AN ABSTRACT OF THE THESIS OF

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Abstract approved: _______________________________
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Medusahead, *Taeniatherum caput-medusae*, an annual grass native to the Mediterranean region of Eurasia, has quickly expanded in the Great Basin on disturbed sites with fine-textured soils. Prior to this study, invasion onto coarser textured soils was thought to be low. Using demographic and growth analysis tools, we examined the likelihood for medusahead to expand onto clay and loamy soils (over two years, 1993-1994, and 1994-1995 growing seasons) where intact native shrub-steppe communities, Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) and Thurber's needlegrass (*Stipa thurberiana* Piper.), range sites already exist. We used different planting times (fall vs. spring) and disturbance treatments (control, defoliation, soil disturbance, severe disturbance-complete removal of all vegetation within a 6 m^2 area.) to simulate different times of seed arrival and different types of disturbances that plants might find upon arrival. Precipitation during the study varied from year to year with 1993 being much drier than 1994. Seeds were sown and emerged plants were censused individually throughout their lifespan. Percent emergence was at least two-fold greater for individuals planted on the clay soil as compared to the loamy soil. In addition, in all cases, plants exposed to the severe disturbance treatment had 5-fold more biomass and seed production per plant than plants in other treatments. In 1994, plants emerging on the clay soil had greater

proportional survival (70 to 85%) than plants on the loamy soil (40 to 70%) depending on the treatment. The severe disturbance treatment resulted in the highest survival and seed production on both sites. Results of this experiment clearly show that an intact native plant community was not necessarily resistant to medusahead invasion. In addition, medusahead expansion onto loamy soils is possible if the right environmental factors are met, such as precipitation at time of germination and a severely disturbed area at the time of seed arrival. It is necessary to maintain a diverse native plant community along with minimal disturbance to restrict the expansion of medusahead onto either clay or loamy soil textures.

Demography of Medusahead on Two Soil Types: Potential for Invasion into Intact Native Communities

by

Heather C. Miller

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorized release of my thesis to any reader upon request.

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Heather C. Miller, Author

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INTRODUCTION

Invasions of organisms onto rangelands have been of great concern to those involved with maintaining native biodiversity of plant communities and food production for wild and domestic animals. The rangelands of the Great Basin region of North America have been greatly affected by this onset of invasive species, in particular annual exotic grasses. Medusahead, *Taeniatherum caput-medusae* ssp. *asperum* (Simk) Melderis, is an annual grass native to Portugal, Spain, southern France, Morocco, and Algeria and was first discovered in the U.S.A. in southeastern Oregon in 1884 (McKell et al. 1962, Young 1992). Since its initial discovery, it has infested thousands of hectares of rangeland in California, Oregon, Washington, and Idaho and continues to expand its influence in these states as well as Nevada and Utah. When introduced into rangelands degraded by overgrazing, fire, or plowing, medusahead quickly expands and dominates these communities (Evans and Young 1970). The competitiveness of this species decreases the structure and diversity of native plant communities in the Great Basin, and changes physical and biological functions of these sites (Bovey et al. 1961, Young 1992).

Medusahead can occupy a variety of soil types, but is customarily associated with finer soil textures such as heavy and silty clays, that appear to facilitate medusahead invasion (Young 1992). The relatively high moisture content of these finer soils allows medusahead to extend its lifecycle later into the summer than other annual plants in this region. Even though surface soils may appear to be loamy and aerated, if the B horizon is clayey, the site is still very susceptible to medusahead establishment (Sharp et al. 1957, Horton 1991, Young 1992). The potential threat of medusahead invasion onto coarser (i.e. loamy) soil textures within intact native plant communities has not been examined. These areas were previously thought to be resistant to medusahead invasion; my study was designed to test this hypothesis. In addition, although medusahead is able to become established on disturbed areas, it is not known if medusahead can establish and maintain itself in a diverse undisturbed native community. Using demographic (emergence, survival and reproduction) and growth analysis (biomass and height) tools, I examined the potential for medusahead to expand onto clay and loamy soils where intact native shrub-steppe communities already exist.

I wished to determine the following objectives: (1) if medusahead establishment and survival are influenced by soil texture; (2.) if defoliation, surface soil disturbance, or severe disturbance- removal of all competitors-affects the establishment and survival of medusahead; (3) if time of planting affects medusahead establishment and survival.

METHODS

Study area

The Great Basin has been classified as a semi-arid ecosystem dominated more or less equally by sagebrush, *Artemisia* spp., and bunchgrasses (West 1983). Within this region, two study sites were selected in Harney County, Oregon, based on their native plant community and soil type. Both sites contain a diverse native shrub steppe community with similar dominant species, but different soil textures, with one site characterized by a clay soil and the other a loamy soil.

Both sites occur on land managed by the Burns District, U.S. Department of the Interior, Bureau of Land Management and had been grazed by livestock prior to the experiments. On the clay site, cattle grazing alternated on a yearly basis, between May-June and August-September with a grazing capacity of 4 ha/AUM. On the loamy site, cattle grazing occurred during the month of October every year, at a capacity of 7.0 ha/AUM.

The clay site was approximately 96 km northeast of Burns, Oregon (SW 1/16, NW 1/4 Sec. 17, T22S, R36E Drewsey Quad. 1150 m elev.). The soil was classified as a fine, montmorillonitic, mesic Duric Paleagrid (xerollic) originating from a combination of lacustrine, alluvium, eolian, and possibly some volcanic ash deposits. The slope was 6-7%, with a northeast aspect. The 4-cm thick A horizon was a loam with 23% clay and 77% silt. The underlying Bt horizons average 49% clay. Roots were common as deep as 64 cm, and occasionally extend 177 cm deep.

The loamy site was approximately 64 km northeast of Burns, Oregon (NE 1/4, Sec. 12, T20S, R33E House Butte Quad. 1139 m elev.). The soil was classified as coarse loamy, mixed, mesic Durixerollic Haplargid (DPV) originating from eolian deposits and alluvium. The slope is 2% with a southeast aspect. The 4-cm thick A horizon is fine sandy loam with 11% clay and 60% sand. The underlying Bt horizons average 66% sand. Roots were common down to 51 cm; a few roots extend 160 cm deep.

Plant community composition was determined in 1995 using the Daubenmire (1959) cover-class method (Table1) for estimating canopy cover by plant species with the following exceptions. I added a seventh cover class for zero percent cover to the traditional six classes. Ten, 5-m transect lines were randomly located and 5 plots/line were systematically placed at each meter interval for a total of fifty plot frames (20-cm by 50-cm) at each site. Medusahead was not present at either site, although it was found within 10 km of the clay site and 48 km of the loamy site.

Climate of the area is typified by hot dry summers and cold moist winters. Annual precipitation ranges from 228 mm to 304 mm, most of which occurs as snow during November through March. Localized, and occasionally severe, convectional storms occur during the summer. Annual precipitation was measured and recorded by the Oregon Climate Service in Drewsey, Oregon. Drewsey is located approximately

Table 1. Values for Daubenmire's coverage estimation technique.

Coverage class	Range of coverage, %	Midpoint of coverage class, %
0	0	0
1	1-5	2.5
2	5-25	15
3	25-50	37.5
4	50-75	32.5
5	75-95	85
6	95-100	97.5

25 km west of the clay site and 25 km east of the loamy site. Overall, the annual 12-month average is approximately 230 mm (Oregon Climate Service 1995). The 1993-1994 growing year (October through September) was slightly drier than average, with only 200 mm of precipitation. The 1994-1995 growing year was slightly higher than average with 372 mm of precipitation. The mean annual air temperature was approximately 11^{0}C with extremes ranging from -7^{0} to 38^{0} C. The frost-free period ranges from 110 to 140 days. Optimum above-ground plant growth occurs from April through June.

Experimental Design and Analysis

In September 1993, two 50-m by 50-m exclosures of a four strand smooth wire fence were constructed at each site to prevent livestock from disturbing plots. No sampling was conducted within a 10-m buffer along both sides of the fence. Fifteen 30-cm by 60-cm plots were randomly located and placed within the 900-m^2 sample area of each exclosure. Plots were established in the interspace, closest to the random location, between perennial plants to cause as little disturbance as possible to the surrounding native vegetation. Surface rocks were removed from plot areas, if needed, so medusahead seeds could be planted in grid locations.

