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ECOLOGY AND MANAGEMENT OF MEDUSAHEAD (*TAENIATHERUM CAPUT-MEDUSAE* SSP. *ASPERUM* [SIMK.] MELDERIS)

James A. Young[1]

ABSTRACT.—Medusahead is another in the extensive list of annual herbaceous species to invade the temperate desert rangelands of the Great Basin. Medusahead is not preferred by large herbivores and apparently is not preferred by granivores. Herbage of this annual grass enhances ignition and spread of wildfires. Medusahead is highly competitive with the seedlings of native species and is probably the greatest threat to the biodiversity of the natural vegetation that has yet been accidentally introduced into the Great Basin. Despite the obvious biological disruptions that are associated with medusahead invasion, the species offers a wealth of opportunities for students to examine the mechanism by which this species is so successful. Students of evolution, plant physiology, and ecology may find this species to be an excellent model for colonization.

Key words: medusahead, Taeniatherum caput-medusae, *annual grass, colonizing species, wildfires, grazing.*

In the management of natural resources there are certain problems that by their persistence, magnitude of ecological disruption, and economic impact refuse to dissipate as a result of being ignored and neglected. Unfortunately for range management, medusahead (*Taeniatherum caput-medusae* [L.] Nevski) is that type of problem. During the 1950s medusahead was considered among the most pressing problems on the rangelands of California, Idaho, and Oregon. A great deal of research effort was devoted to solving the medusahead problem. Valuable information was learned about the ecophysiology and synecology of medusahead. Control methods were developed using herbicides. The fatal link in integrated programs for the suppression of medusahead populations proved to be artificial revegetation technologies after medusahead was controlled. The nature of the sites infested had more to do with this failure than the weed itself, especially in the Intermountain area. The recent discovery of medusahead in northern Utah has renewed interest in suppressing this rangeland weed.

My purpose in this review is to refresh our collective memories about medusahead ecology and management.

TAXONOMY

As is often the case with an introduced species, there has been confusion about the correct scientific taxon for medusahead. The first description of medusahead in a North American flora used the taxon *Elymus caput-medusae* L. (Howell 1903). There is apparent agreement that medusahead is a member of the tribe Triticeae of the grass family. There is also apparent agreement among morphologists and cytogeneticists that medusahead does not fit in the genus *Elymus*. Various authors have placed medusahead in *Hordeum* or *Hordelymus*. Nevski (1934) proposed that medusahead was truly a different genus and published the name *Taeniatherum*. Jack Major of the University of California suggested in 1960 that material introduced to the United States was *Taeniatherum asperum* (Major et al. 1960). Based on the European and Russian literature, Major reported that *Taeniatherum* contained three geographic and morphologically distinct taxa, *T. caput-medusae, T. asperum,* and *T. crinitum.* These three species are found in the Mediterranean region and extend eastward into central Asia. After examining the European material, growing in place, Major decided the United States introduction was *T. asperum.*

The Danish scientist Signe Frederiksen revised the genus in 1986. He kept the same three taxa, but reduced them to subspecies of *Taeniatherum caput-medusae.* Positive identifi-

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[1] Agricultural Research Service, U.S. Department of Agriculture, 920 Valley Road, Reno, Nevada 89512.

cation to the lowest level possible is absolutely essential for any proposed biological control program for medusahead. According to Frederiksen's revision, subspecies *crinitum* has a very strict spike. Subspecies *caput-medusae* has a large open spike with straight awns. The spike of subspecies *asperum* is intermediate with angled awns. Subspecies *asperum* is the only one of the three with pronounced barbs coated with silica on the awns. Apparently, the correct taxon for the medusahead of western North America is *Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis (Frederiksen 1986).

Taeniatherum caput-medusae ssp. *caput-medusae* is mostly restricted to Portugal, Spain, southern France, Morocco, and Algeria. It has been collected outside this area in Europe and Asia, but Frederiksen considers it adventitious in these areas. Subspecies *crinitum* is found from Greece and Yugoslavia eastward into Asia. Subspecies *asperum* completely overlaps the distribution of the other two subspecies. All three subspecies integrate with each other. Apparently only the one subspecies occurs in North America. Does this indicate one or very limited introductions?

