respectively (Fig. 4.1C). Nevertheless, the addition of salt (GS) or the adjuvant (RT3) had no impact on relative biomass reduction of these two forage types compared to that observed for glyphosate alone (G). The lack of difference in relative biomass among the glyphosate treatments may have been a consequence of the sub-lethal dose applied; as rate decreases, the likelihood of a plant intercepting a quantity sufficient for lethality is reduced (i.e., efficacy of the active and inert ingredients) (Hartzler, 2001). Furthermore, there were no differences in relative biomass across all chemical treatments applied regarding all other forage types assayed, which may be a consequence of varying susceptibilities between plant species to sub-lethal rates of glyphosate. Low doses of glyphosate have been shown to increase root and shoot biomass in a variety of species (Coupland and Caseley, 1975; Velini et al., 2008), possibly explaining the lack of biomass reduction in species other than medusahead and annual forbs.

Seed production is the primary means by which annual grass propagation occurs

(Pyke, 1994). Glyphosate targets the plant shikimate pathway and inhibits enzyme production, arresting plant growth (Franz et al., 1997), and consequently prevents seed production when applied prior to seed head emergence. This was thought to be a contributing factor in > 95% control of medusahead when glyphosate was applied prior to seed head emergence (Kyser et al., 2012). The glyphosate-containing treatments in our study similarly arrested medusahead growth and prevented seed head emergence, which likely decreased one years' worth of seeds within the soil seed bank. In contrast, medusahead in the ADJ and CTRL treatments continued to grow, with prominent seed heads observed during the grazing period of the study. Thus, glyphosate application prior to viable seed production, over multiple application years, may be used to deplete the soil seed bank and provide a viable tool of medusahead control.

Forage Quality and Availability

Herbivores' preferences are not only based on the biochemical characteristics of the forages on offer (i.e., quality), but also on the relative abundance of these forages within the plant community (Stephens and Krebs, 1986). Medusahead and ventenata are fairly new invaders to Utah, and with the addition of other invasive annual grasses (e.g., cheatgrass), are beginning to replace desirable plant species within the plant community (Young and Evans, 1970). This was evident in the treatment plots by the greater biomass availability and foliar cover of these species (> 50% for both variables), with lower abundances for perennial grasses and forbs (Table 4.1 and 4.2). Thus, it would be expected that forages with greater abundance in the plant community would be consumed to a greater extent than those of a lesser abundance, and thus in direct proportion to the relative likelihood of encounter rate (Stephens and Krebs, 1986). However, quality also plays a key role in foraging preferences by livestock, particularly silica, protein, and fiber content.

High concentrations of undigestible amorphous silicon (i.e., silica) in grasses has been proposed as a defense mechanism against herbivory (McNaughton et al., 1985), as it forms a varnish on the epidermis of awns, culms, leaves and glumes (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964), which reduces digestibility of the plant (Hunt et al., 2008; Montes-Sánchez and Villalba, 2017). In support of this, the concentration of acid insoluble ash (AIA), an indicator of silica content in forages (Charca et al., 2007), was high in both medusahead (7.5 to 9.2%, range) and ventenata (5.9 to 7.0%, range; Table 4.3) during the present study.

Sub-lethal doses of glyphosate have been shown to reduce silica concentrations in quack grass (*Elymus repens*) (Coupland and Caseley, 1975), and similar results were predicted to occur for medusahead and ventenata. Nevertheless, glyphosate in any of its treatment forms appeared not to alter the concentration of AIA in either of these plant species. As medusahead matures, silica concentrations in the plant have been reported to decrease by only 1 to 3 percentile units (Swenson et al., 1964), or increase by only 1 percentile unit (Bovey et al., 1961), depending on ecological site. Furthermore, the values of AIA found in this study for ventenata were more than double of the values typically reported (e.g., Pavek et al., 2011), and silica content across phenological stages have not been explored for this species. The elapsed time between pre- and post-chemical application was small (10 d), which could explain the lack of differences in AIA between glyphosate-treated and non-treated plants, particularly when considering that the active ingredient arrests plant growth and that differences in silica content only range between 1 and 3 percentile units across phenological stages. Stronger differences may have occurred if more time elapsed between sampling times.

In addition to alterations in silica content, sub-lethal doses of glyphosate have been shown to preserve the nutritional quality of the treated forages (Siever-Kelly et al., 1999). For instance, glyphosate in the form of its isopropylamine salt was applied at low rates prior to anthesis of annual ryegrass (*Lolium rigidum* Graudin), which subsequently increased nitrogen concentrations, preserved soluble carbohydrates, and increased digestible dry matter compared to untreated plants (Armstrong et al., 1992; Gatford et al., 1999). We used a different glyphosate formulation than the aforementioned study (glyphosate in the form of its potassium salt), although the performance of different glyphosate formulations have been reported to be similar (Hartzler, 2001), thus we expected a similar trend for the nutritional value of glyphosate-treated forages. As grasses mature, protein levels often decline, while concentration of structural carbohydrates (e.g., fiber) increase (Buxton et al., 1995; Van Soest, 1994). Thus, arrested growth of medusahead and other annual grasses was expected to preserve the nutritional quality of the grasses over that of non-glyphosate treated plants. Contrary to these assumptions, CP content did not differ for medusahead, perennial grasses, annual or perennial forbs across treatments and sampling times (Table 4.3). Nevertheless, the glyphosate-containing treatments in medusahead, ventenata, other annual grasses, and in annual forbs promoted reductions in fiber (i.e., acid and neutral detergent fiber; ADF and NDF) contents relative to the CTRL and ADJ treatments, which could be explained by a reduction in the accumulation of structural carbohydrates due to arrested growth (Gatford et al., 1999). In contrast, perennial grasses and perennial forbs showed incremental increases in fiber contents with plant maturity (i.e., 10 days after chemical applications).

Grazing Preference

Grazing has been described as the preferred method for medusahead control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015). Confining sheep at high densities, prior to the emergence of medusahead seed head, was shown to increase consumption of this grass in medusahead-infested rangeland (DiTomaso et al., 2008; Lusk et al., 1961). Nevertheless, utilization of standing medusahead vegetation and litter by livestock is often unsuccessful as grazing animals tend to avoid consuming the grass (Davies and Svejcar, 2008; Hironaka, 1961). However, the interplay between forage abundance and quality in response to the application of glyphosate and its chemical constituents was evident by the pattern of medusahead biomass removal by cattle in this study. Despite the reduced medusahead and annual forb biomass caused by the application of glyphosate-containing chemicals (Table 4.1), livestock removed a greater proportion of medusahead (Fig. 4.1B) and annual forbs (Fig 4.1D) in the glyphosate containing treatments than ADJ or non-treated (CTRL) plots. Medusahead biomass only declined by 2.5% in the CTRL strips from before to after grazing, and it even increased by 21% in the ADJ treatment, suggesting low to nil use (i.e., avoidance), respectively. In contrast, medusahead biomass declined from before to after grazing by 75, 55 and 80% in the GS, RT3 and G (i.e., containing glyphosate treatment plots), respectively. The increased removal of biomass in the glyphosate-treated plots could be partially explained by a greater digestibility of medusahead, attributed to lower fiber (ADF and NDF) content. As fiber levels in plants increase (e.g., due to plant maturation), digestibility has been found to decrease (Buxton and Redfearn, 1997; Van Soest et al., 1991), and thus lower fiber concentration allow for greater energy extraction (i.e., digestion of plant cell solubles) and improved fermentation kinetics (Chapter 5), which collectively increase medusahead palatability (Montes-Sánchez and Villalba, 2017). The same mechanism could explain the greater removal of glyphosate-treated annual forbs as this forage type also displayed lower levels of fiber when treated by the herbicide.

Nevertheless, despite similar reductions in fiber content to that of medusahead, annual grasses other than ventenata only showed a tendency for greater biomass removal in RT3 and G treatments than in CTRL and ADJ, although the GS plot revealed a large increase in biomass for this plant category post-grazing (> 300%). The reason for this low use in the GS plot is unknown, but it could be attributed to the spatial distribution of these plants within the community, likely away from other forage types that animals preferred. Foraging preferences for unpalatable plants by herbivores are influenced by the identity, diversity and chemistry of neighboring plants in the community (Underwood et al., 2014). Glyphosate also reduced fiber contents in ventenata and yet no differences in grass disappearance post-grazing were observed among treatments. It is likely that the delayed maturation of ventenata (i.e., before the appearance of developed awns) compared to that observed in medusahead, or the structural characteristics of the plant (i.e., a tall plant (50 to 70 cm) with a few stems that only branch at the root crown) contributed to the lack of differences in biomass removal through grazing.

Livestock discriminate and display strong preferences for forages of higher nutritional value (Provenza, 1996, 1995), and such discrimination occurs even when differences in nutritional quality among forages are subtle, (i.e., 1% difference in the concentration of soluble carbohydrates) between forage alternatives (Burritt et al., 2005).

Nevertheless, selection of glyphosate-treated forages was not detected in the bite count assessment, except for a tendency on greater number of bites on annual grasses other than ventenata or medusahead in the RT3 plot, and lower number of bites in the ADJ plot (Fig. 4.2C). Bite count determinations were performed during a small portion of the total grazing time (3.5 h out of 10 h per day), and although assessments were done at peaks of foraging activity (morning and evening), they only encompassed a representation of the total foraging events that took place daily. In addition, observers did not assess the size of each bite which could have been greater in the glyphosate-treated than in the CTRL plots given the greater nutritional quality of medusahead in the former treatment.

Bites on medusahead, ventenata and other annual grasses increased towards the last day of the study, reflecting the decline in the relative abundance of perennial grasses and forbs, which were preferred due to their greater nutritional quality. In support of this, there was a decline in the proportion of bites recorded on perennial grasses from the beginning to the end of the grazing period, caused by a decline in their abundance within the community and consequently a decline in the likelihood of encounter rate. Bite counts on annual forbs also declined over the duration of the grazing period, but to a lesser extent than those values recorded for perennial grasses.

Ruminants have evolved cravings and preferences for the taste of salt, in order to satiate their dietary needs for different minerals (Schulkin and Schulkin, 1991). However, when a particular forage or nutrient is consumed in excess (i.e., satiety), a mild to strong aversion can occur (Distel and Villalba, 2018; Provenza, 1996). Cattle had available *ad libitum* amounts of trace mineral blocks, and thus mineral requirements were expected to be met in all animals throughout the study. In this context, avoidance for minerals added to medusahead (i.e., in the form of RT3, GS and ADJ) was expected as ruminants avoid mineral sources present in feeds when their mineral requirements are met (Villalba et al., 2008; Villalba and Provenza, 1996). Despite this assumption, cattle still removed a high proportion of biomass in the salt-containing treatments (e.g., RT3, GS), which was comparable to that observed in the glyphosate-only treatment. Tradeoffs exist when animals graze diverse forages in order to satisfy their multiple and dynamic needs, evident when one nutrient is consumed in excess in order to meet the physiological need for another nutrient which is in deficit (Langhans, 1995). For instance, lambs deficient in energy supply showed greater preferences for flavors associated with sodium propionate than for flavors associated with a vehicle (water), even when they avoided sodium chloride because their physiological needs for sodium were already met (Villalba and Provenza, 1996). Thus, energy-deficient lambs prefer a source of energy (the volatile fatty acid sodium propionate) despite the fact that they avoid sodium when this element is not tied to the calories that they need (i.e., in the form of NaCl). It is likely that the greater nutritional value (i.e., lower fiber contents, greater digestibility) of glyphosate-treated medusahead overrode the effects of satiety imposed by salt in RT3 or GS treatments. In support of this, the application of adjuvant alone, which provided chemicals in the herbicide without improvements in forage quality (i.e., due to the absence of the active ingredient glyphosate) led to forage avoidance. This was evident by observing that biomass of medusahead in the ADJ treatment, which increased after grazing and indicates a very low to nil use of this treatment by cattle. Additionally, medusahead in the RT3 treatment, which also contained the inert ingredient (i.e., adjuvant), was consumed to a relatively lesser extent than other glyphosate containing treatments (G and GS). The adjuvant may provide an undesirable taste dynamic to medusahead, which contributes to reduced grazing selection of this plant, indicated by nil use in the ADJ plot and < 50% in the RT3 plot compared to the other glyphosate containing treatments (Fig. 4.1B).

Animals also tended to spend a greater proportion of their grazing time in the ADJ, CTRL and GS plots (Fig. 4.3). Cattle develop preferences for vegetation patches in heterogenous landscapes, particularly when that vegetation is of greater nutritional quality and bulk density (i.e., quantity of forage) (Bailey, 1995). In addition, when physiological needs are not met, animals tend to search for patches that will satisfy these demands compared to when these needs are met (Egea et al., 2014; Provenza et al., 1998). The difference in residence time across treatments may in part be explained by the increase in searching time for more palatable species in the non-treated plots which also presented a greater bulk density than glyphosate-treated plots and thus more plants to search for preferred species. Despite longer residence times in patches of greater bulk density, cattle ingested very little (CTRL) to nil (ADJ) amounts of forage, evidenced by the high levels of biomass recovered post-grazing.

CONCLUSION

A low-rate of glyphosate application, whether with or without adjuvant or salt (G, GS, RT3), arrested medusahead growth preventing large increases in biomass production (chemical control). In contrast, no chemical application (CTRL) or spraying the adjuvant alone (ADJ) led to large increases in medusahead biomass. All glyphosate containing treatments prevented the emergence of a seed head, which counters viable seed production and contributes to deplete the soil seed bank, particularly when repeated applications occur on medusahead-infested landscapes.

Glyphosate applications did not influence the concentration of crude protein or silica in medusahead plants, although they reduced the concentration of fiber in medusahead and annual forbs relative to non-treated or adjuvant-treated plants. This improvement in nutritional quality enhanced biomass removal after cattle grazing. In contrast, livestock avoided grazing adjuvant-treated medusahead, clearly showing that it was the active ingredient in the herbicide formulations and not the adjuvant that improved nutritional quality of the grass, causing increased medusahead utilization by cattle. Overall, the integrated approach of glyphosate application and grazing, independent of adjuvant and salt, suggests improvements in the forage value of medusahead and represents a novel and efficient alternative to weed control in medusahead-infested landscapes.

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TABLES AND FIGURES

Table 4.1. Biomass availability of associated forage classes across different chemical treatments and sampling times during a grazing study in northern Utah.

Treatments	Pre-chemical	Post-chemical/Pre-Graze	Post-graze
		Medusahead (kg · ha^{-1}dry matter)	
CTRL	128.9 ± 128.1^{abc}	590.4 ± 128.1^{abc}	622.3 ± 128.1^{ab}
ADJ	145.7 ± 128.1^{abc}	443.2 ± 128.1^{a}	564.0 ± 128.1^{ab}
GS	132.0 ± 128.1^{abc}	402.5 ± 128.1^{abc}	140.1 ± 128.1^{abc}
G	110.2 ± 128.1^{abc}	204.1 ± 128.1^{bc}	14.7 ± 128.1^{c}
RT3	70.6 ± 128.1^{bc}	227.4 ± 128.1^{abc}	29.4 ± 128.1^{abc}
		Ventenata (kg · ha^{-1}dry matter)	
CTRL	265.0 ± 133.1	320.8 ± 133.1	114.21 ± 133.1
ADJ	260.9± 133.1	267.5 ± 133.1	58.4 ± 133.1
GS	452.8 ± 133.1	304.1 ± 133.1	82.7 ± 133.1
G	206.6 ± 133.1	273.6 ± 133.1	82.7 ± 133.1
RT3	161.4 ± 133.1	253.8 ± 133.1	170.1 ± 133.1
		Annual Grass (kg · ha^{-1}dry matter)	
CTRL	360.9 ± 118.7^{ab}	576.1 ± 118.7^{a}	377.2 ± 118.7^{ab}
ADJ	415.7 ± 118.7^{ab}	565.5 ± 118.7^{ab}	484.8 ± 118.7^{ab}
GS	304.1 ± 118.7^{ab}	216.8 ± 118.7^{b}	332.0 ± 118.7^{ab}
G	422.8 ± 118.7^{ab}	373.1 ± 118.7^{ab}	90.4 ± 118.7^{b}
RT3	467.0 ± 118.7^{ab}	346.7 ± 118.7^{ab}	169.0 ± 118.7^{ab}
		Perennial Grass (kg · ha^{-1}dry matter)	
CTRL	267.0 ± 104.7^{ab}	202.0 ± 104.7^{ab}	62.9 ± 104.7^{cde}
ADJ	290.9 ± 104.7^{abcde}	219.3 ± 104.7^{abcde}	113.2 ± 104.7^{de}
GS	210.7 ± 104.7^{abcde}	297.5 ± 104.7^{abcd}	148.7 ± 104.7^{bcde}
G	311.2 ± 104.7^{abc}	306.1 ± 104.7^{abcd}	108.6 ± 104.7^{de}
RT3	221.3 ± 104.7^{bcde}	344.2 ± 104.7^{a}	46.2 ± 104.7^{e}
		Annual Forb (kg · ha^{-1}dry matter)	
CTRL	233.0 ± 81.0^{a}	257.9 ± 81.0^{ab}	120.3 ± 81.0^{abc}
ADJ	232.5 ± 81.0^{ab}	418.8 ± 81.0^{a}	146.2 ± 81.0^{bcd}
GS	342.6 ± 81.0^{a}	167.0 ± 81.0^{abc}	45.7 ± 81.0^{cd}
G	420.3 ± 81.0^{ab}	100.0 ± 81.0^{cd}	9.1 ± 81.0^{d}
RT3	256.4 ± 81.0^{ab}	215.2 ± 81.0^{abc}	21.8 ± 81.0^{d}
		Perennial Forb (kg · ha^{-1}dry matter)	
CTRL	116.2 ± 41.1^{ab}	122.3 ± 41.1^{ab}	39.6 ± 41.1^{abc}
ADJ	220.8 ± 41.1^{abc}	32.5 ± 41.1^{bc}	20.3 ± 41.1^{bc}
GS	77.2 ± 41.1^{abc}	108.6 ± 41.1^{abc}	57.9 ± 41.1^{bc}
G	49.7 ± 41.1^{a}	115.7 ± 41.1^{a}	35.5 ± 41.1^{bc}
RT3	79.7 ± 41.1^{abc}	29.9 ± 41.1^{bc}	12.2 ± 41.1^{c}

CTRL = control with no chemical application.