Medusahead seed was collected each year from the same location (approximately 10 km from the clay site and 48 km from the loamy site) and was stored in paper bags until use. There were three seeding and four harvest dates for medusahead (Table 2). Six thousand medusahead seeds (100 seeds/plot) were individually planted at each seeding date. Seeds were uniformly planted with one seed per location just below the soil surface. Seed locations were determined by 100, 5-mm holes evenly spaced at 5-cm intervals in a 30-cm by 60-cm by 5-mm thick sheet of plexiglass. Plots were for relocated using 10-cm PVC pipe pounded into the ground at the corners of the plot frame (30-cm by 60-cm). A metal flag was placed next to one of the pipes in the ground so that there was a marker, and the plot frame could be oriented in the same direction at each census date. In the fall 1993 planting, the medusahead seed (lemma, palea, and filled caryopsis) with the awn attached was planted so the seed was 3 to 5 mm deep, but the awn remained exposed. I suspect that rodents were attracted by the awns and ate many seeds, because awns without seeds were seen on the soil at later census dates, and few seedlings germinated. In subsequent plantings, awns were removed and seeds were planted just below the soil surface. Because of the suspected rodent predation, an additional set of randomly located plots (15 plots/exclosure) was established and 6000 additional seeds were planted in spring 1994. Some seeds planted at this date remained dormant in the soil and were censused in the 1994-1995 growing season.

I conducted a census of each seed location approximately every four weeks after the initial seeding, (when sites were accessible) to determine emergence and survival. For each census, I used a 30-cm by 60-cm plot frame, constructed of 2-cm diameter PVC pipe with nylon string threaded through the holes to create 84 squares

Table 2. Dates of data collection and treatments analyzed for each planting of medusahead seeds.

Planting Date	Harvest Date	Census Dates	Treatments Analyzed
Fall 1993 9 September	Summer 1994 25 June	19 November 1993 25 March 1994 4 April 1994 24 May 1994 8 June 1994 25 June 1994	Soil Disturbance Control Defoliation
Spring 1994 24 March	Summer 1994 25 June	4 April 1994 24 May 1994 8 June 1994 25 June 1994	Soil Disturbance Control Defoliation
	Summer 1995 16 June	30 March 1995 22 April 1995 10 May 1995 16 June 1995	Soil Disturbance Control
Fall 1994 15 September	Summer 1995 16 June	30 March 1995 22 April 1995 10 May 1995 16 June 1995	Soil Disturbance Control Defoliation Severe Disturbance

(5-cm on a side). This plot frame allowed data collection without damaging study plants. The plot frame was oriented in the same direction at each plot whenever data were recorded. Each seed or plant had a unique coordinate corresponding to the center of each square. The height (the distance in mm from the soil to the tallest part of the plant) of 20 randomly selected medusahead plants per treatment per soil type, was measured during each census. At the end of the growing season (approximately late June), all surviving plants were harvested flush with the soil surface and bagged individually. The number of seeds was recorded for each harvested plant. Plants were oven dried (70^0 C for 48 hours) and weighed individually.

To examine the importance that disturbance plays in medusahead's ability to invade a community, each 30-cm by 60-cm plot was randomly assigned one of three treatments: defoliation, shallow soil disturbance, or undisturbed control. Each treatment was replicated five times within each exclosure. For the defoliation treatment, grasses and forbs within a 1.5-m radius of the plot center were clipped to 3 cm above the soil in early May and early June; this corresponds to the spring grazing season for livestock in the region. The shallow soil disturbance treatment was applied to the plot area at the time of planting by using a 3-pronged hand rake to disturb the soil approximately 1 cm to 3 cm deep prior to planting the seed. The shallow disturbance treatment corresponds to a light disturbance, such as hoof impacts by livestock or soil disturbance by rodents.

I repeated the study at the same sites in the fall of 1994 and seeds were censused during the 1994-1995 growing season. An additional severe disturbance treatment was added; this treatment was established in two adjacent 38-m by 38-m exclosures at each site which were erected in September 1994. Fence line buffers were established as before. Nine, 6-m by 6-m macroplots, were evenly spaced with a one-meter buffer among plots, in the central sampling area (18-m by 18-m) of each exclosure. Four of these 6-m by 6-m macroplots were randomly selected for placement of the 30-cm by 60-cm plot frames. All shrubs and grasses were cut, dug, and removed from the four randomly chosen plots using a pulaski. Approximately the first 20 cm of soil was disturbed. One, 30-cm by 60-cm plot was placed in the center of each macroplot, and was planted with medusahead seeds as described above.

The experimental design for the first year was a two by three factorial split-plot design with two soil texture classes (clay and loamy) as the whole plot factor, (each exclosure is one replicate therefore, there were two replicates per soil type), and with disturbance level (none, defoliation, shallow soil disturbance) as the split-plot factor. The following year, an additional severe soil disturbance treatment was added, resulting in a two by four factorial split-plot design.

Differences in survival rates (proportion alive over the series of census dates) of medusahead plants between treatments and soil types were treated as censored data and analyzed it using Peto and Peto's logrank test (Pyke and Thompson 1986, PROC

LIFETEST SAS 1994). Each soil type was analyzed separately to detect differences among disturbance treatments.

Differences in medusahead heights, biomass, and seed production between soil types, treatments and the interaction between treatments and soil types were tested with ANOVA using the PROC MIXED procedure (SAS 1994). Repeated measures were not used to analyze height data due to death of individual plants. Biomass data were log-transformed, and seed production was square-root-transformed to normalize the data. In addition, the MIXED procedure accounts for the unbalanced design in the fall 1994 planting (the severe disturbance treatment had four plots verses five plots of the soil disturbance, defoliation, and control treatments) (Personal Communication, L. Ganio 1996). Only two treatments, shallow soil disturbance and control, were examined in the spring 1994-to-summer-1995 treatment. These treatments were chosen to reduce confounding factors of carryover from spring of 1994 to spring of 1995 because they were applied at the time of planting, whereas the defoliation treatment was applied after the seedlings were established. When applicable, I report means (when necessary reporting the back-transformed means) and the 95% confidence intervals around the means.

RESULTS

Both sites were classified on BLM range site descriptions as Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) and

Thurber's needlegrass *(Stipa thurberiana* Piper.*)* range sites, however, the results I obtained using cover classes revealed that differences did exist in species composition between these sites. At the clay site Sandberg's bluegrass *(Poa secunda* J.S. Presl spp. *secunda)*, and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata)* were the dominant grasses (Table 3). On the loamy soil types, bottlebrush squirreltail (*Elymus elymoides* (Raf.) (Swezey)), Thurber's needlegrass, and needle-and-thread grass *(Stipa comata* Trin. and Rubpr.) were similar in community dominance. In addition, the percent cover of Wyoming big sagebrush was notably higher on the clay site than the loamy site, whereas the loamy site contained green rabbitbrush ((*Chrysothamnus viscidiflorus* (Hook)) and bitterbrush (*Purshia tridentata* (Pursh) DC.) and the clay site did not (Table 3).

Emergence and Growth

I found differences in the emergence of seeds in relative to soil type, disturbance treatments, and year of planting (Fig. 1, Table 4). The most dramatic differences were between the fall of 1993 and fall of 1994 seedings. For both soil types I found at least a two-fold increase across all treatments in the percent emergence from the fall 1994 seeding as compared to the fall 1993 seeding. In addition, there was a three to nine-fold higher emergence percentage on the clay as compared to the loamy soil.

Table 3. Percent cover and relative composition of all species that existed on both soil types. Collected in summer 1995. Percent cover and relative compositions represented by T are less than one percent.

