Invasion of Medusahead into the Great Basin[1]

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Abstract. We characterized soil and vegetation assemblages, many of which are infested with medusahead (*Taeniatherum asperum* (Sim.) Nevski), on the margin of the Great Basin. Interpretations of these assemblages provide an index of the validity of the basic environmental unit of this ecosystem which can be manipulated through weed control and revegetation techniques. Vertisol (churning clay soils) sites with sparse native plant communities are more susceptible to medusahead invasion than more complex low sagebrush (*Artemisia arbuscula* Nutt.) or low sagebrush-woodland communities on related clay soils. If the more complex communities are degraded to a low seral state, medusahead can invade and occupy the site. Wet meadows and burned coniferous forest sites at high elevations were the only sites where medusahead occurred on soils with textures other than clay. Big sagebrush (*Artemisia tridentata* Nutt.) communities on medium to coarse textured soils were very resistant to medusahead invasion. The restriction of medusahead to certain sites controls the mechanism of invasion and interacts with the breeding system of the species to influence its evolution.

INTRODUCTION

A succession of alien species has been introduced into the seral plant communities of the Great Basin. In one brief century, man through domesticated animals and use and suppression of fire, has revolutionized stand renewal processes in plant communities of the arid interior basin of western North America. The suppression of these native plant communities and the introduction of grazing animals have created voids in the herbaceous vegetation which have been exploited by highly competitive alien annual species. This alien invasion is of sufficient magnitude and duration that the annual grass, downy brome (*Bromus tectorum* L.), which occupies the highest seral position among the aliens, characterizes millions of acres of rangeland. Piemeisel (26) astutely described the steps in succession of these seral alien communities from Russian thistle (*Salsola kali* L. var. *tenuifolia* Tausch) infestations to downy brome dominance. The recent introduction of medusahead (*Taeniatherum asperum* (Sim.) Nevski) and its subsequent spread to the edge of the Great Basin threatens to add a new dimension to succession among the aliens.

Medusahead has been a highly successful invader of plant communities since its introduction from Europe or Asia to southwestern Oregon late in the nineteenth century (32). Spreading through a series of mountain valleys, medusahead reached the upper Sacramento Valley of California by 1900 (25). Since then, medusahead has spread through the annual-dominated ranges of northern and central California. Besides expanding its range to the south, medusahead has spread across the Cascade Mountains into eastern Oregon and the Columbia Basin. In western Idaho, this species has increased its distribution from a few isolated patches to more than 750,000 acres in 15 years (14). In eastern Oregon and Idaho, medusahead has successfully invaded seral communities and replaced downy brome as the dominant alien grass.

Medusahead has slowly progressed across the mountainous plateau of northeastern California until infestations are poised on the edge of the interior basin of northeastern California, northern Nevada, and western Utah.

The consequences of the phytosociological intrusion of medusahead have ramifications throughout the ecosystem of the invaded area. The replacement of other alien annuals by this species dramatically modifies the food supply of caryopses-eating birds and small mammals (29). The replacement of downy brome removes an important source of forage for grazing animals. The carrying capacity of rangeland for domestic livestock has been reduced by 40 to 50% following invasion of medusahead (20). The accumulation of medusahead litter greatly increased the hazard of wildfires.

To counter and suppress the effect of medusahead on the infested ecosystem, wildland managers are attempting to reduce its dominance of plant communities by tillage, burning, spraying of herbicides, and grazing management.

Almost all of the limited studies of the ecology of medusahead have been concerned with its control and suppression after it has become established (16, 17, 23, 31). With the notable exception of the investigations by McKell *et al.* (22), little is known of the mechanism of invasion of this or any other weedy species in relation to the characteristics of the effective environments being invaded or the genetic complement of the invader.

This investigation was to characterize the soil and vegetation assemblages on the margin of the Great Basin where medusahead infestations occur. These assemblages are the basic units of the ecosystem for vegetation manipulations such as weed control. This characterization is used to infer a mechanism of invasion by this species. In essence, this provides a stratification of the environment based on the susceptibility of plant communities to invasion.

METHODS

We described soil and vegetation assemblages (effective environments) on the margin of the Great Basin starting at Reno, Nevada, and continuing for 200 miles through northeastern California to the boundary between California and Oregon. This is the area where medusahead infestations have reached or extended into the physiographic province of the Great Basin (19). The area of the investigations is shown in Figure 1.

Climatic patterns. Throughout the investigation area, the bulk of the precipitation occurs during the winter as snow. Summer precipitation is largely confined to in-

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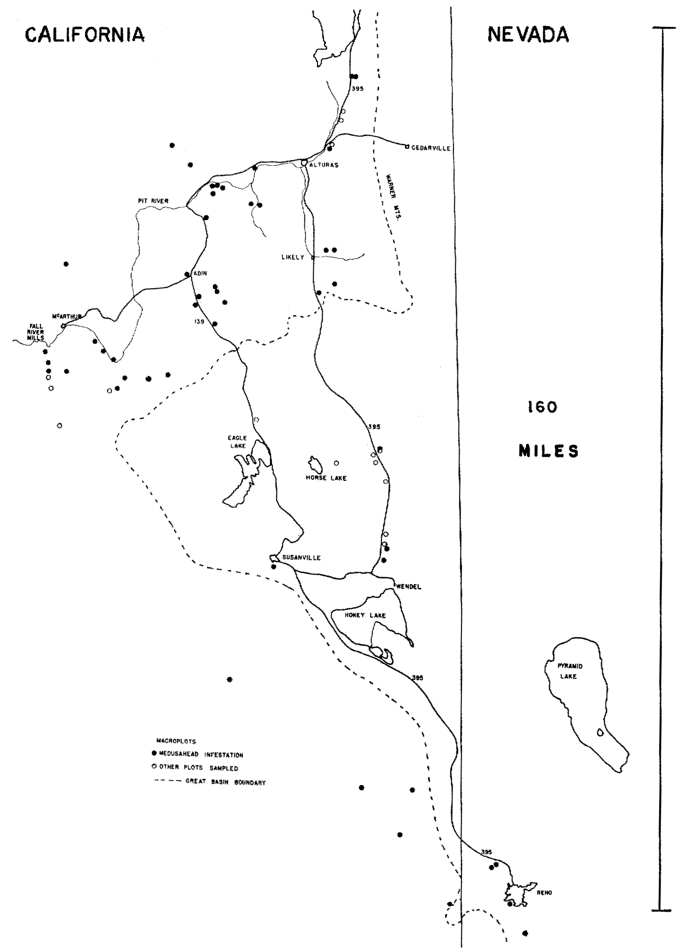