ADJ= the inert ingredients of the herbicide applied at 285.9 mL ha^{-1}.

GS = glyphosate as its potassium salt only applied at 788 g ae ha^{-1}.

G = glyphosate of the herbicide only applied at 788 g ae ha^{-1}.

RT3 = glyphosate as its potassium salt with inert ingredients applied at 788 g ae ha^{-1}.

$^{a-e}$ Means followed by the same superscript within plant type are not different at $P > 0.05$.

Table 4.2. The proportion of vegetation foliar cover within the plant community (as a percent) of different forage types prior to chemical application across five strips during a grazing study conducted in northern Utah.

	Chemical Treatment				
	CTRL	ADJ	GS	G	RT3
	Foliar Cover, %				
Medusahead	9.0	20.8	7.5	22.3	25.6
Ventenata	29.1	26.6	10.4	13.8	29.2
Annual Grass	24.8	12.4	34.5	18.2	5.6
Perennial Grass	10.2	5.7	13.3	7.5	10.7
Annual Forb	13.8	13.9	16.5	17.8	14.1
Perennial Forb	7.6	9.3	7.7	4.7	4.6
Thatch	1.8	8.2	3.0	7.5	5.4
Bare Ground	3.6	3.0	7.1	8.1	4.7

SEM = 2.9
CTRL = control with no chemical application.
ADJ = the inert ingredients of the herbicide applied at 285.9 mL ha^{-1}.
G = glyphosate of the herbicide only applied at 788 g ae ha^{-1}.
GS = glyphosate as its potassium salt only applied at 788 g ae ha^{-1}.
RT3 = glyphosate as its potassium salt with inert ingredients applied at 788 g ae ha^{-1}.

Table 4.3. Nutrient content of different forage types Pre- and Post-herbicide application during a grazing study conducted in northern Utah.

Medusahead (g · kg dry matter)

	CP		ADF		NDF		AIA	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
CTRL	109.0	80.0 ± 5.4	375.0	419.3 ± 12.4	579.0	697.3 ± 7.4^{a}	85.6	92.5 ± 5.4
ADJ	117.0	82.3 ± 4.7	335.0	408.8 ± 10.7	528.0	669.5± 6.4^{a}	80.5	82.8 ± 4.7
GS	98.0	88.5 ± 6.6	395.0	396.5 ± 15.1	601.0	630.0 ± 9.0^{b}	82.7	82.2 ± 6.6
G	119.0	78.0	354.0	395.0	564.0	637.0	78.3	75.3
RT3	100.0	82.0	369.0	391.0	551.0	615.0	76.8	81.7

Ventenata (g · kg dry matter)

	CP		ADF		NDF		AIA	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
CTRL	90.0 ± 6.1^{a}	69.5 ± 6.1^{b}	350.0 ± 11.5	399.0 ± 11.5	575.0 ± 43.6	670.5 ± 43.6	59.8 ± 3.8	60.9 ± 3.8
ADJ	86.5 ± 6.1^{ab}	76.0 ± 6.1^{ab}	369.5 ± 11.5	426.0 ± 11.5	579.0 ± 43.6	664.0 ± 43.6	69.8 ± 3.8	59.2 ± 3.8
GS	85.3 ± 4.3^{a}	68.7 ± 5.0^{b}	366.0 ± 8.1	376.2 ± 11.4	543.5 ± 30.8	620.5 ± 43.6	67.4 ± 2.7	61.5 ± 3.8
RT3	68.8 ± 7.1^{ab}	80.0 ± 6.1^{ab}	360.3 ± 16.1	380.5 ± 11.5	598.0 ± 61.7	608.0 ± 43.6	66.2 ± 5.4	58.8 ± 3.8
G	82.0 ± 6.1^{ab}	80.0 ± 6.1^{ab}	355.5 ± 11.5	380.0 ± 11.5	595.0 ± 43.6	619.0 ± 43.6	69.2 ± 3.8	63.9 ± 3.8

Other Annual Grasses (g · kg dry matter)

	CP		ADF		NDF	
	Pre	Post	Pre	Post	Pre	Post
CTRL	93.5 ± 4.6^{ab}	75.8 ± 4.6^{ab}	328.8 ± 9.2	389.8 ± 9.2	550.0 ± 13.9^{c}	655.0 ± 13.9^{a}
ADJ	92.3 ± 4.6^{ab}	73.3 ± 4.6^{b}	324.0 ± 9.2	378.3 ± 9.2	550.0 ± 13.9^{c}	631.0 ± 13.9^{ab}
GS	87.5 ± 4.6^{ab}	73.8 ± 6.3^{ab}	346.0 ± 9.2	366.2 ± 12.9	569.3 ± 13.9	584.6 ± 19.3^{abc}
RT3	99.5 ± 4.6^{a}	81.3 ± 4.6^{ab}	315.3 ± 9.2	353.5 ± 9.2	544.8 ± 13.9^{c}	578.3 ± 13.9^{bc}
G	88.3 ± 4.6^{ab}	81.8 ± 4.6^{ab}	344.8 ± 9.2	354.3± 9.2	568.0 ± 13.9^{bc}	578.0 ± 13.9^{bc}

Table 4.3. Continued.

	Perennial Grasses (g · kg dry matter)					
	CP		ADF		NDF	
	Pre	Post	Pre	Post	Pre	Post
CTRL	75.5 ± 8.6	74.7 ± 11.8	295.0 ± 14.4	370.6 ± 19.3	517.0 ± 23.7	676.3 ± 33.0
ADJ	71.0 ± 8.6	59.9 ± 11.8	368.5 ± 14.4	357.5± 19.3	683.7 ± 23.7	616 ± 33.0
GS	75.0	63.0	337.0	332.0	576.0	610.0
RT3	96.0 ± 8.6	58.0 ± 8.6	331.0 ± 14.4	339.0 ± 14.4	587.0 ± 23.7	612.5 ± 23.7
G	89.8 ± 6.1	78.4 ± 8.3	337.0 ± 10.2	359.5 ± 13.6	604.5 ± 16.7	633.0 ± 23.4
	Annual Forbs (g · kg dry matter)					
	CP		ADF		NDF	
	Pre	Post	Pre	Post	Pre	Post
CTRL	114.0 ± 9.1	94.5 ± 9.1	332.0 ± 17.8	340.5 ± 17.8	361.5 ± 17.6	384.0 ± 17.6
ADJ	99.2 ± 8.9	98.7 ± 7.5	332.9 ± 17.1	353.7 ± 14.5	367.8 ± 16.9	432.0 ± 14.4
GS	94.0 ± 6.5	114.3 ± 12.3	307.8 ± 12.6	257.4 ± 22.8	358.3 ± 12.5	291.6 ± 22.6
RT3	130.0 ± 7.5	112.9 ± 8.9	286.3 ± 14.5	267.8 ± 17.1	348.0 ± 14.4	343.2 ± 16.9
G	99.7 ± 7.5	116.4 ± 12.3	340.7 ± 14.5	264.4 ± 23.1	373.0 ± 14.4	301.1 ± 22.9
	Perennial Forbs (g · kg dry matter)					
	CP		ADF		NDF	
	Pre	Post	Pre	Post	Pre	Post
CTRL	118.0	137.0	208.0	288.0	267.0	364.0
ADJ	117.5 ± 8.8	99.0 ± 8.8	265.5 ± 29.2	303.0 ± 29.2	333.5 ± 24.3	296.0 ± 24.3
GS	127.5	89.0	350.5	348.0	394.0	384.0
RT3	122.0	107.0	197.0	336.0	251.0	410.0
G	110.0	121.0	225.0	282.0	350.0	344.0

CP = Crude protein.
ADF = Acid detergent fiber.
NDF = Neutral detergent fiber.
AIA = Acid insoluble ash.
CTRL = control with no chemical application.
ADJ = the inert ingredients of the herbicide applied at 285.9 mL ha^{-1}.
G = glyphosate of the herbicide only applied at 788 g ae ha^{-1}.
GS = glyphosate as its potassium salt only applied at 788 g ae ha^{-1}.
RT3 = glyphosate as its potassium salt with inert ingredients applied at 788 g ae ha^{-1}.
$^{a-c}$ Means followed by the same superscript within forage type and nutrient type are not different at P = 0.05.

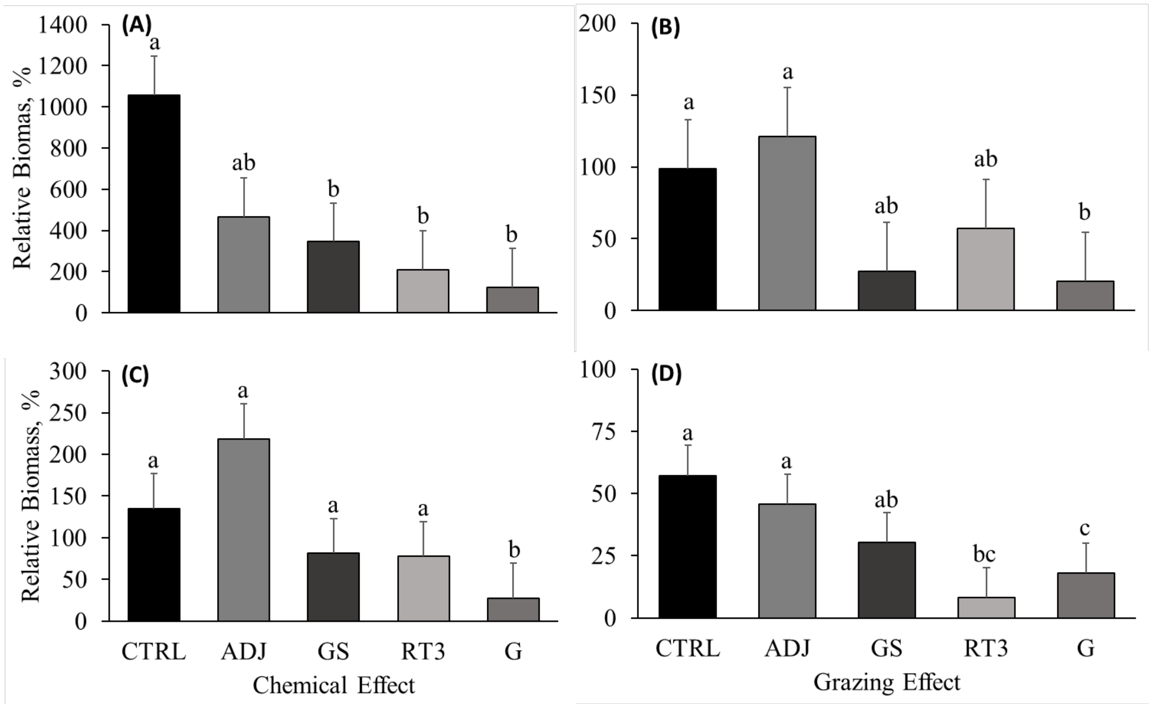

Figure 4.1. Percentage of plant biomass reduction from before to 10-d after herbicide treatment (chemical effect) and from before to after cattle grazed herbicide-treated vegetation in medusahead-infested rangeland. Panels A-B Medusahead (*Taeniatherum caput-medusae* (L.) Nevski; Panels C-D: Annual forbs. Herbicide treatments were applied in strips, such that cattle could select to graze in vegetation treated with: (1) the glyphosate-containing herbicide RT3 Roundup®; (2) glyphosate in the form of its potassium salt with inert ingredients (RT3), (3) glyphosate only (G), (4) glyphosate in the form of its potassium salt without inert ingredients (GS) at 788 g ae ha^{-1}, and (4) inert ingredients (ADJ) at 285.9 mL ha^{-1} (the same quantity in RT3). There was also a control strip with no chemical application (CTRL). Bars represent means for 4 spatial replications with their SEMs. Same letters are not significant ($P > 0.05$).

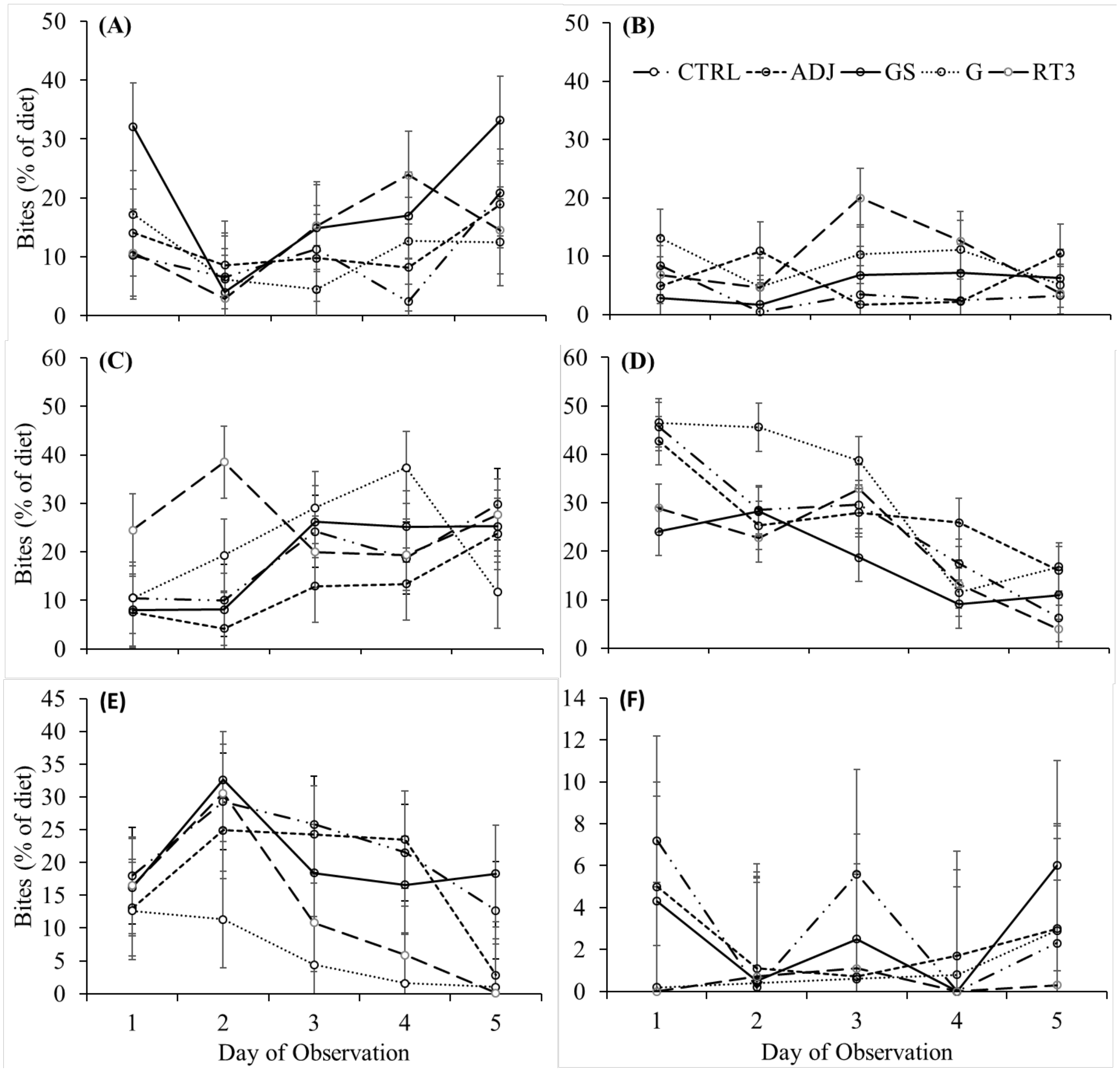

Figure 4.2. Proportion of daily bites on forage types recorded when cattle could choose among five strips of medusahead-infested vegetation previously treated with (1) the herbicide Roundup RT3®, (2) glyphosate only (G), (3) glyphosate in the form of its potassium salt without inert ingredients (GS), and (4) inert ingredients of the herbicide (ADJ). A fifth strip had no chemical application (CTRL). Panel (A) medusahead, Panel (B) ventenata, Panel (C) annual grasses, Panel (D) perennial grasses, Panel (E) annual forbs, and Panel (F) perennial forbs. Points represent means for 4 spatial replications. Vertical bars represent the standard error of the mean.

