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Medusahead Ecology and Management: California Annual Grasslands to the Intermountain West

Aleta M. Nafus and Kirk W. Davies*

The spread of medusahead across the western United States has severe implications for a wide range of ecosystem services. Medusahead invasion reduces biodiversity, wildlife habitat and forage production, and often leads to increased fire frequency and restoration costs. Medusahead is problematic in the Intermountain West and California Annual Grasslands. The last review of medusahead ecology and management was completed 20 years ago. Since the last review, there have been scientific advances in medusahead management suggesting a significant need to develop an up-to-date synthesis. Medusahead continues to pose a serious threat to rangeland ecosystems. In this synthesis, we present new information regarding the ecology of medusahead, suggest a framework for managing medusahead based on invasion level, and identify research needs to further improve management of this invasive annual grass. Success of different management practices varies between the Intermountain West and California Annual Grasslands, signifying that the best management practices are those specifically tailored with consideration of climate, soil, plant community characteristics, and management objectives. Prevention and control treatments that are useful in the Intermountain West may not be practical or effective in the California Annual Grasslands and vice-versa.

Nomenclature: Medusahead, *Taeniatherum caput-medusae* (L.) Nevski; ELYCM.

Key words: Control, exotic annual grass, invasive plant prevention, restoration, revegetation.

Medusahead [*Taeniatherum caput-medusae* (L.) Nevski] is a vigorously growing exotic, annual grass invading rangelands throughout the western United States. Its invasion is a serious management concern because it reduces biodiversity, decreases forage production, degrades wildlife habitat, and alters ecosystem function (Davies 2011; Davies and Svejcar 2008). Medusahead invasion is associated with substantial decreases in native vegetation and plant diversity (Davies 2011; Davies and Svejcar 2008; Young 1992). Medusahead infestations threaten the diversity of many types of plant communities including juniper woodlands, dry forests, big sagebrush, low sagebrush, and perennial and annual grasslands (Davies 2011; Davies and Svejcar 2008; Evans and Young 1970; Young 1992). Medusahead invasion can reduce the grazing capacity of rangelands by at least 50–80% (Hironaka 1961); heavily invaded plant communities produce only 13% of the native plant biomass of noninvaded plant communities (Davies and Svejcar 2008). The loss of native vegetation associated with medusahead invasion may have severe ramifications for wildlife (Davies and Svejcar 2008) including potentially threatened sagebrush obligates such as sage-grouse (*Centrocercus urophasianus*) (Connelly et al. 2000).

Once medusahead enters a plant community, it generally spreads rapidly from one location to the next and soon becomes the dominant species. Since its arrival in the U.S. sometime prior to 1887, medusahead has spread to become a serious problem across the western USA (USDA, NRCS 2012). Although estimates of its current range are difficult to obtain, estimates suggest it has invaded at least 2.2 million hectares (5.4 million ac)across the western US (Duncan and Jachetta 2005; Duncan et al. 2004) with well over 25 million additional hectares of public land in the Great Basin at risk of annual grass invasion (Pellant and Hall 1994). With an estimated expansion rate of 12% a year (Duncan and Jachetta 2005), effectively managing existing populations and preventing further medusahead spread should be a high priority (Davies and Johnson 2008).

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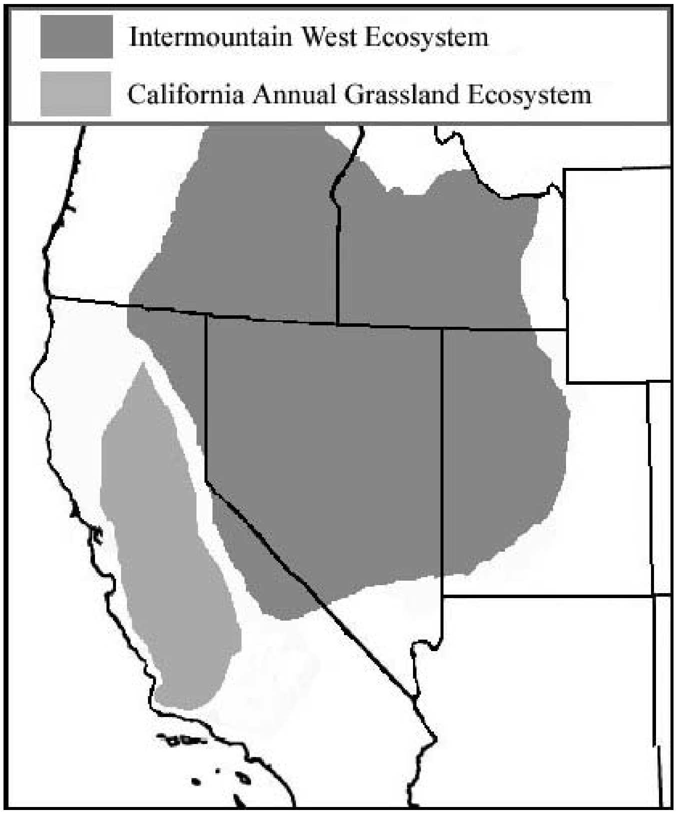

Figure 1. Map of the Intermountain West and California Annual Grassland regions in the western United States.

Because medusahead occurs across such a broad array of ecosystems, development of uniform guidelines to prevent invasion from occurring and manage and restore rangelands where it already exists have been difficult (Davies and Johnson 2011; Young 1992). There are many management options for the control of medusahead but there are no thorough summaries of the current management options across the range of the problem.

