AN ABSTRACT OF THE THESIS OF

David Clausnitzer for the degree of Master of Science in Rangeland Resources presented on August 15, 1996. Title: Field Study of Competition Between Medusahead (*Taeniatherum caput-medusae*) and Squirreltail (*Elymus elymoides*).

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Abstract approved: ______________________
Michael Borman

Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) is a Eurasian annual grass that infests large areas of U.S. rangelands, dominating former bunchgrass/shrub sites. Squirreltail (*Elymus elymoides* (Raf.) Swezey) is a native perennial grass that has demonstrated the ability to establish in stands of medusahead.

A study conducted on two sites near Burns, OR had the objectives of quantifying competition between medusahead and squirreltail, and determining the effect of moisture availability on competition. Two hundred plots were arranged in a factorial design. Measurements were taken of plant growth, seed production, soil moisture, and climate.

Results for the two years are contrasting. The first year was very dry. Medusahead grew and reproduced well, producing a seed crop up to 10 times the amount planted; squirreltail grew poorly and did not reproduce. Samples of squirreltail seed retrieved from the plots in late summer were found to have remained dormant since seeding. The second year had above-average precipitation. Medusahead grew and reproduced well again. Squirreltail grew and reproduced abundantly on one of the sites, both on freshly-seeded plots and on plots containing dormant seeds and surviving plants from the previous year.

In all cases, medusahead exhibited stronger interspecific and intraspecific competitive effects than did squirreltail seedlings. With adequate soil moisture, squirreltail reduced average weight and median seed production of individual medusahead plants, but did not reduce medusahead seed production per square meter. Medusahead succeeded in a drought year by utilizing deep soil moisture, and utilized shallower moisture in a wet year. During a wet year in plots containing mature squirreltail, medusahead utilized shallower moisture, while squirreltail strongly utilized much deeper moisture.

Interspecific competitive interference by medusahead on squirreltail seedlings suggests the potential benefits of suppressing medusahead during the seeding year for squirreltail in a rehabilitation effort, especially if climatic conditions are conducive to squirreltail germination and establishment.

Field Study of Competition Between Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) and Squirreltail (*Elymus elymoides* (Raf.) Swezey)

by

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David Clausnitzer, Author

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INTRODUCTION

The ecosystems of eastern Oregon have been disrupted by the spread of alien weed species which have established themselves primarily by taking advantage of human-caused disturbances. The original native vegetation is able to reclaim the sites only very slowly if at all. (Hironaka and Tisdale 1963, Sharp and Tisdale 1952). Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) is one of the most widespread and competitive of the exotic species in the Great Basin.

Medusahead is successful in competition with other plants for a number of reasons. The seeds are able to germinate at low temperatures when moisture is available (Young, Evans, and Eckert 1968). Fall germination allows the leaves to develop before winter (Sharp, Hironaka, and Tisdale 1956) and the roots to grow through much of the winter, thus preempting resources from plants that germinate in spring or go dormant in winter. The roots have a heavily suberized endodermis that may allow it to transport deeply-stored water through dry upper horizons (Harris 1965). The species has a high reproductive rate which is very plastic. When densities are high, plants usually produce one seed head per plant. At lower densities the number of culms is commonly three to five per plant. In one rare instance a plant produced 133 seed heads (Sharp, Hironaka, and Tisdale 1957). The plant's tissues are high in silica (Bovey, Le Tourneau, and Erickson 1961), making it nearly inedible and producing a litter that, due to its slow decomposition, can build up into a thick layer that inhibits the germination of seeds other than its own (Hironaka 1965).

Revegetating areas in the face of medusahead competition has proven to be very difficult (Evans 1961). Medusahead roots develop earlier and faster than those of most perennials, greatly reducing the ability of the perennial seedlings to survive their first season due to competition for water (Harris 1977, Harris and Wilson 1970). Efforts to reduce medusahead populations are necessary if reseeding efforts are to succeed. These efforts have included herbicides, discing, plowing, and burning (Harris and Goebel 1976, Furbush 1953, Kay 1965). Rough ground, shallow soils, inaccessibility, and regulations make some of these treatments impractical or expensive (Sharp and Tisdale 1952, Turner 1965). Medusahead is able to grow in Vertisols on which reestablishment of other vegetation is difficult due to the churning and cracking of these soils (Young and Evans 1970).

An inexpensive and possibly effective means of reducing medusahead dominance is suggested by the observation that squirreltail (*Elymus elymoides (Raf.) Swezey*) may be able to invade stands of medusahead and bring about decreases in weed populations (Hironaka and Tisdale 1963). Squirreltail is a native perennial that exhibits strong competitive characteristics: abundant production of highly germinable seed, rapid physiological development of seedlings, and ability to increase on disturbed or harsh sites (Whitson et. al 1988, Young and Evans 1977). The emergence of squirreltail has been shown to be almost as good on unfavorable sites as that of crested wheatgrass, a widely used exotic perennial forage grass (Wood et al. 1982). Squirreltail plays a seral role in native sagebrush-bunchgrass communities, and is not a major component of the climax vegetation (Schlatterer and Hironaka 1972, Young and Evans 1977). Establishment of squirreltail in stands of medusahead may be a first step in restoring a semblance of the original plant community.

Squirreltail has already exhibited the ability to establish itself when broadcast-seeded into medusahead stands with densities exceeding 1000 per square meter (Hironaka and Sindelar 1973). Additive design greenhouse experiments and field studies have shown squirreltail to be successful when grown in competition with medusahead. The squirreltail germinated in the fall, grew and survived the following year, and had some reproductive success (Hironaka and Sindelar, 1973 and 1975). Although shoot growth of squirreltail was unspectacular, root growth was strong, which probably explains its competitive ability and survivability through the dry season. However, squirreltail seeds have not shown the ability to germinate well when suspended in medusahead litter. This indicates that removal of thick medusahead litter would be necessary before reseeding (Young and Evans 1977).

Squirreltail seedlings have also been observed to do better on medusahead-dominated sites than on sites dominated by squirreltail (Hironaka and Sindelar 1973). Although this may have been due to frost heaving on the bare interspaces between squirreltail plants, the squirreltail intraspecific competition needs to be explored. In a replacement experiment with Arizona fescue (*Festuca arizonica* Vasey), squirreltail was more negatively affected by intraspecific competition than by interference from the other species (Cook and White 1985).

Species or populations of plants interact with each other in a variety of ways that may be positive, negative, or neutral. The effect that a plant has upon the environment of its neighbors is termed interference, and is caused by consumption of limited resources, production of stimulants or toxins, predation, or protection (Radosevich and Holt, 1984). One form of negative interference is competition, which is the mutually adverse effects of plants which utilize a resource in short supply (Barbour et al. 1980). The critical resources and their interactions can be integrated into the concept of space, the utilization of which can be measured using the plants as biological indicators. An individual resource may also be identified and considered independently when that resource is suspected as being of overriding importance.

Negative interference between plants of the same species is termed intraspecific competition. This form of competition can be very intense because the plants share the same needs and means for satisfying those needs. Interspecific competition exists between plants of different species, and is theoretically minimized through evolution, allowing coexistence of different species in varied niches within communities. A plant can have a direct uptake effect on a resource through consumption, or through direct effects such as the reduction of surface temperature and evaporation by shading and litter, or the accumulation of nutrients around plant bases (Goldberg 1990).

Plant growth is affected by density: increasing density brings about a decrease in the average size of the plants in the population. Within a given environment, the yield per unit area increases as the population increases until the resources become limiting, resulting in a constant final yield regardless of further increase in population, due to the plasticity of plant growth. As density increases, both mortality (self-thinning) and variation in plant size increase (Firbank and Watkinson 1990).

The traits that determine competitive success depend on the structure of the competing populations. Seedling establishment is often the critical life history stage in population persistence (Harper 1977), and the main consideration is whether seedlings are competing with each other (size-symmetric competition) or with mature plants (size-asymmetric competition). In revegetation efforts against medusahead, size-symmetric competition will be the initial and deciding arena; in this situation, success will be determined by traits related to early and aggressive resource capture rather than tolerance of low-resource conditions (Goldberg 1990).

