Medusahead (*Taeniatherum caput-medusae*) Outperforms Squirreltail (*Elymus elymoides*) through Interference and Growth Rate

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Understanding the ecological processes that foster invasion and dominance by medusahead is central to its management. The objectives of this study were (1) to quantify and compare interference between medusahead and squirreltail under different concentrations of soil nitrogen (N) and phosphorous (P) and (2) to compare growth rates of medusahead and squirreltail under field soil N and P availabilities. We grew medusahead and squirreltail in an addition series in a greenhouse and applied one of four nutrient treatments weekly: (1) low N low P (no N or P added), (2) low N high P (added 250 ml of 600 µM P solution in the form of calcium phosphate), (3) high N low P (added 250 ml of 8,400 µM N solution in the forms of calcium nitrate and potassium nitrate), and (4) high N high P (added solutions as listed above for high N and high P). After 70 d density and biomass by species were sampled. We also grew individual medusahead and squirreltail plants in control soil conditions. Biomass, leaf area, and root length were determined for each species at 14-d intervals over 72 d. Regression models for medusahead and squirreltail suggested N appeared to be playing a much larger role than P in interference between the species. The high N treatment did not increase medusahead's interference ability relative to squirreltail as we had hypothesized. Medusahead typically imposed a two-to-seven-times stronger influence on interference relationships than squirreltail. Medusahead accumulated biomass, leaf area, and root length twice as fast as squirreltail. Results from our study suggest that medusahead seedlings will likely dominate over squirreltail seedlings. To restore squirreltail to medusahead-infested rangeland, medusahead densities should be reduced with integrated weed management strategies. On medusahead-free rangeland, prevention and early detection and eradication programs are critical.

Nomenclature: Medusahead, *Taeniatherum caput-medusae* (L.) Nevski ELYCM; squirreltail, *Elymus elymoides* (Rafin.) Swezey SITHY.

Key words: Competition, interference, invasive plants, revegetation, weed management.

Medusahead is a nonindigenous, invasive winter-annual grass that threatens rangeland systems in the intermountain West. Medusahead was first identified in 1884 near Roseberg, OR, and its distribution quickly increased throughout the 20th century to central and eastern Oregon, Washington, Idaho, California, Nevada, and Utah (Miller et al. 1999; Whisenant 1990). Medusahead is estimated to occupy 2 million hectares in the Great Basin (Miller et al. 1999), where it displaces native vegetation and forms exclusive stands. It may disrupt nutrient, water, and fire cycles (Miller et al. 1999) and is almost worthless forage for

livestock (Turner 1965). When present, medusahead may reduce forage production up to 80% (Hironaka 1961).

Medusahead has several attributes that may enable its invasion and dominance. It forms dense stands that produce copious amounts of seed (Sharp et al. 1957). Medusahead germinates in the fall and grows rapidly in the spring. Its litter decomposes slowly because of its high silica content, thereby accumulating and forming a physical barrier to the establishment of other species (Bovey et al. 1961; Harris 1965). However, medusahead seeds can germinate within its litter layer and seedlings can develop a new root if the initial root becomes desiccated (Young 1992).

Rangeland dominated by medusahead is often devoid of competitive desirable plants. In such cases, introducing and establishing competitive plants is essential for successful management of infestations and the restoration of desirable plant communities (Borman et al. 1991; Larson and McInnis 1989; Mangold et al. 2007). Squirreltail has been identified as a potential species for restoration of medusa-