The most recent review of the ecology and management of medusahead occurred over 20 years ago (Young 1992). Advances since then have provided us with a better understanding of medusahead ecology and given us improved management options. The goals of this synthesis are to provide a comprehensive update on the knowledge of medusahead ecology and management and articulate the differences between the two main epicenters of medusahead invasion, the California Annual Grasslands and the Intermountain West. We also provide suggestions for future research directions to improve the effectiveness and efficiency of medusahead management.

In this paper, we will use the delineation of "Intermountain West" to describe an area including parts of California, Oregon, Idaho, Utah, Washington and Nevada located between the Rocky and Cascades/Sierra Mountain Ranges where the climate is characterized by warm summers and cool winters (Figure 1). The natural community is a shrub-bunchgrass steppe where the dominant shrub is sagebrush (most commonly *Artemisia tridentata* Nutt. and *Artemisia arbuscula* Nutt.). In relatively intact plant communities, bunchgrasses are the dominant herbaceous vegetation, including bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Great Basin wildrye [*Leymus cinereus* (Scribn. & Merr.) A. Löve], Idaho fescue (*Festuca idahoensis* Elmer), bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], needle-and-thread grass [*Hesperostipa comata* (Trin. & Rupr.) Barkworth], Sandberg bluegrass (*Poa secunda* J. Presl), and Thurber's needlegrass [*Achnatherum thurberianum* (Piper) Barkworth]. The "California Annual Grasslands" for the purposes of this paper are areas with a Mediterranean climate characterized by warm winters where the current dominant vegetation consists of introduced annual grasses and forbs (Figure 1). Remnant native perennial bunchgrasses include purple needlegrass [*Nassella pulchra* (Hitchc.) Barkworth], California oatgrass (*Danthonia californica* Bol.), blue wildrye (*Elymus glaucus* Buckley), and one-sided bluegrass (*Poa secunda* ssp. *secunda*). Characteristic introduced annual grasses include wild oats (*Avena fatua* L.), soft brome (*Bromus hordeaceus* L.), ripgut brome (*Bromus diandrus* Roth), red brome (*Bromus rubens* L.), mouse barley (*Hordeum murinum* L.), and rattail fescue [*Vulpia myuros* (L.) K.C. Gmel.].

Ecology

Medusahead occurs across a wide variety of climatic and soil conditions. It occurs in areas that receive 250 to1000 mm (9.8 to 39.3 in) of precipitation arriving predominantly in the fall, winter, and spring with a dry summer (Major et al. 1960; Sharp et al. 1957; Torell et al. 1961). Medusahead germination occurs with fall precipitation, typically from October through November, though it can continue through winter and spring (Young 1992). Leaf development in fall can reach several inches before cold weather stops the growth process (Young 1992), and root growth can continue throughout winter (Hironaka 1961). Above-ground growth resumes in spring, and flowering typically occurs sometime in early June with most seedheads maturing by July (Sharp et al. 1957). Like all annuals, seed production is essential to the continuation and further spread of a medusahead infestation. Medusahead can exhibit high phenotypic plasticity in seed production; an isolated plant without neighbors can produce as many seeds as 1,000 more densely packed plants (Young 1992). Although average production is less, in ideal conditions a stand of medusahead can produce well over 10,000 seeds·m^{-2} (10,000 seeds 10.8 ft^{-2}) (Clausnitzer et al. 1999). Medusahead seed dispersal begins in summer with dispersal mainly occurring in August although seeds will continue to disperse from the parent plant into fall (Davies 2008). Seed dispersal is accomplished in a number of ways. In the absence of water, large animal, vehicle or human vectors of dispersal, medusahead generally disperses relatively short distances; 75% of seeds land less than 0.5 m (1.7 ft) from the invasion front and most of the remaining seeds disperse no further than 2 m from the invasion front (Davies 2008). Although most seed probably remains in, or near, the infestation, spread into medusahead free areas is possible through a variety of vectors. Medusahead seeds have long awns covered in small barbs that facilitate dispersal by adhesion to animals and vehicles (see Davies 2008 and Davies and Sheley 2007a). Medusahead seeds may be transported and cached by small mammals (Miller 1996). Davies and Sheley (2007b) found medusahead seed can also be dispersed by wind over short distances [typically less than 10 cm (3.9 in)]. Whole plants may disarticulate and be carried by the wind, ride along on travelling tumbleweeds such as tumble mustard (*Sisymbrium altissimum* L.) or Russian-thistle (*Salsola tragus* L.), or get transported in the mud adhering to a vehicle or to the foot of an animal (personal observations). Medusahead infestations are more common near roads than at other locations, suggesting that vehicles are probably an important vector for its dispersal, possibly, in part, because roadside areas are conducive to medusahead establishment (Davies et al. 2013). An increase in the numbers of vectors available to spread seed probably results in a higher seed introduction rate and, therefore propagule pressure, into an area (Davies 2008).

Medusahead is highly competitive on sites with high clay content and shrink-swell potential and is most problematic on these soils (Sheley et al. 2008; Stromberg and Griffin 1996). Medusahead is also able to invade loamy soils (Miller 1996) but is less likely to invade well-drained, coarser, sandy textured soils (Dahl and Tisdale 1975). Soil disturbance leads to increased medusahead potential for dominance on all soil types (Miller 1996).