The general objective of this project was to determine whether or not reseeding with squirreltail can be an effective and inexpensive means of reducing domination of rangeland sites by medusahead. More specifically, we wished to quantify the relative competitive abilities at different densities and proportions of squirreltail and medusahead from germination through the growing season to determine the growth, reproduction, and survivability of squirreltail seedlings in medusahead stands. We also wished to quantify and separate interspecific and intraspecific competition in the system with the aim of determining if squirreltail can be an effective reseeding species in medusahead stands, and the level of control of medusahead populations needed before seeding with squirreltail. Long-term plots have been established to allow the expression of any successional advantage squirreltail may have because it is a perennial. Last, we wished to measure soil moisture utilization by the two species in order to determine niche separation between them.

MATERIALS AND METHODS

Study Site

Two study sites are located near the northwest shore of Warm Springs Reservoir in Harney County, Oregon. Mean annual temperatures range from 9 to 12 degrees C (48 to 52 degrees F), with summer maximums reaching 38 degrees C (100 degrees F) and winter minimums dropping to -37 degrees C (-35 degrees F). Annual precipitation usually ranges from 20 to 30 cm (8 to 12 inches), and the frost-free period is 110 to 140 days. Precipitation occurs primarily from September through April; summer precipitation is rare and usually so light as to not affect soil moisture levels. Elevation is 1070 m (3475 feet).

The native vegetation of the area is sagebrush-bunchgrass steppe, dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Nutt.), bluebunch wheatgrass (*Pseudoroegneria spicatum* (Pursh) Scribn. & Smith), Thurber's needlegrass (*Stipa thurberiana* Piper), and Basin wildrye (*Elymus cinereus* Scribn. & Merr.). The land has long been grazed by cattle and, in the past, sheep. Due to historical overgrazing, fires, and cultivation and abandonment, much of the area has degraded to domination by alien annual species. Large sections have been seeded to crested wheatgrass.

The two sites were chosen because they are on contrasting soils and aspects and are now entirely dominated by stands of annual weeds that are likely to be invaded by medusahead, although this has not yet noticeably occurred. Medusahead-dominated sites do occur in the general area.

The site designated ST is at T22S R36E section 27 NE 1/4 of the NW 1/4. It is on a hillside stream terrace. The soil is a well-drained, fine, montmorillonitic, mesic Durixerollic Haplargid originating from lacustrine deposits, alluvium, and some eolian deposits. The slope is 5%, with a NE aspect of 30-40 degrees. The 5 cm thick A horizon is a loam with 16% clay and 18% gravel and cobbles. The underlying Bt horizons average 35% clay. Roots are common to many as deep as 100 cm; a few roots extend down to 125 cm. The current vegetation is primarily clasping pepperweed (*Lepidium perfoliatum* L.) with a few scattered crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Wyoming sagebrush plants. Isolated medusahead and squirreltail plants can be found within 75 meters of the plots. Soil samples were kept in a greenhouse and watered in order to determine the seed bank, which was found to include cheatgrass (*Bromus tectorum* L.), *Vulpia* spp., and native bluegrass (*Poa sandbergii* Vasey) in addition to the above species.

The site designated VT is at T22S R36E section 22 SE 1/4 of the SE 1/4. It is on a residual hill. The soil is a well-drained, fine, montmorillonitic, mesic Xerollic Haplargid originating from lacustrine deposits, residuum, and some eolian deposits. The slope is 8%, with a SE aspect of 150-160 degrees. The 5 cm A1 horizon is a silt loam with 25% clay and no coarse fragments. The underlying A2 and Btk horizons average 35% clay. Roots are common to many to as deep as 100 cm; a few roots extended down to 180 cm. The soil has many cracks, 0.5 to 3 cm wide and as deep as 60 cm. The current vegetation is Russian thistle (*Salsola iberica* Sennen), tumble mustard (*Sisymbrium altissimum* L.), and spiny lettuce (*Lactuca serriola* L.) with a few scattered crested wheatgrass plants. A few plots contain rhizomes which may be Western wheatgrass (*Agropyron smithii* (L.)

Pers.). One squirreltail plant was found 30 meters from the plots, and a few medusahead exist nearby. The seedbank was found to contain cheatgrass in addition to the above species.

Site Preparation and Maintenance

Four strand smooth wire fences enclose each site as rectangles 50 meters on a side to exclude cattle. One inch mesh 36 inch high poultry wire erected on the same fence posts is intended to exclude jackrabbits.

Weeds on the sites were mowed and hand-pulled. Selective hand-weeding was continued throughout the study period. The soil was rototilled lightly to a depth of about 1/2 inch. Cobbles, stones, and some of the coarser gravel were removed by hand and light raking at Site ST, and the soil surface was levelled by raking.

Two inch diameter PVC pipes were included in each plot to provide access for soil moisture measurements. Each was cut to a length of one meter. A cap was glued to the bottom end of each length, and a removable cap put on the top. Holes were drilled with a hand auger near the center of each plot and a pipe was buried with the top end exposed in each.

Seed Collection and Processing

Squirreltail and medusahead seeds were collected from nearby range sites in mid-July each year. Seeds were processed to remove awns and other extraneous material using an air screen scalper and sorting drum. Awn removal was very good, with no noticeable seed damage.

Seeds were stored at room temperature until planting. Germination tests performed by the USDA Seed Laboratory at OSU indicated seed viabilities for both species in the range of 90-99%.

Seeds were sown by hand into each plot and lightly covered with soil in September 1993. Extra seed was sown to compensate for less than complete germination. The number of seeds sown was doubled for the lowest density plots, while 10% extra seed was added for the other densities.

Design and Analysis

Site layout is a randomized block design with a factorial arrangement. Each block contains 25 randomly-assigned plots seeded with the two species at levels of 0, 10, 74, 550, and 4074 seeds per square meter. This allows observations of competitive effects at all combinations of density and proportion, which, along with allowing detection of interactions, is the advantage of the factorial arrangement (Snaydon 1991).

Each of the 25 plots within a block is 1.5 meters on a side (2.25 square meters). One meter wide strips separate all the plots within each block; these provide access and a uniform edge effect for each plot. The strips were seeded with crested wheatgrass in an attempt to suppress weeds. Buffer zones of at least 5 meter width exist around each block. Small plots of the species under study were grown in the buffer zone. These plants were harvested and weighed to provide samples for nondestructive estimation of plant growth within the experimental plots.

Three blocks at each of the two sites were constructed and seeded in 1993 for a total of 150 plots for observing competition between seedlings. One additional block was constructed at each site in August 1994 for a total of 200 plots. All surviving squirreltail plants from the 1994 spring growing season were removed from one original block at each site; these blocks as well as the newly prepared blocks were seeded exactly as described above for the 1994 growing season in order to observe seedling competition in 1995. The remaining original blocks were cleared of dead medusahead, but any surviving squirreltail plants were allowed to remain. This allowed observation of competition among annual medusahead, squirreltail seedlings, and mature squirreltail. These blocks were reseeded to the seed densities produced in each plot during the 1994 growing season.

Data analysis focused on effects of varying densities and proportions of the two species on individual plant weight, seed production per plant, and soil moisture use at four depths due to each species. Multiple linear regression produced models estimating effects of numbers or total plot weights of medusahead, squirreltail seedlings, and mature squirreltail plants on the above variables, within the range of densities occurring in the plots. The regression intercept estimated weight or seed production of an individual plant not affected by competition. Results were very similar whether the independent variables were plant numbers or total biomass per species in each plot.

Soil moisture use was estimated between two dates: the first, the date early in the growing season after significant precipitation had stopped and plant growth began to produce discernible reductions in moisture; and the second, the date of harvest of medusahead plants after seed set and senescence.

The difference in soil moisture between the two dates was regressed against plant numbers within the ranges of densities that grew in the plots, allowing estimation of soil moisture use (percent by volume or centimeters) attributable to the maximum occurring densities of each species as well as evaporation from bare control plots. The regression intercept estimated moisture reduction on bare plots. Loss of soil moisture is indicated by a positive number; gain of soil moisture in lower soil horizons due to redistribution is indicated by a negative number.