Figure 1. Study area showing Great Basin boundary and sampling locations.

frequent and highly variable thundershowers. Sufficient rainfall for germination of annuals before cold temperatures in the fall is highly variable among years. Spring precipitation can extend into June, creating ideal conditions for the growth and reproduction of annuals or be virtually nonexistent after the winter storms. In general, annual precipitation declines at similar elevations as one moves from west to east and enters the Great Basin (Table 1).

Sampling procedure. We located sites to be described along three transects. The most western transect is completely cismontane running northward from Fall River Mills to Davis Creek, California. This transect roughly follows the route of Highway 299 and the main course of the Pit River. In this area, the valleys are devoted to intensive agriculture and the mountains are heavily forested. The foothills have almost all suitable sites infested with medusahead. Where wildfires have burned into the forest, medusahead forms extensive colonies in higher elevation sites which formerly were ponderosa pine (*Pinus ponderosa* Dougl.) and western juniper (*Juniperus occidentalis* Hook) woodlands. The plant communities, 6 miles southwest of Fall River Mills where the transect begins, contain many species such as digger pine (*Pinus sabiniana* Dougl.) which are characteristic elements of the woodland vegetation of the cismontane foothills of the Sierra Nevada (24).

Table 1. Average annual precipitation in inches for reporting stations in study area.[a]

Transects: Western	inches	Central	inches	Great Basin	inches
Adin	18	Jess Valley	17	Fort Bidwell	14
Alturas	13	Madeline	15	Termo	15
Davis Creek	24	Loyalton	25	Secret Valley	11
Canby	17	Susanville	24	Wendel	9
Fall River	17			Doyle	17
				Cedarville	13

[a]Climatological Data, Environmental Science Services Administration. U. S. Department of Commerce, Vol. 15, 16, 17 and 18.

We initiated the second transect on the broad crest of the mountainous plateau which separates the drainage of the Pit River Basin from the Susan River watershed which drains into the Great Basin. This transect extends northeastward among the jumble of mountains between the interior basin and the drainage of the Pit River. Along this transect we found the most easterly extensions of continuous medusahead infestations. Characteristically, infestations along this transect were small isolated stands far in advance of the continuous front. This transect started in islands of low sagebrush (*Artemisia arbuscula* Nutt.) among park-like stands of ponderosa pine and white fir (*Abies concolor* (Gord. and Glend.) Lindl.) and ended among western juniper and low sagebrush woodlands on the southwestern extensions of the Warner Mountain Range.

The third transect was initiated at Reno, Nevada, and followed the course of Highway 395 northward to the south end of the Warner Mountain Range. This transect was entirely in the Great Basin. The landscape is characterized by long mountain slopes covered with a series of big sagebrush (*Artemisia tridentata* Nutt.) communities. At higher elevations western juniper/low sagebrush woodlands are encountered. Along the base of the Sierra Nevadas, ponderosa pine and Jeffrey pine (*Pinus Jeffreyi* Grev. and Balf.) forest merge with the big sagebrush shrub steppe.

When we initiated this investigation in 1965, there were only three small and isolated infestations of medusahead known in the Great Basin. The first known infestation in the Great Basin was discovered in 1963 at Verdi, Nevada (33). Subsequently, small infestations were located southwest of Reno, Nevada and at Susanville, California.

Selections of sites to be described. We started sampling in 1965 on the first cismontane transect where medusahead infestations are almost continuous. After preliminary reconnaissance, we located macroplots in each plant community infested with medusahead. As we moved from south to north along the transect, we added plots in each community infested with this species. These additional plots may have been similar soil-vegetation assemblages to those already described or new communities of differing potentials.

We followed the same procedure on the second transect. However, besides sampling all the infested communities encountered, we also sampled communities which, based on the results of the first transect, we considered to be potential sites for establishment of medusahead if given the chance for introduction.

On the third transect, other than the three known infestations, we expected to inventory and describe the number and extent of effective environments which, based on the results of the first two transects, would have potential for the introduction of medusahead. While describing these sites, we discovered a number of new medusahead infestations in the Great Basin. Location of plots sampled is shown in Figure 1.

Macroplots. In the actual sampling of each community, we employed the phytosociological concepts of Braun-Blanquet (5), Daubenmire (7), and Poulton and Tisdale (27) in stratifying macroplots within ecologically homogeneous areas. Daubenmire (7) defines the interpretive unit in this stratification as the collective area which is capable of supporting the same relatively homogeneous climax plant association.