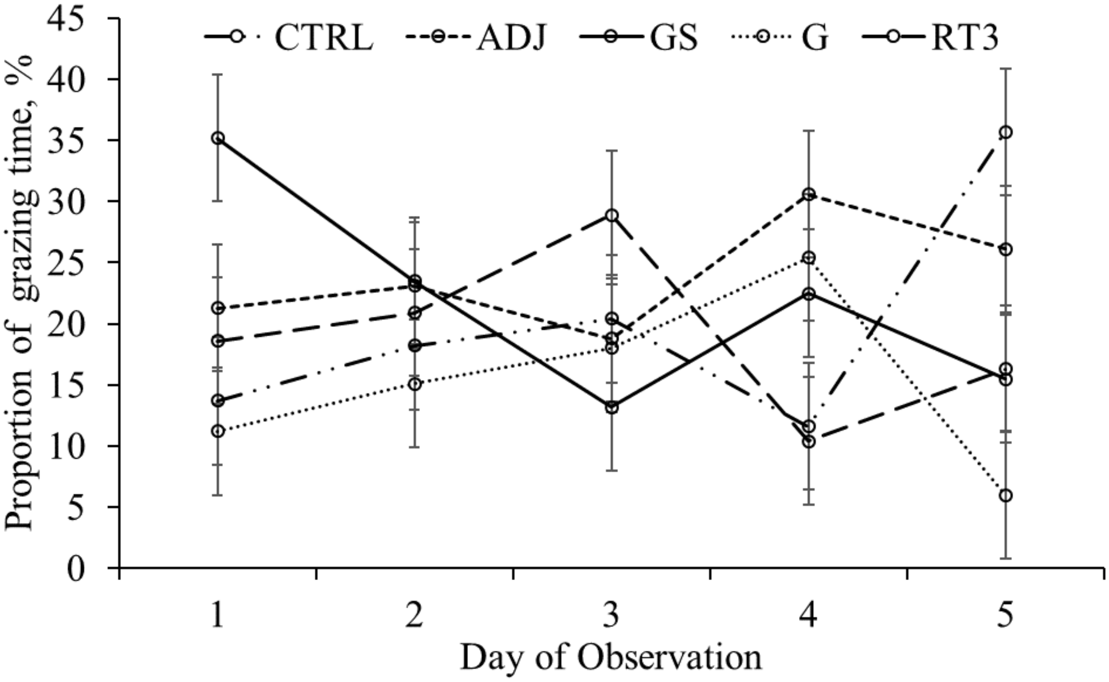

Figure 4.3. Percentage of daily grazing time (residence time) cattle spent in each of five strips of medusahead-infested vegetation previously treated with (1) the herbicide Roundup RT3®, (2) glyphosate only (G), (3) glyphosate in the form of its potassium salt without inert ingredients (GS), and (4) inert ingredients of the herbicide (ADJ). A fifth strip had no chemical application (CTRL). Points represent means for 4 spatial replications. Vertical bars represent the standard error of the mean.

CHAPTER 5

FERMENTATION KINETICS OF MEDUSAHEAD TREATED WITH DIFFERENT GLYPHOSATE RATES AT DIFFERENT PLANT PARTICLE SIZES[5]

ABSTRACT

Medusahead (*Taeniantherum caput-medusae* (L.) Nevski) treated with a glyphosate herbicide has been shown to increase grazing preference by livestock, explained through an arrest in plant growth that preserves nutritional quality. The objective of this study was to determine the *in vitro* apparent digestibility and gas production kinetics of medusahead treated with different glyphosate rates (788 g $ae \cdot ha^{-1}$ (High), 394 g $ae \cdot ha^{-1}$ (Low), and 0 g $ae \cdot ha^{-1}$ (Control; CTRL), and at different plant particle sizes (1, 20, 30, and 40 mm). Medusahead was treated with glyphosate during the late vegetative to early reproductive stage at two locations, Utah (UT) and Washington (WA). *In vitro* gas production from fermentable substrates were measured over 120 h of incubation, and gas production kinetics were adjusted using a single phasic model with three parameters (A, B, C). Apparent digestibility (dDM, dOM) and silica content of the substrates were also determined. Across herbicide rates, medusahead silica concentrations were CTRL > Low > High, and silica was greater for the UT location ($P < 0.05$), whereas apparent digestibility, rates of fermentable gas production, and fermentation efficiency were greater for the WA location ($P < 0.05$). The smallest plant particle size, promoted the greatest apparent digestibility, and rates of fermentation ($P < 0.05$), whereas the High and Low herbicide rates led to greater apparent digestibility,

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[5] Co-authored with Clint Stonecipher

rates of fermentation and fermentation efficiencies ($P < 0.05$). These results suggest that the lowest particle size and herbicide treatments improved the digestion of medusahead, explaining in part the greater palatability of the grass. Increased particle sizes also impinged an inhibitory effect on medusahead digestibility, which may also explain the typically low and variable medusahead intakes by livestock. Increasing the digestibility of medusahead through herbicide application shows promise as a control tool for managing the weed within the plant community.

1. Introduction

Medusahead (*Taeniatherum caput-medusae* (L.) Nevski) is currently one of the most detrimental invasive plants impacting western rangeland sustainability and livestock operations (Davies and Johnson, 2008; Miller et al., 1999; Young, 1992); it decreases the abundance and quality of forage available to livestock and wildlife, negatively impacts plant diversity, and increases the frequency of fires (Davies and Johnson, 2008). These negative effects are further compounded by the fact that traditional control techniques (i.e., mechanical, cultural, and chemical) are often unsuccessful.

Livestock grazing has been shown to be the preferred method of medusahead management and control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015). However, livestock utilization of standing medusahead vegetation and litter is often low as grazing animals tend to avoid consuming the grass (Davies and Svejcar, 2008; Hironaka, 1961). Such avoidance is in part due to the high concentration of silica in the plant's tissues (Hamilton et al., 2015; Swenson et al., 1964), which interferes with cell wall digestion (Van Soest 1994) and creates an undesirable oral texture (McNaughton 1985). Herbicide treatments of 2, 4-D, tebuthiuron, picloram, and glyphosate have been shown to increase palatability of treated plants (Kisseberth et al., 1986; Scifres et al., 1983), attributed to a delay in loss of water-soluble carbohydrates and an increase in *in vitro* dry matter digestibility caused by arrested plant growth (Gatford et al., 1999). In addition, arrested plant growth due to inhibition of plant metabolic pathways prevents the accumulation of plant defenses and antinutritional compounds (Fedtke, 2012) such as silica, which also contributes to enhance palatability of the grass.

Previous studies have shown that medusahead has a fairly high nutritional value (Hamilton et al., 2015; Villalba and Burritt 2015), which is in stark contrast to its low palatability. In fact, the dry matter digestibility of medusahead at 48 h (60-75%) is comparable to or greater than values reported for much more palatable forages such as tall fescue (*Festuca arundinacea*) or alfalfa (*Medicago sativa*) hay (Montes-Sánchez and Villalba, 2017). The epidermal silicon in plants comprises a varnish that limits the degradation of unsilicified organic constituents beneath (Van Soest and Jones 1968; Mayland and Shewmaker 2001; P. J. Van Soest 2006). In addition, the silicified cuticle layer and cell wall may work as a hard physical barrier resistant to mechanical breakdown (i.e., through chewing and rumination), constraining particle size reduction and thus the digestion rate of feed particles in the rumen (Bae et al., 1997; Hunt et al., 2008; Van Soest, 1994). These effects negatively impact food intake and preference by livestock (Allen, 1996). Classical estimates of digestibility do not consider these variables and thus overestimate “real” digestibility values of the grass. For instance, the typical grinding process before analyses (e.g., to 1 mm particle size) creates an artifact that increases surface area, which reduces the aforementioned inhibitory effects of the epidermal coating of silica on medusahead digestibility (Montes-Sánchez and Villalba, 2017).

The *in vitro* fermentation kinetics of forages is a more reliable predictor of nutritional value than estimates of forage digestibility as it considers the speed at which forages are fermented, instead of just the final extent of fermentation (Van Soest 1994). Quantitative expressions of the kinetics of digestion are needed to more precisely estimate the quantity and composition of nutrients digested from feeds and their subsequent efficiency of utilization by the animal (Mertens, 1993). In addition, the *in vitro* kinetics of forage fermentation at different particle sizes of the substrate may represent a more reliable estimate of medusahead utilization by livestock because such tests reduce the bias induced by grinding the forage to a powder that masks the inhibitory (structural) effects of silica on forage fermentation.

Thus, the objectives of this study were to 1) determine the nutritional composition and digestibility of medusahead treated with glyphosate using different herbicide rates at different locations across the intermountain U.S, and 2) determine if particle length of medusahead plays a role in digestibility of the herbicide-treated plant material.

2. Materials and methods

Fermentable substrate gas production kinetics and apparent digestibility was determined using the gas production technique described by Theodorou et al., (1994), and modified by Mauricio et al. (1999).

2.1. Substrates and experimental design

Four replicated medusahead-infested areas (12 x 15 m) arranged side-by-side in Ritzville, WA (47º03.86’N, 118º13.51’W, 522 m) within a 97 ha pasture and three replicated plots (18 x 15 m) in the foothills of Mantua, UT (41º31.38'N, 111º55.33'W, 1686 m), also arranged side-by-side, within a 210 ha pasture were selected to collect plant material for the study. The Washington site (WA) soil consists of a coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic typic hapoxeroll (Benge very stony silt loam) within a 254-406 mm precipitation zone and has been degraded to consist primarily of invasive annual grasses, of which medusahead comprised ~60 percent of the vegetation cover (Chapter 2). The Utah site (UT) consisted of a Mountain Stony Loam ecological site with stony, cobbly, or gravelly loam, Xerolls soil (Goring-Yeates Hollow association) in a 457 mm precipitation zone with invasive annual grasses beginning to take over the plant community, of which medusahead comprised ~30 percent of the vegetation cover (Chapter 4).

Each plot was sub-divided into three treatment areas of 3 x 15 m (WA location) and 6 x 15 m (UT location). Each area then received one of three application rates of glyphosate in the form of its potassium salt (Roundup RT 3$^{(R)}$; Bayer Crop Science, Lenexa, KS, USA): 1) 0 g ae ha^{-1} (CTRL), 2) 394 g ae ha^{-1} (Low), and 3) 788 g ae ha^{-1} (High). Herbicide application took place on April 26, 2016 at the WA site, while medusahead was in the mid-vegetative phenological stage, and on June 2, 2016 at the UT location, while medusahead was in the late vegetative phenological stage. All vegetation within each plot and replicated area was hand-harvested by clipping plants to a 1 cm stubble height, 15 d post-herbicide application at the WA location and 10 d post-herbicide application at the UT location. Samples were subsequently sorted to only include medusahead plants. Non-herbicide treated medusahead in WA had progressed to the late vegetative phenological stage upon collection and to the early reproductive phenological stage in UT, whereas treated plants remained in the phenological stage at which the chemical application occurred.

Representative samples of medusahead from each replicated plot, herbicide treatment, and location were ground using a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 1 mm screen for nutritional analyses. Additional samples were composited across replicated areas and representative samples were subsequently prepared at different particle sizes: 1) ground in a Wiley mill to pass through a 1 mm screen, or hand-cut to particle sizes of 2) 20, 3) 30, and 4) 40 mm (4 particle sizes) for both locations for the fermentation kinetics study. An in-house alfalfa hay standard was obtained from the Poisonous Plants Research Laboratory (Logan, UT, USA) in order to compare the consistency of digestibility across runs.

Four hundred milligrams of each herbicide-treated substrate at different particle sizes at the two locations were weighed in small aluminum cups and placed in 125 mL serum flasks (Wheaton, Boston, USA) in triplicate. A total of 72 flasks of medusahead substrate (24 treatments x 3 replicates) plus 3 blanks and 3 alfalfa standards were incubated in each run, and 4 sequential runs were conducted during the study.

2.2. Inoculum

Rumen fluid was collected the day of gas production measurements. The inoculum was taken 4 h post-feeding from a rumen-cannulated Angus cow fed an *ad libitum* diet of tall fescue hay fed at 0700 h (Utah State University Institutional Animal Care and Use Committee, Approval #10196). Rumen liquid and contents were placed in a pre-warmed (39º C) thermal flask of 2 L. The inoculum was immediately transported to the laboratory, homogenized in a commercial blender (Waring 34BL97; New Hartford, CT), strained through four layers of cheesecloth, and kept in a water bath at 39º C with a constant flow of CO_2. Rumen fluid pH was measured and averaged 6.6 ± 0.3 (Poteneiometer HI 991002; Hanna Instruments, Woonsocket, RI, USA).

2.3. In vitro fermentation procedure and gas production measurements

Forty mL of buffer medium was prepared with deionized water according to Menke and Steingass (1988) and added to each 125 mL serum flasks. The buffer medium consisted of micro- and macro-mineral solutions, artificial saliva, reducing solution and resazurin (Sigma-Aldrich, Milwaukee, WI, USA). Flasks were subsequently flushed for five seconds with CO_2 before being sealed with 20 mm butyl rubber stoppers and aluminum crimp caps (Wheaton Cia, Boston, USA). Sealed flasks were stored overnight at 4º C. The following morning, serum bottles were warmed in an incubator to 39º C and 20 mL of collected rumen fluid was injected into the sealed flasks. Upon injection, this was considered time zero where the incubation process began. The extra gas pressure from injection of the inoculum was allowed to escape prior to removing the needle from the stopper. Flasks were then gently swirled to homogenize the contents and placed in a preheated incubator (Percival, Boone, IA, USA) at 39º C.

Head-space gas pressure was measured (psi unit) using a USB output pressure transducer (PX409-015GUSBH; Omega Engineering Inc., Stamford, CT, USA) connected to a PC that enabled to chart, log, display, and output the data coming from the transducer (Mauricio et al., 1999). Readings were taken at 2, 4, 6, 8, 10, 12, 18, 24, 36, 48, 72, 96, and 120 h during the incubation period, using a 23-gauge needle inserted through the rubber stoppers which was attached to the transducer using a luer fitting-type connector. After each reading, gas pressure was allowed to return to zero before removing the needle. Upon completion of the last reading, flasks were placed in a refrigerator at 4º C to halt the digestion process and contents were immediately filtered for substrate disappearance.

2.4. Apparent digestibility

In situ digestion bags (5 x 10 cm, 50 µ porosity; Ankom Technologies, Macedon, NY, USA), were weighed prior to transferring the digestion residual into individual bags. Digestion bags were rinsed with deionized water until the water became clear, sealed with a heat sealer (120v 50/60HZ; Ankom Technologies, Macedon, NY, USA), and subsequently dried in a forced air oven at 60º C to constant weight. Residual dry matter weights were determined by subtracting the empty bag weight from the residual dry matter weights. Dry matter disappearance (dDM) was determined by differences between the original substrate weight and residue dry matter weight, adjusted by the blank residual weight. Organic matter disappearance (dOM) was determined by differences between the ash weight of fermentation residuals and residual dry matter weight and subtracting the difference from the substrate organic matter (OM) weight (see chemical analyses section below for the ashing procedure and OM determination).

2.5. Fermentation kinetics parameters

Gas pressure values for each incubation time were converted to gas volume using the equation reported by Frutos et al., (2002) (Gas volume (mL) = 5.3407 x gas pressure (psi)). Gas volumes were corrected by the amount of the amount of OM incubated and gas pressure of the blanks (ruminal fluid plus buffer medium without substrate). The gas production parameters were estimated using a single phasic model of Groot et al., (1996):

$G = A/(1 + (B^{c}/t^{c}))$ where G represents the amount of gas produced (mL) per gram of organic matter incubated at time t after the beginning of the incubation; parameter A is the asymptotic gas production (mL per gram of OM); parameter B (h) is the time after starting the incubation at which half of the asymptotic amount of gas has been formed; and parameter C is a constant determining the sharpness of the switching characteristics of the curve. As the value of parameter C increases, the curve becomes sigmoidal with an increasing slope, and both B and C parameters indicate the fermentation rate of the substrate. The maximum rate of gas production (R_{max}; R_{max} (mL h^{-1}) = $(A*B^{C}*C*T_{max}^{(-C-1)})/((1 + B^{C}*T_{max}^{-C})^{2}))$ and the time at which it occurs (T_{max}; T_{max} (h) = $B*(((C-1)/(C+1))^{1/C}))$ were calculated according to the equations proposed by Bauer et al., (2001). Finally, substrate disappearance allows for the calculation of a partitioning factor (PF) (Blümmel et al., 1997), which relates the amount of dOM to the final gas volume produced by such amount, providing an estimate of fermentation efficiency.

2.6. Chemical analyses

Medusahead substrates were analyzed for crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), organic matter (OM), ash, silica (Si) content. Nitrogen (N) content was determined using the combustion method (AOAC, 2000: method 990.03) using a Leco FP-528 Series Nitrogen Analyzer (Leco Corp., St. Joseph, MO). Crude protein (CP) was determined by multiplying N content x 6.25. Neutral detergent fiber and ADF was analyzed using procedures modified for use in an ANKOM-200 fiber analyzer (ANKOM Technologies Corp., Fairport, NY) according to Van Soest et al., (1991). Ash concentrations were obtained by burning substrates at 550º C for 6 h (Allen, 1989) in a muffled furnace. The OM content was determined by calculating the difference between substrate ash content and the original substrate dry matter weight, corrected by an empty ashed bag weight. Silica is quantitatively recovered in the ADF residues (Van Soest, 1994); thus, ADF residues were incinerated in a muffled furnace to measure Si concentration in the samples (550º C for 6 h).

2.7. Statistical analyses

Treatments consisted of a combination of two locations, three herbicide rates, and four particle sizes. Substrates and blanks were run four times per treatment (experimental unit), on different weeks with three serum bottles (measurement units) per treatment, totaling 72 bottles per run. Gas production parameters were estimated using PROC NLIN in SAS/STAT (SAS Inst., Inc. Cary, NC; Version 9.4 for Windows) with A = 200, B = 20, and C = 1, as initial values.

The dDM and dOM, fermentation kinetics parameters (A, B, and C), R_{Max}, T_{Max}, and PF were compared using a three-way factorial mixed model with location, herbicide rate, and particle size as the fixed factors and run as the random effect. Nutritional content of substrates (CP, NDF, ADF, OM, Ash, and Si) were analyzed using a two-way factorial mixed model with location and herbicide rate as the fixed factors and spatial replication as the random effect. Analysis were performed using PROC GLIMMIX in SAS. The model diagnostics included testing for a normal distribution and homoscedasticity. Data was transformed when needed according to the Box-Cox method but non-transformed data is reported (mean ± standard error of mean). Least square means (LSMeans) were compared using Tukey's multiple comparison test when F-ratios were significant ($P < 0.05$) and reported with their standard error of means (SEM).