Squirreltail failed to appear during both years of the study at the ST site, while medusahead growth and reproduction were strong. This may have been due to the harshness of the site which was not apparent during site selection. Considerable frost heaving was apparent in winter, followed by crusting of the soil surface as drying occurred. Although medusahead growth was strong, it appeared to concentrate in small depressions and cracks. Cheatgrass from the soil seed bank germinated and grew strongly within ST plots, but not outside the plots where the soil had not been disturbed by site preparation.

Vegetation Measurements

The measurement of competition requires a measurement of plant growth, such as total biomass, plant size, or seed output. A single harvest of each species at the end of the season gives a good measurement of the outcome of competition. Frequent measurements during the growing season can help define the mechanism of the competition through differential growth rates (Radosevich and Holt 1984).

All plant measurement and collection were done in only the central square meter of each plot. This reduced data collection to a manageable level and provided an additional buffer against influences from outside the plots.

Periodic measurements of plant height, leaf number, and density were made in each plot during the growing season. Actual harvest of individual plants from the extra plots allowed development of regression equations for estimating biomass within the experimental plots based upon nondestructive measurements.

The outcome of competition was analyzed by clipping all end-of-season vegetative growth at ground level on two blocks at each site, storing in labeled paper bags, drying at 70° C for 48 hours, and weighing. All seed was harvested, stored in paper bags, and air-dried. Seeds were counted, weighed, and tested for viability.

About 20% of the medusahead seedheads in the VT site were clipped off, apparently by grasshoppers, just before harvesting. Many clipped seedheads were on the ground in the plots, but could not be positively identified as coming from any given plot. In order to salvage the situation, culms from which seedheads had apparently been removed were counted and assigned the average number of seeds per head counted in remaining seedheads in each plot.

Soil Moisture Measurements

Volumetric soil moisture content was measured using a frequency domain reflectometer at depths of 15, 30, 45, and 60 cm on all plots. Measurements were done concurrently with plant measurements. Units of measurement are percent water per volume of dry soil, which are numerically the same as centimeters of water. The reflectometer was calibrated at each depth and site by taking gravimetric soil samples and bulk density measurements.

Climatic Measurements

Instruments and data recorders at each site provided measurements of air temperature, precipitation, and soil temperature at 15 and 30 cm depth. Measurements were stopped or interrupted by the theft of equipment from the ST site and battery leakage at the VT site.

RESULTS AND DISCUSSION

Site Differences

Squirreltail failed to emerge on the ST site in 1994 and 1995. This site consistently had slightly higher soil temperatures than the VT site. Soil moisture on the ST site was less than on VT at 15 cm, but greater at 30 and 45 cm. The most striking difference between the two sites was the nature of the soil surface. The ST site showed evidence of frost heaving during cold temperatures and developed a hard crust upon drying, while the VT surface soil remained soft and loose under all conditions.

Because this study is concerned with competition between the two species, all data and conclusions presented will deal with the VT site.

Squirreltail Seed Dormancy

Sample lots of all seeds were tested for germination and viability in the OSU Seed Laboratory before planting. Squirreltail seed showed 82% germination and 11% dormant for a total of 93% viability before planting. Due to the low emergence rate of squirreltail on the VT site in 1994, seeds were sifted from soil taken from buffer areas within plots in late summer and submitted for retesting. No attempt was made to estimate seed density in the soil bank, but squirreltail seeds were easy to find and abundant. A tetrazolium test indicated that the retrieved seeds were 84% normal, 6% abnormal (probably dying), and 10% dead for a total of 84% viability at the end of summer.

Growing Season Development

Climatic conditions contrasted sharply between the two years of the study (Table 1). Precipitation in 1994 was lower and earlier than in 1995; soil warmup was also earlier in 1994. Although distinguishing between grass seedlings is very difficult, both species appeared to be present on the VT site inspection in early January 1994. Presence of seedlings of either species was not detectable in 1995 until the middle of May.

A difference between the ratio of surviving plants:seeds planted was apparent between the two years. Medusahead survival was much better with the fall germination of the 1993-1994 growing season than with the spring germination of the 1994-1995 season. Surviving squirreltail plants:seeds planted was better in the wetter 1994-1995 season, even with the late germination time. The 1994 growing season produced noticeable growth in both species by April 15, about a month ahead of the 1995 season. Maximum plant size, however, was considerably lower in 1994 than in 1995 (Figures 1 and 2). Squirreltail growth after medusahead harvest continued well into July during the wet 1995 year, but showed no increase in the summer of 1994.

Competition Effects

Intraspecific competition had more effect than interspecific competition on dry vegetative weight and seed production of individual medusahead plants in 1994 (Table 2; Figures 1 and 3). The effect of maximum medusahead density (700/m^2) on mean dry weight of an individual medusahead plant was to reduce the weight by 0.245 g compared with an individual medusahead plant without competition. This is biologically significant in that mean dry weight was 0.20 g and maximum dry weight was 0.48 g. Squirreltail at

Table 1. Precipitation and Temperature Data, VT Site.

	3/31	4/30	5/24	6/11	6/27	7/14	8/1
1994							
Precipitation[1]	147	163	197	202	206	207	209
Air Temp.(C)							
Average	8	9	15	24	23	27	27
Max.	17	27	29	40	38	38	39
Min.	-1	-5	5	10	8	11	15
Average Soil Temp.(C)							
15 cm	-	11	malfunction			29	30
30 cm	-	12	malfunction			29	30
1995							
Precipitation[1]	175	199	238	252	268	270	284
Air Temp.(C)							
Average	7	7	12	12	26	23	27
Max.	18	17	20	22	38	36	38
Min.	-1	-1	1	7	13	11	17
Average Soil Temp.(C)							
15 cm	7	8	12	15	21	23	24
30 cm	7	8	12	15	21	22	23

[1]Cumulative precipitation in millimeters.

Figure 1. Medusahead Weight per Plant (VT Site)