	Clay Soil Type		Loam Soil Type	
SPECIES	**Percent Cover**	**Relative Composition**	**Percent Cover**	**Relative Composition**
Shrubs				
Artemisia tridentata Nutt. *wyomingensis*	35	37	13	20
Chrysothamnus viscidiflorus (Hook)	0	0	11	18
Purshia tridentata (Pursh) DC.	0	0	T	1.5
Perennial Grasses				
Pseudoroegneria spicatam (Pursh) A. Love ssp. *spicatum*	18	18	0	0
Elymus cinereus Scribn. & Merr.	0	0	T	T
Achnatherum hymenoides (Roemer & Schultes) Barkworth	T	T	T	T
Poa secunda J.S. Presl spp. *secunda*	25	24.5	1.6	2.5
Elymus elymoides (Raf.) (Swezey)	5.4	5.0	7.6	12
Stipa comata Trin. & Rupr.	0	0	8	13
Stipa thurburiana Piper	T	T	8	13
Annual Grasses				
Bromus tectorum L.	2.3	2.1	T	T
Perennial Forbs				
Agoseris glauca (Pursh) Raf.	T	T	T	T
Allium sp.	T	T	0	0
Antennaria sp. Gaertn.	0	0	T	T
Arenaria congesta Nutt.	T	T	0	0
Astragalus purshii dougl.	T	T	T	T
Aquilegia sp. L.	T	T	0	0
Calochortus macrocarpus Dougl.	T	T	0	0

Table 3. Continued

SPECIES	**Percent Cover**	**Relative Composition**	**Percent Cover**	**Relative Composition**
Chaenactis sp. DC.	T	T	T	T
Cirsium vulgare (Savi) Tenore	T	T	0	0
Crepis acuminata Nutt.	T	T	0	0
Delphinium bicolor Nutt.	0	0	T	T
Eriogonum aphanactis (Gray) Greene	T	T	0	0
Eriogonum ovalifolium Nutt.	T	T	T	T
Leptodactylon pungens (Torr.) Nutt.	0	0	1.5	2.4
Lomatium dissectum (Nutt.) Math. & Const.	0	0	T	T
Phlox longiforlia Nutt.	T	T	2.0	3.3
Tragopogon dubius Scop.	T	T	0	0
Zygodenus sp. Michx.	0	0	T	T
Annual Forbs				
Blepharipappus scaber Hook.	2.23	2.43	0	0
Collinsia parviflora Lindl.	T	T	3.0	4.8
Crypatantha sp. Lehm.	0	0	T	T
Descurainia pinnata (Walt.) Britt.	T	T	0	0
Draba verna L.	T	T	0	0
Epilobium minutum Lindl.	T	T	2.68	4.24
Epilobium paniculatum Nutt.	1.88	1.99	T	T
Erigeron poliospermsis Gray	0	0	T	T
Lactuca serriola L.	T	T	T	T
Layia glandulosa (Hook.) H. & A.	0	0	T	T
Lepidium perfoliatum L.	1.63	1.70	0	0
Mentzelia sp.	0	0	T	T

Table 3. Continued

SPECIES	**Percent Cover**	**Relative Composition**	**Percent Cover**	**Relative Composition**
Mimulus nanus H. & A.	0	0	T	T
Polygonum douglasii Greene	T	T	0	0
Sisymbrium altissimum L.	T	T	0	0
TOTALS	**98.65**	**100**	**63.15**	**100**

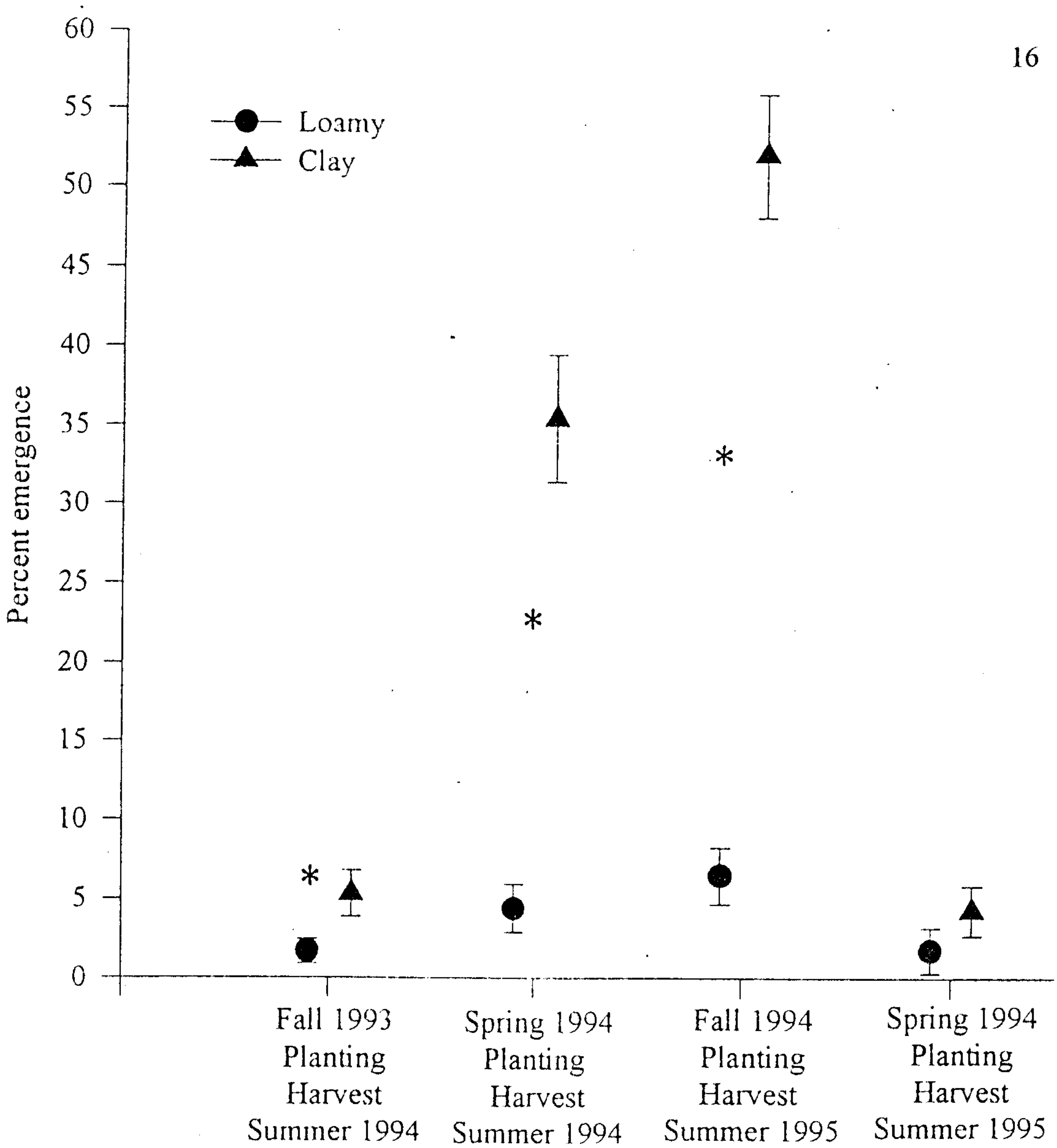

Figure 1. Percent emergence of seeds planted (mean per plant and 95% confidence interval) for different planting and harvest dates. Means are combined across all disturbance treatments. Significant differences ($P<0.05$) between soil types are noted with an asterisk (*) above those planting and harvest dates.

Table 4. Results of ANOVA for effects of planting and harvest dates, soil types (S), and disturbance (D) treatments on plant height, biomass and seed number.