Competition from established vegetation can limit medusahead establishment. Medusahead establishment was negatively correlated with the density of tall tussock perennial bunchgrasses (Davies 2008). Removal of perennial grasses resulted in the greatest increase (almost double) in medusahead density and biomass compared to the removal of any other plant functional group (Sheley and James 2010). Established perennial bunchgrasses in the Intermountain West may successfully reduce medusahead seedling establishment through reduced resource availability. Other plant functional groups in the Intermountain West, however, do not appear to have as much influence on medusahead establishment. The susceptibility of a plant community to medusahead invasion does not appear to be correlated with the density of Sandberg bluegrass or forbs (Davies 2008), although the loss of rhizomatous forbs may result in greater medusahead density and biomass (Sheley and James 2010).

If medusahead is able to establish successfully in a community, it may be able to displace native vegetation by forming a dense thatch layer; creating an ideal habitat to promote further medusahead germination and establishment while generally limiting germination and establishment of other species (HilleRisLambers et al. 2010; James et al. 2011b). The formation of these thick, persistent, thatch layers not only helps to inhibit growth of rival species, but also increases the amount and continuity of fine fuels (Davies and Svejcar 2008; Torell et al. 1961; Young 1992; Young et al. 1972) leading to increased fire frequency. This increased fire frequency is detrimental to the less fire-adapted native vegetation and beneficial to further medusahead dominance, thereby causing a grass-fire cycle that promotes medusahead dominance to the detriment of native vegetation (D'Antonio and Vitousek 1992). In addition to being well adapted to fire, medusahead is more tolerant of intense grazing pressure than are many native species (Pyke 2000).

Established medusahead communities may also inhibit native vegetation through more rapid uptake of soil nutrients. Medusahead seedlings are better at acquiring soil resources than native grass seedlings because they have higher growth rates, even under low nutrient conditions, than native seedlings (James 2008a, 2008b; Mangla et al. 2011; Monaco et al. 2003b; Young and Mangold 2008). The exact mechanisms by which medusahead outcompetes other plants have been difficult to elucidate (Arredondo et al. 1998; James 2008a, 2008b; James et al. 2010). A reciprocal transplant experiment suggests that medusahead may be highly invasive in the United States because of elevated availability of soil nutrients relative to its native Europe (Blank and Sforza 2007).

Management

We propose a framework for management of medusahead based on the level of invasion (Figure 2) adapted from general frameworks for invasive species developed by Hulme (2006) and Simberloff et al. (2013). Medusahead management is separated into to three different management stages in our framework: (1) prevention, (2) early detection, and (3) rehabilitation. Dissimilar to Hulme (2006) and Simberloff et al. (2013), we are dealing with one invasive species that has already been introduced into the region. Thus, our recommendations for prevention are focused on limiting its spread within an area where it has already been introduced. The objective of early detection is to locate new infestations (satellite populations) and attempt to eradicate them. When medusahead invasion has progressed to established infestations, often near monocultures, medusahead management shifts to rehabilitation.

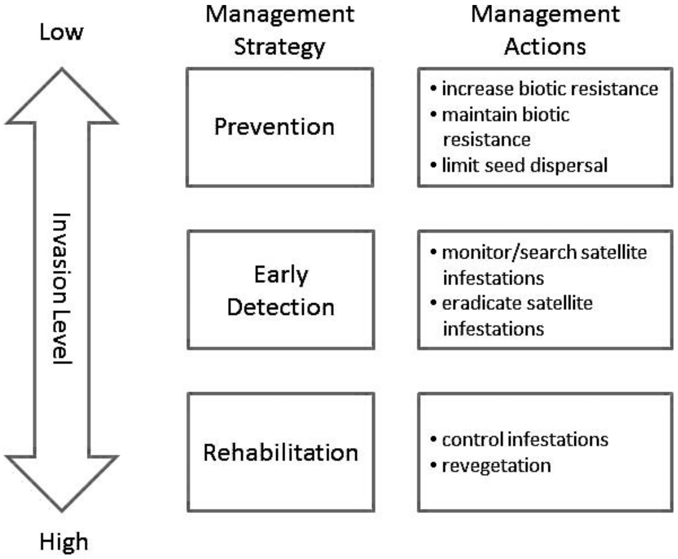

Figure 2. Framework for managing medusahead based on invasion level (Adapted from Hulme 2006 and Simberloff et al. 2013).

Rehabilitation begins with medusahead control and is often followed by revegetation. We place a heavy emphasis on prevention and early detection because of the high cost of control and revegetation, as well as the loss of species diversity associated with medusahead invasion (Davies 2011). In addition, even though short-term control has been achieved with a variety of treatments, successful revegetation after medusahead control has been less common (Monaco et al. 2005; Sheley et al. 2007). If revegetation is not successful, medusahead rapidly regains dominance of the plant community (Davies 2010; Monaco et al. 2005).

Prevention. Preventing medusahead from invading desired landscapes cannot be overemphasized as the best use of resources and the most effective management strategy, mostly because of the low rates of success in rehabilitating invaded communities. There are two important strategies in developing effective prevention programs. The first is to prevent medusahead from reaching a site and the second is to prevent medusahead seed that reaches a site from establishing by promoting the biotic resistance of the desired plant community. Unfortunately, it is hard to quantify the effectiveness of prevention methods (Davies and Johnson 2011), but useful strategies for medusahead prevention have recently been developed.