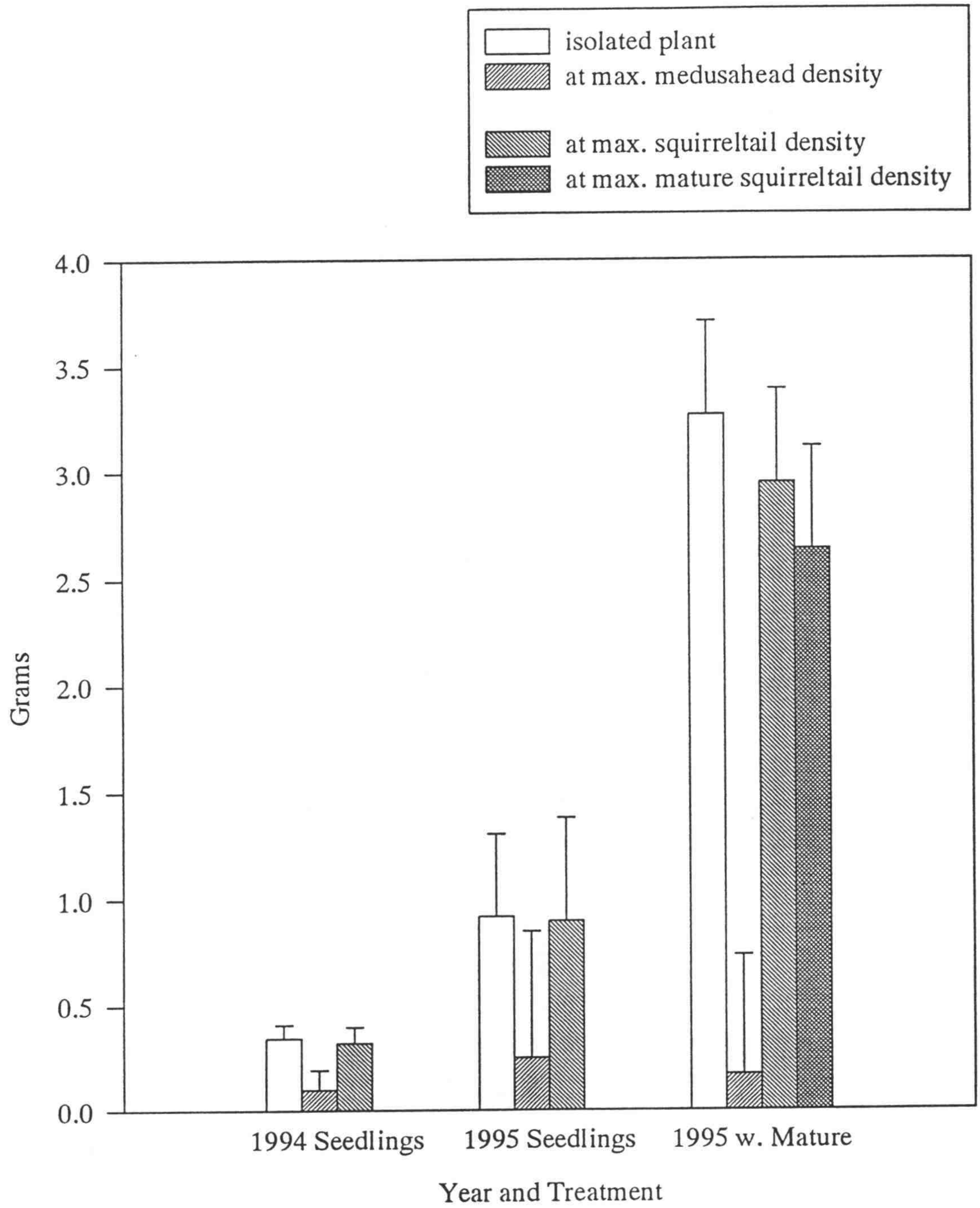


Figure 2. Seedling Squirreltail Weight per Plant (VT Site)

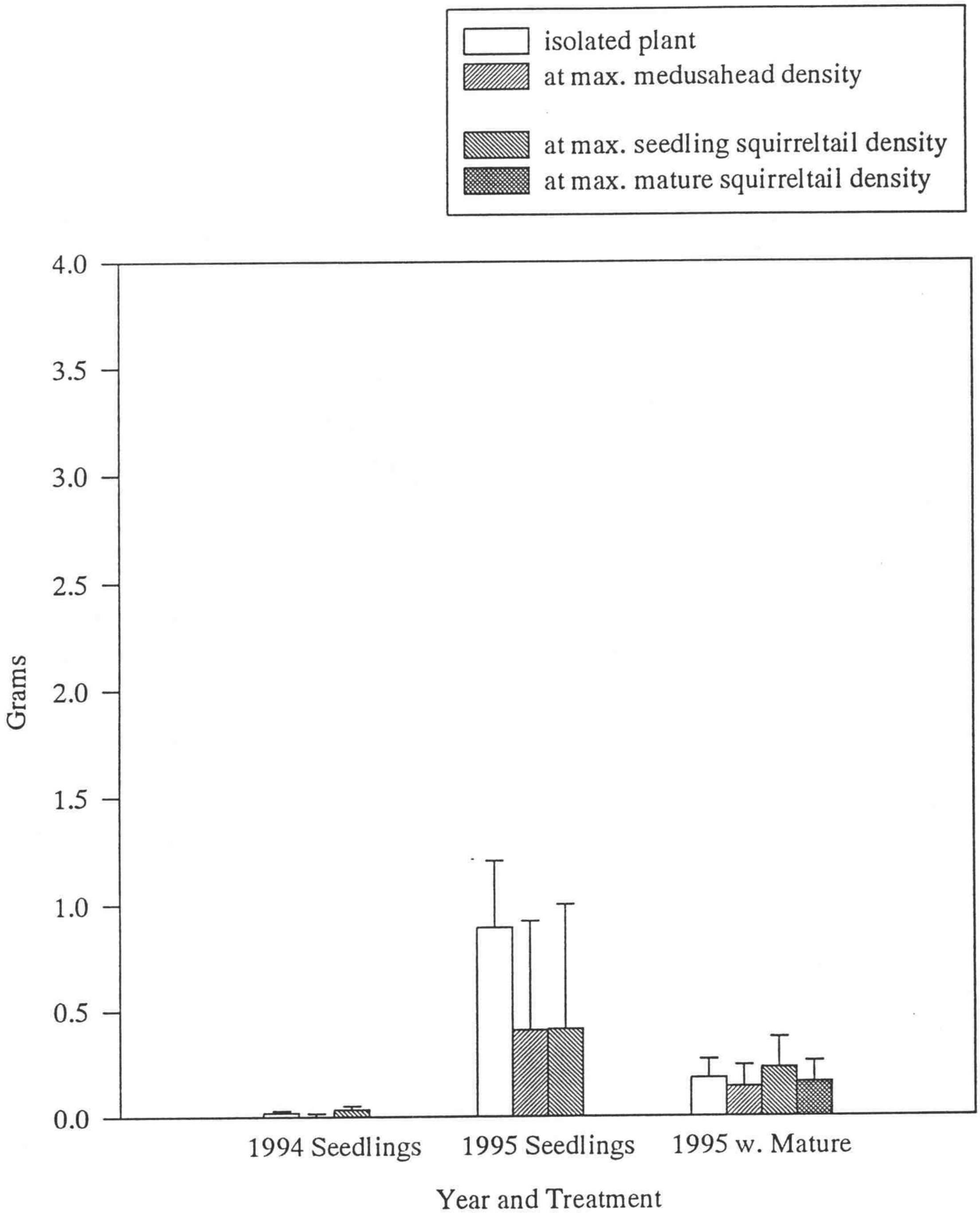
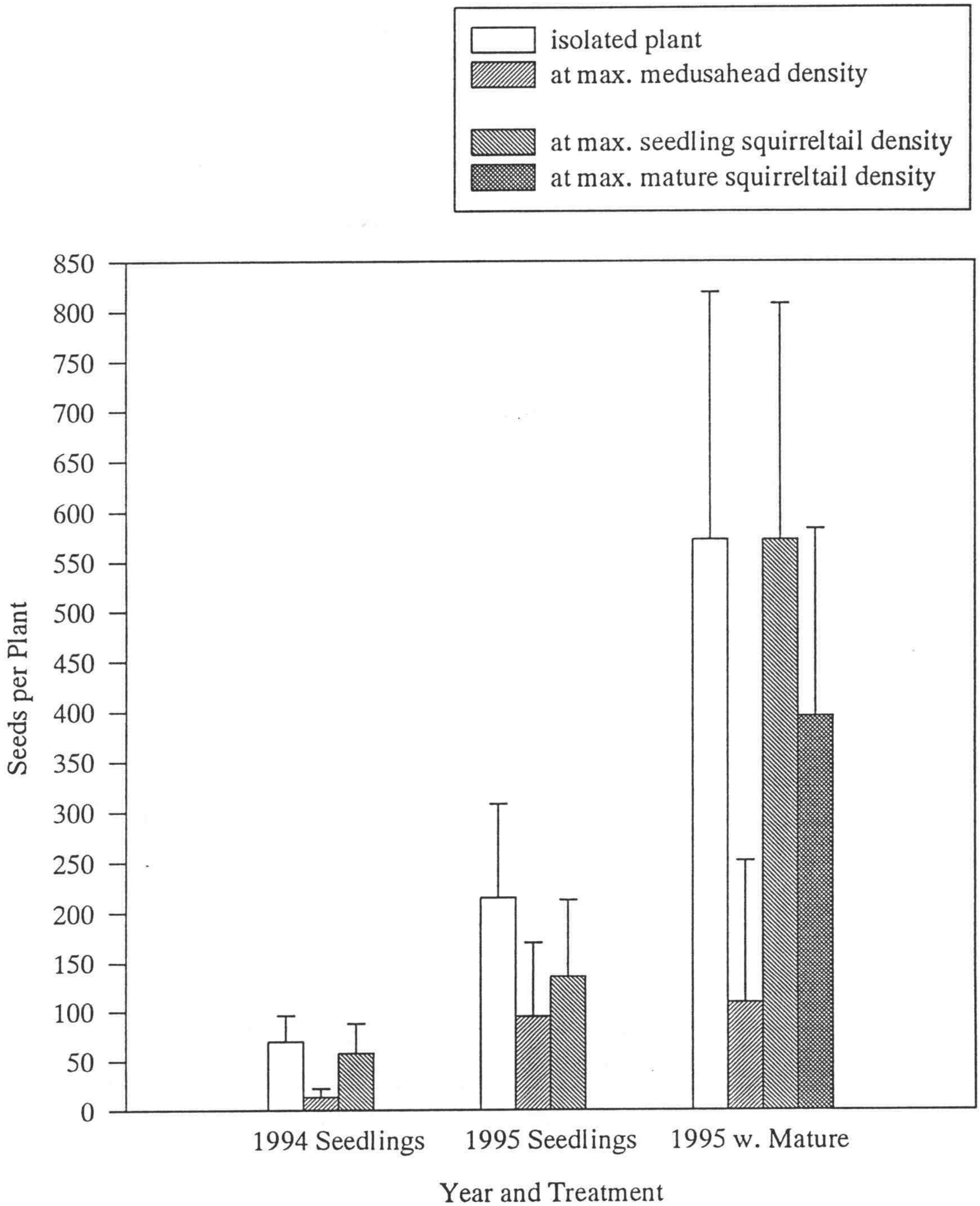


Table 2. Competitive effects on medusahead weight per plant due to treatments, with confidence intervals (VT Site).