		Effect								
Plant Parameter	Date	Soil Type			Disturbance			S x D		
	Seeded: Fall 1993 Harvested: Summer 1994	df (effect, error)	*F*	*P*	df (effect, error)	*F*	*P*	df (effect, error)	*F*	*P*
Emergence		1,54	16.61	<0.01	2,54	0.50	0.61	2,54	0.67	0.52
Height	November 19	1,34	26.72	<0.01	2,34	0.02	1.0	2,34	1.36	0.30
	March 25	1,28	9.71	<0.01	2,28	.40	0.70	2,28	0.01	1.0
	April 4	1,23	1.84	0.19	2,23	.12	0.89	2,23	.91	0.45
	May 24	1,22	19.48	<0.01	2,22	0.05	0.95	2,22	0.34	0.72
	June 8	1,15	1.29	-----	2,15	1.02	-----	1,15	0.34	-----
Biomass		1,2	1.93	0.30	2,36	0.21	0.81	2,36	0.18	0.83
Seed Number		1,38	6.26	0.02	2,38	0.31	0.79	2,38	0.52	0.60

Table 4. Contiuned

		Effect								
Plant Characteristic	Date	Soil Type			Disturbance			S x D		
	Seeded: Spring 1994 Harvested: Summer 1994	df (effect, error)	*F*	*P*	df (effect, error)	*F*	*P*	df (effect, error)	*F*	*P*
Emergence		1,56	206.32	<0.01	2,56	0.25	0.78	2,56	2.21	0.12
Height	June 25	1,2	2.33	0.27	2,38	1.8	0.18	2,38	3.08	0.06
Biomass		1,46	3.36	0.07	2,46	0.58	0.60	2,46	0.56	0.60
Seed Number		1,46	0.00	-----	2,46	0.00	-----	2,46	0.00	-----
	Seeded: Spring 1994 Harvested: Summer 1995									
Emergence		1,16	3.34	0.09	1,16	0.02	0.90	1,16	0.58	0.46
Height	April 22	1,16	6.78	0.02	1,16	0.03	0.87	1,16	0.03	0.87
	May 10	1,2	1.72	0.32	1,16	0.29	0.60	1,16	0.13	0.72
Biomass		1,2	4.34	0.17	1,19	0.36	0.55	1,19	1.74	0.20
Seed Number		1,21	13.45	<0.01	1,21	0.70	0.41	1,21	1.23	0.28

Table 4. Continued

		Effect								
Plant Characteristic	Date	Soil Type			Disturbance			S x D		
	Seeded: Fall 1994 Harvested: Summer 1995	df (effect, error)	*F*	*P*	df (effect, error)	*F*	*P*	df (effect, error)	*F*	*P*
Emergence		1,68	385.21	<0.01	3,68	0.12	0.95	3,68	0.50	0.68
Height	March 30	1,2	53.40	0.02	3,66	0.84	0.48	3,66	1.73	0.17
	April 22	1,2	9.71	0.09	3,61	0.08	0.96	3,61	1.23	0.30
	May 10	1,66	67.72	<0.01	3,66	2.93	0.04	3,66	1.96	0.13
	June 16	1,61	21.24	<0.01	3,61	10.81	<0.01	3,61	1.00	0.40
Seed Number		1,2	29.12	0.03	3,66	52.51	<0.01	3,66	0.07	1.0
Biomass		1,68	0.06	0.80	3,68	10.94	<0.01	3,68	0.33	0.80

Aboveground biomass for medusahead plants seeded during the first year did not differ significantly (P>0.05) between soil types or among disturbance treatments regardless of time of planting (fall 1993 or spring 1994) or of harvesting (summer 1994 or 1995). During the wetter growing season (fall 1994 to summer 1995), only the severe soil disturbance treatment (the treatment added that year) differed significantly from the others with a five-fold increase in aboveground biomass (Fig. 2, Table 4).

In the drier year (fall 1993 to summer 1994), medusahead height was examined on six census dates. All plants measured for height died on the loamy soil by the fifth census date. Only the soil disturbance and defoliation treatments were analyzed on the clay soil type for the last two census dates, because all plants that were measured for height in the control treatment died by the fifth census date. During this year, plant height did not differ significantly (P>0.05) among disturbance treatments on any census date. However, heights were significantly greater on the clay soil type, three out of four census dates in which plants were present on both soil types (Fig. 3, Table 4). On the loamy soil, plants attained most of their maximum height by April, whereas those on the clay soil continued to increase height for nearly two more months. For plants seeded in spring and harvested in summer 1994, too few plants emerged before the June date to allow examination of treatment differences in height.

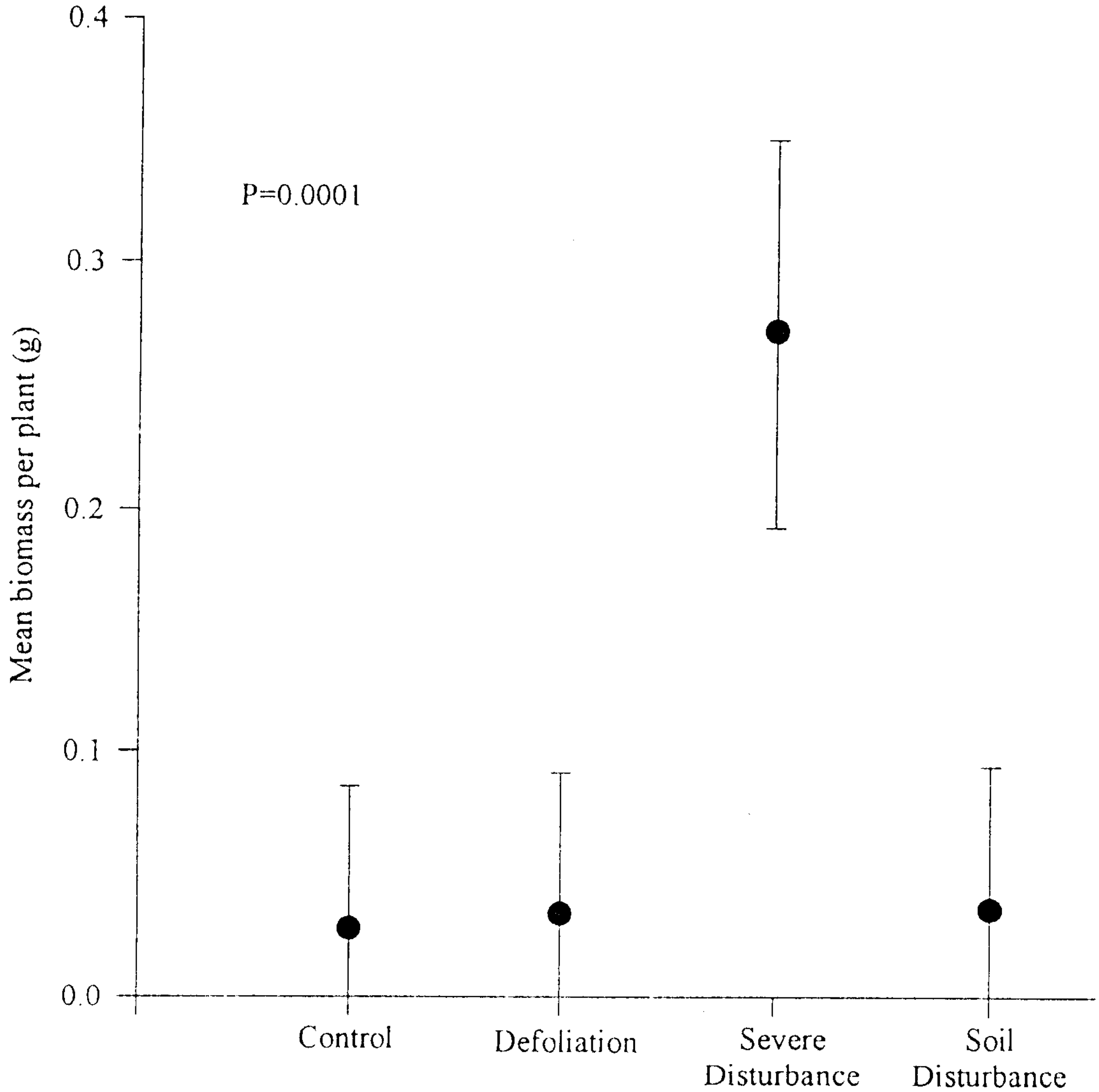

Figure 2. Medusahead biomass (mean per plant and 95% confidence interval) for all plots across both soil types, and among disturbance treatments for plants seeded in fall 1994 and harvested in summer 1995.