Interpretive Summary

Understanding the mechanisms and processes that foster invasion and dominance by medusahead is central to its management. We simultaneously conducted two studies that evaluated the effects of nitrogen and phosphorus on interference between medusahead and squirreltail and compared growth rates of the two species. We grew medusahead and squirreltail in growth tubes in various combinations of density. We applied one of four nutrient treatments to each growth tube. Additionally, we grew individual medusahead and squirreltail plants and measured their growth over a 72-d period. We found that medusahead typically imposed a two-to-seven-times stronger influence than squirreltail on plant–plant interactions. Medusahead accumulated biomass, leaf area, and root length twice as fast as squirreltail. Our data suggest medusahead outperformed squirreltail in all aspects of interference and growth rate. We believe that medusahead may be outperforming squirreltail by growing faster and therefore increasingly gaining access to resources. The results from our study suggest that squirreltail cannot effectively compete with medusahead. To restore squirreltail to medusahead-infested rangeland, medusahead densities should be reduced with integrated weed management strategies. On medusahead-free rangeland, prevention and early detection and eradication programs are critical.

head-infested range and wild land (Jones 1998) and has been observed to establish in medusahead stands over time (Hironaka and Sindelar 1973; Hironaka and Tisdale 1963; Young 1992). An early to midseral native bunchgrass common to western rangeland, it germinates across a range of soil temperatures and its cool season root growth may help explain its ability to compete with annual grasses (Hironaka and Tisdale 1972; Young and Evans 1977). A variety of other attributes may help squirreltail compete with medusahead, including self-pollination, wide ecotypic variation, and efficient seed dispersal mechanisms (Arredondo et al. 1998; Jensen et al. 1990; Jones 1998).

We conducted an addition-series study that evaluated the effects of N and P additions on the interference between medusahead and squirreltail. Another study compared growth rates of the two species. The overall objectives were (1) to quantify and compare interference between medusahead and squirreltail under different concentrations of soil N and P and (2) to compare growth rates of medusahead and squirreltail under soil N and P availabilities found in field soil collected locally. We hypothesized that (1) N and P additions would increase medusahead's interference ability relative to the native grass in the interference study and (2) medusahead would display higher growth rates and biomass accumulation than squirreltail.

Materials and Methods

The two studies were simultaneously conducted in a greenhouse at the Eastern Oregon Agricultural Research Center in Burns, OR, from May to August 2005. Average daily temperature in the greenhouse during the studies was 22.0 C (71.6 F). In the summer of 2003, medusahead seed was collected locally by hand and stored in a cool, dry location. The following summer seed was cleaned and partially deawned with a rubbing board and Ferrell-Ross seed cleaner.[1] Squirreltail seed[2] was purchased in spring 2004. Germination tests in June 2004 yielded 66% squirreltail germination and 87% medusahead germination. Later germination tests conducted prior to planting in March 2005 yielded 70% squirreltail germination and 99% medusahead germination. Seeding densities were increased to account for the lower percentage of germination.

Polyvinyl chloride (PVC) pipe (15 cm diam) was used to construct growth tubes 0.5 m deep for the interference study and 1.0 m deep for the growth analysis study. Weed barrier fabric secured with tape and/or perforated PVC end caps covered the bottoms of the tubes. Soil that had supported squirreltail and medusahead was collected from two sites near John Day, OR, and sieved through a 0.6-cm screen to remove rocks and large roots. Soil was mixed with concrete-grade sand in a 1 : 1 ratio by volume and placed in the growth tubes. Potting medium was saturated prior to planting with approximately 2.3 L of tap water. Growth tubes were allowed to drain to column capacity, then seeds of both species were uniformly scattered across the surface of each, depending on the experiment, and covered with approximately 2 mm of field soil.

Interference Study. Medusahead and squirreltail were planted into the prepared growth tubes in an addition-series design (Spitters 1983). Five density levels of medusahead (0, 1, 5, 25, or 125 pure live seeds per pot) were fully mixed with the same five density levels for squirreltail for a total of 25 density combinations. Each grouping of the 25 density combinations received one of four nutrient treatments and was replicated three times in each of two separate trials. Growth tubes were arranged in a randomized block design. Each trial lasted approximately 70 d, with Trial 1 running May 26 through August 4, 2005, and Trial 2 running June 14 through August 23, 2005.