Medusahead is predominantly self-pollinated. Genetically the genus appears to stand alone in genomic relations within the Triticeae (Schooler 1966, Sakamoto 1973). Apparently *Taeniatherum* has a genome that is distinct, but faintly related to those of *Psathyrostachys*, *Dasypyrum*, *Eremopyrum*, or *Hordeum* (Frederiksen and Bothner 1989).

HISTORY IN NORTH AMERICA

Medusahead was first collected in the United States near Roseburg, Oregon, on 24 June 1887 by Thomas Jefferson Howell (1903). It was next collected near Steptoe Butte in eastern Washington in 1901 by George Vasey (Piper and Beattie 1914), followed by a collection near Los Gatos, California, in 1908 by Charles Hitchcock (Jepson 1923). Medusahead certainly attracted the noted agrologist. McKell, Robinson, and Major (1962) commented on this strange initial distribution reaching 390 miles north and 450 miles south from the point of initial collection. Early herbarium specimens show a rapid spread to the south into California.

J. F. Pechanec made the first collection in Idaho in 1944 near Payette or about 180 miles south of Steptoe Butte (Sharp and Tisdale 1952). Fred Renner told Jack Major he had seen medusahead near Mountain Home, Idaho, as early as 1930, and Lee Sharp had reports from ranchers that the species occurred in Idaho as early as 1942. The medusahead infestation in Idaho increased to 30,000 acres by 1952. Min Hironaka estimated that 150,000 acres were infested by 1955, and the Bureau of Land Management estimated 700,000 acres were infested by 1959. At that rate of spread it appeared that all of Idaho would be infested by the end of the next decade. The spread of medusahead slowed and nearly continuous infestations remained confined to Gem, Payette, and Washington counties in southwestern Idaho. There were several spot infestations in surrounding counties (Hironaka and Tisdale 1958).

Medusahead spread south in California to Santa Barbara on the southern coast and Fresno County in the interior valleys. The rapid spread from southwestern Oregon through northern and central California occurred in annual-dominated grassland, oak (*Quercus*) woodland, and chaparral communities. These areas have a Mediterranean type climate with hot, dry summers and cool, moist falls, winters, and springs. Germination occurs in the fall and flowering and seed set in the spring.

In northeastern California, east of the Sierra Nevada–Cascade rim, medusahead invasion occurred at a much slower rate. In the Pitt River drainage, vegetation is an intergrade of Oregon white oak (*Quercus garryana*) woodlands, cismontane California species, western juniper (*Juniperus occidentalis*), ponderosa pine (*Pinus ponderosa*) woodlands, and sagebrush (*Artemisia*)/bunchgrass communities more typical of the Intermountain area.

Medusahead was discovered in the Great Basin at Verdi, Nevada, in the early 1960s. Isolated infestations were subsequently found along the eastern front of the Sierra Nevada in areas where range sheep bands used to concentrate while waiting for mountain summer pastures to be free of snow.

In northeastern California in the Great Basin during the early 1960s, there were two small infestations in city lots in Susanville and a small infestation at the old sheep-shearing site of Viewland along the railroad above Wendel, California. Another isolated infestation occurred at the mouth of Fandango Pass in Surprise Valley. By the early 1970s, medusahead was nearly continuous over about 60,000 acres of the Willow Creek–Tablelands northeast of Susanville. Currently, after four years of extreme drought, medusahead spot infestations occur over perhaps an additional million acres on the western margin of the Great Basin.

BIOLOGY OF MEDUSAHEAD

Medusahead, in some ways, is a rerun of cheatgrass (*Bromus tectorum*) invasion. Cheatgrass dominates secondary succession in a majority of sagebrush/bunchgrass communities in the Great Basin and provides a significant portion of the forage base for livestock grazing. However, there are highly significant differences in the ecology of the two grass species (Harris and Wilson 1970, Al-Dakheel 1986).

GERMINATION.—The caryopsis of medusahead is less than a millimeter wide with a very sharp callus and an elongated, non-geniculated awn. The medusahead caryopsis is covered with small barbs of silica. Vicious is the best description for this grass caryopsis. Bovey et al. (1961) determined that medusahead had a much higher ash content (over 10%) than other grass species and the ash was about 75% silica. Heavy deposition of silica occurs on the barbs of awns and the epidermis of leaves.