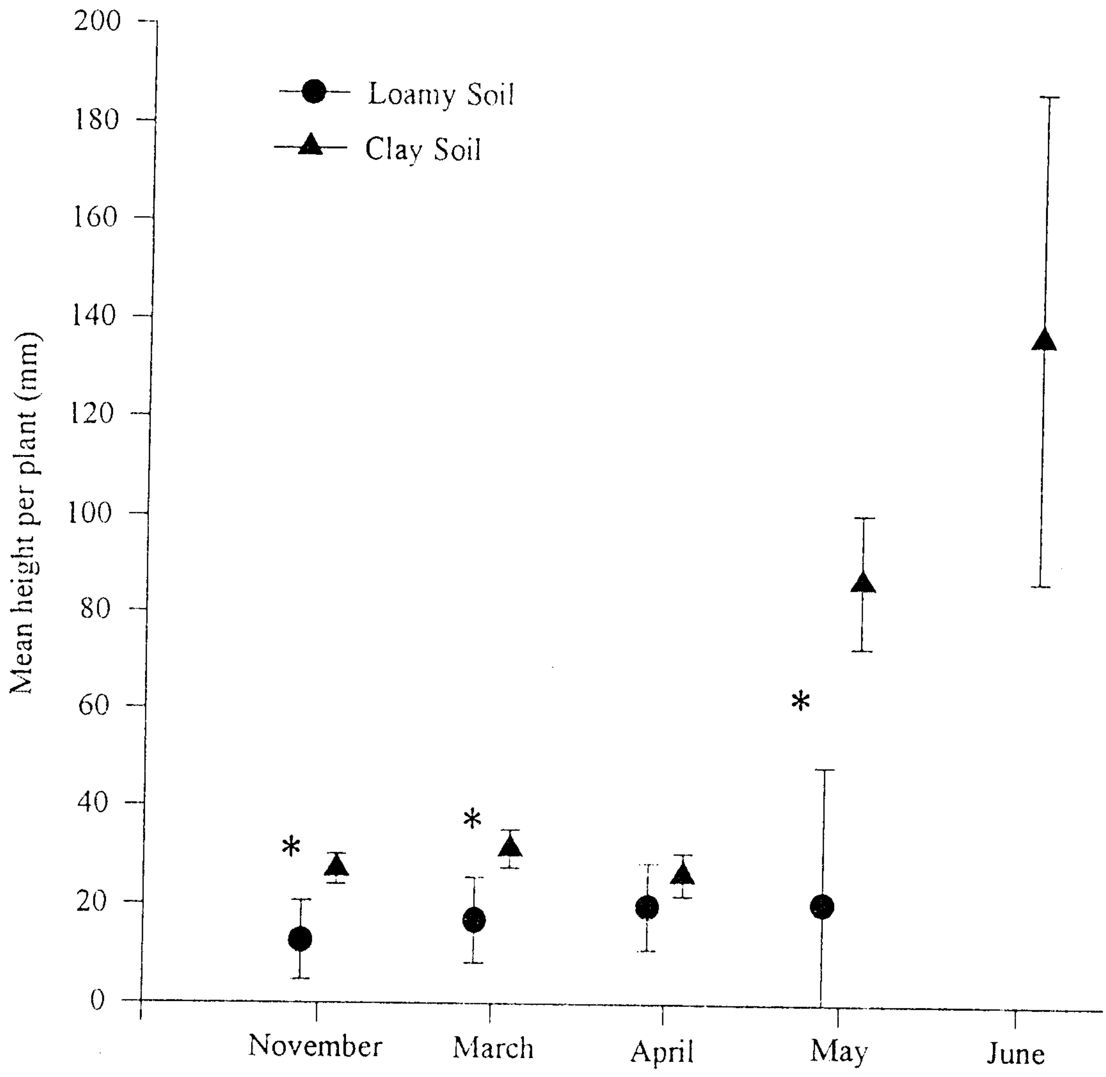

Figure 3. Height of medusahead plants seeded in fall 1993 and harvested in summer 1994 (mean per plant and 95% confidence intervals) growing on two soil types, measured at five dates (19 November, 25 March, 4 April, 24 May, 8 June, 25 June) during the 1993-1994 growing season. Significant differences ($P<0.05$) between soil types for a date are noted with an asterisk (*) above that pair of heights. Means are combined across all disturbance treatments. All plants being measured on the loamy soil were dead by the June census date.

During the wetter year (fall 1994 to summer 1995), plants seeded in fall 1994 continued to increase in height on both soils throughout the year. Similar to the previous year, heights were significantly ($P<0.05$) greater on the clay soil for three out of four census dates (Fig. 4A, Table 4). Differences between disturbance ($P<0.05$) treatments occurred on the last two census dates, but were largely driven by the greater height of plants in the severe disturbance (Fig. 4B, Table 4).

For plants seeded in spring 1994, heights of spring 1994 emergent plants did not differ between soil types, however, fall emergent plants did differ. Plants at the loamy site were taller than those at the clay site only in April 1995. However, heights at the clay site increased in the following months, as was true for the other planting dates (Fig. 5, Table 4).

Survival and Seed Production

Because few plants emerged during the first year, no significant differences were noted among disturbance treatments or soil types in their survival rate to summer 1994 (proportion alive out of proportion emerged = 0.09 ± 0.03, $\bar{x} \pm SE$, n= 12, $P>0.05$). The spring 1994 seeded and emerged plants differed significantly among disturbance treatments in survival time on the clay soil type ($P=0.0001$), but not on the loamy soil type. The plants affected by the shallow soil disturbance treatment on average lived ten days longer than the control treatment, and five days longer then the

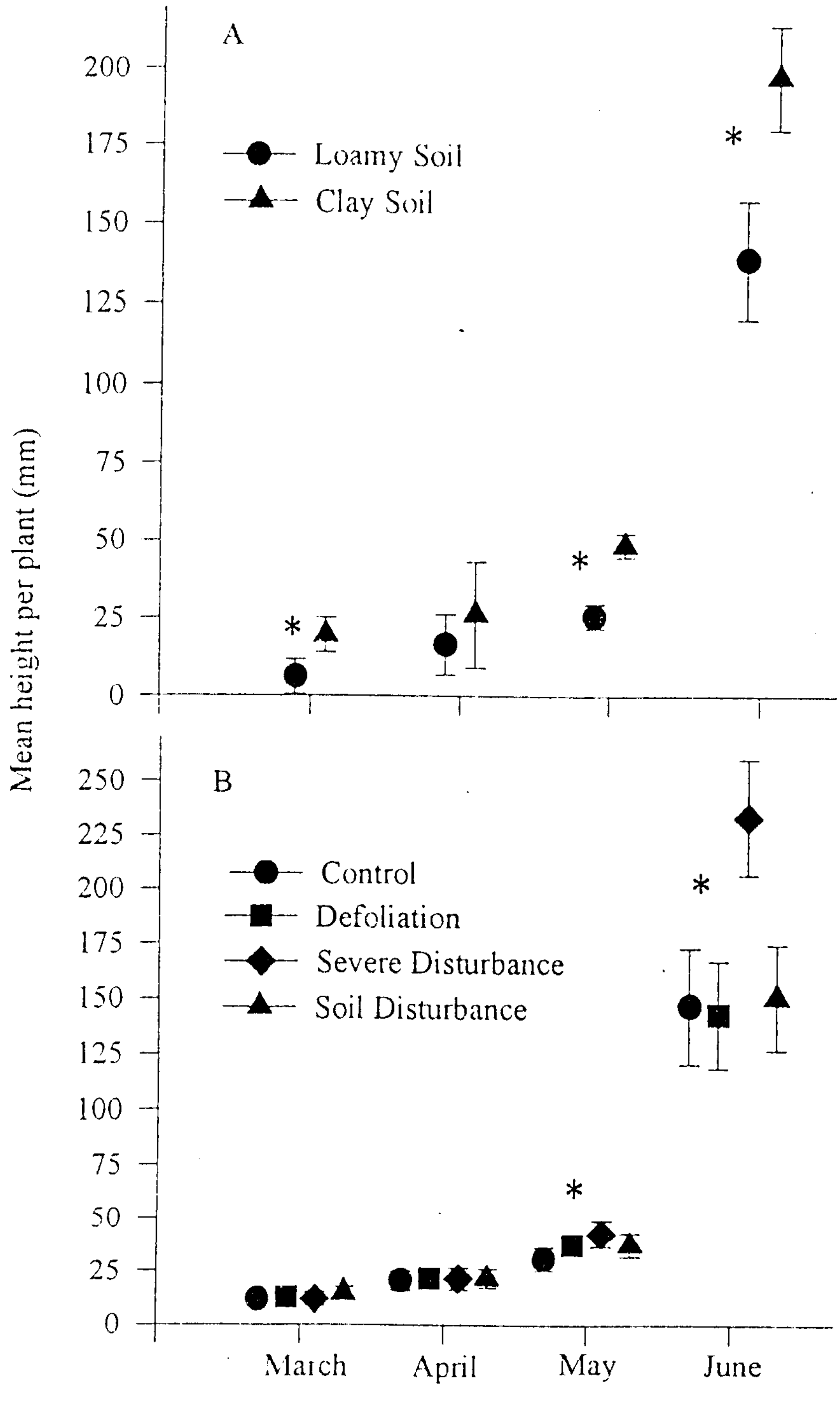

Figure 4. Height of medusahead plants (mean per plant and 95% confidence intervals) seeded in fall 1994 and harvested in summer 1995, growing on two soil types, measured at four dates (30 March, 22 April, 10 May, 16 June) during the 1994-1995 growing season. Significant differences ($P<0.05$) between soil types (A) and among disturbance treatments (B) are noted with an asterisk (*) above those heights.