Nutrient treatments began immediately after planting. Growth tubes were covered with clear plastic for 6 to 7 d to maintain humidity conducive to germination. Each planting matrix received one of four nutrient treatments weekly: (1) low N low P was the control with no N or P added to the pots, (2) low N high P added 250 ml of a 600 µM P solution in the form of calcium phosphate, (3) high N low P treatment added 250 ml of an 8,400 µM N solution in the forms of calcium nitrate and potassium nitrate, and (4) high N high P treatment added 250 ml of an 8,400 µM N and 600 µM P solution in the forms of calcium nitrate, potassium nitrate, and potassium phos-

phate. The high N and P treatments were roughly equivalent to 60% strength modified Hoagland's solution. Essential macro- and micronutrients (K, Ca, Mg, S, Fe, Cl, Mn, Zn, Cu, B, and Mo) were applied in a 10 to 20% modified Hoagland solution along with N and P treatments to ensure that plant growth was not limited by nutrients other than N or P (Table 1). Growth tubes were misted twice daily as needed throughout the study to prevent water stress. Volunteer seedlings of undesired species were removed as necessary. After 70 d, density per growth tube of each species was counted and aboveground biomass clipped approximately 5 mm above the soil surface. Aboveground biomass was dried for 72 h at 50 C (122 F) and weighed.

Data were grouped by treatment for each trial and fit to multiple linear regression ($n = 75$, df $= 2$) (Spitters 1983). The inverse of medusahead and squirreltail individual aboveground biomass per plant was predicted using medusahead and squirreltail final densities per growth tube as independent variables. Models were of the following form:

$$y_m^{-1} = \beta_{m0} + \beta_{mm}N_m + \beta_{ms}N_s \text{ (medusahead)}$$

$$y_s^{-1} = \beta_{s0} + \beta_{ss}N_s + \beta_{sm}N_m \text{ (squirreltail)}$$

where y_m and y_s represented the average aboveground biomass per plant for medusahead and squirreltail, respectively. The regression coefficients β_{m0} and β_{s0} represented the maximum aboveground biomass for a medusahead and squirreltail plant grown in isolation, respectively. A smaller number indicates greater biomass due to the inverse operation. β_{mm} and β_{ss} represented the effect of species density upon its own biomass (intraspecific interference) from the medusahead and squirreltail models,

respectively. β_{ms} and β_{sm} represented the effect of the neighboring species' density on the mean biomass of the response species (interspecific interference). N_m and N_s represented the density per growth tube of medusahead and squirreltail, respectively.

Slopes from the regression models for each nutrient treatment were compared by calculating variance ratios using the following equation:

$$\text{Variance ratio}_i = VR_i =$$

$$[(RSS_i - RSS_1)/(df_i - df_1)]/(RSS_1/df_1)$$

where RSS_i is the pooled residual sum of squares, RSS_1 is the combined residual sums of squares of the treatments being compared, df_i is the pooled error degrees of freedom, and df_1 is the combined error degrees of freedom of the treatments being compared. A variance ratio larger than the critical $F_{(\alpha, dfnumerator, dfdenominator)}$ value ($\alpha = 0.05$) rejects the null hypothesis that the slopes of the regression lines are similar (Snedecor and Cochran 1980).

The relative interference ability for both species under each nutrient treatment was calculated by dividing the intraspecific interference coefficient by the interspecific interference coefficient (Spitters 1983). By multiplying together the relative interference abilities from both models $[(\beta_{mm}/\beta_{ms})(\beta_{ss}/\beta_{sm})]$, niche differentiation was determined (Spitters 1983). The farther the niche differentiation value was from unity (1.0), the greater the resource partitioning between species. Zero was used for all nonsignificant coefficients and a constant of 0.0001 was used for ratio calculations (Jacobs et al. 1996; Roush 1988).