Year and Treat-ment	Weight of Isolated Medusahead	Inde-pendent Variable	p	Range of x[1]	Point Est.[2]	Lower 95%	Upper 95%
1994 Seedlings Only	0.345	Medusahead Density	.0001	700	-0.245	-0.34	-0.154
		Squirreltail Density	.543	107	-0.024	-0.10	0.053
1995 Seedlings Only	0.921	Medusahead Density	.034	283	-0.669	-1.29	-0.05
		Squirreltail Density	.931	227	-0.021	-0.50	0.46
1995 Seedlings & Mature	3.271	Medusahead Density	.00001	201	-3.010	-3.68	-2.52
		Squirreltail Seedling Density	.147	52	-0.317	-0.75	0.12
		Squirreltail Mature Density	.011	5	-0.629	-1.11	-0.15

[1]Maximum density of independent variable.
[2]Difference in weight (g) between isolated medusahead plant and mean weight at maximum density of independent variable.

Figure 3. Medusahead Seeds per Plant (VT Site)



maximum density ($107/m^2$) reduced mean individual medusahead dry weight by 0.01 g, a statistically insignificant effect.

Medusahead seed production at maximum medusahead density was 20% that of a medusahead plant with no medusahead competition. Medusahead seed production at maximum squirreltail density was 83% that of a medusahead plant with no squirreltail competition; again, this result was statistically insignificant (Table 3; Figure 3).

Squirreltail vegetative weight was reduced at maximum medusahead density by 0.02 g from estimated weight of an isolated plant. Maximum squirreltail density increased squirreltail weight by 0.01 g (Table 4; Figure 2). This result is both statistically and biologically significant. Most plots that contained low numbers of squirreltail were also plots that had high medusahead density that suppressed individual squirreltail weight. Where medusahead density was lower, squirreltail plants survived in greater numbers and grew larger. Only two squirreltail seeds were produced among all the plots in 1994.

Squirreltail seedlings exerted more influence on the outcome of competition in 1995, although still not as strongly as medusahead. Maximum medusahead density reduced mean medusahead dry weight per plant by 0.67 g compared to the mean medusahead plant with no medusahead competition. Squirreltail effect on medusahead weight was biologically and statistically insignificant at 0.02 g reduction (Table 2; Figure 1). Squirreltail had a significant effect on medusahead seed production, reducing it to 63% of the level of an isolated medusahead plant. Maximum medusahead density reduced medusahead seed production per plant to 44% that of production at no intraspecific competition (Table 3; Figure 3).

Table 3. Competitive effects on medusahead seed production per plant due to treatments, with confidence intervals (VT Site).

Year and Treatment	Seed Prod. of Isolated Medusahead	Independent Variable	p	Range of x[1]	Point Est.[2]	Lower 95%	Upper 95%
1994 Seedlings Only	70	Medusahead Density	.0001	700	0.20	0.12	0.32
		Squirreltail Density	.373	107	0.83	0.56	1.25
1995 Seedlings Only	215	Medusahead Density	.007	283	0.44	0.24	0.79
		Squirreltail Density	.048	227	0.63	0.40	0.99
1995 Seedlings & Mature		Medusahead Density	.00001	201	0.19	0.08	0.44
	572	Squirreltail Seedling Density	.997	52	1.00	0.70	1.43
		Squirreltail Mature Density	.059	5	0.69	0.46	1.02

[1]Maximum density of independent variable.
[2]Percent of an isolated medusahead plant's seed production produced by a medusahead plant at maximum density of independent variable.

Table 4. Competitive effects on squirreltail seedling weight per plant due to treatments, with confidence intervals (VT Site).

Year and Treatment	Weight of Isolated Squirreltail	Independent Variable	p	Range of x[1]	Point Est.[2]	Lower 95%	Upper 95%
1994 Seedlings Only	0.020	Medusahead Density	.004	700	-0.023	-0.04	-0.005
		Squirreltail Density	.042	107	0.014	0.002	0.03
1995 Seedlings Only	0.894	Medusahead Density	.065	283	-0.488	-1.01	0.03
		Squirreltail Density	.097	227	-0.483	-1.06	0.10
1995 Seedlings & Mature		Medusahead Density	.350	201	no		
	0.1815	Squirreltail Seedling Density	.470	52	significant		
		Squirreltail Mature Density	.727	5	effects		

[1]Maximum density of independent variable.
[2]Difference in weight (g) between isolated squirreltail plant and mean weight at maximum density of independent variable.

Maximum medusahead density reduced mean squirreltail dry weight by 0.49 g, comparable to squirreltail's effect on itself of a 0.48 g reduction (Table 4; Figure 2). Maximum medusahead density reduced squirreltail seed number per plant to 11% of that without interspecific competition; maximum squirreltail density reduced squirreltail seed production per plant to 63% of maximum (Table 5; Figure 4).

Competitive effects in plots that contained mature squirreltail, seedling squirreltail, and seedling medusahead were more complicated and harder to differentiate due to smaller sample sizes (not all plots in these blocks actually contained mature squirreltail).

Maximum medusahead density reduced mean medusahead weight per plant by 2.52 g. Mature squirreltail reduced medusahead by 0.63 g, while squirreltail seedlings had an insignificant effect on medusahead dry weight (Table 2; Figure 1). Medusahead seed production per plant was reduced to 19% that of an isolated plant by maximum intraspecific competition. Mature squirreltail had the effect of reducing medusahead seed production to 69% of that without competition from mature squirreltail. Again, no significant effects due to squirreltail seedlings were detectable (Table 3; Figure 3).