Reducing Dispersal. Medusahead seeds appear to be primarily transported by humans (often via vehicles) and animals (Davies et al. 2013). If human and animal transport of medusahead is restricted, medusahead seeds generally disperse relatively short distances (Davies 2008). Sheley et al. (2003) suggest that a barrier to spread can be created by spraying herbicide along the border of existing invasive plant infestations. Maintaining neighboring vegetation taller than the invasive species can physically intercept seeds and thereby limit the spread of medusahead (Davies and Sheley 2007b). For example, Davies et al. (2010b) found that seeding crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] around infestations reduced the invasion of medusahead into nearby non-invaded plant communities. Depending on the availability of transport vectors, it is probable that these barriers would not need to be very wide to be effective. Once a barrier is established, vehicle, human and livestock travel from infested to uninfested areas should be restricted as much as possible, especially during seed dispersal.

Maintaining or Increasing Biotic Resistance. Competition from other species may prevent medusahead from establishing on a site or prevent medusahead from regaining dominance following successful control (Davies 2008; James et al. 2008), possibly by limiting the resources available to medusahead. In the warm-winter annual grasslands of California, more desirable annual grasses may provide the best competition against medusahead (Kyser et al. 2008). In the semi-arid, cool-winter areas of the Intermountain West, it is important to maintain intact perennial bunchgrass communities as they are the most important functional group to successfully inhibit medusahead establishment (Davies 2008; James et al. 2008; Sheley and James 2010).

In the Intermountain West, the perennial bunchgrasses with the most promise as competitors against medusahead are crested wheatgrass and squirreltail (Arredondo et al. 1998; Harris and Wilson 1970; Monaco et al. 2003b). Squirreltail has successfully established in near-monocultures of medusahead, but its presence does not appear to result in further succession (Hironaka and Sindlelar 1973; Hironaka and Tisdale 1963; Young 1992). Although squirreltail will establish in stands of medusahead, it does not appear to be able to compete effectively with medusahead, especially at the seedling stage (Harris and Wilson 1970; Young and Mangold 2008). Plant communities seeded with crested wheatgrass were much more resistant to medusahead invasion compared to non-seeded plant communities (Davies et al. 2010b).

Though reducing soil resource availability (water, N, etc.) has been speculated to shift the competitive advantage from exotic annual grasses to native perennial grasses, recent research indicates exotic annual grasses are more competitive than native perennial grasses even under low resource availability (James 2008a, 2008b; Monaco et al. 2003a), especially at the seedling stage (James et al. 2011a). However, reductions in nitrogen availability did reduce growth differences between native perennial bunchgrasses and medusahead, limiting medusahead growth to an extent that perennial grasses might be able to compete successfully (Monaco et al. 2003a). Reductions in nitrogen can reduce biomass and seed production of medusahead (Brunson et al. 2010). This implies if soil N is maintained at low levels for multiple years, established perennial bunchgrasses might be able to compete more effectively with medusahead than when soil N is elevated (James et al. 2011a). At higher temperatures, medusahead is better able to utilize N suggesting that a warmer climate may increase the success of medusahead relative to native perennial bunchgrasses (Leffler et al. 2013), increasing the importance of maintaining functional plant communities with high biotic resistance. Amendments to reduce nitrogen availability, (e.g. barley straw, sucrose, sawdust) tend to be short-lived and expensive to apply on a large scale (Alpert and Maron 2000; Brunson et al. 2010; Monaco et al. 2003a). Water can also be an important limiting factor of plant growth in rangelands (Chambers et al. 2007). Drought may slightly reduce medusahead's competitiveness against native bunchgrasses (Clausnitzer et al. 1999; Mangla et al. 2011) but can also limit bunchgrass establishment (Kyser et al. 2013; Sheley et al. 2012a). Although drought years can drastically reduce the medusahead seedbank, a single wet year may allow for complete replenishment (Young et al. 1998). Even though resource limitation may reduce medusahead success, it is unlikely that resource limitations will eliminate medusahead from a community (Clausnitzer et al. 1999; Mangla et al. 2011; Young et al. 1998). Maintaining an ecologically functional, competitive plant community is important to help limit resource availability and provide resistance to medusahead invasion (Davies 2008; Sheley and James 2010).

In some circumstances, carefully utilized management may be used to help maintain a resistant plant community and increase the resistance of the plant community to invasion. In the Intermountain West, low to moderate levels of grazing may increase the ability of a community to resist invasion following a fire disturbance compared to no grazing. On relatively intact Wyoming big sagebrush sites, cheatgrass density was nearly 40-fold higher following a prescribed burn in areas where grazing was excluded for 60+ years than on adjacent moderately grazed sites (Davies et al. 2009). Grazing in this system reduced the buildup of litter, which reduced the severity of the fire and decreased fire-induced mortality in the perennial grasses component (Davies et al. 2010a, 2009). Though medusahead invasion was not explicitly tested, the loss of perennial bunchgrasses would open the plant community to medusahead invasion (Davies 2008; James et al. 2008; Sheley and James 2010). In the Intermountain West, grazing practices that favor perennial bunchgrasses may be the best approach to manage medusahead. For example, fall defoliation (clipping) of a crested wheatgrass stand reduced the density and biomass of medusahead by 50% relative to spring and early summer defoliation (Sheley et al. 2008), whereas early spring defoliation reduced the competitive ability of bluebunch wheatgrass against medusahead (Sheley and Svejcar 2009).