Growth Analysis Study. In two separate trials, five seeds of medusahead or squirreltail were uniformly scattered across

Table 1. Nutrient treatment concentrations (μM) in solution added weekly to potting medium.

Nutrients	Nutrient treatments			
	low N low P	low N high P	high N low P	high N high P
NO$_3$–N	0	0	8,400	8,400
P	0	600	0	600
K	1,000	1,000	3,600	3,400
Ca	400	700	2,400	2,800
Mg	200	200	200	200
S	1,100	1,100	200	200
Fe	4	4	4	4
Cl	10	10	10	10
Mn	0.4	0.4	0.4	0.4
Zn	0.4	0.4	0.4	0.4
Cu	0.1	0.1	0.1	0.1
B	5	5	5	5
Mo	0.1	0.1	0.1	0.1

the surface of 40 (20 for each species per trial) prepared growth tubes and covered with approximately 2 mm of field soil. Growth tubes were arranged in a completely randomized design and covered with clear plastic for 6 to 7 d following planting to maintain humidity conducive to germination. The density of each growth tube was reduced to one vigorous seedling following establishment. Growth tubes were misted twice daily as needed throughout the study to prevent water stress. Each trial lasted approximately 70 d, with Trial 1 running May 26 through August 4, 2005, and Trial 2 running June 23 through August 14, 2005. No nutrient treatments were applied, so N and P levels were equivalent to the low N low P (control) treatment in the interference study.

Every 14 d, above- and belowground biomass of four randomly selected squirreltail and four randomly selected medusahead plants were harvested with the following exception: in Trial 1 the second growth period (GP2), between sample dates (SD) 28 and 35 d postplanting (dpp), was 7 d and the third growth period (GP3), between SD 35 and 56 dpp, was 21 d instead of 14 d. Above- and belowground biomass was separated and leaf area was quantified[3] and root length determined.[4] Above- and belowground biomass was dried (72 h at 50 C [122 F]) and weighed. Root : shoot ratio was calculated from above- and belowground biomass measurements.

Data were natural-log transformed and fit to a linear regression to estimate the instantaneous growth rate based on total biomass, leaf area, and root length over the 70-d period (Hunt 1982). Slopes were compared by calculating variance ratios using the extra sums of squares

procedure as described above (Snedecor and Cochran 1980).

Results and Discussion

Interference Study. For both Trial 1 and Trial 2, all models predicting medusahead or squirreltail aboveground biomass were highly significant ($P < 0.01$). Biomass was higher in Trial 2, therefore the two trials were modeled separately.

Regression-model coefficients for both species generally differed between the high and low N treatments, but not between the high and low P treatments (Tables 2 and 3). The only exception to this was for the squirreltail model in Trial 2 where the low N low P treatment differed from all other treatments (Table 3). Nitrogen appeared to be playing a much larger role than P in interference between medusahead and squirreltail, which supports evidence suggesting additions of N influence plant community dynamics and biomass production to a much greater degree than additions of P (McLendon and Redente 1991; Rauzi 1972).

The invasive grass medusahead outperformed the native grass squirreltail in all aspects of interference, and high nutrient availability did not increase medusahead's interference ability relative to squirreltail as hypothesized. In a similar study, additions of N did not alter the interference relationship between the native grass bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] and the invasive forb spotted knapweed (*Centaurea maculosa* Lam.) (Herron et al. 2001). Other studies suggested that invasive plants are

Table 2. Trial 1 and Trial 2 multiple linear regression models with medusahead and squirreltail growth tube density predicting the inverse of individual medusahead biomass (g plant^{-1}).[a,b]