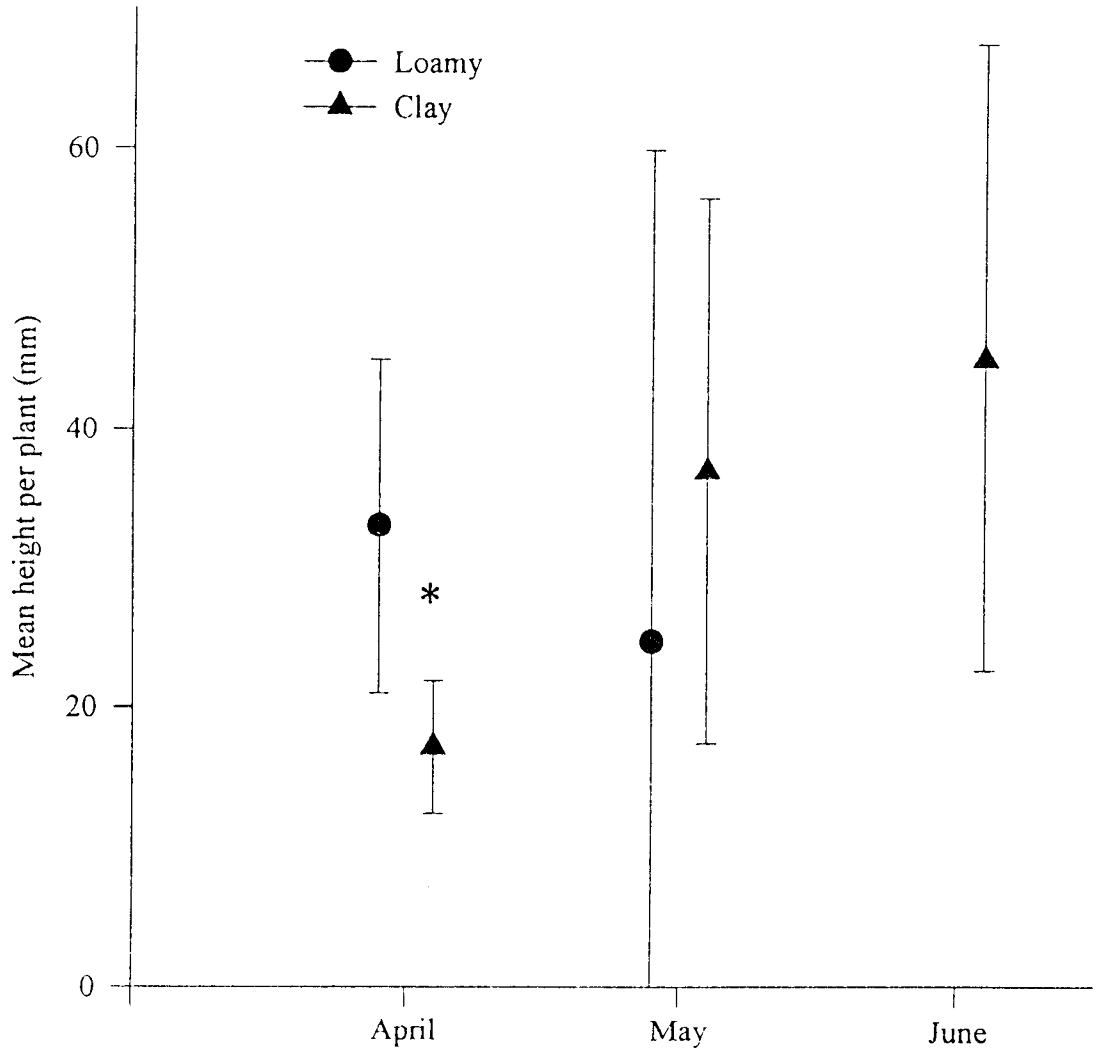

Figure 5. Height of medusahead plants (mean per plant and 95% confidence intervals) seeded in spring 1994 harvested in summer 1995, growing on two soil types measured on three dates (22 April, 10 May, 16 June) during the 1994-1995 growing season. Means are combined across all disturbance treatments. Significant differences ($P<0.05$) between soil types are noted with an asterisk (*) above those heights. All individuals were dead on the loamy soil by the last census date.

defoliation treatment. Although longevity was greatest in the shallow soil disturbance treatment, they died within 45 days of emergence. Plants from this spring 1994 seeding that remained dormant during summer 1994 and emerged in fall 1994 did not differ significantly in survival rate among treatments on either soil type (proportion alive out of proportion emerged = 0.26 ± 0.04, $\bar{x} \pm$ SE, n = 4, P>0.05).

Survivorship curves for medusahead planted in fall 1994 and harvested in summer 1995 significantly differed among disturbance treatments within each soil type (Fig. 6; P=0.01 and P<0.01, for the loamy and clay sites respectively). Plants on the loamy soil within the severe disturbance treatment had the shortest lifespan, on average 60 days, as compared to 80 days for plants within the other treatments. Plants on the clay soil type lived to approximately 80 days, individuals affected by the severe disturbance and shallow soil disturbance treatments had the highest proportion alive at the end of the lifespan for that growing season.

Seed production per medusahead plant was two- to four-fold greater (P=0.02) on the clay soil than the loamy soil for plants sown in fall or for those that remained dormant until fall (Fig. 7, Table 4). Plants that were sown and emerged in spring 1994 did not reproduce regardless of soil type or treatment. In the wetter year, plants sown in fall 1994 produced five-fold more seeds in the severe soil disturbance than any other treatment (P<0.01) (Fig. 8, Table 4).