Regardless of management, some sites are more susceptible to invasion than other sites and even the best management may not prevent medusahead invasion. Sites with high clay content and shrink-swell potential favor medusahead and can be marginal for perennial grass survival (Sheley et al. 2008; Stromberg and Griffin 1996). On these sites, medusahead may invade regardless of the presence or absence of grazing. On a low sagebrush site with high clay content medusahead frequency was approximately 30% on both, a site that had been protected from grazing for over 30 years and on a nearby grazed site, though neither site had medusahead at the time the exclosure was constructed (Wagner et al. 2001).

Early Detection. Despite well planned and implemented prevention efforts, medusahead plants will probably establish in previously non-invaded areas. A system should be in place to detect these new infestations early to improve the probability of successful eradication and to reduce costs (Davies and Johnson 2011; Sheley et al. 2003). It is much more effective to control a new small infestation than a larger infestation (Moody and Mack 1998; Smith et al. 1999). Sheley et al. (2003) outlined general steps for detecting and eradicating weed introductions. They suggested that a survey plan that includes inventory techniques, the area to be surveyed, and survey time periods must be developed for each management area. Survey efforts should be primarily concentrated on roads, secondarily on animal trails, and then on random areas because roads appear to not only be the primary vector pathway for medusahead spread into new areas but, roadsides may provide an ideal environment for medusahead establishment (Davies et al. 2013). When medusahead infestations are found, the plants must be controlled, taking care to minimize further seed dispersal. After control treatments have been applied, continued monitoring should be performed to ensure that treatment was successful.

Rehabilitation. Even with the best prevention and early detection of medusahead infestations, there are millions of hectares already invaded by medusahead (Duncan and Jachetta 2005; Duncan et al. 2005; Pellant and Hall 1994) that will need to be rehabilitated. In addition, there is a high probability that new infestations will continue to occur and grow large enough that they will need to be rehabilitated even with well-developed prevention and early detection programs. For successful rehabilitation, medusahead must first be controlled. Control of exotic plants is often accomplished with biological control, prescribed fire, herbicides, mechanical treatments, grazing, or integrated approaches that use some combination of these individual treatments. Near-monocultures of medusahead have little remaining desirable vegetation (Davies 2011) and thus seeding of desired plants is often required following medusahead control (Davies 2010).

Biological Control. Biological control agents are not currently commercially available for managing medusahead. Although many types of fungus that cause crown and root rot have successfully reduced seed production in medusahead, they have also proved to also be fairly detrimental to desirable native grasses and/or cereal grain crops (Berner et al. 2007; Grey et al. 1995; Siegwart et al. 2003). No insects have been identified for use in the management of medusahead. A native rhizobacterium, *Pseudomonas flourescens* strain D7 (*Pf* D7), was shown to be deleterious to medusahead in the laboratory, and field tests currently in progress are indicating promising reductions in medusahead density three years after application (Ann Kennedy, personal communication).

Prescribed Fire Control. Medusahead populations are able to rapidly recover after fire (D'Antonio and Vitousek 1992). However, under certain circumstances burning can be an effective tool for reducing medusahead. Medusahead seed production is later than many other annual species in the California annual grassland, allowing for selective burning to reduce medusahead and favor more desirable annual species (Kyser et al. 2008; Meyer and Schiffman 1999). The effectiveness of burning is influenced by many factors including: fuel loading, preburn species composition, fire characteristics, and weather conditions during and after the burn (Harrison et al. 2003; Kyser et al. 2008). A temporary reduction in viable medusahead seed can be achieved through prescribed burning if a slow burn that maximizes heat intensity is performed during the late dough stage before seedheads mature (McKell et al. 1962; Pollak and Kan 1998; Sharp et al. 1957; Sheley et al. 2007). Medusahead seed mortality is greater when burned prior to seed drop because seeds on the soil surface are less likely to receive sufficient heat to exceed the mortality threshold than are seeds still in the inflorescence (Sweet et al. 2008). Multiple burns in consecutive years may be required to successfully reduce medusahead, as a single burn may leave sufficient seeds to re-colonize the site (Blank et al. 1996). In the low elevation, warm winter areas of California, high fuel loads of annual grasses are conducive to burning in the several consecutive years necessary to achieve successful medusahead control (Kyser et al. 2008), and burning may be timed to favor more desirable annual grasses (Murphy and Lusk 1961). In contrast, in semiarid, cold-winter areas of the Intermountain West, timing of burning and insufficient combustible biomass to conduct multiple consecutive burns may make it difficult to achieve satisfactory medusahead control (Kyser et al. 2008). In these ecosystems, burning medusahead, especially after seed maturation, generally only serves to increase medusahead dominance unless further treatments are applied (Davies 2010; Davies and Sheley 2011; Maret and Wilson 2005; Young et al. 1972).