Within each macroplot, we sampled the structure and composition of the vegetation with 100-sq-ft frequency plots and ten 32-sq-ft cover plots. We determined frequency by the ratio between the number of sample plots where a species was present and the total number of sample plots (6). Herbage cover was estimated by a vertical projection of the herbage canopy on to the ground surface within each cover plot. Both frequency and cover plots were arranged within each sampling area following the method of Evans and Love (12).

Soils and physiography. We excavated and described a soil profile on each plot, using methods described in the Soil Survey Manual (3).

We added more plots in 1966, 1967, and 1968. Each year we sampled all previously established plots.

We constructed association tables, using species composition based on frequency and cover at the end of each year's sampling to assist in the development of an understanding of the various vegetation assemblages (6). Mean figures of all years of sampling were employed for final analysis and data presentation.

Results

Medusahead infestations were restricted to a small group of recurring, easily-recognized plant communities. It also was evident that these plant communities were associated with a series of very heavy clay soils or vertisols (2), and that these soils were closely associated with the physiography of the landscape (Figure 2).

Vertisols. Vertisols normally are developed in montmorillonitic parent material derived from basic igneous rocks. Shrinking, cracking, and shearing of the vertisols and mass movement of the soils, make them unstable and introduce severe problems for plant growth (3).

The sites infested with medusahead that have clay vertisols, separate into three groups based on presence and frequency of annual grasses (Table 2). In one group, medusahead is the dominant annual grass to the virtual exclusion of downy brome. Perennial grasses are absent from these sites.

The native forb, sunflower, (*Helianthus annuus* L. ssp *lenticularis* (Dougl.) Ckll.) is abundant on all plots located on these sites. Panicle willowweed (*Epilobium paniculatum* Nutt.) and gumweed (*Grindelia nana* L.) have a relatively high frequency on plots located in the western and central transect, but are absent from the plot at Reno, Nevada in the eastern transect. Prickly lettuce (*Lactuca scariola* L.) maintains a low frequency in all of the medusahead dominated sites.

The second grouping of clay vertisol sites contains stands where medusahead and downy brome share dominance (Table 2). The short-lived perennial grasses squirreltail (*Sitanion hystrix* (Nutt.) J. G. Sm.) and Sandberg bluegrass (*Poa secunda* Presl.) are present in varying frequencies on these sites. Among the native forbs, California goldenrod (*Solidago californica* Nutt.) is a constant component of the vegetation assemblage of sites where downy brome shares dominance, but is absent from sites where medusahead is the sole or overwhelming dominant annual grass. The introduced forb, redstem filaree (*Erodium cicutarium* (L.) L'Her.), is constant to all the sites where downy brome shares dominance, but is absent from the other shrubless vertisol sites. The forbs with high constancy on the medusahead dominated sites have low and erratic frequencies on the sites with considerable downy brome.

The native perennials, adobe beardtongue (*Penstemon laetus* Gray.) and povertyweed (*Iva axillaris* Pursh) have

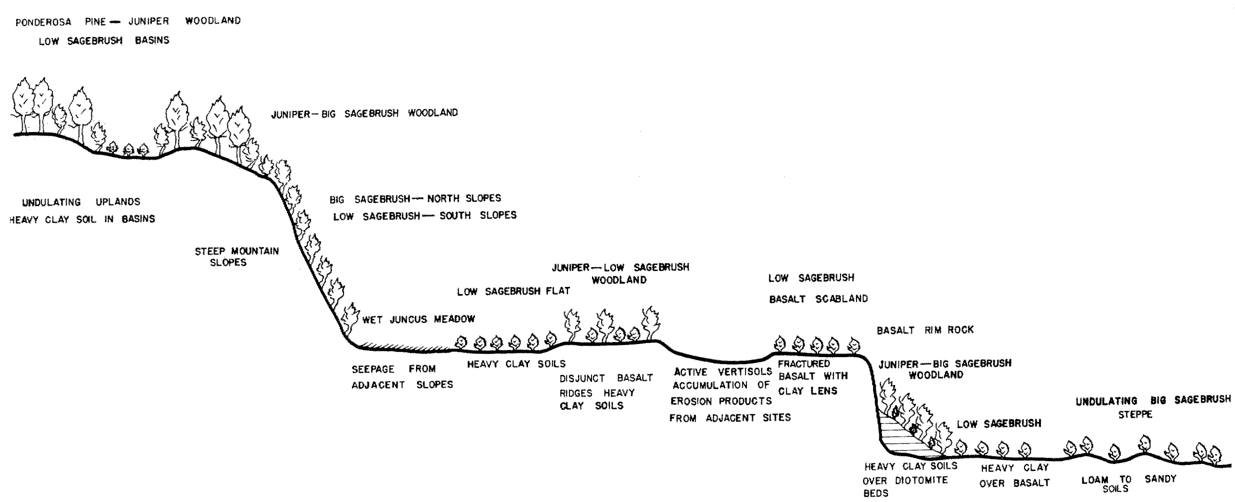

Figure 2. Physiographic, soil, and vegetation relations of communities investigated.