For the vast majority of collections of cheatgrass from the Intermountain area, seeds are ready to germinate when they are mature. No pregermination treatments are necessary (Young and Evans 1982). For collections from the Great Plains and perhaps the Columbia Basin, seeds may have a brief afterripening dormancy. In contrast, seeds of medusahead have a temperature-related afterripening, and germination will not occur except at cold incubation temperatures for about 90–120 days after maturity (Young et al. 1968). Nelson and Wilson (1969) found this dormancy was controlled by materials located in the awn.

The high silica content on the herbage of medusahead makes the litter very slow to decompose. Harris (1965) described the choking accumulations of medusahead litter that built up for several years. We evaluated the germination of seeds of various annual grass species in medusahead litter (Young et al. 1971a). Allelopathy was not suspected, but rather the physical holding of seeds out of contact with the surface of the seedbed. Medusahead seeds germinate very well without the callus end of the seeds touching a moisture-supplying substrate. In this situation, germination of medusahead seeds is controlled by the relative humidity within the litter and the incubation temperature, which of course influences the relative humidity. The needlelike, vitreous caryopses of medusahead appear hydrophobic rather than hygroscopic. Not only can medusahead seeds germinate under these conditions, but they can be dried until the primary root is dead; then, following remoistening, a new adventitious root will develop.

Raymond Evans and I demonstrated what a great modifying influence litter cover can be to the surface of seedbeds on temperate desert rangelands in terms of reducing extremes in temperature and conserving moisture (Evans and Young 1970, 1972). Caryopses of squirreltail (*Elymus hystrix*) are very similar in morphological appearance to those of medusahead. As I will discuss later, squirreltail seedlings are one of the few native species that can become established in undisturbed medusahead stands. Both *Taeniatherum* and *Elymus* are members of the tribe Triticeae, but they do not share the same genome.

Medusahead populations easily exceed 1000 plants per square foot, and they are phenotypically plastic enough that a population of 1 plant per square foot can exceed the seed production of 1000 plants per square foot (unpublished research, ARS, Reno, Nevada). Huge seed banks develop in medusahead communities in the litter and soil. Medusahead seed acquires a dormancy in the field similar to that of cheatgrass (see Young et al. 1969). These dormant seeds respond to enrichment of the seedbed with nitrate and gibberellin (Evans and Young 1975).

LIFE CYCLE.—Medusahead seeds can germinate in the fall, winter, or spring; and seedlings from all seasons can produce flowers and seeds early in the summer. The striking thing about the medusahead life cycle is that it matures from 2 to 4 weeks later than other annual grasses. All those famous botanists and range scientists who were out on the range discovering new infestations of medusahead were led to the populations by the bright green color when all other annuals in either cismontane California or the Great Basin were brown.

R. L. Piemeisel recognized the dominance of alien plant species in the secondary succession of disturbed sagebrush communities in the

Intermountain area (Piemeisel 1951). Working on the Snake River plains of Idaho during the 1930s, Piemeisel enumerated dominance from Russian thistle (*Salsola australis*) to tumble mustard (*Sisymbrium altissimum*) to cheatgrass. Continued disturbance tended to perpetuate cheatgrass dominance. According to Piemeisel, the annual species that germinates first, reaches maximum growth and maturity first, has the capacity to withstand crowding, and has high seed production is the one that will occupy and persist in seral sagebrush plant communities. Piemeisel always noted that no one species had a clear dominance on all these characteristics, but on balance cheatgrass was the clear winner.

Medusahead contradicts several of Piemeisel's criteria. Medusahead seeds are initially dormant with temperature-related afterripening requirements, while cheatgrass seeds have no such restraints. This works only for initial establishment because once seed banks are established with seeds with acquired dormancy, our research indicates that cheatgrass and medusahead seeds have equal chances of germination with the initial moisture event in the fall. Medusahead does take much longer to mature than cheatgrass and perhaps tumble mustard. Min Hironaka and his students have conducted a series of excellent experiments comparing the cumulative growth curves for roots and aerial structures of medusahead and other grasses (Hironaka 1961, Hironaka and Sindelar 1973, 1975). Dr. Hironaka concluded from these studies that the comparative growth phenology restricts medusahead to areas with surplus soil moisture after cheatgrass normally matures.