Herbicide Control. A number of herbicides have been successfully applied to control medusahead. Herbicide selection depends on a number of factors including the present and desired plant community, revegetation plans, and local regulations. Glyphosate is a broad spectrum herbicide often used on rangelands. Proper timing (at medusahead tillering) of glyphosate application at low rates [158 to 315 g ae ha^{-1} (2.2 to 4.4 oz product acre^{-1})] can maximize medusahead control while minimizing damage to non-target species such as sagebrush (Kyser et al. 2012a). It has been shown to be effective against medusahead, although multiple years of treatment may be required because it does not inhibit establishment from the seedbank (Kyser et al. 2012a). Imazapic and rimsulfuron have, in recent years, been widely tested for controlling medusahead, especially in the Intermountain West (Davies 2010; Davies and Sheley 2011; Kyser et al. 2007, 2012b; Monaco et al. 2005; Sheley et al. 2007). These herbicides can be fall applied for preemergence control or spring applied for post emergence control. Fall imazapic (70 g ae ha^{-1}) application provided better medusahead control and relatively fewer deleterious impacts on perennial vegetation than spring application (Kyser et al. 2007; Monaco et al. 2005). Imazapic and rimsulfuron are less likely to have deleterious impacts on perennial grasses and forbs than nonselective herbicides such as glyphosate (Sheley et al. 2007; Shinn and Thill 2004). However, imazapic and rimsulfuron show inconsistent control of medusahead in the California Annual Grassland (Kyser et al. 2007, 2012b). In the case of imazapic this may be because of binding in the thatch layer (Kyser et al. 2007). Inconsistencies in the control of medusahead with rimsulfuron may be because of rapid degradation in warmer soils, allowing for later season medusahead germination and establishment (Kyser et al. 2012b). Even in high-elevation, cool-winter areas, the effectiveness of preemergent herbicide treatments such as imazapic may be influenced by soil type, with clay soils exhibiting reduced herbicide activity compared to sandy loam soils (Hirsch et al. 2012). In the Intermountain West, imazapic provided the longer term control of medusahead (80% after 2 years) than rimsulfuron (Kyser 2013). In the California Annual Grassland, a high rate (245 g ae ha^{-1}) preemergent application of aminopyralid, typically used as a broadleaf herbicide, showed promise by reducing medusahead and some broadleaf species and allowing more desirable annual grasses to increase (Kyser et al. 2012b). However, depending on sensitivity, preemergent herbicide treatments may cause injury to desired plants, especially if there are desired annual grasses or annual forbs in the plant community (Davies 2010; Davies and Sheley 2011; Kyser et al. 2007; Louchaichi et al. 2012).

Mechanical Control. In the California Annual Grasslands, mechanical treatments have been used to temporarily reduce medusahead. Plowing, disk harrowing, furrowing, mowing, tilling or raking can reduce medusahead 65 to 95% for one year following treatment, although medusahead may quickly reinvade and mechanical treatments may result in increased exotic forb cover (Cox and Allen 2008; Harwood 1960; Kyser et al. 2007; Young et al. 1969). Mechanical treatments in these areas were generally intended as preparation for herbicide application and, although few details are present, were performed in spring (Cox and Allen 2008; Young et al. 1969) or fall (Harwood 1960; Kyser et al. 2007). Mechanical treatments to control medusahead have not been evaluated in the Intermountain West. However, chaining treatments to reduce cheatgrass and increase seeding success of perennial grasses have had mixed success (Ott et al. 2003; Pierson et al. 2007). Mechanical treatments are often expensive and can be destructive to soils and remnant native plants (Mattise and Scholten 1994; Pierson et al. 2007). They are also limited by factors such as rockiness and slope of the site (Mattise and Scholten 1994), precluding their use on many rangelands.

Grazing Control. Given the proper conditions, grazing can be used as a tool to reduce medusahead cover and seed production, increase the abundance of native forb species, or increase the resistance of plant communities to invasion (DiTomaso et al. 2008; Griggs 2000; Reiner and Craig 2011). Although medusahead has poor palatability, it will be eaten early in the season before seedheads emerge (Bovey 1961; Lusk et al. 1961; Torell et al. 1961).

Timing and intensity of grazing treatments is important in both the California Annual Grasslands and the Intermountain West (DiTomaso et al. 2008; Sheley et al. 2008; Sheley and Svejcar 2009). In established medusahead infestations in the California Annual Grasslands, high intensity grazing with sheep or cattle successfully reduced medusahead cover (DiTomaso et al. 2008; George et al. 1989; Lusk et al. 1961). The success of sheep grazing treatments to control medusahead may be increased by grazing during the stem elongation phase. Mid-spring (April/May) grazing reduced medusahead cover by 86 to 100% (DiTomaso et al. 2008) and increased forb cover, native forb species richness and abundance, and overall plant diversity (DiTomaso et al. 2008; Griggs 2000). In contrast, early spring (March) or fall (October/November) grazing did not reduce medusahead cover (DiTomaso et al. 2008), and year-round grazing was associated with greater medusahead frequency (Harrison et al. 2003).

Integrated Management. Although control of medusahead has been achieved with individual treatments, combining treatments tends to increase effectiveness (Davies 2010; Davies and Sheley 2011; Kyser et al. 2007; Monaco et al. 2005). The use of prescribed fire, mechanical methods, or grazing to remove the thatch layer prior to herbicide application not only reduced the amount of herbicide needed but also resulted in greater control of medusahead, greater establishment of bunchgrasses, and increased the longevity of medusahead suppression compared to any of the treatments applied alone (Davies and Sheley 2011; Kyser et al. 2007; Sheley et al. 2007, 2012a). Prior removal of medusahead thatch by burning or clipping increased the effectiveness of sheep grazing as a tool for reducing medusahead (Lusk et al. 1961).

Revegetation. Seeding forbs, more desirable annual grasses or perennial grasses may be a necessary component of effective management after medusahead control (Seabloom et al. 2003). However, revegetation of invaded plant communities has proven challenging and is often unsuccessful. Revegetation efforts, especially when using native perennial species, have high rates of failure (James et al. 2011b). Medusahead is more competitive in the seedling stage than perennial bunchgrasses (Harris and Wilson 1970; Hironaka and Sindlear 1973; Young and Mangold 2008); thus, successful control of medusahead is often needed for effective establishment of desired vegetation (Davies 2010).