Table 2. Species composition (frequency) of communities found on clay vertisols.[a]

Species	Species frequency per sq ft											
	Annual grass domination									Forb domination		
	Medusahead				Medusahead and downy brome							
Annual grasses												
Medusahead	96	96	96	97	98	78	84	84	84	7	1	3
Downy brome				1	58	72	99	40	85			
Hairy chess	4	4	1									
Perennial grasses												
Squirreltail						1		2	29	1		1
Sandberg bluegrass					21		1					
Bluebunch wheatgrass[b]									1			
Native forbs												
Adobe beardtongue	2	1	1	1	1	1	2	1	1	1	3	1
Red buckwheat	3	14	16			20				6	29	11
California goldenrod					2	16	10	25	10			
Annual sunflower	46	18	31	41				1	25	36	9	63
Gumweed	32	2	16		2							
Naked lomatium					1							
Povertyweed	8	1	1		1	3		6	14	55		68
Introduced forbs												
Redstem filaree					28	6	1	11	9			
Prickly lettuce	5	2	1	2				1		8	1	7
Physiographic features												
Slope (%)	basin	basin	0–2	0–2	5	3	3	2	6	0–2	basin	basin
Litter cover (%)	60	60	40	45	25	95	5	29	29	0	0	0
Surface stone cover (%)	30	0	15	90	85	50	40	50	35	85	70	80
Solum depth—inches	60+	48	48	72+	36	24	20	32	34	48+	50+	40

[a]Frequency is relative expression of presence or absence.
[b]Bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Sm.).

high constancy on sites both with and without downy brome.

The third subdivision of shrubless vertisols includes four sites found on the eastern transect beyond the range of medusahead (Table 2). The frequency of downy brome and hairy chess *(Bromus commutatus* Schrad.) is low, or nonexistent in one plot, even without medusahead. Both of the species of *Bromus* were abundant in the vegetation surrounding the vertisol site. These plots are almost devoid of perennial grasses. The frequencies of native forbs is very similar to those found on the medusahead dominated stands farther west. An exception is the lack of gumweed. Two of the plots are dominated by the perennial povertyweed.

The medusahead and forb-dominated sites occupy flat micro-basins without drainage. The sites where downy brome and medusahead share dominance tend to be located on the margins of basins with some slope for drainage. The heavy clay vertisols are quite deep, especially in the medusahead and forb-dominated sites. On all sites where loose rocks occur, they have largely been sorted to the surface of the soil.

On most of the sites where medusahead is established, a heavy litter has accumulated. This species is the greatest known plant accumulator of silica (4, 30). The high silica content of medusahead litter probably explains its persistence.

Not all plots are completely free of shrubs. Some support very sparse stands of the semi-woody Douglas rabbitbrush *(Chrysothamnus viscidiflorus* (Hook.) Nutt.)

Site potential. Two major differences in potential are evident in this series of plots. The forb-dominated plots in the eastern transect apparently represent sites where, if the chance introduction of medusahead occurred, this species would dominate the site to the exclusion of downy brome. It appears that sites where medusahead and downy brome are codominants have a slightly different inherent potential from sites where medusahead is the sole dominant. Some of the subtle differences separating these two sites apparently are in their physiographic position and solum depth. The lack of downy brome dominated vertisol sites on the eastern transect is puzzling. This may be due to the dynamic nature of vertisols. There is considerable evidence that vertisols develop in these areas after the erosion of coarser textured surface soils.[3]

Degrading sites with heavy clay soils and any remnant shrub cover were placed under the low sagebrush grouping. These eroding low-sagebrush sites may be the last stages in the development of a type of vertisol which has the potential to support mixed stands of medusahead and downy brome. The erosion products of the degrading low sagebrush sites accumulate in basins which have potential for dominance by the native forbs, sunflower, povertyweed, or the alien grass, medusahead, depending upon the chance of introduction.

Low sagebrush sites. Medusahead infestations were found most frequently in low sagebrush communities on very heavy clay soils. Next to low sagebrush, the most frequently occurring community is that of big sagebrush. We never found medusahead in big sagebrush communities on medium to coarse textured soils. Low sagebrush communities occupy a number of physiographic positions in the investigation area (Figure 2). These communities occupy heavy clay soil flats among timbered ridges on the highest mountainous plateaus. The most widespread vegetation assemblages of the rocky, clay soils of south-facing slopes in the foothill region are dominated by low sagebrush. The low sagebrush flat on broad stairstep benches formed by disjointed basalt flows is the remembered image of northeastern California and northwestern Nevada.

The topo-edaphic factors of these low sagebrush sites have a powerful influence on the environment. Low sagebrush communities at Fall River, California, (annual precipitation 17 inches) situated in a matrix of digger pine

[3]Personal communication from Harry Summerfield, Soil Scientist, Soil Conservation Service, U. S. Department of Agriculture.

and California black oak (*Quercus kelloggii* Newb.) have virtually no differences in native species composition from low sagebrush communities interspersed in a matrix of coniferous forest on the flanks of Mt. Lassen (estimated annual precipitation 25 inches), or with low sagebrush communities at Viewland (annual precipitation 9 inches) in the Great Basin.

Influence of medusahead invasion on the structure of low sagebrush communities. A comparison of the structure of low sagebrush communities dominated by medusahead with those with little annual grass reveals some striking differences in floristic composition (Table 3).

Table 3. Comparison of low sagebrush communities dominated by medusahead and by perennial grasses.[a]

Species	Medusahead dominated Cv	F	C	Perennial grass dominated Cv	F	C
Annual grasses	58			6		
Medusahead	38	70	100	1	3	27
Downy brome	15	37	100	3	11	72
Hairy chess	4	11	64	1	2	27
Rattlesnake brome[b]	1	1	7	T	T	9
Perennial grasses	8			24		
Squirreltail	3	7	71	7	23	100
Sandberg bluegrass	4	4	64	12	33	90
Columbia needlegrass	T	2	28	4	11	63
Thurbers needlegrass	T	T	7	T	2	9
Bluebunch wheatgrass	T	T	14	T	2	36
Junegrass[b]	T	T	7	T		
Native forbs	7			3		
Panicle willowweed	1	23	100	2	13	63
Showy tarweed	2	4	42	T	2	18
California goldenrod	2	4	28		T	18
Adobe beardtongue	T	T	7	T	T	9
Annual sunflower	T	T	7	T	1	18
Lupine spp.	T	2	7	T	2	18
Douglas phlox[b]	T	2	14	T	1	9
Red buckwheat				T	1	18
Flattop buckwheat				T	2	18
Naked lomatium				T	2	18
Povertyweed	T	2	7			
Alien forbs	3			1		
Redstem filaree	1	2	42			
Prickly lettuce	T	1	21	1	1	9
Yellowflower pepperweed	T	2	7			
Shurb cover	4		100	21		100
Low sagebrush	3		100	2		8
Douglas rabbitbrush	T		37	2		8
Horsebrush	T		2			
Number of plots			14			11