Differences among LSMeans with $P < 0.05$ were considered statistically significant. A trend was considered when $0.10 > P > 0.05$.

3. Results

3.1. Nutritional composition

Nutritional composition of medusahead treated with different rates of glyphosate at two locations in the Intermountain West are reported in Table 5.1. The crude protein (CP) content of medusahead across locations was the greatest at the Low herbicide rate (herbicide rate effect: $P < 0.001$). The Washington (WA) location displayed greater CP contents across all herbicide rates than the UT location (location effect: $P < 0.001$). The CTRL and Low herbicide rate in WA revealed similar and the greatest CP contents, whereas the CTRL treatment in UT displayed the lowest CP concentrations (herbicide rate by location interaction: $P < 0.001$).

The neutral detergent fiber (NDF) content of medusahead across locations for the different herbicide treatments was the highest for CTRL (herbicide rate effect: $P < 0.001$). The UT location across all herbicide rates (location effect: $P < 0.001$), and the CTRL treatment in UT displayed the greatest NDF concentrations, whereas the High and Low herbicide rates in WA showed the lowest values recorded (herbicide rate by location interaction: $P < 0.001$).

The acid detergent fiber (ADF) content of medusahead across locations for the different herbicide rates was High > CTRL > Low (herbicide rate effect: $P < 0.001$). The WA location displayed the lowest ADF contents across all herbicide rates (location effect: $P < 0.001$), and the High herbicide rate in UT had the greatest ADF contents, whereas the High herbicide rate in WA showed the lowest concentration (herbicide rate by location interaction: $P < 0.001$).

The organic matter (OM) content for medusahead across locations for the different herbicide rates was Low > CTRL > High (herbicide rate effect: $P <0.001$). The WA location displayed greater OM contents ($P < 0.001$), and Low and CTRL herbicide rates in WA revealed the greatest OM percentages (herbicide rate by location interaction: $P < 0.001$).

The ash contents of medusahead across locations for the different herbicide rates was High > CTRL > Low (herbicide rate effect: $P < 0.001$). The UT location showed greater ash contents across herbicide rates (location effect: $P < 0.001$), and the CTRL and Low herbicide rate in WA revealed the lowest values (herbicide rate by location interaction: $P < 0.001$).

The silica content of medusahead across locations for the different herbicide rates was CTRL > Low > High (herbicide rate effect: $P = 0.006$). The UT location showed greater silica contents across herbicide rates (location effect: $P < 0.001$), with the High herbicide treatment displaying the greatest concentrations, and the opposite pattern occurring for the WA location (herbicide rate by location interaction: $P < 0.001$).

3.2. Apparent digestibility

Apparent digestibilities of dry matter (dDM) and organic matter (dOM) of treated medusahead are reported in Table 5.2. Final gas production volumes of the alfalfa standard were fairly consistent across runs (ranging between 57.8 and 68.8 mL).

The application of glyphosate to medusahead increased dDM across particle sizes and locations with Low > High > CTRL (herbicide rate effect: $P < 0.001$). The smallest particle size (1 mm) and samples collected at the WA location revealed the greatest dDM (particle size effect: $P < 0.001$; location effect: $P < 0.001$). Regardless of location, particles > 1 mm and without herbicide application (CTRL) led to lower dDM (herbicide rate by particle size interaction: $P < 0.045$; particle size by location interaction: $P < 0.001$). The WA location showed greater values of dDM regardless of herbicide rates (location effect: $P < 0.001$), whereas no herbicide application (CTRL) at the UT location displayed the lowest values of this parameter (herbicide rate by location interaction: $P < 0.001$). Finally, the smallest particle size (1 mm) promoted the greatest dDM, regardless of herbicide rate or location, whereas medusahead collected at the UT location with no herbicide application and > 1 mm particle size led to the lowest observed values of this parameter (herbicide rate by particle size by location interaction: $P = 0.003$).

The same pattern described above for herbicide rate, particle size, location, and their interactions was observed for dOM ($P < 0.05$), except that no interaction of herbicide rate by particle size was detected ($P = 0.146$), so that regardless of rate of herbicide application or location, particles > 1 mm led to lower dOM ($P < 0.05$).

3.3. Fermentation kinetics parameters

The parameters describing the cumulative gas production for medusahead treatments are reported in Table 5.2, and gas production curves are reported in Figs. 1 and 2. The application of glyphosate to medusahead increased the asymptotic gas production parameter (A) across particle sizes and locations with High > Low > CTRL rate (herbicide rate effect: $P < 0.001$). Regardless of herbicide rate or location, the smallest particle size (1 mm) led to the lowest values of parameter A, while the 20 mm size revealed the greatest value of this parameter (particle size effect: $P < 0.001$; herbicide rate by particle size interaction: $P = 0.005$). No differences between locations were detected for parameter A across herbicide rates or particle sizes ($P = 0.788$), and no particle size by location interaction was detected ($P = 0.875$). Averaged across particle sizes, the High and Low herbicide rates revealed the greatest A values for the UT location (herbicide rate by location interaction: $P < 0.001$).

Parameter B (time at which half of the asymptotic amount of gas was produced) across particle sizes and locations was High > Low = CTRL (herbicide rate effect: $P = 0.001$). As observed for parameter A, the smallest particle size (1 mm) led to the lowest values of parameter B, regardless of herbicide rate or location (particle size effect: $P < 0.001$; herbicide rate x particle size interaction; $P = 0.058$). There were no differences between locations across herbicide rates and particle sizes for parameter B ($P = 0.788$), and no herbicide rate by location and particle size by location interactions was detected ($P > 0.05$).

The sharpness of the switching characteristics of the gas production curve (C) across particle sizes and locations was CTRL > Low = High (herbicide rate effect: $P < 0.001$). Regardless of herbicide rate or location, the 1 mm particle size showed the greatest parameter C values (particle size effect: $P < 0.001$; herbicide rate by particle size interaction: $P <0.001$; particle size by location interaction: P < 0.001). Additionally, the UT location showed greater parameter C values across herbicide rates and locations (location effect: $P < 0.001$). Finally, the UT location with greater particle sizes and the Low and High herbicide rates showed greater values of parameter C (herbicide rate by particle size by location interaction: $P < 0.001$).

The maximum gas production rate (R_{Max}) across particle sizes and locations was

Low > High = CTRL (herbicide rate effect: *P* < 0.001; Table 5.2, Fig. 5.2). The smallest particle size (1 mm) led to the greatest R_{Max} values, regardless of herbicide rate or location (particle size effect: *P* < 0.001; particle size by location interaction: P = 0.008; Fig. 5.1), and no herbicide rate by particle size interaction was detected (*P* = 0.662). The WA location produced a greater RMax (location effect: P < 0.001) across herbicide rates and particle sizes, whereas the CTRL and High herbicide rates in UT revealed the lowest values (herbicide rate by location interaction: *P* = 0.019). Finally, greater particle sizes in UT led to the lowest R_{Max} values (herbicide rate by particle size by location interaction: *P* = 0.004).

The time (h) at which maximum gas production rate occurs (T_{Max}) across particle sizes and locations was CTRL > High = Low (herbicide rate effect: *P* < 0.001; Fig. 5.1), and 40 > 1 = 30 > 20 mm for different particle sizes across locations and herbicide rates (particle size effect: *P* = 0.032; herbicide rate by particle size interaction: P < 0.001; Fig. 5.2). The UT location displayed higher T_{Max} values than the WA location averaged across herbicide rates and particle sizes (location effect: *P* < 0.001; herbicide rate by location interaction: *P* < 0.001), and particles > 1 mm in WA also led to the lower values (herbicide rate by location interaction: *P* < 0.001). Finally, CTRL in UT at larger particle sizes led to greater T_{Max} values (herbicide rate by particle size by location interaction: *P* = 0.001).

The estimate of fermentation efficiency (PF) averaged across particle sizes and locations was High > Low > CTRL rate (herbicide rate effect: *P* = 0.014), but there were no differences among particle sizes (*P* = 0.224) and no herbicide rate by particle size interaction was detected for this parameter (*P* = 0.763). The WA location led to greater

PF values averaged across herbicide rates and particle sizes (location effect: $P = 0.016$), and the High and Low treatments at this location also promoted greater values (herbicide rate by location interaction: $P = 0.005$). No particle size by location interaction ($P = 0.246$), and no herbicide rate by particle size by location interaction (P = 0.283) were detected for the PF parameter.

4. Discussion

4.1. Nutritional composition

We determined whether the application of a glyphosate-containing herbicide to the unpalatable grass medusahead would preserve the nutritional quality of the plant due to the reported arrest in plant growth caused by this chemical on annual grasses (Gatford et al., 1999). The unpalatability of medusahead is in part explained by the presence of high concentrations of undigestible amorphous silicon (i.e., silica), which forms a varnish on the epidermis of awns, culms, leaves and glumes (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964) reducing the digestibility of the plant in the rumen (Hamilton et al., 2015; Hunt et al., 2008; Montes-Sánchez and Villalba, 2017). Previous studies have reported concentrations of silica in medusahead ranging between 6 and 16 % DM (Bovey et al., 1961; Hamilton et al., 2015; Montes-Sánchez et al., 2017; Montes-Sánchez and Villalba, 2017; Swenson et al., 1964; Villalba and Burritt, 2015), consistent with concentrations observed in this study (6.5 to 7.5 percent; Table 5.1).

Sub-lethal doses of glyphosate have been shown to reduce silica concentrations in quack grass (*Elymus repens*) (Coupland and Caseley, 1975), and similar results were predicted to occur for medusahead. Consistent with this idea, glyphosate applications at the High rate reduced silica concentrations (e.g., by ~ 1 percentile unit), and although significant, this difference resulted in a concentration that was still high, and was likely not enough to overcome the reduced intakes typically observed by livestock consuming this grass (Hamilton et al., 2015; Montes-Sánchez et al., 2017). As medusahead matures, silica concentrations in the plant have been reported to decrease by only 1 to 3 percentile units (Swenson et al., 1964), or increase by approximately 1 percentile unit (Bovey et al., 1961), depending on location. The elapsed time between chemical application and forage sampling was short (10 and 15 d), which in addition to the small changes reported for silica content throughout the plant's phenology, may explain the small differences in silica concentration observed between treated and non-treated medusahead plants in this study.

As grasses mature, protein levels often decline, while concentration of structural carbohydrates (e.g., fiber) increase (Buxton et al., 1995; Van Soest, 1994). Glyphosate is a non-selective herbicide that targets the shikimate pathway and inhibits enzyme production for plant growth (Franz et al., 1997). Thus, as non-treated medusahead plants continued to mature, glyphosate-treated plants experienced an arrest in growth that preserved the contents of crude protein (CP) and fiber, explaining the differences observed between treated and control plants. As predicted, CP concentration at the Utah (UT) location was greater in for glyphosate-treated than in non-treated medusahead, but this difference was absent in Washington (WA); in fact, CP content declined at this location with the application of herbicide relative to no chemical treatment (CTRL). This contrasting responses across locations may be explained by the different phenological stages at which glyphosate was applied in UT and WA. For instance, medusahead is known to mature rapidly (i.e., bolting), going from the vegetative stage to the presence of seed head within a time frame of 2-4 weeks (Brownsey et al., 2017; Young, 1992). Since herbicide application at the UT location occurred during the late vegetative phenological stage, it is likely that the CTRL plants began to lose nitrogen content with continued maturation (i.e., leading to greater nitrogen content in glyphosate-treated plants with arrested growth), whereas plants at the WA location were treated at the mid-vegetative phenological stage, when the process of nitrogen accumulation was still occurring (i.e., leading to greater nitrogen content in CTRL plants). Furthermore, and as predicted, fiber content (neutral and acid detergent fiber; NDF and ADF) in general decreased with glyphosate application, with the exception of ADF for the High herbicide rate which increased. Greater organic matter (OM) and lower ash contents in glyphosate-treated plants were also in line with a preservation of nutritional quality due to arrested growth by chemical application, although differences were small (~ 1 percentile unit), which may not represent the main reason for improved palatability in glyphosate-treated plants.

Low rates of glyphosate have been shown to increase digestible dry matter (dDM) of annual rye grass pastures and incremental increases in herbicide rate (0, 45, 90, 180, and 360 g ai · ha^{-1}) were positively correlated with incremental increases in dDM (Gatford et al., 1999). Thus, the High herbicide rate was expected to increase digestibility to a greater extent than the Low rate in this study. Contrary to this assumption, the Low herbicide rate appeared to have preserved the nutritional quality of medusahead to a greater extent than the High rate (e.g., greater CP and OM contents, lower ash and ADF contents). It is possible that the different rates at which growth was arrested in response to the different doses of herbicide allowed for different rates of preservation, favoring the

Low treatment. For instance, lower rates of glyphosate may allow for delayed plant death compared to higher rates, thus allowing for accumulation of nutrients but preventing those nutrients from being metabolized in to cellular structures (i.e., lignin or fiber synthesis) (Gatford et al., 1999). Furthermore, the High rate in this study was more than double the highest rate applied by aforementioned study suggesting that a threshold of herbicide rate may exist beyond which the nutritive value of the sprayed plant begins to decline rather than just preserve nutrient contents.

4.2. Particle size

Particle size had the greatest influence on apparent digestibility and gas production parameters, followed by herbicide application at the two locations. Mastication of forages is the primary means by which particle sizes are reduced prior to entering the rumen, thus increasing the digestion efficiency and passage rate (Allen, 1996). Nevertheless, silica has been associated with resistance to mechanical breakdown (Hunt et al., 2008), which reduces the rate and efficiency of particle size reduction and thus the digestibility of the forage (Mayland and Shewmaker, 2001; Van Soest and Jones, 1968). Van Soest and Jones (1968) demonstrated that for every unit of increase in silica content there is a 3 unit decrease in digestibility of grasses, attributed to constraints in particle size reduction. Furthermore, Welch (1967) demonstrated that when 150 g of longer indigestible fibers (7 cm) were placed in the rumen of sheep, intake of chopped alfalfa decreased by 30 percent. Classical estimates of digestibility do not take into consideration the limitations associated with the mechanical reduction of particle sizes through mastication, particularly for plants that possess anti-nutritional factors such as lignin or silica. For instance, the typical grinding process before digestion analyses (e.g., reduction of particles to a size of 1 mm) creates an artifact that increases the surface area per unit of mass, and thus overestimates “real” digestibility values. The effect of the grinding process was evident with the 1 mm particle size increasing dDM and digestible organic matter (dOM) by approximately 6 and 4 percentile units, respectively, over that of larger particles (Table 5.2). No differences in digestibility were observed when particles increased in size from 20 to 40 mm, suggesting that above the threshold of 1mm, particle size did not have an influence on this parameter.

Forage selection by livestock is directly related to greater amounts of gas production within the first 8 h after intake (e.g., digestion of substrates encompassing the fraction of highly digestible cell solubles), and less gas production later in digestion (e.g., digestion of structural carbohydrates), which contributes to greater energy production and reduced gut fill (Blümmel et al., 2005). Therefore, the shorter time to reach the asymptote (smaller values of parameter B) corresponds to greater rates of gas production at earlier stages of incubation, which parallels with increments in forage intake (Blümmel et al., 2005), reflected in this study for the lower values of parameter B obtained with the substrate at 1 mm particle size. It took 3 to 4 times longer to reach half the amount of gas produced by larger-particle substrates than by the 1 mm particle size (Table 5.2). Likewise, the greater rates of fermentation at earlier stages of incubation for substrates at 1 mm particle size were also reflected in lower values of parameter A (the amount of gas produced; asymptote) and greater values of parameter C (sharpness of the curve). These values indicate there was rapid initial increases in fermentation (relative to larger particles), but the extent of fermentation over the duration of the incubation period was lower as a consequence of artificially reducing the larger fermentable structural carbohydrates through the grinding process, and thus instead of experiencing digestion later in the fermentation process, the finely ground structural carbohydrates were likely digested within a time frame that was closer to fermentation of cell solubles. In contrast, the larger particle sizes produced more gas later in the incubation period as structural carbohydrates were being digested, evidenced by greater values of parameters A and B, and lower values of parameter C.

With an increasing gradient of particle sizes of substrates, it would be expected that parameters A, B, and C would respond similarly across a gradient of magnitudes. Contrarily, particle sizes did not display this gradient. In fact, the opposite gradient occurred, with the 20 mm particle size displaying the greatest values for parameter A and B, and the lowest values for parameter C. As particle size increased (i.e., from 20 to 40 mm) parameters A and B decreased while parameter C increased. Nevertheless, differences between 20, 30, and 40 mm were much less pronounced than differences between 1 mm and the rest of the particle sizes assayed. These values are in line with a previous *in vitro* gas production kinetics study for medusahead (Montes-Sánchez and Villalba, 2017), suggesting that reduction of medusahead particle size plays a significant role in fermentation kinetics and possibly contribute to greater consumption of medusahead by livestock.

Similar to values observed for parameters A, B, and C at 1 mm particle size, there was a greater maximum gas production rate (R_{Max}) for this small particle size, which would indicate a greater initial digestibility, contributing to the greater likelihood of the forage being consumed (Blümmel et al., 2005). Nevertheless, T_{Max} values (maximum time at which R_{Max} occurs) were similar for the 1 and 30 mm particle sizes, and the same gradient for the larger particle sizes and parameters described previously was displayed for T_{Max} (i.e., 20 > 30 > 40). Furthermore, there were no differences in the fermentation efficiency (PF), likely as a consequence of the extended incubation time (120 h), which diluted differences among the different particle sizes assayed. Regardless of location, the substrate at 1 mm particle size produced ~33% more gas per h than substrates formed with larger particles even though T_{Max} and PF values did not reflect this difference.