Treatment	β_{m0}	β_{mm}	β_{ms}	β_{mm}/β_{ms}	R^2
			Trial 1		
low N low P	3.16 (1.25)	0.34 (0.02)	0.06 (NS)	3.4×10^3 (a)	0.86
high N low P	0.33 (NS)	0.11 (0.00)	0.04 (0.01)	2.57 (b)	0.96
low N high P	3.47 (1.52)	0.37 (0.02)	0.04 (NS)	3.7×10^3 (a)	0.83
high N high P	0.16 (NS)	0.11 (0.00)	0.06 (0.01)	1.92 (b)	0.97
			Trial 2		
low N low P	1.39 (NS)	0.29 (0.01)	0.06 (0.02)	4.74 (a)	0.92
high N low P	−0.03 (NS)	0.11 (0.00)	0.04 (0.00)	2.87 (b)	0.98
low N high P	1.30 (NS)	0.31 (0.01)	0.04 (0.02)	7.05 (a)	0.89
high N high P	0.03 (NS)	0.11 (0.00)	0.04 (0.00)	2.98 (b)	0.96

[a] β_{m0}, inverse mean biomass of an individual medusahead plant grown in isolation; β_{mm}, effect of medusahead density on medusahead biomass per plant; β_{ms}, effect of squirreltail density on medusahead biomass per plant; β_{mm}/β_{ms}, relative interference ratio of the two species; N, nitrogen; P, phosphorus; R^2, coefficient of determination; NS, not significant.

[b] Numbers in parentheses are standard errors for coefficients significantly different from zero ($P = 0.05$). Slopes of models with different letters in parentheses in the relative interference ratio column are statistically different from one another.

Table 3. Trial 1 and Trial 2 multiple linear regression models with medusahead and squirreltail growth tube density predicting the inverse of individual squirreltail biomass (g plant^{-1}).[a,b]

Treatment	β_{s0}	β_{ss}	β_{sm}	β_{ss}/β_{sm}	R^2
			Trial 1		
low N low P	15.02 (5.30)	0.41 (0.13)	0.52 (0.10)	0.80 (a)	0.43
high N low P	1.89 (NS)	0.12 (0.04)	0.43 (0.03)	0.26 (b)	0.82
low N high P	16.13 (NS)	0.42 (0.20)	0.76 (0.14)	0.55 (a)	0.44
high N high P	3.61 (NS)	0.10 (NS)	0.40 (0.05)	2.5×10^{-4} (b)	0.62
			Trial 2		
low N low P	6.71 (2.86)	0.33 (0.05)	0.44 (0.04)	0.75 (a)	0.73
high N low P	3.62 (NS)	0.12 (0.04)	0.26 (0.03)	0.45 (b)	0.60
low N high P	6.81 (2.68)	0.31 (0.05)	0.58 (0.04)	0.54 (b)	0.83
high N high P	0.92 (NS)	0.18 (0.03)	0.24 (0.02)	0.73 (b)	0.74

[a] β_{s0}, inverse mean biomass of an individual squirreltail plant grown in isolation; β_{ss}, effect of squirreltail density on squirreltail biomass per plant; β_{sm}, effect of medusahead density on squirreltail biomass per plant; β_{ss}/β_{sm}, relative interference ratio of the two species; N, nitrogen; P, phosphorus; R^2, coefficient of determination; NS, not significant.

[b] Numbers in parentheses are standard errors for coefficients significantly different from zero (P = 0.05). Slopes of models with different letters in parentheses in the relative interference ratio column are statistically different from one another.

just as successful as native species when resource availability is low (Lowe et al. 2002; Mangold 2004; Monaco et al. 2003). In the low N treatments for Trial 1, the predicted maximum aboveground biomass for an isolated medusahead plant (β_{m0}) was about 0.3 g (1/3.16 for low P and 1/3.47 for high P), whereas the high N treatments resulted in a nonsignificant regression coefficient for predicted maximum aboveground biomass. The predicted maximum aboveground biomass for an isolated squirreltail individual (β_{s0}) ranged from about 0.07 g (1/15.02) to 0.15 g (1/6.71 and 1/6.81) in the low N treatments across trials. As with medusahead, high N treatment models resulted in a nonsignificant regression coefficient for predicting maximum aboveground biomass of squirreltail. A nonsignificant regression coefficient suggested the maximum biomass of an isolated individual would be very large because of the reciprocal operation (i.e., 1/≈ 0). In all cases, the predicted maximum aboveground biomass for an isolated medusahead plant was greater than that of an isolated squirreltail plant.