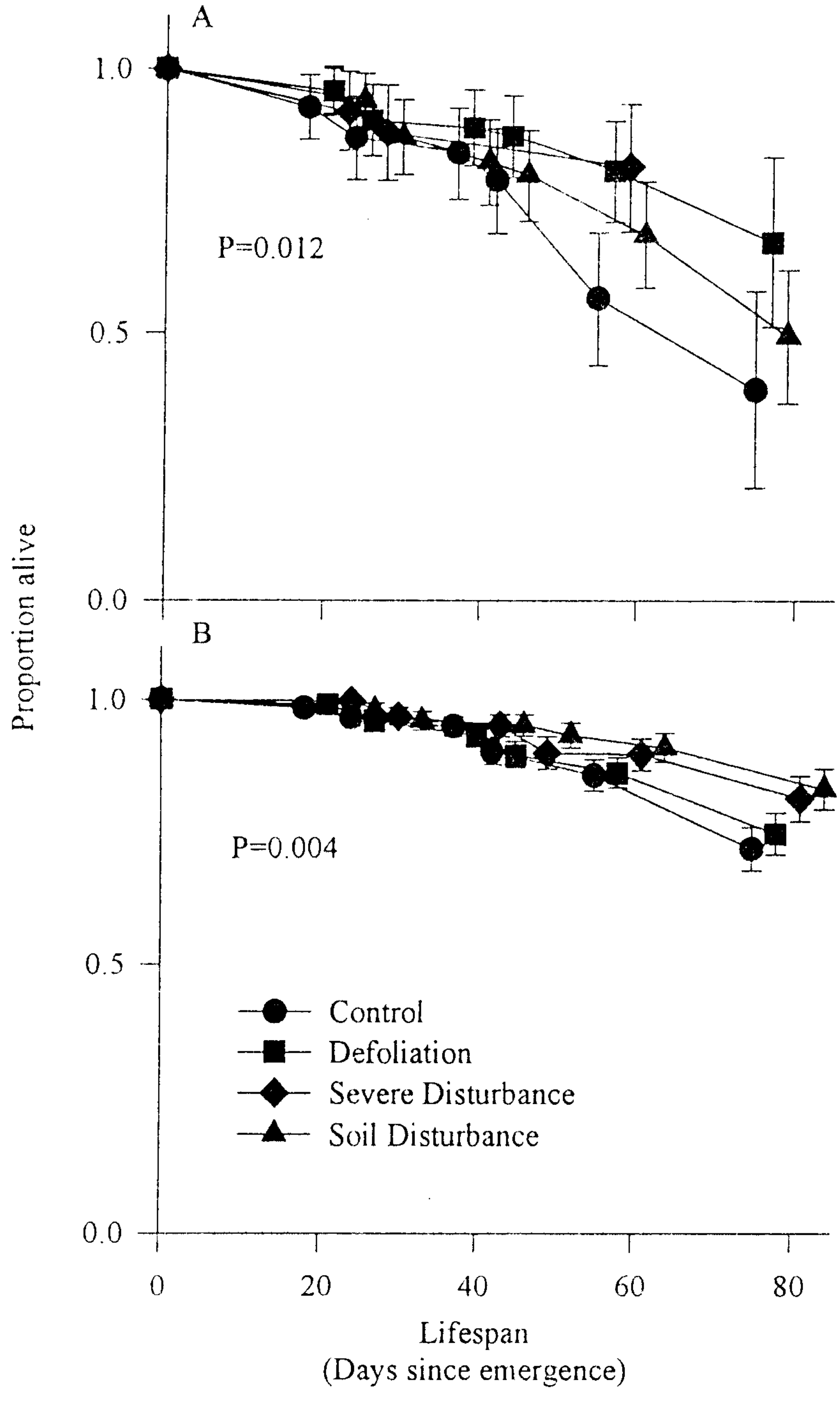

Figure 6. Proportion of medusahead plants alive at increasing lifespans for plants seeded in fall 1994 (mean and 95% confidence intervals) growing on two soil types, loamy (A) and clay (B) soil types.

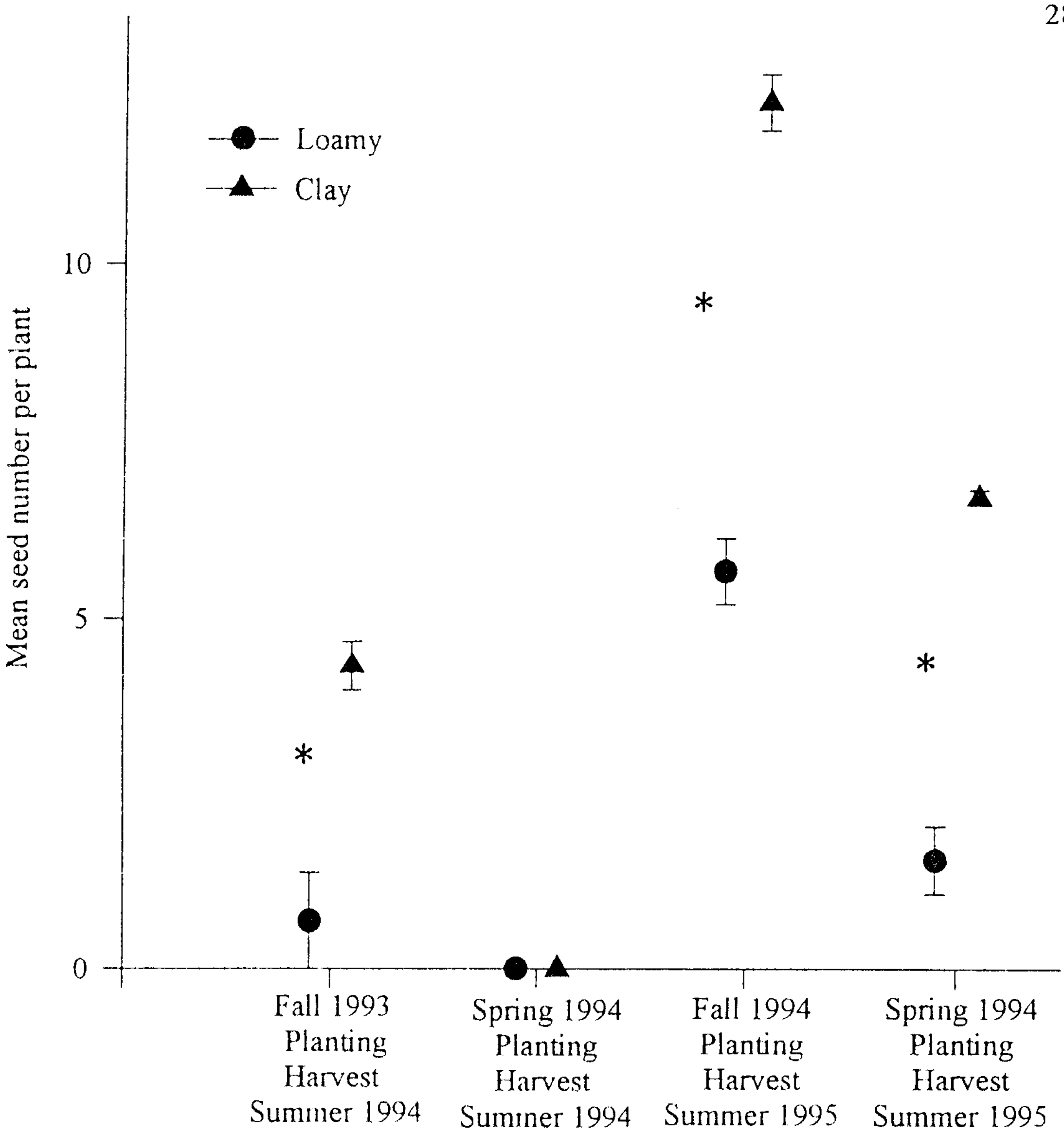

Figure 7. Mean number of seeds produced by medusahead plants (mean per plant and 95% confidence interval) for different planting and harvest dates. Means are combined across all disturbance treatments. Significant differences ($P<0.05$) between soil types are noted with an asterisk (*) above those planting and harvest dates.