[a]Symbols: Cv—percent projected herbage cover—area of herbage canopy when projected on ground; F—frequency per sq ft; C—constancy—expression of presence or absence among stands: T—less than 1%.
[b]Rattlesnake brome (*Bromus brizaeformis* Fisch and May.), Junegrass (*Koeleria cristata* (L.) Pers), yellowflower pepperweed (*Lepidium perfoliatum* L.), Douglas phlox (*Phlox douglasii* Hook.)

The three dominant native perennial grasses, squirreltail, Sandberg bluegrass, and Columbia needlegrass (*Stipa columbiana* Macoun.), have lower cover, frequency, and constancy on the medusahead-infested plots. The negative relation between perennial grass and annual grass cover is statistically significant at the 1% probability level. Medusahead mainly accounts for this relation and apparently downy brome plays a very minor role in the structure of the community.

The relation of medusahead invasion to the presence of native forbs in the low sagebrush communities is more complex than for perennial grasses. Mean native forb cover is higher in the medusahead-infested communities (Table 3). However, there is a negative relation between annual grass cover and native forb cover (Table 4). Regression lines for low sagebrush, perennial grass, and native forb cover in relation to annual grass cover are compared in Figure 3. Panicle willowweed cover was negatively related to annual grass cover; the frequency and constancy of this native perennial increased on the

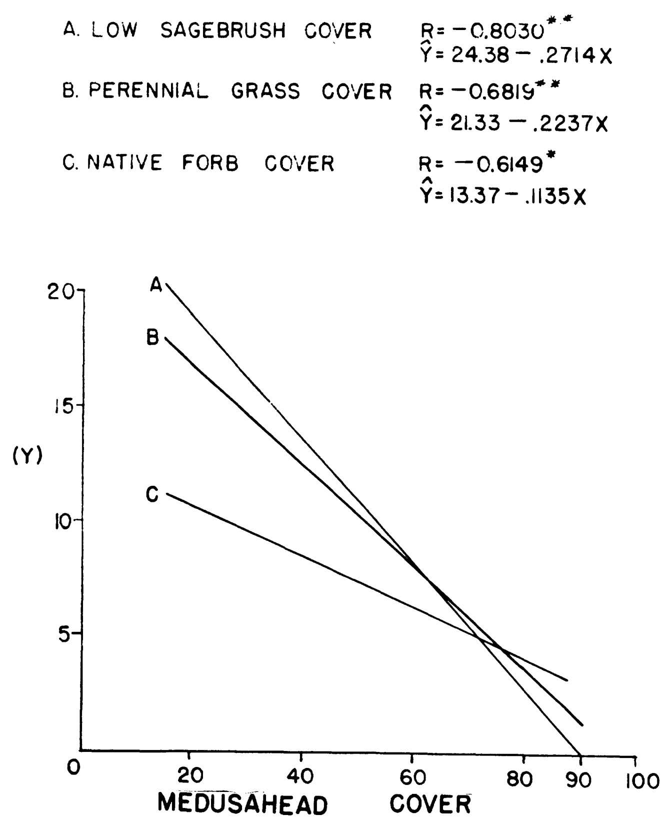

Figure 3. Relation of medusahead cover to low sagebrush, perennial grass, and native forb cover.

Table 4. Matrix of correlation coefficients of the species composition of low sagebrush communities.[a]

Species	Projected herbage cover[b]: Low sagebrush	Alien forbs	Native forbs	Panicle willowweed	Perennial grass cover	Squirreltail	Sandberg bluegrass
Medusahead	−0.769**	−0.259	−0.456	−0.461	−0.682**	−0.253	−0.379
Downy brome	0.229	0.149	−0.089	−0.387	−0.162	−0.012	−0.039
Annual grass cover	−0.800**	−0.280	−0.615*	−0.623*	−0.682**	−0.594*	−0.419
Squirreltail	0.252	−0.011	0.707**	0.420			
Sandberg bluegrass	0.355	0.450	0.336	0.633*			
Perennial grass cover	0.425	0.267	0.589*	0.746**			
Panicle willowweed	0.387	0.397					
Native forbs	0.332	0.102					
Alien forbs	−0.010						

[a]Symbols: ** indicates significance at 0.01 probability level; * indicates significance at 0.05 probability level.
[b]Area of herbage canopy when vertically projected on ground.

medusahead-infested plots. Both showy tarweed *(Madia elegans* D. Don) and California goldenrod increased in cover, frequency, and constancy on medusahead-infested low sagebrush sites. The native forbs, red buckwheat *(Eriogonum sphaerophalum* Dougl.), flat top buckwheat *(Eriogonum umbellatum* Torr.), and naked lomatium *(Lomatium nudicaule* (Pursh.) Coult. and Rose) were absent from the medusahead-infested communities (Table 3).