The type and timing of pretreatment actions may affect the success of revegetation efforts and will probably depend vary by species, herbicide type, and site characteristics. In the Intermountain West, Monaco et al. (2005) found a greater increase in perennial grass cover with fall than spring herbicide application for both imazapic and sulfometuron, especially on sites with lower medusahead thatch layers. Imazapic application resulted in higher perennial grass cover than sulfometuron application. Burning prior to herbicide application can increase the diversity of remnant vegetation released from medusahead suppression compared to herbicide alone (Sheley et al. 2012a). If prescribed burning is performed prior to herbicide application, the season of burn can play a role. Both fall and spring burns followed by fall imazapic application resulted in greater perennial grass cover and overall plant diversity than either burning or herbicide alone, but spring burning resulted in slightly more perennial grass cover while fall burning was more advantageous for perennial forbs (Davies and Sheley 2011). Although seedings of desirable species are likely to be more successful if they are done one year following herbicide application, increased density of desirable plants and reduced treatment costs and time may be possible with a single application approach (in which seed and herbicide are applied simultaneously) although results will be heterogeneous across large landscapes (Sheley et al. 2012a,b). Successful annual grass control with imazipic application is likely to result in high mortality of simultaneously seeded species (KW Davies, unpublished data; Madsen et al. 2014). In the California Annual Grassland, medusahead seed production is later than many other annual species allowing for selective burning to reduce medusahead and favor more desirable annual species (Kyser et al. 2008; Meyer and Schiffman 1999).

In the California Annual Grasslands, strategically timed grazing of medusahead infestations may be used to encourage establishment of more desirable vegetation (DiTomaso et al. 2008; Mac Lauchlan et al. 1970; Menke 1992). Early spring grazing treatments may help reduce annual grass abundance and seed production, allowing for increased abundance of native perennial bunchgrasses (Menke 1992). The intensity of grazing treatments is also important. At high levels of grazing, neither exotic annual grasses nor native perennial grasses were able to establish in medusahead stands, but at low grazing intensity, limited establishment of more desirable exotic annual grasses can occur (Suding and Stein 2010).

Native vs. Introduced Species. Although it is often desirable to revegetate with native species, they are frequently more difficult to establish and may be less resistant to reinvasion (Arredondo et al. 1998; James et al. 2011b). In the Intermountain West, crested wheatgrass, an introduced perennial bunchgrass, is often used in revegetation projects, because it is less expensive and germinates and establishes more successfully than native species (Boyd and Davies 2010; Eiswerth et al. 2009). Introduced species, such as crested wheatgrass, are typically more competitive and easier to establish (Davies et al. 2010b; James et al. 2011b), and may provide similar ecosystem function as more desirable native species (Davies et al. 2011). However, the issue of revegetating an area with introduced species can be controversial (Davies et al. 2011). For example, crested wheatgrass can be highly competitive with native plants and may limit native species diversity (Asay et al. 2001; Hull and Klomp 1967). Introduced species may result in plant communities that do not provide as good of habitat for some native wildlife as native plant communities (McAdoo et al. 1989; Reynolds and Trost 1981). When faced with the high probability of failure when attempting to establish native species, it may make more sense to revegetate with introduced species, at least in the short term, to occupy the site to limit medusahead reinvasion. Once the medusahead seedbank has been greatly reduced, it may be possible to replace the introduced species with native species (Cox and Anderson 2004; Seabloom et al. 2003). A potential revegetation scenario is that crested wheatgrass can provide a bridge between exotic annual grass infestations and native dominated plant communities (Cox and Anderson 2004). However, because of the highly competitive nature of crested wheatgrass, it may be difficult to replace it with native species (Fansler and Mangold 2011; Hulet et al. 2010).

It is potentially possible to select native plants to improve the probability of revegetation success. Revegetation success probably varies by the source and genetic subtype of native vegetation species. For example, big squirreltail (*Elymus multisetus* M.E. Jones) plants removed from an area with high levels of cheatgrass invasion initiated growth faster after transplanting than did plants collected from nearby uninfested sites (Leger 2008). Ecotypic variation in squirreltail species may be part of the reason squirreltail has had mixed success as a competitor against medusahead (Arredondo et al. 1998; Hironaka and Sindlear 1975; Hironaka and Tisdale 1963; Young and Mangold 2008). In the Intermountain West, the likelihood of successfully establishing native species also increases as sites become cooler and wetter.

In the California Annual Grassland, introduced forbs such as Lana vetch (*Vicia dasycarpa* Ten.) have been developed to more effectively compete with medusahead (Mac Lauchlan et al. 1970), although the fertilizer amendments necessary for successful establishment may be impractical for large scale restoration efforts. Although restoration of native perennial grasses in the California Annual Grassland is often a management objective, the authors were unable to find sufficient research to indicate the relationship between medusahead control and perennial grass restoration in this area. Although perennial grass restoration into stands of introduced annual grasses may be possible with proper grazing management, burning treatments, and reseeding efforts in the California Annual Grassland (Menke 1992; Seabloom et al. 2003), this has not been evaluated for medusahead-invaded California Annual Grassland communities.