4.3. Herbicide rate

Herbicide rate increased the apparent digestibility and the fermentation efficiency of medusahead (assessed by parameter PF; High rate; Table 5.2). Sub-lethal doses of glyphosate have been shown to reduce silica concentrations in quack grass (Coupland and Caseley, 1975), and increase *in vitro* dry matter digestibility in annual rye grass (Gatford et al., 1999). Increases in digestibility of glyphosate-treated annual ryegrass were attributed to the disruption or arrest of the lignification process. Alteration in the lignin structural complex may have weakened the fibrous bonds within the plant, thus allowing for increased digestibility. Furthermore, decreases in fiber content with the application of glyphosate likely increased the efficiency of digestion of medusahead with an approximate 4 to 5 percentile unit increase in dDM and dOM (Fig. 5.2). Consistent with the effect of High and Low herbicide rates on nutritional parameters, the Low dose showed the greatest values of dDM and dOM, likely attributed to greater contents of CP and lower contents of fiber for this treatment. However, as described under “nutritional composition” section, it is likely that there is an herbicide rate threshold beyond which the arrested growth constraints the nutritional quality of the forage and consequently its digestibility.

Apparent digestibility values were greater in the WA location, likely due to the greater nutritional quality described for this site. Furthermore, the R_{Max}, T_{max}, and PF values were also greater indicating greater speed and efficiency of fermentation, again linked to the nutritional parameters and the amount of dOM present in the forage. Nevertheless, parameters A and B were not different between locations likely attributed to the extended period of fermentation.

The potential gas production (parameter A) and the time at which half the gas production is reached (Parameter B; High rate) were lower for non-treated (CTRL) medusahead than for glyphosate-treated plants, although these differences were much less pronounced than for 1mm substrate and the rest of particle sizes. Likewise, parameter C was greater in CTRL, although differences were similarly less pronounced than those observed between 1mm and the rest of the particle sizes. Greater values for parameter A and B in glyphosate-treated medusahead suggest a greater amount of gas being produced by fermentation in a prolonged period of time, instead of a significant volume of gas being produced initially (as described for the 1 mm particle size above). Fermentation in glyphosate-treated substrates was extended in time with greater amounts of gas being produced, which allowed for greater degradability of structural carbohydrates in medusahead. Furthermore, lower T_{Max} for glyphosate-treated medusahead suggests that Rmax occurred at earlier times than for CTRL substrates. These results were likely a consequence of smaller declines in gas production once the maximum rates were reached at earlier times for herbicide-treated medusahead relative to CTRL substrates. Similar to the greater A and B parameters, PF values were higher for the glyphosate treatments than that of CTRL, further indicating more efficient digestion.

5. Conclusions

High silica concentrations have been proposed as a contributing factor to reduced digestibility and low intakes of medusahead by livestock. Disruption of this defense mechanism is key to increasing consumption of the plant and its control within the plant community. The WA location appeared to have better nutritional quality to that of UT which may have been a consequence of phenological stage at which the plant was collected. Herbicide application also increased digestibility and the efficiency of digestibility of the grass. However, a smaller particle size (1 mm) appears to play the largest role at enhancing fermentation kinetics as increased surface area per unit weight promotes greater microbial recruitment and eliminates the silica-associated defense. In a rangeland setting, processing the plant material to this size is unlikely and therefore, herbicide application appears to be a more practical approach to increasing consumption of the grass. Overall, the integrated approach of glyphosate application and livestock grazing shows promise at controlling the spread of medusahead in rangelands, as herbicide applications increases the nutritional quality and digestibility of the grass, which in turn enhance palatability and nutrition, potentially promoting greater utilization of medusahead by livestock.

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Table 5.1. Nutritional composition of medusahead (*Taeniatherum caput-medusae* (L.) Nevski) treated with different rates of glyphosate at two locations in a 2016 fermentation kinetics study.

	CP[1]	NDF[2]	ADF[3]	OM[4]	Ash	Silica
Herbicide Rate			*(g · kg dry matter)*			
CTRL	93.6 ± 1.5^{b}	622.2 ± 3.3^{a}	351.8 ± 1.7^{b}	896.8 ± 0.9^{b}	103.2 ± 0.9^{b}	72.0 ± 0.9^{a}
Low	101.5 ± 1.5^{a}	547.1 ± 3.3^{b}	340.0 ± 1.7^{c}	900.9 ± 0.8^{a}	99.1 ± 0.8^{c}	70.0 ± 0.8^{ab}
High	93.6 ± 1.5^{b}	548.2 ± 3.3^{b}	380.7 ± 1.7^{a}	891.8 ± 0.9^{c}	108.2 ± 0.9^{a}	68.3 ± 0.9^{b}
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	0.006
Location			*(g · kg dry matter)*			
UT	86.0 ± 1.4^{b}	604.3 ± 2.4^{a}	368.8 ± 1.4^{a}	891.7 ± 0.8^{b}	108.3 ± 0.8^{a}	75.0 ± 0.9^{a}
WA	106.5 ± 1.2^{a}	540.6 ± 3.4^{b}	346.3 ± 1.4^{b}	901.3 ± 0.7^{a}	98.7 ± 0.7^{b}	65.2 ± 0.8^{b}
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Herbicide Rate and Location			*(g · kg dry matter)*			
UT						
CTRL	74.4 ± 2.3^{d}	676.9 ± 3.7^{a}	346.4 ± 2.4^{b}	890.1 ± 1.4^{b}	109.8 ± 1.4^{a}	74.4 ± 1.3^{ab}
Low	96.0 ± 2.3^{b}	563.1 ± 3.7^{b}	343.0 ± 2.4^{c}	892.8 ± 1.1^{b}	107.2 ± 1.1^{a}	71.8 ± 1.1^{bc}
High	87.5 ± 2.3^{c}	523.3 ± 3.7^{b}	416.9 ± 2.4^{a}	892.0 ± 1.4^{b}	108.0 ± 1.4^{a}	78.8 ± 1.3^{a}
WA						
CTRL	112.8 ± 2.0^{a}	567.4 ± 5.2^{b}	357.3 ± 2.4^{b}	903.4 ± 1.1^{a}	96.6 ± 1.1^{b}	69.6 ± 1.1^{bc}
Low	107.0 ± 2.0^{a}	531.0 ± 5.2^{c}	337.0 ± 2.4^{c}	909.0 ± 1.1^{a}	91.0 ± 1.1^{b}	68.1 ± 1.1^{c}
High	99.6 ± 2.0^{b}	523.3 ± 5.2^{c}	344.6 ± 2.4^{c}	891.5 ± 1.1^{b}	108.5 ± 1.1^{a}	57.8 ± 1.1^{d}
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

[1]Crude protein; [2]Neutral detergent fiber; [3]Acid detergent fiber; [4]Organic matter; CTRL = no herbicide application; Low = glyphosate in the form of its potassium salt applied at a rate of 394 g ae·ha^{-1}; High = glyphosate in the form of its potassium salt applied at a rate of 788 g ae·ha^{-1}; UT = Mantua, Utah location; WA = Ritzville, Washington location.

$^{a-c}$ same letters within column and treatment are not significantly different ($P > 0.05$).

Table 5.2. Apparent digestibility and gas production kinetics parameters of medusahead (*Taeniatherum caput-medusae* (L.) Nevski) at different glyphosate herbicide rates and particle sizes at two locations incubated for 120 h.

	Apparent Digestibility (g · kg)		Gas production kinetics parameters					
	dDM	dOM	A	B	C	R$_{max}$	T$_{max}$	PF
	Herbicide Rate							
CTRL	779.2^{c}	828.8^{c}	105.5^{c}	83.3^{b}	1.3^{a}	1.0^{b}	14.0^{a}	5.19^{b}
Low	830.5^{a}	876.3^{a}	114.2^{b}	87.4^{b}	1.2^{b}	1.2^{a}	5.8^{b}	5.25^{ab}
High	819.6^{b}	866.0^{b}	124.0^{a}	114.4^{a}	1.1^{b}	1.1^{b}	6.8^{b}	5.38^{a}
SEM	6.0	5.2	7.8	13.5	0.1	0.1	2.1	0.05
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.014
	Particle Size (mm)							
1	850.0^{a}	889.0^{a}	83.2^{c}	37.7^{c}	1.4^{a}	1.5^{a}	8.7^{ab}	5.25
20	796.2^{b}	846.7^{b}	139.0^{a}	146.0^{a}	1.1^{c}	0.9^{b}	8.0^{b}	5.37
30	795.8^{b}	846.5^{b}	120.2^{b}	102.4^{b}	1.2^{b}	1.0^{b}	8.6^{ab}	5.24
40	797.1^{b}	845.8^{b}	115.8^{b}	94.2^{b}	1.2^{b}	1.0^{b}	10.2^{a}	5.25
SEM	6.2	5.4	8.0	14.0	0.1	0.1^{b}	2.1	0.06
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.032	0.224
	Location							
UT	781.3^{b}	836.7^{b}	114.5	98.0	1.3^{a}	1.0^{b}	12.4^{a}	5.21^{b}
WA	838.3^{a}	877.3^{a}	114.7	92.2	1.1^{b}	1.2^{a}	5.2^{b}	5.34^{a}
SEM	5.7	4.9	7.6	13.0	0.1	0.1	2.1	0.04
P-value	<0.001	<0.001	0.788	0.077	<0.001	<0.001	<0.001	0.016

dDM: Coefficient of dry matter disappearance; dOM: Coefficient of organic matter disappearance; A: Asymptotic gas production (mL·g OM); B: time to half of the asymptote (h); C: Constant determined the sharpness of the curve; R$_{Max}$: maximum gas production rate (mL·h^{-1}); T$_{Max}$: time at which R$_{Max}$ occurs (h); PF: Partitioning factor (mg dOM·mL gas produced); CTRL = no herbicide application; Low = glyphosate in the form of its potassium salt applied at a rate of 394 g ae·ha^{-1}; High = glyphosate in the form of its potassium salt applied at a rate of 788 g ae·ha^{-1}; UT = Mantua, Utah location; and WA = Ritzville, Washington location.

$^{a\text{-}c}$ same letters within column and treatment are not significantly different ($P > 0.05$).

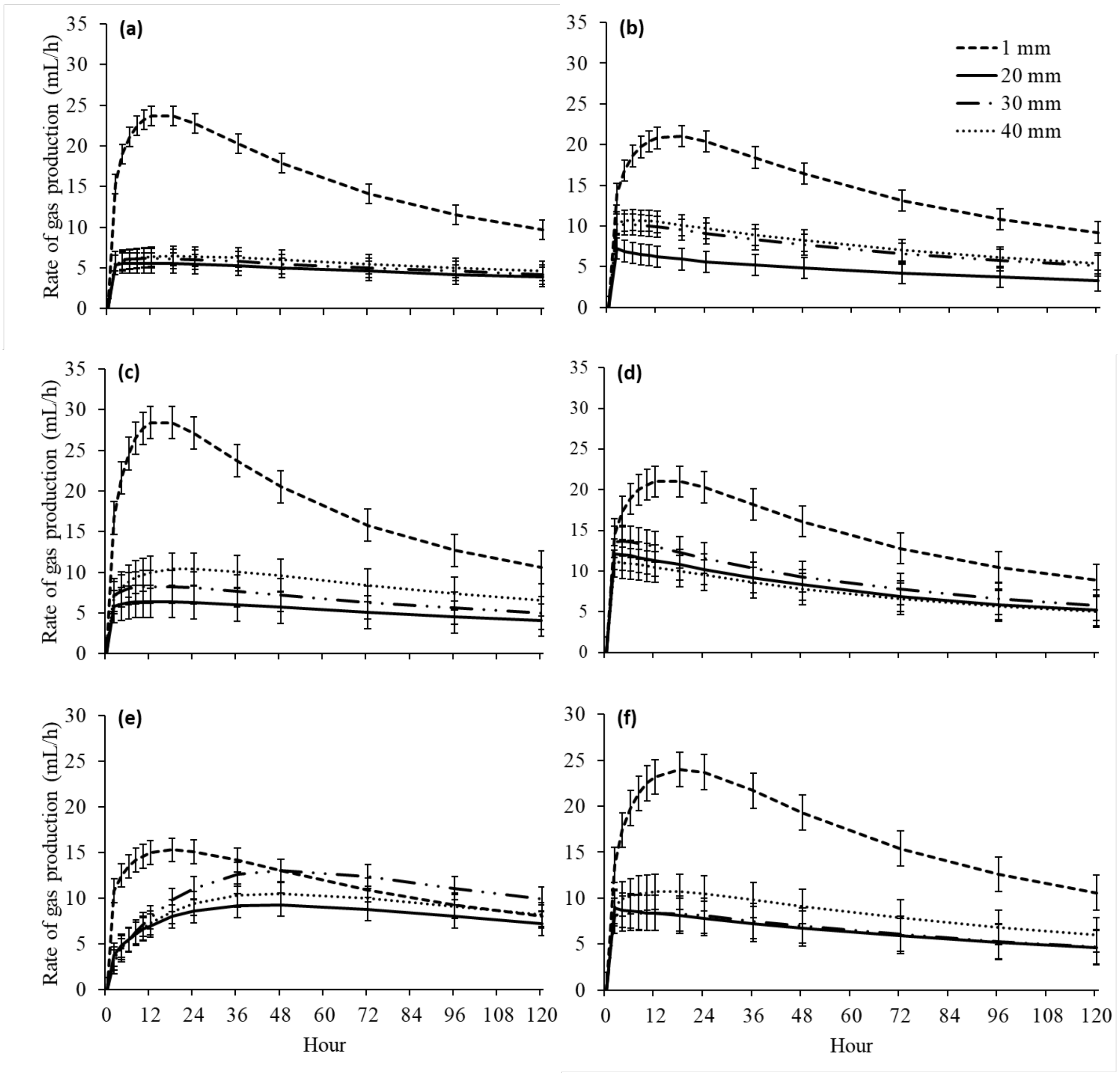

Fig. 5.1. Rate of gas production profiles for medusahead (*Taeniatherum caput-medusae* (L.) Nevski) at different particle lengths treated with glyphosate at: (a) 788 g ae·ha^{-1} in Utah (UT); (b) 788 g ae·ha^{-1} in Washington (WA); (c) 394 g ae·ha^{-1} in UT; (d) 394 g ae·ha^{-1} in WA; and (e) 0 g ae·ha^{-1} in UT; (f) 0 g ae·ha^{-1} in WA. Bars represent standard error of mean (SEM).

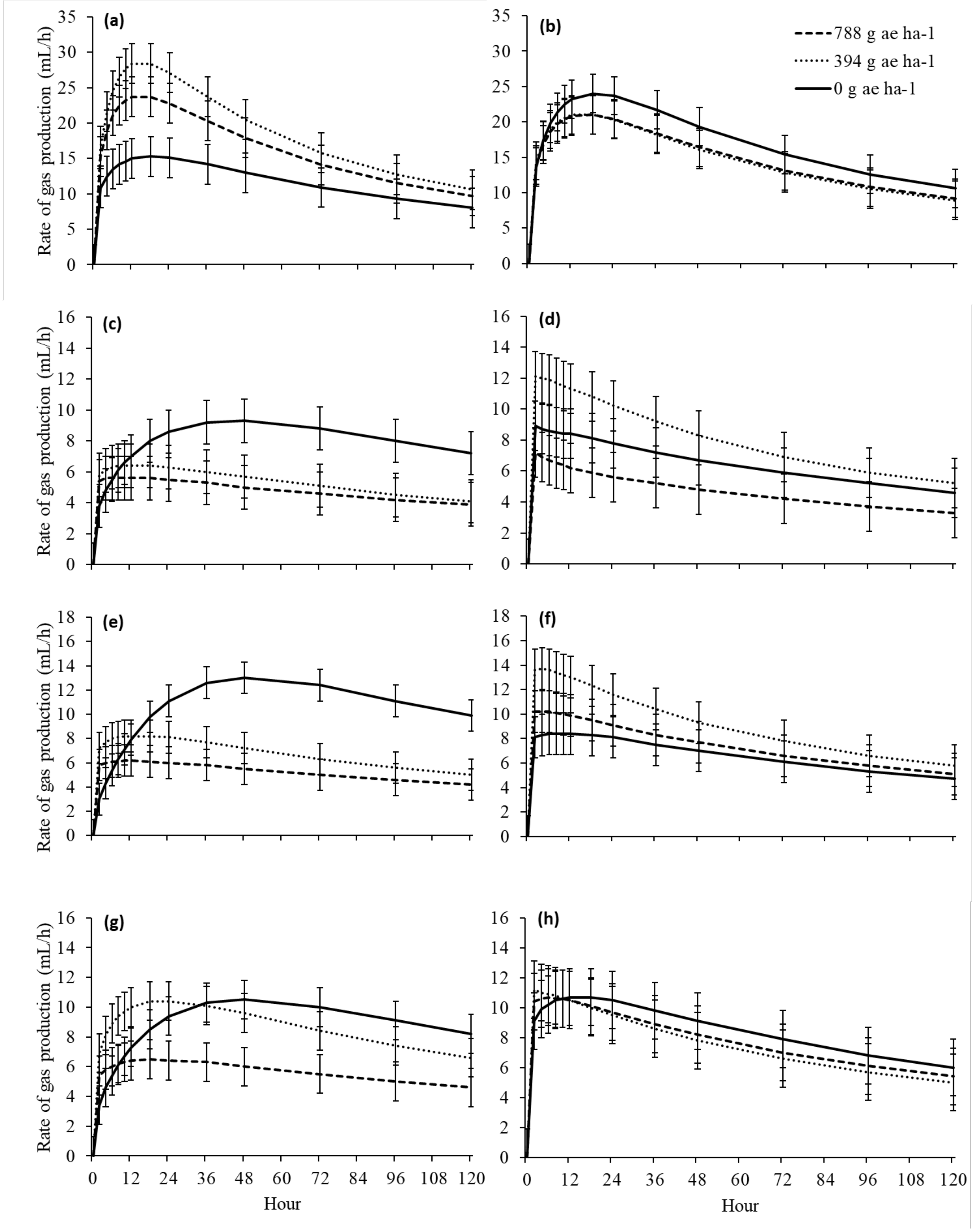

Fig. 5.2. Rate of gas production profiles for medusahead (*Taeniatherum caput-medusae* (L.) Nevski) treated with different glyphosate rates for: (a) 1 mm particle length in nUtah (UT); (b) 1mm particle length in Washington (WA); (c) 20 mm in UT; (d) 20 mm in WA; (e) 30 mm in UT; (f) 30 mm in WA; (g) 40 mm in UT; and (h) 40 mm in WA. Bars represent standard error of mean (SEM).