Alien forbs were infrequent on the low sagebrush sites sampled. Except for prickly lettuce, they were restricted to the medusahead-dominated communities.

There is a negative relation between low sagebrush cover and annual grass cover (Table 4). Mean shrub cover was much lower on the medusahead-dominated sites than on the perennial grass-dominated sites. There was no statistically significant correlations between low sagebrush cover and perennial grass or native forb cover. Apparently, low sagebrush plays a role in the suppression of annual grasses and probably the perennial grasses.

Variation in density of medusahead among years sampled. Due to extensive sampling, minor year to year differences in weather conditions tended to compensate for each other. In 1966, virtually no precipitation was received in northwestern Nevada and extreme northeastern California after January 1, while precipitation was average in the southwestern portion of the study area. Less than 3 inches of precipitation from July 1, 1965 to June 30, 1966 was received at Reno, Nevada, and 90% of the established medusahead seedlings failed to reproduce. Several infestations of medusahead sampled in 1965 on the plateau near Likely, California (Likely Table) were absent in 1966 (less than 1% of our total macroplots). We observed 80 to 90% mortality in downy brome populations in the same areas (37). During this drought period, medusahead stands failed to reproduce on the Likely Table and as far north as Alturas. It had taken years (probably more than 20) for medusahead to gradually spread over this same area.[4] We located a small infestation in a burned-over area at a considerable higher elevation across the Pit River from the Likely Table. This outlying population reproduced during the drought of 1966, giving medusahead a disjunct distribution. During the favorable spring of 1967, all medusahead populations successfully renewed themselves from residual caryopses in litter and soil. Studies of downy brome populations showed that the commitment of reserve reproduction potential is conditioned by the seasonal potential of environment (37). In 1966, medusahead responded in like manner to environmental conditions.

Woodland communities. Although infestations of medusahead are most extensive in the low sagebrush communities, this species also is abundant in a series of woodland communities.

Low sagebrush-western juniper woodlands. Low sagebrush-western juniper woodlands are very extensive in northeastern California, although not as extensive as low sagebrush communities without a western juniper overstory. We established 25 macroplots in low sagebrush communities and found many more sites infested with medusahead which we sampled at reconnaissance level. We located only six low sagebrush-western juniper communities infested with medusahead and established macroplots in four of these infested communities. Some medusahead-infested woodland stands were several thousand acres in extent; however, it was apparent little of the potential area of these woodlands were infested in comparison to the non-forested, low sagebrush sites. In species composition, there are few apparent differences between the vegetation assemblages of the low sagebrush and those of the low sagebrush-western juniper woodland communities (Table 5).

[4]Personal communication from B. L. Kay, Agronomy Department, University of California, Davis, California.

Table 5. Mean species cover, frequency, and constancy of woodland communities infested with medusahead.[a]

	Low sage brush-juniper			Big sage-brush-juniper			Ponderosa pine		
Species	Cv	F	C	Cv	F	C	Cv	F	C
Annual grasses	69			82			65		
Medusahead	38	52	100	79	87	100	40	63	100
Downy brome	28	59	100	3	15	100	25	59	100
Hairy chess	3	4	75	T	1	25			
Perennial grasses	11			3			18		
Squirreltail	6	2	75	2	2	100	2	3	66
Sanb lerg bluegrass	4	2	50	T	1	25	3	1	33
Pine bluegrass							6	23	100
Columbiana needlegrass	T	3	50	T	1	25	4	4	33
Thurbers needlegrass							3	4	33
Mountain brome[b]	T	1	25	T	1	25			
Native forbs	6			1			7		
Panicle willowweed	2	6	75				T	3	33
Showy tarweed	2	1	25	T	5	100	T	10	66
California goldenrod	2	3	50	T	2	50			
Lupine spp.				T	1	25			
Adobe beardtongue	T	1	100	T	2	100			
Western buttercup[b]							2	6	66
Bighead clover[b]							T	3	100
American lotus[b]							T	3	33
Povertyweed				T	1	25	2	1	33
Alien forbs	3			8			4		
Yellowflower pepperweed	2	1	25	4	7	25	1	6	33
Prickly lettuce	1	4	50	2	3	25			
Redstem filaree				1	1	25	T	2	33
Povertyweed									
Field bindweed							2	7	66
Tumble mustard[b]							T	1	33
Shrubs	37			24			18		
Low sagebrush	35		100						
Big sagebrush				23		100	2		25
Bitterbrush[b]							5		50
Douglas rabbitbrush	2		75	T		25	4		25
Sierra plum[b]				T		25	7		50
Trees	30			10			21		
Western juniper	30			10			T		
Ponderosa pine							20		

[a]Symbols: Cv—projected herbage cover—area of herbage canopy when vertically projected on ground; F—frequency (per sq ft)—expression of presence or absence; C—consistency—expression of presence or absence among stands; T—less than 1%.

[b]Mountain brome (*Bromus marginatus* Nees.); western buttercup (*Ranunculus occidentalis* Nutt.); bighead clover (*Trifolium macrocephalaum* Poir.); American lotus (*Lotus americanus* (Nutt.) Bisch.); bitterbrush (*Purshia tridentata* (Pursh) DC.); tumble mustard (*Sisymbrium altissimum* L.); Sierra plum (*Prunus subcordata* Benth.).

Physiographically, the woodland sites tend to be upland with lateral drainage and less subject to water impoundment during the spring periods of snow melt (Figure 2).