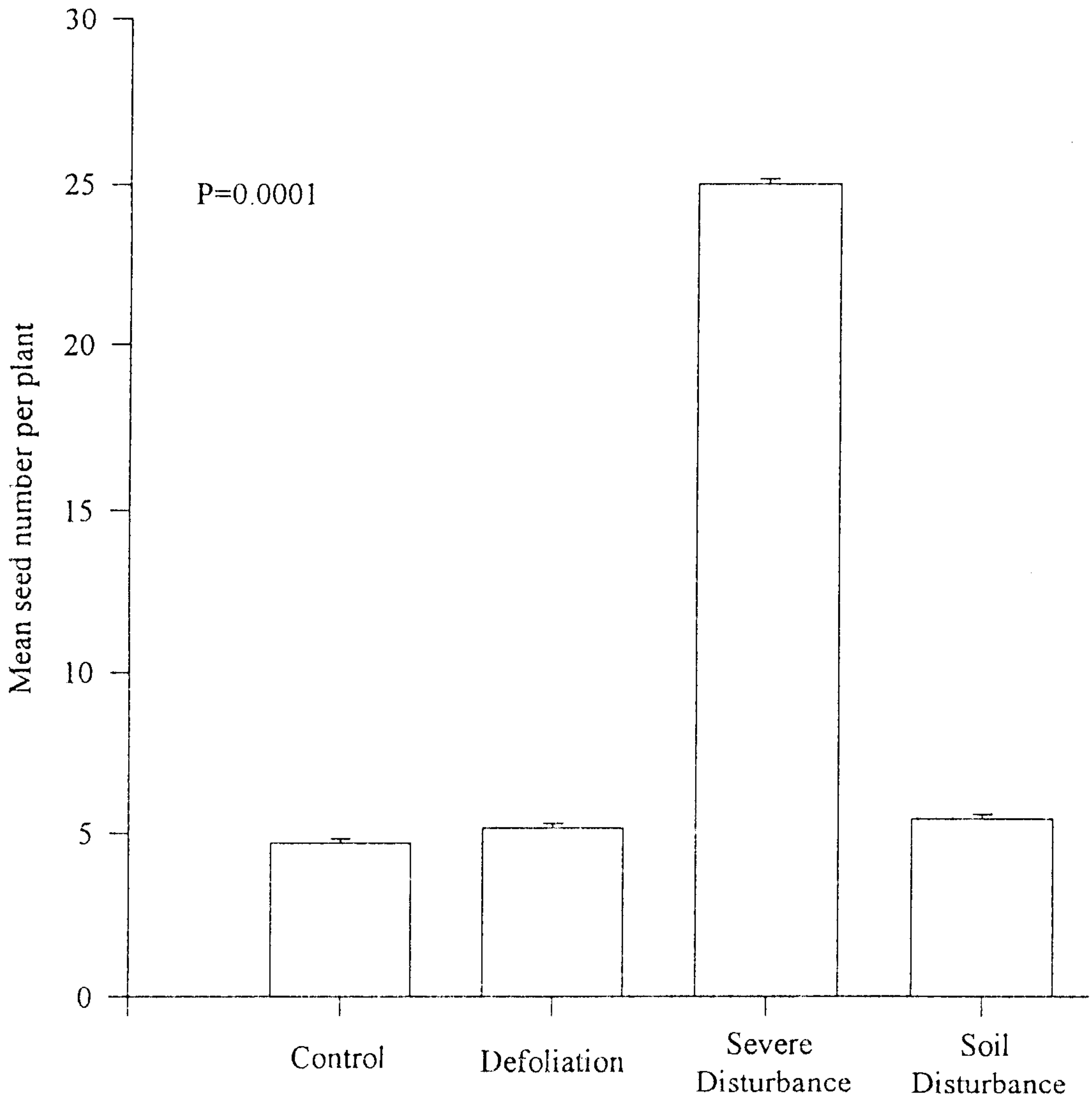

Figure 8. Mean number of seeds produced by medusahead plants (mean per plant and 95% confidence interval) for all plots across both soil types, and among disturbance treatments for plants seeded in the fall of 1994 and harvested in summer 1995.

DISCUSSION AND CONCLUSION

Results of this experiment clearly demonstrate that invasion of medusahead onto coarser textured soil types within native shrub-steppe communities was possible, but that its maintenance was more likely on finer-textured soils where emergence, survival, and reproduction are high. On loamy soils, wetter than normal weather conditions may be necessary for medusahead to maintain a viable population if a native plant community remains intact. However, severe disturbances enhance the growth and fitness parameters of emerged individuals on clay and loamy soils, leading to a higher potential for medusahead dominance. Prior to this study, Young and Evans (1970) observed that wet meadows and burned coniferous forests at high elevations were the only sites where medusahead occurred on soils other than clay. In addition, they suggested that big sagebrush (*Artemisia tridentata*) communities on medium to coarse textured soils were resistant to medusahead invasion. Later, Young (1992) recognized the possibility of expansion onto coarser textured soils. My results appear to lend support to these observations while providing evidence for conditions that may contribute to our understanding of how medusahead may expand into sagebrush grasslands.

Consistent with the earlier predictions regarding medusahead expansion, medusahead emergence and survival is enhanced when soil texture is dominated by clay. My results indicate that medusahead is able to expand onto coarser soil textures under the appropriate climatic conditions (wetter than normal), and to establish within a native perennial shrub-grass community.

Maintenance of intact native plant communities clearly inhibits expansion of medusahead populations. In almost all cases, minor disturbances, such as defoliation of surrounding plants or shallow soil disturbances, did not enhance growth or fitness parameters beyond that of the control. Reduced survival and reproduction of medusahead in intact native plant communities when compared to those in the severe disturbance treatment, are likely a result of a release from resource competition with surrounding native vegetation. Small (36 m^2), but severe disturbances that denude vegetation are adequate for medusahead to maintain a viable population. This fact emphasizes that medusahead expansion and dominance is more likely on areas where the community composition of plants has shifted from many years of overgrazing, from plowing, or from fire. If a seed source exists under these circumstances, medusahead will dominate available space.

Although my experiment was not designed to investigate granivory, my observations provide the first evidence of animal use of medusahead seeds. In the only reported granivore study involving medusahead, Savage et al. (1969) showed that chukar partridges (*Alectoris chukar* (Gray)) did not eat medusahead seeds in a feeding trial. Although I did not directly observe seed use, my observations of detached awns laying on the soil within our plots lead us to suspect rodents may use and transport medusahead seeds.

Further evidence was noted the following spring, when small pockets of medusahead plants were seen within my exclosures, but outside of our plots. These plants were found in small (<3 cm diameter) patches that contained up to approximately 15 plants per patch. I suspect these patches arose from seed caches created by the animals that removed our seeds in the fall. No patches were observed in 1995; removal of awns apparently resulted in removal of the animal's search cue for locating seeds.

Survivorship in the 1994-1995 growing year on the clay soil type indicated that soil disturbance, both shallow and severe, enhanced the survival of medusahead. The shorter lifespan for medusahead in the severe disturbance treatment on the loamy soil type does not reflect mortality before reproduction, but it is a result of later emergence than other treatments. Plants in this treatment produced the highest seed production of all disturbance treatments on loamy soils.

Regardless of soil type, timing of seed arrival plays a critical role in the success of individual plants. My observations of seed caches, that I believe were likely produced in the fall, provides an excellent example of a minor soil disturbance at the time of seed burial, similar to my shallow disturbance treatment, created in the fall. Plants derived from seeds germinating in the fall have higher overall rates of seed production, biomass, and survival than plants germinating in the spring. Being a winter annual, medusahead, germination usually occurs in October or November as moisture becomes available from fall rains, but growth is limited until the soil temperature warms in March and April (Sharp et al. 1957, Murphy and Turner 1959, Harris and Wilson 1970). In spring, development is rapid with seedheads beginning to appear in May. Medusahead allocates biomass to roots during the winter months and is able to maintain root growth in colder soil temperatures than many native species. This ability allows medusahead to expand its root length relative to seedlings of native species (Harris and Wilson 1970). As soil temperatures warm in late winter, medusahead pre-empts the available moisture and nutrients before native annuals and bunchgrass seedlings begin active growth (Harris and Wilson 1970, Hilken and Miller 1980).

Care should be taken to minimize dispersal of medusahead seeds to sites during summer and fall to reduce the potential for fall germination thereby reducing the likelihood of medusahead establishing a viable population. This may include actions such as restricting access to susceptible sites for livestock or vehicles that have previously been in areas with medusahead.

Seeds that remained in the soil from spring 1994 and germinated in fall 1994 were more successful than seeds planted and harvested in spring/summer 1994. Medusahead seed is capable of entering dormancy, allowing it to survive the summer drought. Medusahead strains from the western United States differ in their seed dormancy characteristics with some strains exhibiting only slight seed dormancy a few weeks after harvest and others remaining dormant for 6 months or longer (Nelson and Wilson 1969, McKell et al. 1962). This latter situation appeared to be the case with some of the seeds planted in spring 1994.

Varying degrees of anthropogenic influences affect the onset of invasions by exotic plant species. Introductions of these species have resulted in observable changes in ecosystem structure and function. Some ecosystems are relatively resistant to invasion, and inhibit expansion of certain weeds. However, after initial growth in favorable conditions, weeds may develop or select genotypes appropriate to a wider range of habitats (Baker 1986, Mooney et al 1986, Novak and Mack 1993).

This study demonstrated that medusahead, an exotic species, has the capability to expand onto loamy and clay soil types within an intact native shrub-steppe community, but continued maintenance of medusahead may be more likely on clay soils. Depending on other factors such as disturbance and climate, the rate of expansion will vary. The maintenance of an intact native plant community along with minimal disturbances are necessary to restrict the expansion of medusahead.

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