SOILS

Raymond Evans noted in the 1950s when medusahead first invaded Glenn and Colusa counties in the northern Sacramento Valley of California that medusahead appeared to be restricted to clay-textured soils (personal communication). Mallory (1960) reported on this relationship at the 1960 meeting of the California section of the Society for Range Management. Burgess Kay made the chilling observation that after a couple of decades this relationship disappeared and medusahead occupied many sites with coarser-textured soils (personal communications).

In the Intermountain area, Maynard Fosberg of the University of Idaho reported that the medusahead infestations along the Columbia River in Washington, Idaho, and Oregon were restricted to clay-textured soils (Fosberg 1965). He suggested that the greater soil moisture-holding capacity of these soils allowed medusahead to complete its life cycle.

Building on the work of Fosberg and Hironaka, I sampled the plant communities in the medusahead invasion area along the western edge of the Great Basin (Young and Evans 1970). Medusahead was found on the margins of many degraded meadows where moisture relationships probably favored it over cheatgrass. A much larger area of infestation was sagebrush/grass communities. The sagebrush communities consisted of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) on soils with sandy loam to loam-textured surface horizons and often well-developed argillic horizons. A second series of sagebrush communities consisted of low sagebrush (*A. arbuscula*) growing on soils with clay-textured surface horizons. Harry Summerfield (retired soil scientist, Soil Conservation Service and Forest Service, USDA) suggests the low sagebrush soils share the same development as the big sagebrush soils, but the surface horizons have been removed by erosion (personal communication). On the Modoc Plateau of northeastern California these two series of plant communities divide the landscape about equally (Young et al. 1977). In the northern Great Basin low sagebrush constitutes only about 10% of the total sagebrush vegetation.

On the western edge of the Great Basin, medusahead, in nonmeadow situations, is largely restricted to low sagebrush potential plant communities. Would this restriction to clay soils change over time as appears to have happened in cismontane California? Remember the studies of Raymond Evans that showed competition in the cismontane portion of the California annual grasslands is initially for light, while in cheatgrass communities of the Intermountain area, competition is overwhelmingly for soil moisture (Evans et al. 1970, 1975).

WILDFIRES

Accumulations of litter, on areas where medusahead is established, will burn. McKell, Wilson, and Kay (1962) had initial results that seemed to indicate that burning was the answer to the control of medusahead. The idea was to burn stands while competing annual grasses were fully mature and medusahead seeds were still in the inflorescences. This study showed burned seeds would not germinate. However, the burned seeds were apparently incubated at 20 C, and unburned fresh seed would not have germinated at that temperature. We tried a series of burning experiments on the Pitt River Indian reservation and found burning favored medusahead (Young et al. 1972). We helped Forest Service range conservationists evaluate burning treatment on low sagebrush communities on the Silver Lake district of Fremont National Forest in Oregon; the off-season burns appeared to favor remnant perennial grasses over medusahead.

Low sagebrush communities, because of lack of herbaceous cover, are relatively resistant to the spread of wildfires. Big sagebrush communities, especially those with cheatgrass understories, are very subject to the spread of wildfires. Invasion of medusahead into low sagebrush communities introduces wildfires to these communities, perhaps for the first time since they were in pristine condition. Perennial grass, forb, and shrub cover are all negatively correlated with medusahead cover in the western Great Basin (Young and Evans 1970).

GRAZING PREFERENCE

It is obvious from the above discussion that preference by grazing animals plays an important part in the successional dynamics of medusahead communities. One of the few studies of medusahead palatability was conducted on the northern coast of California using sheep in small hurdle plots (Lusk et al. 1961). Under the confined conditions of the study, sheep utilized medusahead when it was green. When faced with no choice, they used some herbage after the medusahead matured. How much utilization of medusahead would occur in temperate desert situations is unknown.

Cheatgrass stands put a tremendous production of grass caryopses into a local ecosystem. Vertebrate granivores have adapted to this food source. Savage et al. (1969) showed in feeding trials that Chukar Partridges (*Alectoris graeca*) could not utilize the caryopses of medusahead as a food source. These birds are dependent on cheatgrass seeds in the fall and winter. We do not know what the influence of medusahead invasion would be on other granivores. Seeds of other recently introduced weeds in temperate desert communities, such as those of barbwire Russian thistle (*Salsola paulsenii*), are heavily preyed upon by granivores. If cheatgrass populations crash because of replacement by medusahead, what happens to cheatgrass seed predators?