CHAPTER 6

CATTLE TRAMPING AS A TOOL FOR REVEGETATION OF MEDUSAHEAD INFESTED LANDSCAPES[6]

ABSTRACT

Supplemental cattle grazing in combination with seed incorporation into the soil through livestock trampling may provide a sustainable approach to medusahead (*Taeniatherum caput-medusae* (L.) Nevski) control and establishment of more desirable forage species. Beef cows (12) were randomly assigned to two treatments in 6 plots (2 animals/plot) in eastern Washington: 1) Supplemented animals grazed improved rangeland (IMP) for 45 min/d and then they grazed medusahead-infested rangeland (SUP; n=3 plots); and 2) control animals grazed medusahead-infested rangeland only (NSUP; n=3 plots). An additional ungrazed plot (UNGR) was established adjacent to the SUP and NSUP plots. All grazing plots were randomly subdivided into a trampling (T) and a non-trampling (NT) treatment. The T treatment was seeded with introduced and native grasses and forbs prior to grazing and the NT treatment was seeded with the same plant species after grazing. Biomass availability was assessed at the beginning and end of the grazing period, and foliar cover was assessed prior to grazing and during 2 ensuing years after seeding the different forage types. Biomass of all species declined with grazing despite treatment. Trampling had no effect on seeding establishment; in fact, all species except for small burnet (*Sanguisorba minor* Scop.) failed to establish likely due to the highly competitive nature of medusahead. Removing medusahead as a competitor

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[6] Co-authored with Clint Stonecipher

is key in revegetation efforts, and once this competitor is removed, trampling may be a tool for establishing other more desirable species if significant reductions of the seed bank of the species can be achieved.

INTRODUCTION

Medusahead is currently one of the most detrimental invasive plants impacting western rangeland sustainability and livestock operations (Davies and Johnson, 2008; Miller et al., 1999; Young, 1992); it decreases the abundance and quality of forage available to livestock and wildlife, negatively impacts plant diversity, and increases the frequency of fires (Davies and Johnson, 2008). These impacts are further compounded by the fact that traditional control techniques (i.e., mechanical, cultural, and chemical) are often unsuccessful.

Livestock grazing has been shown to be the preferred method of medusahead management and control due to its low-cost and practicality (Hamilton et al., 2015; James et al., 2015), although livestock typically display low intakes of the grass due to its low nutritional value (Bovey et al., 1961; Epstein, 1999; Swenson et al., 1964). When protein concentrates are made available to livestock, the increase in nitrogen inputs to the rumen facilitates the digestion of forages that are low in protein and high in fiber (Van Soest, 1994), which can potentially enhance consumption of the low-quality grass.

Revegetation efforts of desirable species on medusahead-invaded rangelands is often more successful when some type of medusahead control is used (Davies, 2010; Nafus and Davies, 2014). Increasing livestock consumption of medusahead through supplementation may increase consumption medusahead and therefore create more conducive conditions for revegetation. Seeding of rangeland grass species is often done by aerial or broadcast seeding, however it is often unsuccessful without some type of disturbance or incorporation of the seed into the soil (Welch and Haferkamp, 1987). Thus, cattle trampling in combination with broadcast seeding has been shown to have similar efficiency at incorporating seeded species into the soil, and revegetation success, to that of more intense disturbance methods (Winkel and Roundy, 1991). Thus, the integrated approach of supplemental livestock grazing to remove medusahead biomass in combination with cattle trampling and broadcast seeding may provide and efficient and low-cost method of restoration on medusahead-invaded rangelands. We evaluated whether control of medusahead through a program of cattle grazing and supplementation with improved pastures, in combination with of seeding perennials plant species using cattle trampling would restore medusahead-invaded rangelands.

MATERIAL AND METHODS

All animal procedures were approved by the Utah State University Institute of Animal Care and Use Committee (#2117) and were conducted under veterinary supervision.

Site Description

The study was conducted on privately-owned land in the Channeled Scablands region of eastern Washington about 26 km south east of Ritzville, Adams County, WA (47º 03.62’N, 118º02.62’W; 544 m). The original study area was predominantly sagebrush steppe (Daubenmire, 1970), however, invasive annual grasses have become the dominant plant species. Medusahead and downy brome constitute the majority of the landscape but other weedy forbs such as bird vetch (*Vicia cracca* L.), fiddleneck (*Amsinckia intermedia* Fish. & Mey), tansy mustard [*Descurainia pinnata* (Walt.) Britt.], rush skeleton (*Chondrilla juncea L.*), black mustard [*Brassica nigra* (L.) Koch in Rochl], redstem filaree [Erodium cicutarium (L.) L'Hér.], prickly lettuce (*Latuca serriola* L.), wooly plantain (Plantago Patagonica Jacq.), western salsify (*Tragopogon dubius* Scop.), and western yarrow (*Achillea millefolium* L. var. *occidentalis* DC.) are also present. Native perennial grasses were sparse with bulbous bluegrass (*Poa bulbosa* L.) being the only perennial grass present at the study site, however, remnants of bluebunch wheatgrass [*Pseudoroegneria spicataI* (Pursh) Á. Löve] and Sandberg bluegrass (*Poa Secunda* J. Presl) could be found in the surrounding landscape.

A plot of 0.9 ha (219.6 x 41.0 m) was disked (McCormick International 480, Duluth, GA) by the owner with four passes prior to planting. Plots were planted with Vavilov II Siberian wheatgrass (*Agropyron fragile* [Roth] P. Candargy) using a Gandy drop seeder (Anertec and Gandy Co., Owatonna, MN, USA) at a rate of 11.2 pure live seed kg · ha^{-1} in November 2010. One pass with a harrow was made after planting to cover the seed. Forage kochia (*Bassia prostrata* [L.] A.J. Scott) seed was broadcast with a Herd Sure-Feed Broadcaster (Herd Seeder Company, Inc., Logansport, IN, USA) in January 2011 at a rate of 2.2 kg · ha^{-1}. This plot constituted the improved pasture (IMP).

The soil typification was coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic typic hapoxeroll (Benge gravelly silt loam). The 30 year mean annual precipitation is 351.4 mm with annual precipitation from 2016-2018 reported in Fig. 6.1 (PRISM Climate Group, Oregon State University). Average precipitation in 2016 was 437.8 mm while in 2016 totals were well above normal at 123.4 mm with 61.5 mm of the precipitation occurring during the study. With adequate moisture, medusahead seeds began to germinate in thatch and by day 5 of the study, seedlings were abundantly present at approximately 3 mm of height.

Experimental Design

Plot Description

Three medusahead-invaded pastures of 0.4 ha (67.0 x 61 m) each were fenced using solar-powered electric fences, arranged side-by-side adjacent to the improved pasture (IMP), delimited by a barbed wire fence. Each of the three medusahead-invaded pastures were randomly assigned to three treatments: 1-Supplementation (SUP), and 2-No supplementation (NSUP), and 3- a non-grazed plot (UNGR) forming plots of 0.186 ha (76.2 x 24.4 m) in each pasture. The IMP pasture was subdivided into three separate plots of 0.3 ha (73.2 by 41.0 m) delineated by electric fences, adjacent to the spatial replications of the SUP plots. A 3.7 m section of barbed wire fencing between SUP and IMP plots was removed and replaced with a steel cattle panel to allow movement of animal between plots. The grazing portion of the study took place from October 7 to 15, 2016.

Animals

Twelve three-year-old Angus cross-breed heifers (511.4 ± 9.5 kg) were used in a grazing experiment (Chapter 2) to remove plant biomass for revegetation efforts. Heifers were randomly paired, and then randomly allocated to SUP and NSUP treatments. Animals assigned to SUP were allowed to graze IMP (45 minutes/day) for nutritional supplementation prior to grazing their respective medusahead-infested treatment. In contrast, NSUP animals were only allowed to graze their respective medusahead-infested plots without improved forage supplementation. Animals had free access to fresh water and trace mineral salt blocks throughout the study. The mineral composition of the blocks was: minimum 96% NaCl, 320 mg · kg Zn, 380 mg · kg Cu, 2,400mg · kg Mn, 2,400 mg · kg Fe, 70 mg · kg I, and 40 mg · kg Co.

Revegetation

Treatment plots (SUP, NSUP, and UNGR) were divided into two sub-plots (38.2 by 24.4 m) and randomly assigned two seeding treatments: 1- trampled (T), and non-trampled (NT; Fig. 6.2). Prior to grazing, the T plots were seeded in a mix of Hycrest II crested wheatgrass (*Agropyron crisatum* [L.] Gaertn), Vavilov II Siberian wheatgrass (*Agropyron fragile* [Roth] P. Candargy), Mountain Home sandberg bluegrass (*Poa secunda* Presl), and Delar small burnet (*Sanguisorba minor* Scop.) at a rate of 11.2 pure live seed kg · ha^{-1} (Table 6.1). The same plant species and rate was seeded after grazing in the NT plots. In January 2017, Immigrant forage kochia (*Bassia prostrata* [L.] A.J. Scott) was seeded on all treatment plots at a rate of 2.2 kg · ha^{-1}. All seeded species were broadcast using a Herd Sure-Feed Broadcaster (Herd Seeder Company, Inc., Logansport, IN, USA).

Vegetation Assessment

Biomass Availability

Above ground vegetation biomass was determined in each grazing plot (SUP, NSUP, and UNGR) and seeding treatments (NT and T) by hand clipping vegetation in treatment plots to a 1 cm stubble height within a 0.0985 m^2 square frame prior to and after the grazing. Three 76.2 m transects were placed parallel to each other every 6.1 m through the UNGR, SUP, and NSUP plots. Clipped samples were taken every 12.7 m along each transect in the T and NT plots for a total of 2 samples per treatment and transect (n=6 per treatment). Clipped vegetation samples were separated and then composited into the forage types: medusahead, other annual grasses, perennial grasses, annual forbs, perennial forbs, and thatch.

Foliar Cover

Foliar cover was estimated using the line-point intercept method (Herrick et al., 2005) prior to the grazing period using the same transects in all treatment plots. Subsequent yearly foliar cover readings were taken on August 24, 2017 and August 8, 2018. Plant foliar cover readings were taken along the same transects described for biomass collections every 1.5 m in all T and NT plots for a total of 24 readings per transect (n=72 per treatment plot). Individual plant counts along the transect were classified according to the same vegetation types in the biomass section with the addition of bare ground, and the seeded plant species.

Belt Transect

The same transects used for the biomass and foliar cover readings were used for the belt transect readings on August 8, 2018. All seeded species were counted within a 1 m wide by 38.1 m long transect within the T and NT plots. Frequency of each plant reading was calculated as a percentage of area within each transect.

Hoof Disturbance

After a period of grazing, hoof imprints were counted within a 0.0985 m^2 square frame along the same transects as the biomass assessment every 12.7 m (n=6 squares per treatment).

Statistical Analyses

The available aboveground biomass was analyzed in a split plot in a randomized block design with repeated measures. Block was the random effect, grazing treatment and seeding treatment were the fixed factors, and sampling time (before and after grazing were the repeated measures in the analysis.

The proportion of foliar cover for each plant type was analyzed in a split plot randomized block design with repeated measures. Block was the random effect, grazing treatment and seeding treatment were the fixed factors, and sampling year was the repeated measure. Seeded species of Sandberg bluegrass, crested wheatgrass, Siberian wheatgrass, and forage kochia were not detected in the foliar cover readings and therefore not analyzed. Additionally, thatch readings were not taken in 2017 and therefore only two years of repeated measures were analyzed.

The proportion of each seeded plant species within the belt transects were analyzed in a split plot randomized block design. Block was the random effect with grazing treatment and seeding treatment as the fixed factors in the analysis. Siberian wheatgrass and forage kochia were not detected in the belt transects and therefore not analyzed. The number of hoof prints (hoof disturbance) was analyzed using the same model as the belt transect analysis

Analyses were computed using the GLIMMIX procedure in SAS (SAS Inst., Inc. Cary, NC; Version 9.4 for Windows). The covariance matrix structure used was the one that yielded the lowest Bayesian information criterion. The model diagnostics included testing for a normal distribution and homoscedasticity. Data was transformed when needed according to the Box-Cox method but non-transformed data is reported (mean ± standard error of mean). Means were analyzed using Tukey's multiple comparison test when F-ratios were significant ($P < 0.05$). A trend was considered when $0.05 < P < 0.10$.

RESULTS

Biomass Availability

Biomass availability of the different vegetation types prior to and after a grazing period for the different treatments and day of sampling are reported in Table 6.2. There was a tendency across seeding treatments and sampling days for medusahead biomass to be greater in the non-grazed (UNGR) treatment and lower but similar values of biomass in the supplemented (SUP) and non-supplemented (NSUP) treatments (grazing treatment effect: $P = 0.095$), but there were no differences among grazing treatments or sampling days for medusahead biomass across sampling days ($P = 0.151$). Medusahead biomass across sampling days was greater in the UNGR treatment with trampling (T) and least in the SUP treatment with T (grazing treatment by seeding treatment interaction: $P = 0.026$). Additionally, there was a strong tendency across treatments for a decline in medusahead biomass from the beginning to the end of the grazing period (sampling day effect: $P = 0.061$), but no interaction of sampling day by grazing and/or seeding treatment was detected for this forage type ($P > 0.05$).

No differences between grazing treatment or sampling day were detected, and no interactions among fixed factors were detected for annual grasses other than medusahead and annual forbs ($P > 0.05$). Biomass of annual grasses other than medusahead was greater across grazing treatments and sampling days for the non-trampling seeding treatment (NT) than for the trampling seeding treatment (trampling effect: $P = 0.006$), but the opposite pattern was observed for annual forb biomass (trampling effect: $P = 0.007$). There was also a reduction in perennial grass biomass across all treatments from the beginning to the end of the grazing period (sampling day effect: $P = 0.010$), but there was no observable difference between grazing or seeding treatments, and no interaction detected for all fixed factors assessed for this forage type ($P > 0.05$). There were no differences in perennial forb biomass among grazing or seeding treatments, or across sampling days, and no interactions among these fixed factors were detected ($P > 0.05$), except that there was a strong tendency for biomass of this forage type to be greatest and lowest for the T treatment at the beginning and end of the grazing period, respectively (sampling day by seeding treatment interaction: $P = 0.056$).

Foliar Cover

The proportion of vegetation foliar cover of different forage types within grazing and seeding treatments across three years is reported in Table 6.3. There were no differences in cover across all forage types assayed for the grazing or seeding treatments, and no interaction was detected for these parameters ($P > 0.05$), except for annual grasses other than medusahead which displayed the greatest cover for the non-grazed (UNGR) treatment with T, and the lowest cover for the non-supplemented (NSUP) grazing treatment with T (grazing treatment by seeding treatment interaction ($P = 0.047$).

There were differences in sampling years across all plant types and across grazing and seeding treatments for foliar cover: 2017 > 2018 = 2016 for medusahead and perennial grasses other than the seeded species (sampling year effect: $P < 0.05$), 2018 >

2017 > 2016 ($P \leq 0.001$) for small burnet, 2016 > 2018 > 2017 ($P < 0.001$) for annual forbs and thatch, 2018 = 2016 > 2017 ($P = 0.008$) for perennial forbs other than seeded species, and 2016 > 2018 ($P = 0.006$) for bare ground. Finally, there were no interactions detected for sampling year across grazing and/or seeding treatments ($P > 0.05$).

Belt Transect

Seeded plant species within belt transects and across grazing and seeding treatments are reported in Table 6.4. The quantity of small burnet plants across seeding treatments within the belt transect were NSUP > SUP > UNGR (grazing treatment effect: $P = 0.001$). Across grazing treatments, the NT treatment displayed higher quantities of small burnet plants within the belt transect than the T treatment (seeding treatment effect: $P = 0.009$). There was a strong tendency for the NSUP and NT treatment to display the greatest quantities of small burnet within the belt transect, whereas UNGR with the T treatment tended to display the lowest quantities (grazing treatment by seeding treatment interaction: $P = 0.057$). There were no differences in the quantity of crested wheatgrass and Sanberg bluegrass within the belt transect across grazing treatments or seeding treatments, and no interaction of these treatments were detected for these plant types ($P > 0.05$).

Hoof Disturbance

Cattle hoof disturbance in grazing and seeding treatments is reported in Table. 6.5). Cattle hoof prints across grazing and seeding treatments were similar, and no interaction among these treatments were detected (*P* > 0.05).