Big sagebrush-western juniper woodlands. These remarkable sites constitute the only big sagebrush community where we found infestations of medusahead. These communities are restricted to the toe slopes of the ridges and rim rocks surrounding old lake beds in northeastern California. The plant communities are supported by a 2 to 3-ft layer of heavy clay overlying thick beds of diatomite which is highly influenced by volcanic ash (Figure 2). Once infested with medusahead, these sites support a dense stand of annual grasses and alien forbs with few native perennial grasses or forbs (Table 5). Panicle willowweed was not found on these sites.

Ponderosa pine woodlands. Following destruction of ponderosa pine-western juniper woodlands by wildfire, medusahead has invaded these sites. Occasional infestations were observed on non-clay soil. Generally these sites are at much higher elevations than other sites infested with this annual grass. We have observed medusahead infestations in this community at the 6,000-ft level. Pine bluegrass (*Poa scabrella* (Thurb.) Benth.) and Thurber needlegrass (*Stipa Thurberiana* Piper.) are important perennial grasses in these medusahead-infested sites (Table 5).

Wet meadow sites. The wet meadow sites infested with medusahead offer a radical departure in site potential and soils from the other effective environments in this investigation. The wet meadows encountered were located at the bottoms of long slopes where water seepage comes to the surface. Soils ranged from clay loams to silt loams in contrast to the heavy clay soils of the other medusahead sites. Other than the perennial grasses, Sandberg and pine bluegrass, the vegetation of these meadows bears little resemblance to the other medusahead-infested communities (Table 6). The frequency and projected herbage cover of downy brome is uniformly low in all the meadows in comparison to medusahead. The native species characterizing the meadows are Baltic rush (*Juncus balticus* Willd.) and meadow barley (*Hordeum brachyantherum* Nevski.). Baltic rush occurs in large clumps with perennial and annual grasses dispersed among the clumps. Field bindweed (*Convolvulus arvensis* L.) abounded in these meadows. Medusahead suppressed field bindweed and any reduction in medusahead cover results in domination of site by this alien perennial forb. We observed more native and alien forb species on meadows where medusahead has not yet been introduced.

Table 6. Species composition and physiographic features of wet meadow sites infested with medusahead[a].

	Frequency					Mean cover
Annual grasses						46
Medusahead	96	70	68	78	100	45
Downy brome		4		1	3	T
Hairy chess				1		T
Perennial grasses and rushes						45
Pine bluegrass	10	9	12	10	10	3
Sandberg bluegrass		1	8	3	13	1
Meadow barley	13	25	18	4	33	4
Baltic rush	63	56	28	49	40	37
Native forbs						
Povertyweed	1		2	1	2	
Showy tarweed		1		1		
Alien forbs						5
Field bindweed	68	18	100	90	89	4
Redstem filaree	1		1		2	T
Physiographic features						
Solum depth (inches)	30	36	36	29	40	
Rock cover (%)	4	5	0	3	0	
Litter cover (%)	40	30	30	50	60	

[a]Species composition based on frequency per sq ft (an expression of presence or absence).

Wet meadows in sagebrush areas are very important in the life cycle of sage grouse (*Centrocercus urophesinus* Bonaparte) (28). The suppression of native forbs by medusahead invasions may have serious effects on populations of this endangered species.

Discussion

The occurrence of medusahead infestations on the margin of the Great Basin is dependent on the potential of specific effective environments and seral status of the plant communities of these environments. The distribution and structure of all the plant communities in the vegetation matrix around the medusahead infestation also are controlled by the effectiveness of their environments. The only integrated measurement of the effectiveness of the myriad of factors and interactions that control inherent differences among these environments is the use of plant communities as a phytometer of site potential (7). The low seral status of medusahead communities makes them reflections of not only the inherent potential but also of past use of the site. This is why interpretation of the soils of these ecosystems is so important. The continued reoccurrence of problems of practical importance in weed control and environmental quality at a population level underscores the legitimacy of studies of groups of organisms (18).

Medusahead infestations are found on a continuum of heavy clay soils with an associated range of plant communities from very sparse stand of Douglas rabbitbrush on vertisols, through a group of low sagebrush communities into a series of low sagebrush woodland communities. The aggression of medusahead from established stands into neighboring plant communities again is dependent on the relation of the existing community to the potential of the site.

Vertisol sites without appreciable vegetation are a very harsh environment with a limited potential for native vegetation. The shrinking and swelling, self-mulching characteristics of the montmorillonite clays coupled with periods of inundation in the spring, place these sites outside the inherent potential of most species.

One vertisol macroplot was visited by a railroad survey expedition in 1855 (1). Lieutenant Abbot of this survey described the vertisol site as a basin with a very heavy clay soil so baked by the sun in late August that his horses crossed the deeply cracked ground with difficulty. He commented on the scanty cover of "sunflowers" (*Helianthus annuus?*) found on the cracked soils. This basin now supports a complete cover of medusahead.

The inherent physiologic systems and morphologic structures of medusahead have the potential to cope with these soils and so this alien can establish, grow, and reproduce vigorously on vertisols. On the vertisol sites, medusahead had only to combat the physical environment once given the chance by introduction. Biologic competition is a minute factor on these sites. Conversely, once medusahead becomes established and fully occupies the limited potential of these sites, they are effectively closed to invasion by naturally or artifically introduced species. The introduction of medusahead to these sites is irreversible and accumulation of large amounts of litter of high silica content on the surface of these self-mulching soils must have, at least, a temporary effect on their potential.