A study conducted at Washington State University illustrates that granivore preference works both ways in plant succession. Bird populations prefer the seeds of native perennial grass species over those of cheatgrass and medusahead (Goebel and Berry 1976).

Utilization of medusahead by large herbivores of infested ranges results in increased incidence of injury from the seeds. Data on the level of injury are not available for domestic livestock and certainly not available for wildlife.

CONTROL OF MEDUSAHEAD

Kay developed highly technical and very successful control and revegetation techniques for the annual-dominated rangelands of cismontane California using the herbicide paraquat (1,1′-dimethyl-4,4′ bipyridinium ion) and specialized seeding equipment (Kay 1963, 1966, Kay and McKell 1963).

This technique was not successful in the Intermountain area because medusahead plants were not susceptible to paraquat in the temperate desert environment and the annual legumes that proved so adapted to cismontane California were not adapted to the sagebrush environment (Young et al. 1971b). Herbicidal fallow techniques using atrazine (6-chloro-N-ethyl-N′-[1-methylethyl]-1,3,5,-triazine-2,4-di amine) or dalapon (2,2-dichloropropanoic acid), and mechanical fallow techniques were developed for use in the Great Basin. Hilken and Miller (1980) provide a summary of herbicidal control measures applied experimentally for the control of medusahead. A large part of the area infested with medusahead in the western Great Basin was never adapted to these treatments because of surface rock cover that prohibited tillage or seed-drilling techniques. The current mass cancellation of federal registration for uses of herbicides on rangelands and the failure of federal land management agencies to adopt the use of herbicidal revegetation techniques have made the use of these techniques impossible. Landforms and soils of the sites where medusahead is spreading into temperate desert rangelands are critical factors in the ecological suppression of this species.

NATURE OF MEDUSAHEAD-INFESTED LANDSCAPES

The landscape of the western Great Basin where medusahead has invaded is composed of a series of fairly recent basalt flows that comprise the Modoc Plateau and the extreme southern extension of the Columbia River Basalts. Superimposed on the flows are clays from a Tertiary-age lake. This lake was much older than pluvial Lake Lahontan, which lapped at the lower margins of the flows. The old lake left thick beds of clay-textured sediments occasionally interbedded with diatomaceous earth. The clay minerals are predominantly double lattice forms that expand and contract with moisture content. This expansion and shrinkage has sorted basalt rock from the buried flows into giant polygons and pressure ridges until portions of the landscape resemble arctic ice packs that are black instead of white.

There are a host of topoedaphic situations within this wilderness that support specific assemblages of plants; however, the landscape is characterized by upland areas of residual soils with loam-textured surface soils that support big sagebrush and clay-textured surface soils that support low sagebrush. Vast, nearly level benches of lake sediments support swirling mosaics of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and a recently discovered type of sagebrush, a subspecies of low sagebrush known as Lahontan sagebrush. The basin big sagebrush occurs in depressions where erosional products accumulate on soils with clay-textured surface horizons, a very unusual occurrence for the Great Basin. The Lahontan sagebrush communities occur on the lake bed clay sediments that are veneered with thin layers of subaerially deposited, coarser-textured soil.

Wind erosion products accumulate under the shrub canopies and, coupled with organic matter from leaffall, build mounds under the shrubs while miniplayas develop in the interspaces. Eckert et al. (1989) have described and experimented with the seedbeds of these mound interspace situations, particularly the vesicular crust that forms in the interspaces and limits establishment of perennial grass seedlings.

The area of medusahead invasion in the western Great Basin is a microcosm where events in soil and plant ecology that influence millions of acres in the Intermountain area are brought, by fortuitous combinations of physical and biological parameters, into sharp focus. In the medusahead invasion area, lake-deposited red clay is in obvious discontinuity with the thin, grayish surface soil. In undisturbed profiles of this situation the influence of alleviation of subaerial deposited material is apparent on the structure of the clay subsoil, indicating the antiquity of this process (personal communication, Robert Blank, soil scientist, ARS, USDA).