In the medusahead models intraspecific interference was more intense than interspecific interference, whereas in the squirreltail models interspecific interference was more intense than intraspecific interference. Intraspecific interference coefficients for medusahead (β_{mm}) decreased from approximately 0.35 with low N treatments to 0.1 with high N treatments in Trial 1 and from 0.30 to 0.11 in Trial 2 (Table 2). In the low N treatments in Trial 1, the interspecific interference coefficient (β_{ms}) was nonsignificant, suggesting squirreltail density had no effect on medusahead biomass. Interspecific interference increased to about 0.05 in the high N treatments in Trial 1 and in all treatments during Trial 2. Squirreltail intraspecific interference coefficients (β_{ss}) decreased from low N treatments to high N treatments with values ranging from 0.41 to 0.10, respectively (Table 3). Interspecific interference coefficients (β_{sm}) ranged from 0.40 to 0.76 and were generally higher in high N treatments.

All of the relative interference ratios (β_{mm}/β_{ms}) for medusahead were greater than one, especially in the high N treatments, whereas the opposite was true for squirreltail ($\beta_{ss}/\beta_{sm} < 1$) (Tables 2 and 3). This suggests medusahead was imposing more interference on both its own biomass and on squirreltail biomass than was imposed by squirreltail on medusahead biomass or its own biomass. The effect of medusahead density on medusahead biomass was generally about two-to-seven times greater than the effect of squirreltail density on medusahead biomass. The effect of squirreltail density on its own biomass was generally about 25 to 80% of the effect of medusahead density on squirreltail biomass. Theory and field evidence predict that intraspecific interference should be greater than interspecific interference because individuals of the same species share identical resource requirements (Fowler 1986; Sheley and Larson 1995; Spitters 1983), but this was not the case with squirreltail in our study.

High N treatments generally resulted in more niche overlap than in the low N treatments. Strong deviations from unity (1.0) occurred for the low N treatments in Trial 1 with values of 2,720 and 2,035 for the low N low P and low N high P treatments, respectively, suggesting little to no interference between the two species. When N was high,

A)

B)