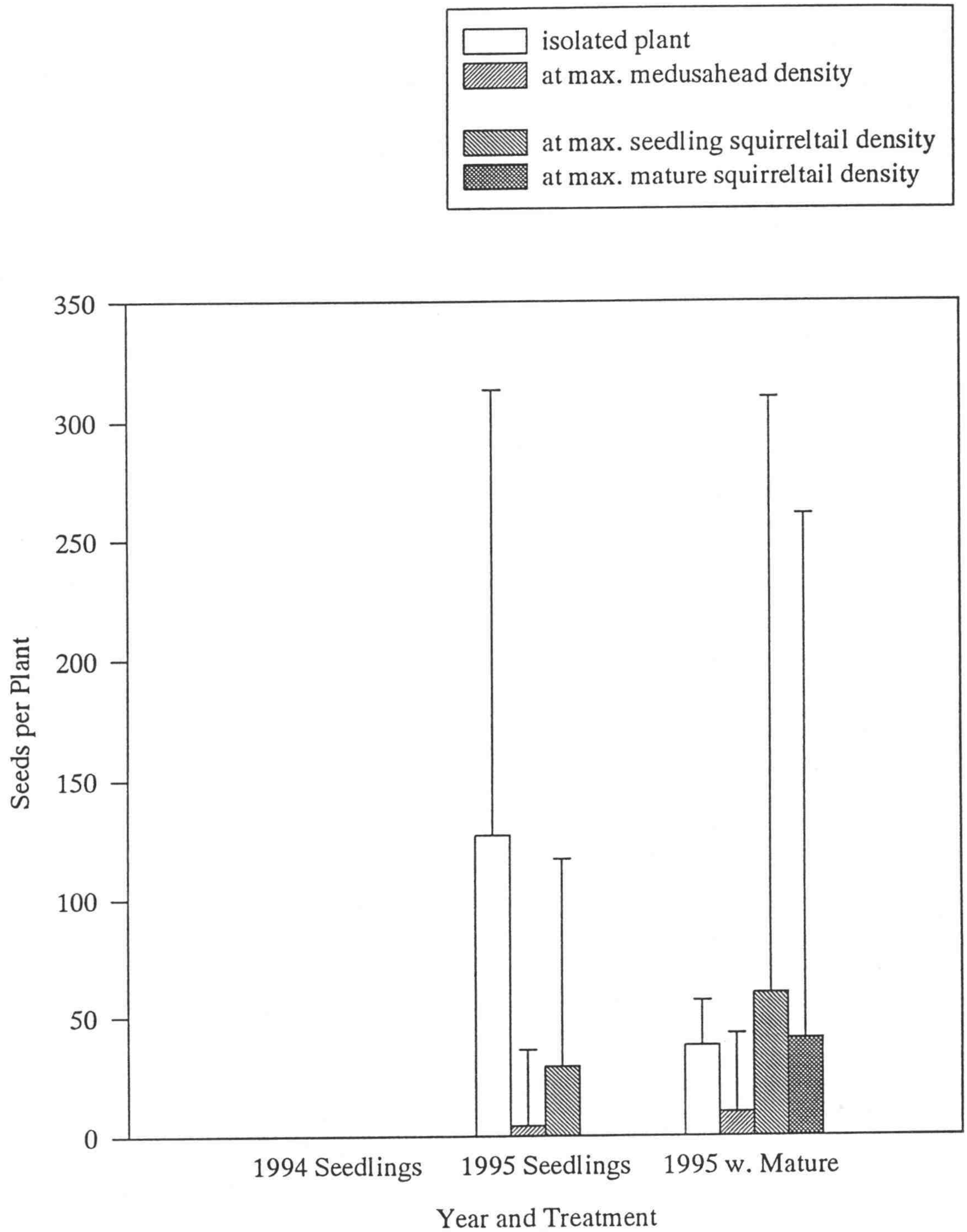
No significant effects upon squirreltail seedling dry vegetative weight per plant or seeds per plant were apparent. No significant effects on mature squirreltail dry weight or seed production could be detected (Tables 4 and 5).

Table 5. Competitive effects on seedling squirreltail seed production per plant due to treatments, with confidence intervals (VT Site).

Year and Treatment	Seed Prod. of Isolated Squirreltail	Independent Variable	p	Range of x[1]	Point Est.[2]	Lower 95%	Upper 95%
1994 Seedlings Only	0	Medusahead Density					
		Squirreltail Density					
1995 Seedlings Only	127	Medusahead Density	.001	283	0.11	0.04	0.36
		Squirreltail Density	.037	227	0.23	0.06	0.92
1995 Seedlings & Mature	38	Medusahead Density	.166	201	no		
		Squirreltail Seedling Density	.737	52	significant		
		Squirreltail Mature Density	.933	5	effects		

[1]Maximum density of independent variable.
[2]Percent of an isolated medusahead plant's seed production produced by a medusahead plant at maximum density of independent variable.

Figure 4. Seedling Squirreltail Seeds per Plant (VT Site)



Soil Moisture Effects

During the drought year of 1994, squirreltail seedling numbers at maximum density had a significant effect only at a depth of 15 cm, reducing volumetric soil moisture by 6.4 cm, compared to an evaporative/redistributive loss of 13.3 cm measured in control plots containing no plants. Squirreltail had no significant effects on soil moisture at greater depths.

Medusahead had significant effects at all depths. At 15 cm depth, medusahead reduced soil moisture by 2.1 cm compared to the 13.3 cm reduction in control plots. At 30 cm depth, medusahead reduced soil moisture by 3.8 cm compared to a gain due to evaporation/redistribution of 0.2 cm in control plots; at 45 cm depth, a reduction of 2.1 cm compared to a gain of 2.1 cm in control plots; and at 60 cm depth, a reduction of 1.7 cm compared to a gain of 3.4 cm in control plots (Table 6; Figure 5).

In the wetter year of 1995, medusahead and squirreltail seedlings both had significant effects at 15 cm. Medusahead reduced soil moisture by 12.6 cm and squirreltail reduced moisture by 6.2 cm compared to an 8.8 cm loss from control plots. At 30 cm depth, medusahead caused a greater reduction than squirreltail, while neither species had any significant effect at greater depths (Table 6; Figure 6).

In 1995 plots that contained mature squirreltail plants, strong medusahead effects on soil moisture were observed at 15 cm and 30 cm depth. Squirreltail seedlings possibly had an effect at 30 cm depth, and showed strong effects at 45 and 60 cm. Mature squirreltail caused a 3.4 cm reduction in soil moisture at 60 cm depth ($p=.10$); this was the only discernible effect of mature squirreltail on soil moisture (Table 6; Figure 7).

Table 6. Soil moisture use (cm) due to evaporation/redistribution from bare soil (control) and transpiration attributable to medusahead, seedling squirreltail, and mature squirreltail. VT Site only. Positive numbers indicate use or loss of moisture from that soil depth; negative numbers indicate gain of moisture due to redistribution.

	1994 Seedlings Only			1995 Seedlings Only			1995 Seedlings and Mature			
Depth	Con-trol	Med-usa head	Squirrel tail	Con-trol	Med-usa head	Squirrel tail	Con-trol	Med-usa head	Sdl. Sq.-tail	Mat. Sq.-tail
15 cm	13.3	2.1	6.4	8.8	12.6	6.2	15.4	8.8	-1.7*	1.0*
30 cm	-0.2	3.8	1.7*	4.7	10.5	3.8	15.3	6.2	4.6	2.4*
45 cm	-2.1	2.1	0.3*	-0.1	1.8*	0.1*	9.7	1.5*	15.6	-0.2*
60 cm	-3.4	1.7	0.2*	-3.5	0.8*	1.4*	0.3	2.5*	10.3	3.4

*Two-sided p-value>0.25. Figures without asterisk have p-values<0.10.

Figure 5. 1994 Soil Moisture Use (VT Site)
Effects not significantly different from 0 are omitted.
Negative use indicates soil moisture increase.