The decision to use native or introduced species to revegetate medusahead-invaded rangelands will ultimately depend on the risk of failure, the risk the manager is willing to take, the resources available, and the objective of the revegetation project. Site characteristics will, of course, influence the risk of failure and will need to be considered when selecting revegetation species. Because seeds of native species are often much more expensive than introduced species, additional resources will be required if natives are used. Additional resources, because of a higher failure rate, will also probably be necessary for reseeding if the initial seeding of native species fails to establish.

Future Research Needs

Successful control of medusahead has been achieved with a variety of herbicides, but revegetation has often failed (Kyser et al. 2013; Monaco et al. 2005; Sheley et al.

2012a). Thus, improving seeded vegetation recruitment is critically needed. James et al. (2011b) identified the emergent stage as a major bottleneck for recruitment of seeded perennial grasses. Determining what mechanisms are limiting emergence, such as physical soil crusts, pathogen attacks, freeze-thaw cycles, and drying of the soil surface, and spatial and temporal extend of these factors would provide valuable information in developing technologies and for selecting plant materials with traits to overcome these limitations. Seed enhancing technologies can enhance germination, emergency, and early growth (Madsen et al. 2014). Therefore, seed enhancing technologies, especially those designed to overcome an ecological barrier to recruitment, should be high priority for future research. Additional research investigating the ability of different plant materials to establish and resist medusahead re-invasion is also needed. Selecting individuals that have higher emergence rates may help overcome the bottleneck at the emergence state. Because plants used to revegetate medusahead-invaded rangelands are likely to face re-invasion by medusahead, selecting plants that are competitive with medusahead is critical. Determining the mechanisms by which some plants are more competitive and then selecting for those traits would be valuable. For example, plants with greater nitrogen uptake at higher temperatures may be more competitive with medusahead (Leffler et al. 2013). Genetic subtypes of native vegetation that are persisting in medusahead infestations may be a promising avenue of research to pursue to select individuals that are more competitive. Remnant native bunchgrasses in cheatgrass-invaded communities grew faster and were more competitive with cheatgrass than bunchgrasses from non-invaded communities (Leger 2008). Therefore, it is highly likely similar traits are present in remnant native plants in medusahead-invaded communities.

The underlying mechanisms that result in variation in revegetation success need to be identified so that areas can be grouped according to their likelihood of being rehabilitated. Revegetation success and the cost to successfully revegetate a unit of land vary considerable across degraded landscapes (Boyd and Davies 2012; Sheley et al. 2012b). Therefore, it would be much more efficient to concentrate efforts in areas where revegetation success is more likely, but information on the causes of revegetation success or failure is generally lacking. Often unsuccessful attempts are anecdotally attributed to ‘‘below-average precipitation’’ (e.g. Kyser et al. 2013). The timing is probably just as important as the amount of precipitation and other environmental/site characteristics likely greatly influence the probability of revegetation success (Boyd and Davies 2012; Boyd and James 2013).

Implementation of prevention plans is constrained by lack of proven methods (Davies and Johnson 2011). Land managers need prevention methods that have been scientifically validated and the benefits of their implementation quantified. Prevention efforts could be improved by determining what plant communities are at the greatest risk of invasion. This would include determining the influence of plant community composition, site characteristics, management actions, climatic variability, disturbances, and their interactions on invasibility. In addition, more information is needed on medusahead invasion patterns from existing infestations to help quantify invasion risk as well as to identify where and what management efforts should be applied to limiting medusahead spread. This information could also be used in models to predict where medusahead infestations are more likely to occur and be used to strategically monitor for new infestations.

Conclusions

Medusahead is a serious problem in the western United States where infestations span a range of climatic and management conditions. Management strategies must be considered over a number of factors including climate, soil, plant community characteristics, and management objectives. Management tools and strategies may not be interchangeable between the Intermountain West and Annual Grasslands of California.

In the California Annual Grasslands, high densities of other annual species may facilitate a burning or grazing regimen to reduce the seed production of medusahead and favor more desirable vegetation, whereas these treatments are less likely to be successful in the Intermountain West. In contrast, pre-emergent herbicides are effective for controlling medusahead in the Intermountain West because of differences in life-cycles between medusahead and most desirable vegetation. However, pre-emergent herbicide applications in the California Annual Grasslands could negatively impact desirable annual grasses. In both the Intermountain West and the California Annual Grasslands, medusahead management appears to require an integrated approach that eliminates or severely reduces medusahead infestations and enables desirable species to become dominant. Seeding with desirable vegetation after medusahead control may be necessary in both regions. Species should be selected with consideration of management objectives and climate, as well as their competitiveness with medusahead.

Although we present a framework with general guidelines for the Intermountain West and California Annual Grasslands, it is important to remember that the most effective management will depend on a variety of site factors including, but not limited to, soil type, climate, level of infestation, success of revegetation and subsequent management. Because of the difficulty and expense of controlling medusahead and then revegetating a site, preventing medusahead from becoming a problem in the first place should be the top priority. Medusahead spread may be reduced by limiting travel through invaded areas, selecting and utilizing management strategies that favor more desirable plants to promote biotic resistance to invasion and by eliminating small medusahead infestations. When treating larger infestations as preparation for restoration, efforts should first focus on areas containing remnant native vegetation. The Intermountain West and California Annual Grassland each contain a diverse assemblage of environmental and site characteristics. Analysis of soils, climatic nuances, and vegetation differences, and the interactions of each of these with medusahead control and revegetation treatments, will advance management of medusahead. Ideally, tools and strategies developed can be effective across a wide variety of sites. However, an understanding of management limitations will help managers choose the best strategy when resources are limited.

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