DISCUSSION

Grazing and Biomass Removal

Medusahead invasion is likely a consequence of a persistent litter layer, which has a smothering effect on other less adapted plant seedlings, and increased herbivory pressure on the established, co-occurring more desirable plant species (Davies and Svejcar, 2008; Evans and Young, 1970; Pyke, 2000). A high abundance of medusahead was present in this study site and was the major plant species within the community (Table 6.3). Utilization of standing medusahead vegetation and litter by livestock is generally low, as grazing animals tend to avoid this grass (Davies and Svejcar, 2008; Hironaka, 1961). This aversive behavior has been associated with high amorphous silicon (i.e., silica) concentrations within the plant, which retards microbial digestion in the rumen (Hunt et al., 2008), thus constraining the availability of nutrients to the animal (Montes-Sánchez et al., 2017). Supplemental nutrients from an established cool season grass was thought to increase consumption of medusahead when a rotational grazing study was implemented. There was a trend detected in the consumption of medusahead but this was likely a consequence of the ungrazed (UNGR) plot as supplemented (SUP) and non-supplmented (NSUP) plot biomass was similar (Table 6.2). There was a decline in medusahead biomass from the beginning to the end of the grazing period, which shows promise for reducing medusahead abundance in order to seed more desirable plant species. Revegetation efforts of desirable species on medusahead-invaded rangelands is often more successful when some type of medusahead control is used (Davies, 2010;

Nafus and Davies, 2014). Perennial grasses were less abundant within the plant community but had a large decrease and were likely selected due their better nutritional quality (see Chapter 2). All other forages had only small declines in their abundance but overall decreases in biomass within the plant community would likely aid in more efficient revegetation efforts.

Seedlings and the Trampling Effect

The revegetation efforts were largely unsuccessful despite having above average precipitation for the year of seeding as well as during the following year (Fig. 6.2). In the spring of 2017, forage kochia was observed to have germinated and was in the two-leaf stage. Nevertheless, when assessments took place in the autumn of the same year, forage kochia was absent. The hot-dry summers associated with eastern Washington, in combination with the presence of abundant invasive annual grasses, likely depleted the soil moisture, and without forage kochia having an established tap-root, the plant withered and died. This may also have been the case for the perennial grass species that were seeded. However, it was difficult to distinguish between the annual grasses and the newly emerged seedlings in the spring, and therefore it was unknown whether the perennial grasses actually germinated. Furthermore, we broadcast seeded these species at a typical prescribed rate without the presence of invasive annual grasses (Hull, 1974), however, higher rates have been suggested to increase establishment when invasive annual grasses are present (Sheley et al., 2006). Thus, a higher rate in this study may have resulted in better establishment of the seeded plant species.

Small burnet was the only seeded species with a high enough establishment rate to detect differences in the efficacy of biomass removal through grazing and trampling

(Table 6.2 and 6.3). For this species, removal of biomass through grazing had the greatest impact on seedling establishment (e.g., comparing UNGR to that of the grazed treatments) than the effects of trampling. Annual grasses, and medusahead in particular, are highly competitive for superficial soil resources such as water and nutrients (Harris, 1977; Harris and Goebel, 1976; James et al., 2010). It was likely that the reduction in medusahead abundance through grazing contributed to more resources available for the seedling, and consequently increased its establishment rate. Nevertheless, the establishment rate of small burnet was low, and medusahead abundance the following year was still high. Additionally, there was greater abundance of small burnet in the non-trampled (NT) treatment than in the trampled (T) treatment, but these differences were small and were likely associated with other environmental factors (e.g., soil, moisture, and nutrient availability).

MANAGEMENT IMPLICATIONS

Medusahead is a superior invader as it is avoided by livestock, increasing the grazing pressure on other desirable species in the plant community. Supplementation had little effect on the overall biomass remaining after grazing but intensively grazing medusahead in a confined setting reduced medusahead abundance similar to that reported in other studies. Trampling by grazing cattle has been found to have similar revegetation success to that of other more intensive disturbance method. Nevertheless, trampling had no effect on the success of seeding. In fact, small burnet was the only species to establish, and those establishment rates were low. Medusahead is highly competitive for resources, and likely contributed to the failure of establishment of more desirable species. Grazing removed biomass for one year, but it was likely that it did not reduce the soil seed bank, thus medusahead continued to compete for resources in subsequent years. Overall, removing medusahead as a competitor is key in revegetation efforts, although medusahead biomass increased (2017) and returned to control values (2018) one and two years after grazing, respectively. This suggest that there is a short time frame for revegetation efforts after grazing and that follow-up treatments are needed to reduce the seed bank of the grass such that competition is reduced during the critical period of establishment of desirable perennials.

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TABLES AND FIGURES

Table 6.1. Plant materials used in the study, common and Latin names, purity of mix, and germination rates.

Variety	Common name	Scientific name	Purity of seed mix %	Germination Rates %
Mountain Home	Sandberg Bluegrass	*Poa secunda* Presl.	24.61	74
Delar	Small Burnett	*Sanguisorba minor* Scop.	24.98	85
Hycrest II	Crested Wheatgrass	*Agropyron cristatum* (L.) Gaertn.	24.55	97
Vavilov II	Siberian Wheatgrass	*Agropyron fragile* (Roth) P. Candargy	24.38	96
Immigrant	Forage Kochia	*Bassia prostrata* (L.) A.J. Scott	-	43

Table 6.2. Biomass availability of different forage types during an 8 d grazing period prior to revegetation with selected plant species in the scablands of eastern Washington.

	SUP		NSUP		UNGR	
	T	NT	T	NT	NT1	NT2
	Medusahead (kg · ha^{-1} dry matter)					
PRE	154.5 ± 72.7	169.8 ± 72.7	178.2 ± 72.7	235.6 ± 72.7	411.7 ± 72.7	112.2 ± 72.7
POST	63.2 ± 72.7	60.3 ± 72.7	50.2 ± 72.7	93.6 ± 72.7		
	Other Annual Grasses (kg · ha^{-1} dry matter)					
PRE	40.6 ± 20.1^{ab}	59.8 ± 20.1^{ab}	49.6 ± 20.1^{ab}	54.4 ± 20.8^{a}	31.6 ± 20.1^{ab}	72.8 ± 20.1^{a}
POST	20.3 ± 20.1^{ab}	25.9 ± 20.1^{ab}	10.2 ± 20.1^{b}	55.8 ± 20.1^{ab}		
	Perennial Grasses (kg · ha^{-1} dry matter)					
PRE	17.5 ± 16.3^{b}	32.7 ± 16.3^{b}	5.6 ± 16.3^{b}	91.4 ± 16.8^{a}	37.2 ± 16.3^{b}	19.7 ± 16.3^{b}
POST	7.3 ± 16.3^{b}	1.1 ± 16.3^{b}	3.9 ± 16.3^{b}	3.4 ± 16.3^{b}		
	Annual Forbs (kg · ha^{-1} dry matter)					
PRE	968.4 ± 309.5^{a}	940.2 ± 309.5^{ab}	2161.3 ± 309.5^{a}	801.2 ± 320.8^{ab}	773.3 ± 309.5^{a}	1713.5 ± 309.5^{a}
POST	825.2 ± 309.5^{a}	331.1 ± 309.5^{b}	1055.3 ± 309.5^{a}	375.1 ± 309.5^{ab}		
	Perennial Forbs (kg · ha^{-1} dry matter)					
PRE	985.9 ± 246.6	73.9 ± 246.6	380.2 ± 246.6	341.4 ± 254.0	54.7 ± 246.6	49.1 ± 246.6
POST	269.6 ± 246.6	690.4 ± 246.6	269.6 ± 246.6	690.4 ± 246.6		

SUP = supplemented grazing cattle treatment.
NSUP = non-supplemented grazing cattle treatment.
UNGR = no grazing treatment.
T = seeding prior to grazing.
NT = seeding after grazing.
NT1-2 = seeding without grazing and trampling.
PRE = prior to grazing.
POST = after grazing.
$^{a\text{-}b}$ Same letter within forage type is not different ($P > 0.05$).

Table 6.3. Proportion of vegetation foliar cover the different vegetation types over 3 years of a revegetation study in eastern Washington.

Year	SUP		NSUP		UNGR	
	T	NT	T	NT	NT1	NT2
			Medusahead %			
2016	29.9 ± 5.2	29.2 ± 5.2	28.8 ± 5.2	28.5 ± 5.2	31.9 ± 5.2	33.6 ± 5.2
2017	36.2 ± 5.2	38.9 ± 5.2	47.9 ± 5.2	46.2 ± 5.2	35.6 ± 5.2	45.6 ± 5.2
2018	31.4 ± 5.2	30.4 ± 5.2	33.2 ± 5.2	36.8 ± 5.2	36.7 ± 5.2	42.8 ± 5.2
			Other Annual Grasses %			
2016	2.3 ± 4.8	2.7 ± 4.8	4.1 ± 4.8	4.6 ± 4.8	3.6 ± 4.8	4.1 ± 4.8
2017	14.5 ± 4.8	16.4 ± 4.8	10.8 ± 4.8	11.7 ± 4.8	25.2 ± 4.8	13.4 ± 4.8
2018	21.2 ± 4.8	19.8 ± 4.8	17.7 ± 4.8	27.4 ± 4.8	31.9 ± 4.8	16.2 ± 4.8
			Other Perennial Grasses %			
2016	2.8 ± 3.7	3.1 ± 3.7	3.6 ± 3.7	4.2 ± 3.7	4.5 ± 3.7	3.2
2017	25.3 ± 3.7	20.9 ± 3.7	17.8 ± 3.7	18.0 ± 3.7	15.0 ± 3.7	15.1 ± 3.7
2018	2.7 ± 3.7	4.4 ± 3.7	2.2 ± 3.7	0.9 ± 3.7	1.8 ± 3.7	6.0 ± 3.7
			Annual Forbs %			
2016	19.6 ± 3.4	21.5 ± 3.4	20.7 ± 3.4	20.5 ± 3.4	18.3 ± 3.4	17.0 ± 3.4
2017	11.5 ± 3.4	9.2 ± 3.4	12.1 ± 3.4	10.0 ± 3.4	13.1 ± 3.4	9.6 ± 3.4
2018	16.6 ± 3.4	16.9 ± 3.4	19.7 ± 3.4	16.9 ± 3.4	13.2 ± 3.4	12.9 ± 3.4
			Other Perennial Forbs %			
2016	13.1 ± 2.8	11.7 ± 2.8	9.5 ± 2.8	8.6 ± 2.8	5.0 ± 2.8	4.1 ± 2.8
2017	3.1 ± 2.8	4.7 ± 2.8	4.2 ± 2.8	5.1 ± 2.8	4.5 ± 2.8	8.2 ± 2.8
2018	10.9 ± 2.8	13.2 ± 2.8	11.7 ± 2.8	11.3 ± 2.8	6.8 ± 2.8	7.4 ± 2.8
			Thatch %			
2016	25.7	25.6	26.6	26.4	27.9	29.2
2018	4.8	5.8	6.9	0.9	3.6	6.0
			Bare Ground %			
2016	6.5 ± 2.6	6.3 ± 2.6	6.8 ± 2.6	7.3 ± 2.6	8.7 ± 2.6	8.8 ± 2.6
2017	9.5 ± 2.6	9.9 ± 2.6	7.3 ± 2.6	9.0 ± 2.6	6.7 ± 2.6	8.1 ± 2.6
2018	10.1 ± 2.6	8.1 ± 2.6	8.2 ± 2.6	4.9 ± 2.6	4.6 ± 2.6	7.8 ± 2.6
			Small Burnett %			
2017	0	0	0	0	0	0
2018	1.4 ± 0.5	0.9 ± 0.5	0.5 ± 0.5	0.9 ± 0.5	1.4 ± 0.5	0.9 ± 0.5

SUP = supplemented grazing cattle treatment.
NSUP = non-supplemented grazing cattle treatment.
UNGR = no grazing treatment.
T = seeding prior to grazing.
NT = seeding after grazing.
NT1-2 = seeding without grazing and trampling.

Table 6.4. Seeded plants in a 2018 revegetation study using the belt transect method to measure the effects of cattle trampling in eastern Washington.

	SUP		NSUP		UNGR	
	T	NT	T	NT	NT1	NT2
	(plants · m^2)					
Small Burnett	0.07 ± 0.02^{b}	0.06 ± 0.02^{cb}	0.05 ± 0.02^{cb}	0.13 ± 0.02^{a}	0.01 ± 0.02^{c}	0.02 ± 0.02^{c}
Sanberg Bluegrass	0.02 ± 0.03	0.03 ± 0.03	0.01 ± 0.03	0.07 ± 0.03	0.00 ± 0.03	0.00 ± 0.03
Crested Wheatgrass	0.01 ± 0.01	0.00 ± 0.01	0.01 ± 0.01	0.00 ± 0.01	0.00 ± 0.01	0.00 ± 0.01

SUP = supplemented grazing cattle treatment.
NSUP = non-supplemented grazing cattle treatment.
UNGR = no grazing treatment.
T = seeding prior to grazing.
NT = seeding after grazing.
NT1-2 = seeding without grazing and trampling.
$^{a\text{-}c}$ Same letters within row are not different ($P > 0.05$).

Table 6.5. Cattle hoof disturbance between treatment in a 2016 revegetation study located in eastern Washington.

	SUP		NSUP	
	T	NT	T	NT
Hoof prints · m^2	37.8 ± 2.9	37.8 ± 2.9	35.5 ± 2.9	34.5 ± 2.9

SUP = supplemented grazing cattle treatment.
NSUP = non-supplemented grazing cattle treatment.
T = seeding prior to grazing.
NT = seeding after grazing.

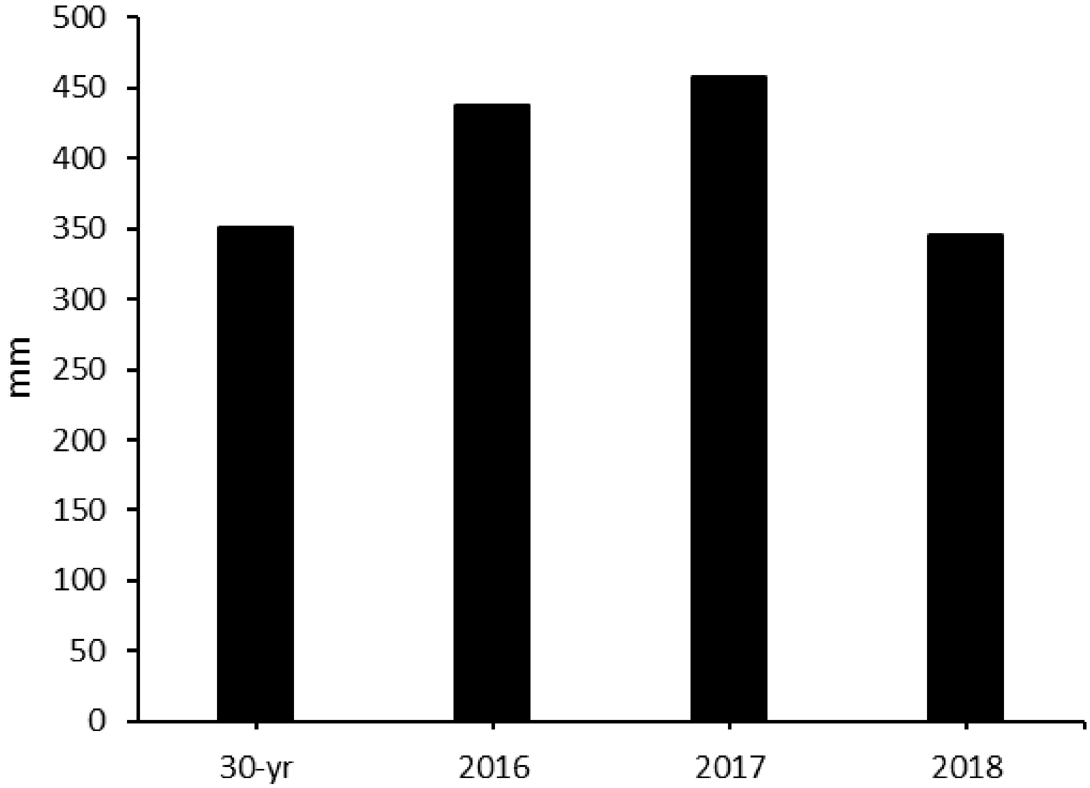


Figure 6.1. Annual precipitation of the study site over 3-years and 30-year average.

Improved			*Improved*			*Improved*		
T	T	NT1	NT2	T	NT	NT2	NT	NT
NT	NT	NT2	NT1	NT	T	NT1	T	T
SUP	*NSUP*	*UNGR*	*UNGR*	*NSUP*	*SUP*	*UNGR*	*SUP*	*NSUP*

Figure 6.2. Experimental plot layout with grazing treatments as supplemented animals (SUP), non-supplemented animals (NSUP), and non-grazed (UNGR). Seeding treatments included seeding prior to grazing (trampling; T), seeding after grazing (non-trampling; NT), seeding with no grazing or trampling (NT1-2).

CHAPTER 7

SUMMARY AND CONLUSION

Attempts to control medusahead (*Taeniatherum caput-medusae* [L.] Nevski), an invasive winter annual grass, have largely been unsuccessful. Limited control can be attributed to the lack of understanding of the link between soluble and insoluble silicon and its associated effects on medusahead invasion. We attempted to conceptualize this relationship through a model explaining a self-reinforcing positive feedback cycle of medusahead invasion. One aspect of the model encompasses, the anti-herbivory effects as a consequence of undigestible amorphous medusahead tissue silicon (i.e., silica) concentrations and was the focus of this dissertation.

Livestock grazing has been shown to be the preferred method of medusahead management and control due to its low-cost and practicality. However, utilization of standing medusahead vegetation and litter by livestock is generally low, as grazing animals tend to avoid this grass, even though the plant has similar nutritional qualities to that of other grasses. This aversive behavior can be partially explained by the silica varnish within the plant, which retards microbial digestion in the rumen, constraining the availability of nutrients to the animal, and promoting an undesirable oral texture. New paradigms on foraging behavior such as the importance of positive experiences with the appropriate supply of nutrients are critical for increasing consumption of less palatable plant species such as medusahead and overcoming the silica-associated restrictions of digestion.