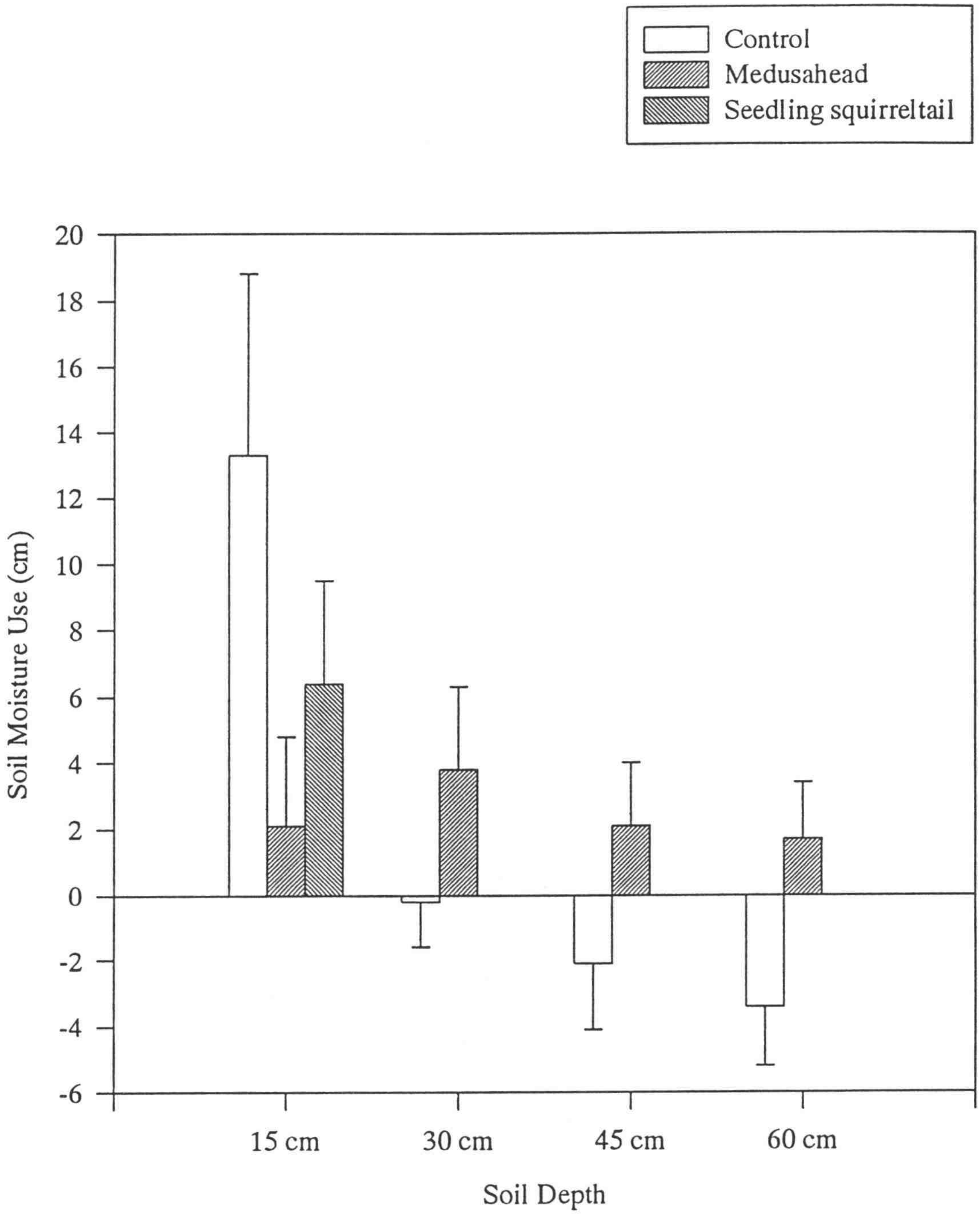


Figure 6. 1995 Soil Moisture Use--Seedlings Only (VT Site)
Effects not significantly different from 0 are omitted.
Negative use indicates soil moisture increase.

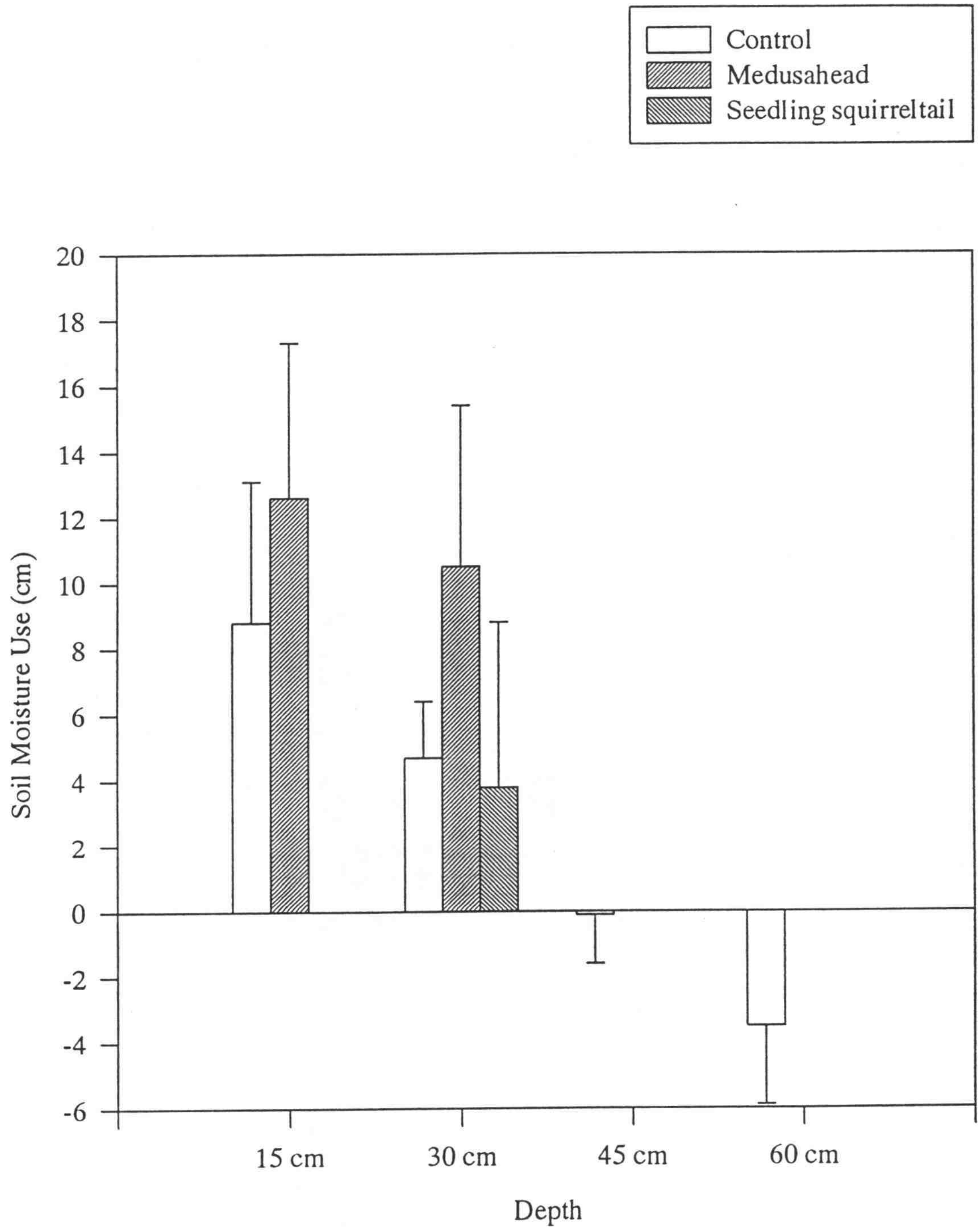
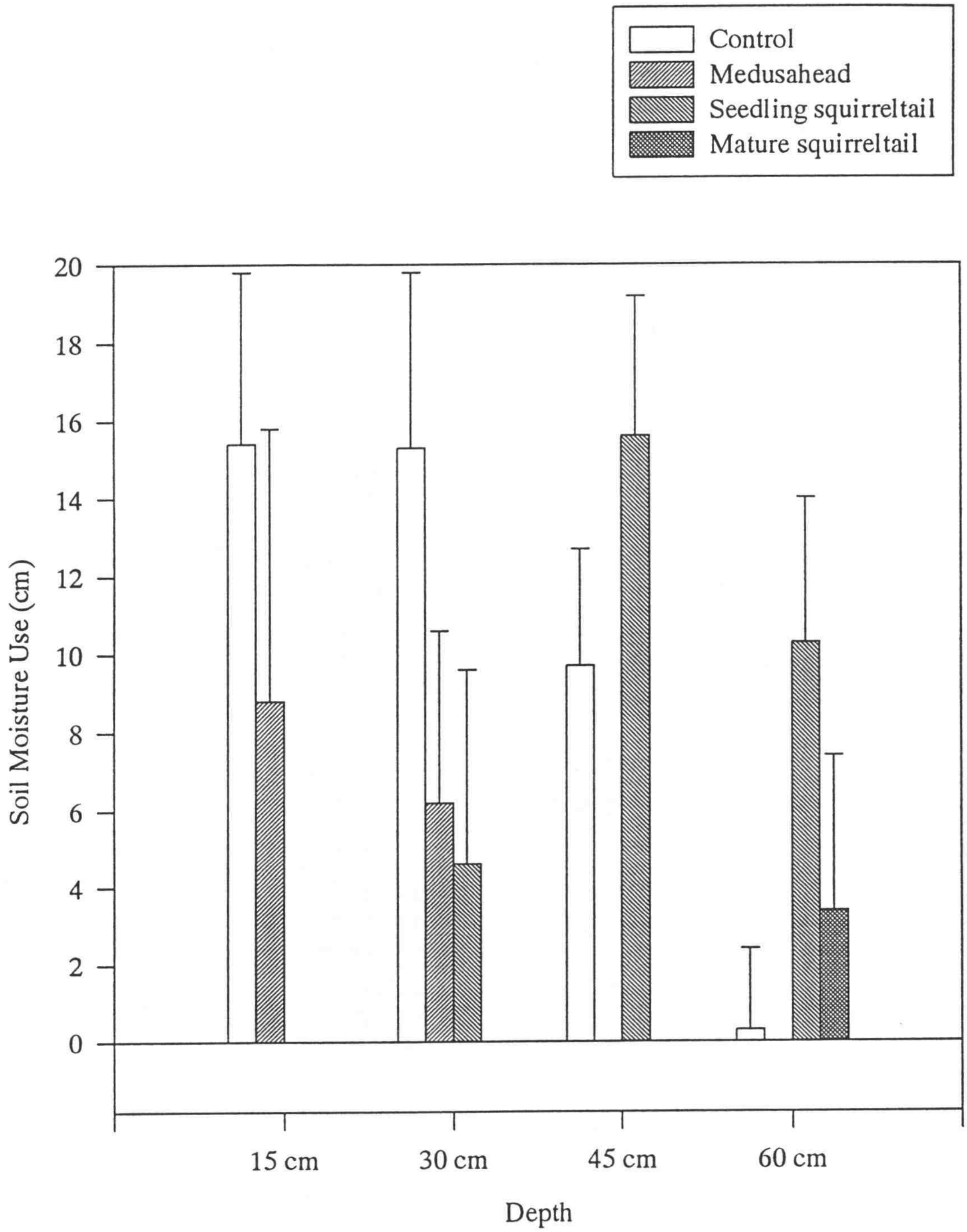