Low sagebrush communities are associated with clay soils and especially heavy clay subsoils (9). The textural B horizon of the soils of many of the low sagebrush sites in this investigation appear identical to the clays of the associated vertisols. On the low sagebrush sites, when given the chance by introduction, medusahead must not only cope with the physical environment, but must also face biologic competition from numerous established perennial species. The seral status of the low sagebrush communities determines the resistance of the site to invasion of medusahead. The perennial grass portion of community is subject to attrition through excessive utilization by livestock. Low sagebrush, itself, is not preferred by domestic livestock or big game and apparently benefits from and contributes to the reduced perennial grass competition. A degraded low sagebrush site with a shrub overstory and a sparse annual and perennial forb understory is resistant to wild fires except at times of extreme fire hazard. The greater the alien annual grass understory, the more early maturing, highly flammable fuel that is available to carry wild fires through low sagebrush stands. These fires destroy the shrub overstory and completely free the potential of the site for medusahead dominance.

Site potential is a two-edge sword in regard to resistance to alien invasion. The greater the potential the more complex the vegetation assemblage, but once this potential is degraded the greater the void available for alien exploitation. If the low sagebrush communities contained a competitive invivo-evolved annual to more fully occupy the potential of the site, their resistance to medusahead invasion would be much higher. Lack of competitive native annuals leaves low sagebrush communities with degraded perennial grass components open to invasion by medusahead. This attrition of the native plant communities is a product of man's passive (unintentional) exploitation of the ecosystem. Man has the technology to defer grazing and, through the application of non-persistent herbicides, to remove the shrub portion of the low sagebrush communities. Application of these manipulations to low sagebrush communities with sufficient remnant stands of perennial grasses should greatly reduce the unused environmental potential otherwise available for medusahead invasion. Perennial grass dominance of these sites would create a much more stable vegetation assemblage in regard to wild fire disturbance.

Besides the quantity of site potential, the specific quality of sites influences susceptibility of communities to invasion (13). The restriction of medusahead to clay soils is a site quality factor which has received considerable attention. Several theories have been put forth to explain this edaphic relation. The high ion exchange capacity of these clays or their high silica content in relation to the tremendous silica accumulation of medusahead have been proposed as possible explanations. The most widely accepted explanation for medusahead abundance on clay soils cites the late maturity of the species in relation to other annual grasses and its subsequent requirements for high water holding capacity clay soils (11, 14). Hironaka (15) reported a similar relation between medusahead infestations, heavy clay soils, and low sagebrush sites in Idaho. He noted that the restriction of medusahead to heavy clay soils became more severe as total annual precipitation decreased. We observed infestations of medusahead in high elevation, ponderosa pine woodlands, and on wet meadows with clay loam or loam soils. In both cases, apparently, soil moisture holding capacity is compensated for by sufficient precipitation or a high watertable. Mallory (21) noted a strong association between medusahead invasion and heavy clay soils on annual grass ranges in the northern Sacramento Valley. Since that time, this association has broken down and medusahead has spread to a number of plant communities on lighter textured soils.[4]

Big sagebrush communities often are open to invasion by alien annuals. However, we encountered only one specific and atypical big sagebrush site that supported medusahead. The heavy clay soils of this site clearly relate it to the other medusahead sites.

Most research and development efforts in the control and revegetation of weedy annual grasses on *Artemisia* rangelands have been concerned with downy brome control (8, 11). The occurrence of downy brome often denotes degraded big sagebrush sites on loam-textured soils. These extensive, mostly level and low rock-cover sites permit the construction of seedbeds for perennial grass seedlings following tillage or herbicide treatments for control of downy brome competition.

The soil environment of medusahead-infested low sagebrush communities forces a basic change in techniques. Heavy clay and rocky soils make seedbed preparation virtually impossible on these sites. Once the moisture level in the soil profile is brought to field capacity, the extremely slow percolation rate of the clay soils causes runoff of much of the precipitation that falls on low sagebrush sites. Consequently, these sites also will release, in runoff water, herbicides which have been applied for medusahead control. The highly erodable nature of fine clay colloids on the soil surface allows herbicides, normally considered virtually insoluble and not subject to leaching, to ride into runoff water on eroded clay particles. Synecological investigations, such as this study, provide a basic inventory and stratification of the environment and allow a weed control research worker to anticipate and account for many of these factors in his research program.

Considering the restriction of medusahead to specific soil and vegetation assemblages and that the frequency of this species within specific sites is dependent on their seral status, the apparent unbroken expanses of big sagebrush on loam soils in the Great Basin seem to offer a bleak future for this alien. Occurrences of vertisols throughout the big sagebrush area and of vast areas occupied by low sagebrush communities at higher elevation change this prognosis. The vertisols provide a favorable line of least resistance through a series of hostile environments. Given a chance by introduction, medusahead should become established on vertisol sites almost any given year. The probability of becoming established in low sagebrush sites is dependent on the seral status of the community and favorable weather conditions occurring in a specific season. Establishment in ponderosa pine woodlands is dependent on occurrence of wild fires and favorable weather conditions following burning and introduction. Webb (33) enumerates the small scale probabilities involved in this type of dispersal and establishment.

Medusahead can become established on vertisols and remain restricted to these sites until conditions of more resistant plant communities become favorable for invasion. Alien introduction to a new site often occurs in very limited numbers and thus of a restricted genotype. The process of introduction is a selection mechanism. Each year that medusahead reproduces on an isolated vertisol involves selection within a circumscribed gene pool under the same macro-climatic conditions of the invasion-resistance surrounding sites. Medusahead populations from the investigation area differ in a number of physiologic characteristics presumably as a result of this mechanism (22, 36, 37).

The occurrence of a vast salt desert basin across northern Nevada may limit the general distribution of medusahead into the Great Basin, but this species apparently can greatly expand its range in the manner described, into this physiographic province. Unfortunately, we have only a limited knowledge of the time scale of this invasion.

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