Improved pastures of established cool season grasses and forbs were thought to provide the appropriate nutrient supply required for increased consumption of medusahead by livestock and mitigate the effects of the silica defense mechanism through increased digestibility when used in a rotational grazing strategy. Grazed areas could be then seeded with more desirable plant species, creating a positive feedback cycle of grazing-restoration which would expand the abundance of nutritious forages in medusahead-infested landscapes. Results from the supplementation study showed that there was reduced incidences of grazing on perennial grasses and increased consumption of medusahead. Medusahead avoidance has been directly correlated with increased grazing pressure on perennial grasses within the plant community. This facilitates a self-reinforcing cycle of medusahead invasion. However, if supplementation increases grazing pressure on medusahead and reduces pressure on perennial grasses, this cycle is interrupted and limits the competitive advantage of medusahead, thus providing an effective and sustainable approach to medusahead management and control.

Sub-lethal rates of a glyphosate containing herbicide have been shown to reduce silica concentrations within plants as well as increase their nutritional quality, and this same result was expected in medusahead. In the sheep and cattle preference study (chapter 3), only small improvements in nutritional composition (reduced fiber contents increased fiber digestibility) were observed, likely due to the late phenological stage at which treatments occurred, thus preventing conservation of the nutritional composition of medusahead at earlier phenological stages. Despite these small responses, sheep and cattle showed increments in the use of this grass, suggesting that a combined treatment herbicide-grazing is a viable option to reduce medusahead abundance within the plant community and 'unlock' the grass as a potential forage source. Salt (KCl) in glyphosate was also thought to increase palatability of medusahead as livestock tend to display preferences for mineral sources that meet there needs. Despite salt application, animals avoided medusahead over that of glyphosate treated and non-treated medusahead.

Similar to the sheep and cattle preference studies, low rates of glyphosate application, may improve the nutritional quality and prevent silica accumulation in the grass. However, it is unknown whether glyphosate, the salt, and/or the inert ingredients are responsible for these changes. Alternatively, the presence of other chemicals in the herbicide (i.e., adjuvants) may increase the palatability of the grass, as sugars and salt represent rewards that may increase selection of forages in livestock. In the cattle grazing study of the different constituents within a glyphosate herbicide, glyphosate applications did not influence the concentration of crude protein or silica in medusahead plants, although they reduced the concentration of fiber in medusahead and annual forbs relative to non-treated or adjuvant-treated plants. This improvement in nutritional quality enhanced biomass removal after cattle grazing. In contrast, livestock avoided grazing adjuvant-treated medusahead, clearly showing that it was the active ingredient in the herbicide formulations and not the adjuvant the cause for improved medusahead utilization by cattle.

Furthermore, classical estimates of digestibility do not consider the consequences of silica concentrations on particle size and glyphosate application thus overestimating “real” digestibility values of the grass. *In vitro* fermentation kinetics of forages is a more reliable predictor of nutritional value than estimates of forage digestibility as it considers the speed at which forages are fermented, instead of just the final extent of fermentation. Smaller particle size (1 mm) appears to play the largest role at enhancing fermentation kinetics as increased surface area per unit weight promotes greater microbial recruitment and eliminates the silica-associated defense. In a rangeland setting, processing the plant material to this size is unlikely and therefore, application of a glyphosate herbicide appears to be a more practical approach for increasing consumption of the grass. The application of the herbicide increased overall efficiency of digestion and fermentation of the grass compared to that non-glyphosate treated medusahead, indicating a more palatable forage. Overall, the integrated approach of glyphosate application and livestock grazing shows promise at controlling the spread of medusahead in rangelands, as herbicide applications increases the nutritional quality and digestibility of the grass, which in turn enhance palatability and nutrition, promoting a more efficient utilization of medusahead by livestock.

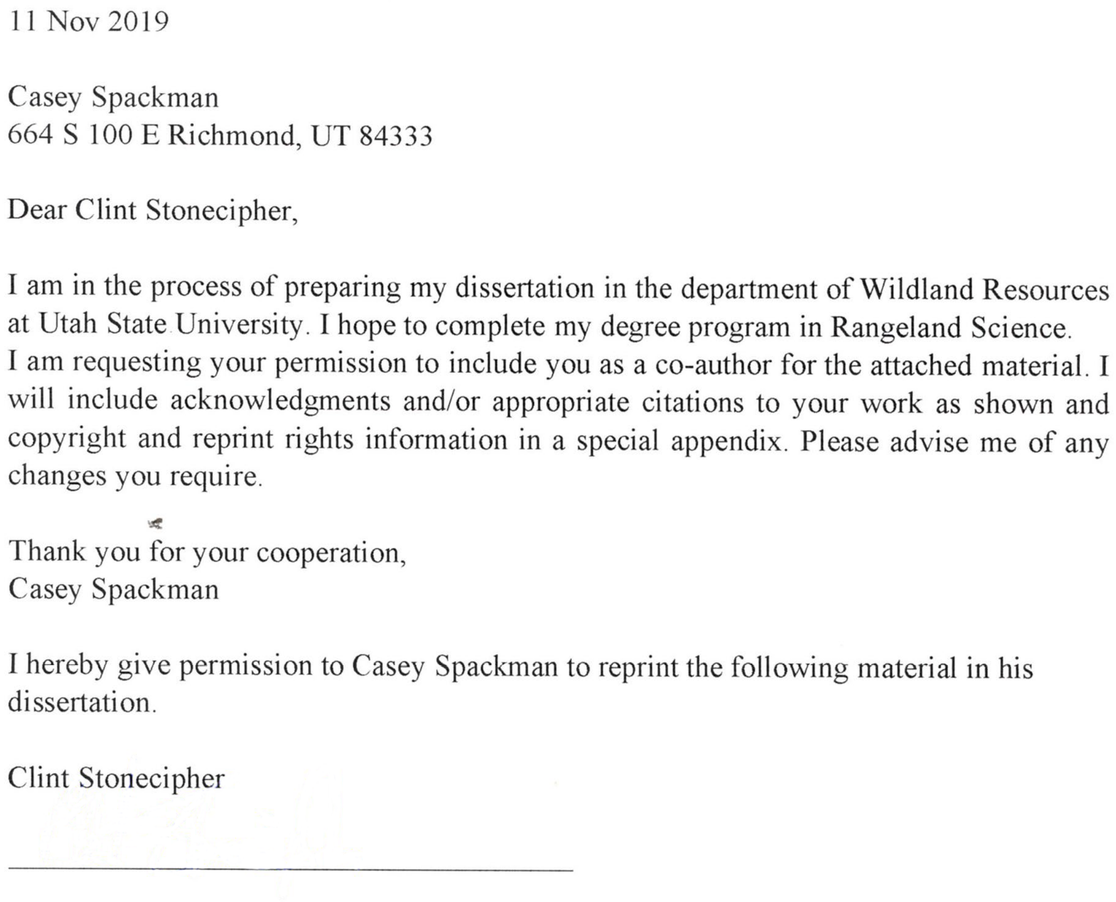
Finally, trampling of broadcasted seeds by grazing cattle has been found to have similar revegetation success to that of other more intensive disturbance method. The integrated approach of removal of medusahead by grazing and incorporating broadcast seeds through trampling was thought to increase establishment of the seeded species. Despite these efforts, trampling had no effect on the success of seeding; in fact, small burnett was the only species to establish, and those establishment rates were low. Grazing removed biomass for one year, but it was likely that it did not reduce the soil seed bank, thus medusahead continued to compete for resources in subsequent years. This suggest that there is a short time frame for revegetation efforts after grazing and that follow-up treatments are needed to reduce the seed bank of the grass such that competition is reduced during the critical period of establishment of desirable perennials.

In summary, this research illustrates that integrated approaches of supplementation or glyphosate herbicide application with grazing provides a tool for medusahead management and control, through increased nutritional quality and digestibility of the grass. These tools of medusahead control address the silica constraints of herbivory, by increasing selection of the grass by grazing livestock, and in turn interrupt the positive feedback cycle of invasion. Mitigation of this cycle provides opportunities to re-establish more desirable plant species and increase the sustainability of rangeland ecosystem function.

APPENDICES

APPENDIX A

PERMISSION LETTER



11 Nov 2019

Casey Spackman
664 S 100 E Richmond, UT 84333

Dear Clint Stonecipher,

I am in the process of preparing my dissertation in the department of Wildland Resources at Utah State University. I hope to complete my degree program in Rangeland Science. I am requesting your permission to include you as a co-author for the attached material. I will include acknowledgments and/or appropriate citations to your work as shown and copyright and reprint rights information in a special appendix. Please advise me of any changes you require.

Thank you for your cooperation,
Casey Spackman

I hereby give permission to Casey Spackman to reprint the following material in his dissertation.

Clint Stonecipher

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EDUCATION

2015-Present	Ph.D., Utah State University, Range Science
2006-2008; 2012-2015	B.S., Utah State University, Animal Science
2009-2011	Study Abroad, University of Sydney, Australia, Veterinary Medicine

PROFESSIONAL EXPERIENCE

2015-Present	Biological Science Technician, U.S Department of Agriculture, Poisonous Plants Research Laboratory, Logan, Utah
2015-2019	Research Assistant, Department of Wildland Resources, Utah State University
2012-2015	Research Technician, Department of Wildland Resources, Utah State University, Logan, Utah
2012-2015	Laboratory Technician, Utah Veterinary Diagnostics Laboratory, Logan, Utah
2009-2011	Veterinary Nurse II, Annandale Animal Hospital, Leichhardt, New South Wales, Australia

GRANTS AND AWARDS

2018-2019	Utah State University Undergraduate Research and Creative Opportunity Grant. **Co-PI** mentoring undergraduate student. $1000
2018-2019	Jeb Stuart Scholarship, Quinney College of Natural Resources, Utah State University $1000
2018	Travel Award, Our Farm Our Future Conference, St. Louis, Missouri. $1250
2017	Society of Range Management. Graduate Student (PhD) Poster Contest. 1st Place. 70th Annual Meeting, St. George, Utah
2016	Utah State University. Graduate Research and Creative Opportunity Grant. **Co-PI.** $1000
2015-2018	Utah State University. Graduate Research Assistantship

2014-2015	Utah Agricultural Leadership Scholarship, College of Agriculture and Applied Sciences, Utah State University. $750
2013	Utah State University, College of Agriculture and Applied Sciences, Utah State University Student Association, Distinguished Service Award.

CURRENT PROJECTS

Stonecipher, C., **Spackman, C.,** 2018-2020. Exploring Different Herbicides to Control Medusahead One and Two Years Post-revegetation in the Scablands of Eastern Washington and Northern Utah. USDA-ARS Poisonous Plants Research Laboratory. Glyphosate application, grazing, and revegetation, took place in 2016 and 2017. Residual medusahead seedbank still existed thus causing a return, but of lower density, of the invasive grass. Our goal was to see if certain herbicides after establishment of seeded plants would work better one year or two years post-revegetation. It is thought that certain herbicides could be used to reduce medusahead abundance while increasing the competitive advantage for the seeded grasses. My role is to provide field support for the execution of this project.

Cooper, A., **Spackman, C**., Stonecipher, C., Villalba, J.J., 2018. Timing of Glyphosate Application to Increase Cattle Consumption of Medusahead. Utah State University Undergraduate Research and Creative Opportunity Grant. Previous research from our lab has shown that cattle prefer medusahead treated with low rates of glyphosate during the phenological boot stage; however, it is unknown if this preference still exists when treated at an earlier stage (seedling) or later stage (reproductive). In addition, other plants in the community may be susceptible to glyphosate depending on their phenological stage, thus determination of when to apply herbicide may have differing effects on desirable plants. My role is to mentor an undergraduate student and facilitate the execution of this project.

Davis, Z., **Spackman, C.,** Grossl, P., 2017. Comparing Selenium Concentrations of Common Rangeland Plants through an Iron Soil Amendment. USDA-ARS Poisonous Plants Research Laboratory. Western aster is a common selenium accumulator on reclaimed mine sites and causes acute toxicity and death in livestock. Iron is thought to change the chemical composition of the selenium thus making it unavailable for uptake. In a greenhouse study, iron will be added to the soil at different concentrations. Alfalfa, western wheatgrass, and western aster will be grown and assessed for above ground biomass production and selenium concentration in both the plant shoots and roots. The overall goal of the study is to determine if iron can be used on a larger scale to reduce selenium uptake and provide non-toxic plants on reclaimed mine sites. My role is to facilitate the execution of this project and run analysis on plant shoots, roots for selenium concentration.

PUBLICATIONS

Stonecipher, C., **Spackman, C.**, Panter, K., and Villalba, J.J. 2019. 'Glyphosate as a Tool to Increase Livestock Consumption of Medusahead (*Taeniatherum caput-medusae).' Animal.* Submitted for Review.

Villalba, J. J., **Spackman, C.,** Lobón, S. 2019 'The Interplay Between Exposure and

Preference for Unpalatable Foods by Lambs.' *Applied Animal Behaviour Science.*

Villalba, J. J., **Spackman, C.,** Goff, B. M., Klotz, J. L., Griggs, T., & MacAdam, J. W. (2015). Interaction between a tannin-containing legume and endophyte-infected tall fescue seed on lambs' feeding behavior and physiology. *Journal of Animal Science,* vol. 94, pp 845-857.

Egea, A.V., Hall, J.O., Miller, J., **Spackman, C.,** and Villalba, J.J. 2014. 'Reduced neophobia: A potential mechanism explaining the emergence of self-medicative behavior in sheep.' *Physiology & Behavior*, vol. 135, pp 189–197.

PRESENTATIONS & REPORTS

Spackman, C., Stonecipher, C., Panter, K., Villalba, J.J, and Burritt, E.J. 2019. Roundup and Grazing: An Integrated Approach to Control Medusahead. Utah State University Extension Research Report 2016. https://www.onpasture.com/wp-content/uploads/2019/02/Roundup-Medusa-2016.pdf

Cooper, A., **Spackman, C.,** Stonecipher, C., and Villalba, J.J. 2019. Timing of Glyphosate Application to Increase Cattle Consumption of Medusahead. Utah State University Student Research Symposium, Logan, UT, April 10-11, 2019. Undergraduate 1st Place Poster Presentation

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2019. Medusahead: A Potential Livestock Forage on Rangelands? 72nd Annual Meeting of the Society for Range Management. Minneapolis, MN, Feb 10-14, 2019. Presentation

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2018. Medusahead: A Potential Livestock Forage on Rangelands? Restoring the West Conference, Logan, UT, October 16-17, 2018. Invited Presentation

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2018. Exploring the Fermentation Kinetics of Medusahead Treated with Glyphosate at Different Particle Lengths. American Society of Animal Science Annual Meeting, Vancouver, BC, Canada, July 8-12, 2018. Presentation

Burrit, E., **Spackman, C**. 2018. Lessons from the Cache Valley Medusahead Task Force. Wyoming Medusahead and Ventenata Education Day, Sheridan, WY, June 19, 2018. Invited Presentation

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2018. An Integrated Approach to Control Medusahead Rye Grass. SARE Our Farm, Our Future Conference, St. Louis, MO, April 3-5, 2018. Speed Presentation

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2018. Training cattle to graze medusahead and avoid velvet lupine: A new tool to sustain the economic viability of livestock operations in the Western US. Our Farm, Our Future Conference, St. Louis, MO, April 3-5, 2018. Poster

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2018. Grazing Rotations on Restored Land as a New Tool for Medusahead Control. 71st Annual Meeting of the Society for Range Management. Sparks, NV, January 28-Feb 2, 2018. Presentation

Stonecipher, C., **Spackman, C.**, Panter, K., and Villalba, J.J. 2018. Glyphosate as a Tool to Increase Livestock Consumption of Medusahead on Annual Grass Invaded Rangelands. 71st Annual Meeting of the Society for Range Management. Sparks, NV, January 28-Feb 2, 2018. Poster

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2017. Glyphosate Application and Cattle Grazing: An Integrated Approach to Control Medusahead. Utah Section Meeting of the Society for Range Management. Midway, UT, November 2-3, 2017. Invited Presentation

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2017. Glyphosate Application and Cattle Grazing: An Integrated Approach to Control Medusahead. 70th Annual Meeting of the Society for Range Management. St George, UT, January 29-February 2, 2017. 1st Place PhD Poster Competition

Spackman, C., Stonecipher, C., Panter, K., and Villalba, J.J. 2016. Grazing rotations on restored land as a new tool for medusahead control. Sagebrush Ecosystem Conservation: all Lands, all Hands. Joint conference of the Great Basin Consortium and a WAFWA-Sponsored Sagebrush Science and Management Meeting. Salt Lake City, Utah, February 23-26, 2016. Poster

TEACHING

2018	Teaching Assistant Biology, Ecology and Management of Weeds Department of Plant, Soils and Climate Utah State University

SERVICE & SOCIETIES

2018	Graduate Student Enhancement Award Review Committee, Utah State University Student Association
2017	Scablands of Eastern Washington Medusahead Field Day Demonstrator, In collaboration with Utah State University, Washington State University Extension, and the USDA-ARS Poisonous Plants Research Laboratory
2017	Graduate Student Representative for the Search Committee of two full-time Assistant Professor Positions (Animal Population Ecology and Movement Ecology), Department of Wildland Resources, Utah State University.
2017, 2019	Society or Rangeland Management
2018	American Society of Animal Science

WEBSITES & PRESS RELEASES

http://medusahead.org/

www.Researchgate.net/profile/Casey_Spackman

Voth, K., 2019. A Rancher's Discovery Shows Promise for Controlling Medusahead Rye. On Pasture. https://onpasture.com/2019/02/25/a-ranchers-discovery-shows-promise-for-controlling-medusahead-rye/