Figure 7. 1995 Soil Moisture Use--Seedlings and Mature (VT Site)
Effects not significantly different from 0 are omitted.
Negative use indicates soil moisture increase.



CONCLUSIONS

Medusahead demonstrated strong competitive abilities, growing and reproducing successfully under a variety of germination times, climatic conditions, and levels of squirreltail competition. Intraspecific competition was the most important factor determining medusahead weight and seed production per plant. The effects of seedling and mature squirreltail on these factors were significant, but did not greatly reduce medusahead seed production per square meter. Squirreltail seedling survival and reproduction were strongly inhibited by medusahead.

Squirreltail does have the possibility of being an effective species for seeding into medusahead stands. The high survivability of squirreltail seeds in a drought year suggests that a seed bank could be accumulated until conditions favor seedling survival and development to maturity. This would at least allow for coexistence of the two species in a stand. More encouraging is the pattern of soil moisture use by the two species. Medusahead depended on deep soil moisture during a drought year. Established squirreltail plants utilized moisture from these same soil depths, suggesting that a population of squirreltail established in wetter years may have strong negative effects on medusahead survival and growth when the inevitable dry years recur. This could result in reducing the density of medusahead, opening up sites for further establishment by other species and reducing fire intensities that can damage perennial grasses.

Based on density-dependent results, suppressing medusahead during the year of squirreltail seeding should help squirreltail establishment, especially if climatic conditions are favorable.

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APPENDIX

Table 1. Multiple regression analysis[1] for the prediction of individual seedling squirreltail plant dry weight (g).[2]

Year and Treatment	B_{SO}	B_{SS}	B_{SM}	B_{SS}/B_{SM}	R^2
1994					
Seedlings	0.020	0.007	-0.008		0.36
	(0.004)	(0.003)	(0.003)		
1995					
Seedlings	0.894	-0.205	-0.199	1.03	0.17
	(0.173)	(0.120)	(0.104)		
1995 Mature and Seedlings	No Significant Variables				

[1] $W_S = B_{SO} + B_{SS} \log N_S + B_{SM} \log N_M$

[2] The intercept B_{SO} estimated the shoot weight of an isolated squirreltail plant. N_S and N_M indicate the number of squirreltail and medusahead seedlings, respectively. Intraspecific interference for squirreltail is measured by the regression coefficient B_{SS} and interspecific interference by B_{SM}. The effect of squirreltail on itself compared to the effect of medusahead on squirreltail is estimated in the ratio B_{SS}/B_{SM}. Numbers in parentheses are standard errors for coefficients. Data points with value of 0 were omitted.

Table 2. Multiple regression analysis[1] for the prediction of individual medusahead plant dry weight (g).[2]

Year and Treatment	B_{MO}	B_{MM}	B_{MS}	B_{MM}/B_{MS}	B_{MMAT}	B_{MM}/B_{MMAT}	R^2
1994							
Seedlings	0.345	-0.086	-0.012	7.17			0.33
	(0.031)	(0.016)	(0.019)				
1995							
Seedlings	0.921	-0.273	-0.009	30.33			0.09
	(0.184)	(0.123)	(0.099)				
1995 Mature							
and Seedlings	3.272	-1.346	-0.185	7.28	-0.901	1.49	0.75
	(0.216)	(0.125)	(0.125)		(0.339)		

[1] $W_M = B_{MO} + B_{MM} \log N_M + B_{MS} \log N_S + B_{SMAT} \log N_{MAT}$

[2]The intercept B_{MO} estimated the shoot weight of an isolated medusahead plant. N_S, N_{MAT}, and N_M indicate the number of squirreltail seedlings, mature squirreltail, and medusahead seedlings, respectively. Intraspecific interference for medusahead is measured by the regression coefficient B_{MM} and interspecific interference by B_{MS} and B_{SMAT}. The effect of medusahead on itself compared to the effect of seedling squirreltail on medusahead is estimated in the ratio B_{MM}/B_{MS}. The effect of medusahead on itself compared to the effect of mature squirreltail on medusahead is estimated in the ratio B_{MM}/B_{MMAT}. Numbers in parentheses are standard errors for coefficients. Data points with value of 0 were omitted.

Table 3. Multiple regression analysis[1] for the prediction of individual seedling squirreltail seed production ($\log_{10}$ number of seeds).[2]

Year and Treatment	B_{SO}	B_{SS}	B_{SM}	B_{SS}/B_{SM}	R^2
1994					
Seedlings	No seed production in 1994				
1995					
Seedlings	2.105 (0.189)	-0.271 (0.124)	-0.384 (0.099)	0.706	0.42
1995 Mature and Seedlings	No Significant Variables				

[1] $W_S = B_{SO} + B_{SS} \log N_S + B_{SM} \log N_M$

[2]The intercept B_{SO} estimated the seed production of an isolated squirreltail plant. Intraspecific interference for squirreltail is measured by the regression coefficient B_{SS} and interspecific interference by B_{SM}. The effect of squirreltail on itself compared to the effect of medusahead on squirreltail is estimated in the ratio B_{SS}/B_{SM}. N_S and N_M indicate the number of squirreltail and medusahead seedlings, respectively. Numbers in parentheses are standard errors for coefficients. Data points with value of 0 were omitted.

Table 4. Multiple regression analysis[1] for the prediction of individual medusahead seed production (log_{10} number of seeds).[2]

Year and Treatment	B_{MO}	B_{MM}	B_{MS}	B_{MM}/B_{MS}	B_{MMAT}	B_{MM}/B_{MMAT}	R^2
1994							
Seedlings	1.842	-0.246	-0.039	6.31			0.44
	(0.070)	(0.036)	(0.043)				
1995							
Seedlings	2.332	-0.146	-0.085	1.72			0.30
	(0.076)	(0.051)	(0.041)				
1995 Mature							
and Seedlings	2.757	-0.309			-0.234	1.32	0.54
	(0.077)	(0.044)			(0.120)		

[1] $W_M = B_{MO} + B_{MM} \log N_M + B_{MS} \log N_S + B_{SMAT} \log N_{MAT}$

[2] The intercept B_{MO} estimated the seed production of an isolated medusahead plant. Intraspecific interference for medusahead is measured by the regression coefficient B_{MM} and interspecific interference by B_{MS} and B_{SMAT}. The effect of medusahead on itself compared to the effect of seedling squirreltail on medusahead is estimated in the ratio B_{MM}/B_{MS}. The effect of medusahead on itself compared to the effect of mature squirreltail on medusahead is estimated in the ratio B_{MM}/B_{MMAT}. N_S, N_{MAT}, and N_M indicate the number of squirreltail seedlings, mature squirreltail, and medusahead seedlings, respectively. Numbers in parentheses are standard errors for coefficients. Data points with value of 0 were omitted.