C)
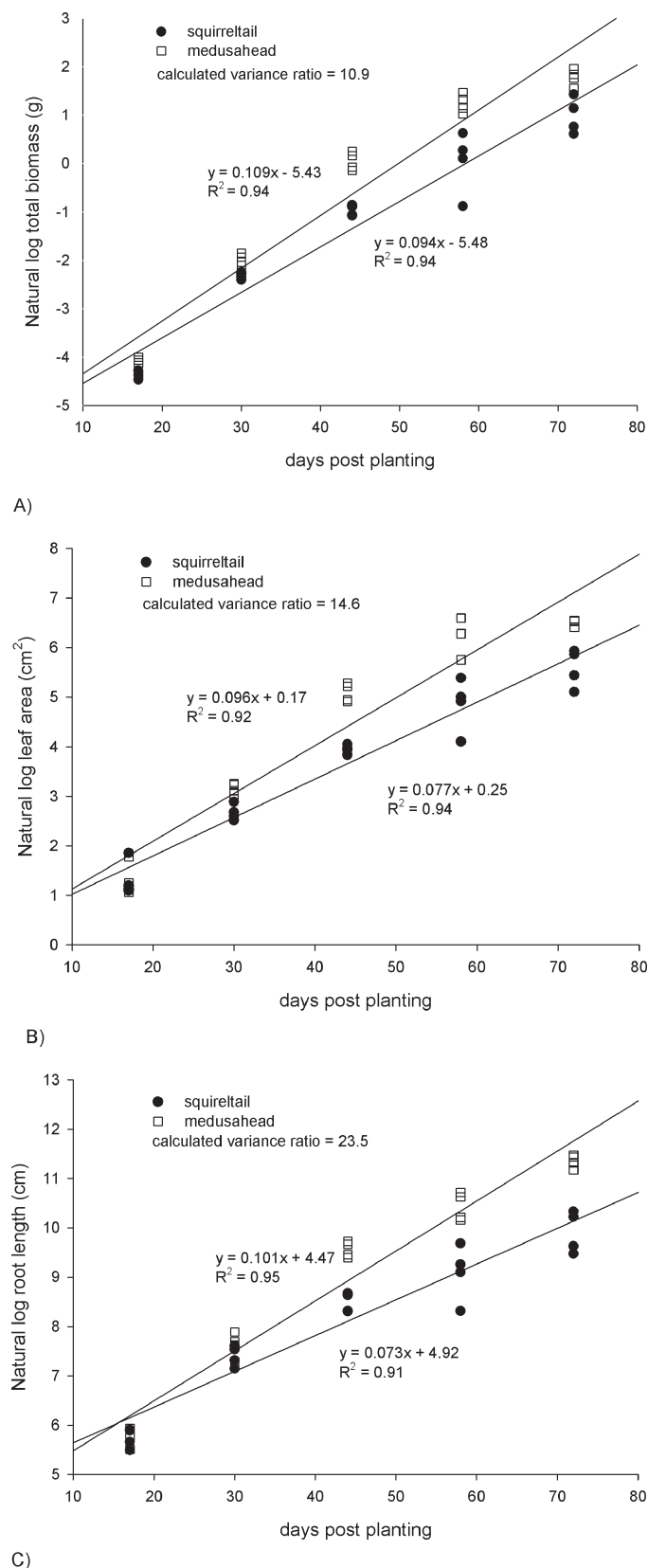
deviation from unity was minimal with values equal to 0.7 and 0.5 for the low P and high P treatments, respectively. Niche differentiation in Trial 2 was more consistent across treatments with values of 3.5, 1.3, 3.8, and 2.2 for the low N low P, high N low P, low N high P, and high N high P treatments, respectively, indicating more niche overlap and interference.

Growth Analysis Study. Data collected from each trial were analyzed separately because biomass accumulation was greater in Trial 2. Only results from Trial 2 are presented graphically (Figure 1), but results were similar across trials.

Consistent with our second hypothesis, we found that medusahead grew bigger and faster than squirreltail in all parameters that were measured. Invasive and/or annual species commonly display high growth rates and large biomass accumulation (Grime and Hunt 1975; Garnier 1992; Arredondo et al. 1998). Medusahead growth rate was higher than that of squirreltail in both trials. Nontransformed data suggested medusahead total biomass increased by 0.11 g/d whereas squirreltail total biomass increased by 0.05 g/d during Trial 2 (Figure 1A). During Trial 1 medusahead total biomass increased by 0.05 g/d compared to a 0.02-g/d increase for squirreltail. A high growth rate is one mechanism that may be critical to medusahead's success. A species with a higher growth rate may dominate because it can establish before, increase in size more quickly, and gain more access to resources than a slower growing species (Radosevich et al. 1997). Medusahead establishes and dominates in what are typically considered infertile environments (i.e., semiarid rangeland). Species typical to infertile environments are often relatively slow-growing and highly competitive for limited resources, or are stress-tolerant (Grime 2001; Tilman 1988). This suggests the mechanism of competition or stress tolerance may be partly responsible for medusahead's success in addition to, or as an alternative to, a high growth rate.