Accumulations of medusahead litter change wildfire characteristics, and the shrub component of the plant community is eliminated. Continued grazing of medusahead-dominated grasslands is extremely deleterious on remnant perennial grasses because of differential grazing preference. In contrast to medusahead, cheatgrass is seasonally preferred forage species, and even the dry herbage of cheatgrass is utilized by livestock. This *dilutes* the effect of grazing as far as the native perennials are concerned. Lack of preference for medusahead *concentrates* the effects of herbivory. Subaerially deposited surface soil is extremely erodible once protection of the shrub canopy and its dependent microphytic crust is lost. Loss of the surface leads to exposure of the clay sediments that then function as Vertisols, shrinking, cracking, and swallowing the surface and reexpanding with moisture. Medusahead is one of the few plant species adapted to these Vertisols. Perhaps some of the soils of these landscapes were always Vertisols where, in wet years, annual sunflowers (*Helianthus annuus*) and turkey mullein (*Eremocarpus setigerus*) formed the only native vegetation. Perhaps excessive grazing converted some of these soils to Vertisols before medusahead arrived. The important point is that medusahead is actively attacking assemblages of native vegetation and changing the physical and biological potential of the sites.

MANAGEMENT OF MEDUSAHEAD INFESTATIONS

It is difficult to revegetate Vertisols in desert environments with both seedlings of woody and herbaceous species, native and exotic. Not only establishment but also subsequent growth are problems on these soils despite both tremendous cation exchange capacity and moisture-holding capacity. The tremendous matric potential of these fine clay soils is always surprising. Moisture is not available for normal plant growth when soils still stick to your boots.

NATURAL SUCCESSION

Dr. Min Hironaka suggests that over prolonged periods perennial seedlings might establish in medusahead-infested sites, especially the short-lived perennial grass squirreltail (Hironaka 1963). Dr. Hironaka and his students followed this aspect of medusahead succession in several studies. He demonstrated that squirreltail can establish in medusahead communities, but he found the perennial grass populations to be cyclic. When the squirreltail plants die, they are replaced by medusahead, not longer-lived perennial grasses (personal communication).

In the western Great Basin, Dr. Hironaka's work is borne out by gradual increases in squirreltail plant density as grazing management systems have been implemented. This has been especially noticeable during the past four years of extreme drought. Densities of one squirreltail plant per 10 square feet began to change the aspect of medusahead-dominated sites, but the fragile nature of this improvement is apparent when bioassay of seed banks shows 250–500 viable medusahead seeds per square foot (down from 1000 per square foot before the drought) and fails to detect any viable squirreltail seeds (unpublished research ARS, USDA, Reno, Nevada).

As you look at medusahead-infested areas on the Vertisols of the western Great Basin, you have a nagging thought that something is missing. The Lahontan and big sagebrush communities of the ancient lake sediments have as their most frequent perennial grass Sandberg bluegrass. This species is completely absent from the medusahead stands and is missing from the stands where squirreltail has begun to return. What factors of seedbed quality exclude the native invader Sandberg bluegrass and are the same factors related to the failure of higher-level perennial grasses to become established in squirreltail/medusahead communities?

The striking difference between native and medusahead communities, other than loss of shrub canopies, is loss of subcanopy mounds and microphytic crust that covers the mounds to extend down to mingle with vesicular crust in the interspaces. The thallophytic crust of mosses, lichens, and liverworts is obviously gone, and we can only speculate on the fate of the microscopic crust of algae, fungi, and bacteria. Prolonged medusahead dominance may decrease populations of mycorrhizae spores in the soil and thus influence growth of artificially established perennial seedlings (personal communication, Jim Trent, soil microbiologist, ARS, USDA, Reno, Nevada).

Specific plant pathogens, developed and marketed by biotechnological companies, may have a role in range weed control. Perhaps a *Fusarium* species exists that would be highly specific for medusahead (personal communication, Joe Antognini, National Program scientist, Weed Science, ARS, USDA).

Taxonomists and geneticists who have worked with medusahead have commented on how variable individual collections may be. Common garden studies have shown this to be true for collections from the American West (McKell, Robinson, and Major 1962, Young et al. 1971b). We found, in common garden studies, a collection from northern California that matured 4 weeks earlier than the average for other collections or on or before the maturity for cheatgrass. As medusahead evolves, we have yet to see the limits of its potential on the western range. The recent discovery of medusahead in Utah illustrates that portions of the eastern Great Basin have the potential to be invaded by this weed (Horton 1991).

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