Medusahead generally accumulated leaf area and root length at a faster rate than squirreltail in both trials. Medusahead leaf area increased by about 4.5 cm^2/d and

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Figure 1. Growth rate (A), leaf area increase (B), and root length increase (C) of isolated individuals of squirreltail and medusahead for Trial 2. Data were linearized by taking the natural log of measured total biomass, leaf area, and root lengths to allow comparison of slopes. Critical value of variance ratio used to compare slopes$_{(\alpha = 0.05)}$ = 6.3. Calculated variance ratio > critical value suggests slopes are different.

13.3 cm^2/d in Trial 1 and Trial 2, respectively (Figure 1B); squirreltail leaf area increased by about 4.9 and 2.3 cm^2/d for Trial 1 and Trial 2, respectively (nontransformed data) (Figure 1B). Root length accumulation showed similar trends with medusahead root length increasing about 2.5 (Trial 1) to four (Trial 2) times faster than squirreltail root length (Figure 1C). However, squirreltail root : shoot ratios based on biomass were approximately 1.5 times greater than medusahead root : shoot ratios in Trial 2 at 30 (0.64 vs. 0.42), 44 (0.53 vs. 0.37), and 58 (0.61 vs. 0.32) dpp.

The growth analysis study supported results of the interference study and offers important insight into why medusahead appeared to impose more interference than squirreltail. When resources such as N are plentiful, the species that is most capable of growing rapidly and exploiting available resources, in this case medusahead, will benefit the most (Firbank and Watkinson 2003; Keddy 2003; Weiner 1985; Weiner 1990). Medusahead may be outperforming squirreltail via resource (i.e., N) preemption because (1) medusahead displayed faster growth rates and greater increases in leaf area and root length than squirreltail, even at the control N levels (low N low P) and (2) medusahead individual plant weight (i.e., total biomass) was always greater than that of squirreltail. Furthermore, the influence of medusahead on its own biomass was more intense than the influence of squirreltail on medusahead's biomass, and this intensity was lessened when N was increased.

Squirreltail has also been observed to establish in medusahead stands over time (Hironaka and Sindelar 1973; Hironaka and Tisdale 1963; Young 1992), which is contradictory to what our results might predict. One reason for this discrepancy may be because squirreltail is highly ecotypic (Hardegree et al. 2002, Jones et al. 2003, Young et al. 2003). Ecotypic variation may provide genotypes that resist medusahead invasion more than others. For example, in studies in which squirreltail established in medusahead (Hironaka and Sindelar 1973; Hironaka and Tisdale 1963), the closely related big squirreltail (*Elymus multisetus* M.E. Jones) was used instead of the bottlebrush squirreltail that was used in our study. Yet another reason may be because our study quantified seedling–seedling interference instead of mature squirreltail–medusahead seedling interference. Humphrey and Schupp (2004) found that the relative growth rate and biomass of 2-yr-old squirreltail plants were less influenced by the annual invasive grass cheatgrass (*Bromus tectorum* L.) than were first-year seedlings, suggesting seedling–seedling interference was more intense than mature plant–seedling interference. The perennial nature of squirreltail and its tendency to have higher root-to-shoot ratios, as indicated in the growth analysis, may confer some advantages over time that we were not able to distinguish in this study.

The results from our study suggest that squirreltail is not likely to effectively compete with medusahead in the seedling stage. Therefore, in order to restore squirreltail to rangeland dominated by medusahead, densities of medusahead seed in the seed bank should be reduced by carefully timing various integrated weed management strategies such as burning (McKell et al. 1962), herbicides (Turner 1965), and grazing (Lusk et al. 1961; Miller et al. 1999). Seeding squirreltail at high rates may also improve establishment success (Sheley et al. 2005; Velegala 1997). Once established, squirreltail may be able to maintain itself through perennial resource allocation patterns as suggested by Hironaka and Sindelar (1975), but would not likely eradicate medusahead. Sheley and Carpinelli (2005) found that several years were required after introducing seeds of desirable species before those species significantly inhibited reinvasion of spotted knapweed. Our short-term study in the greenhouse may not accurately forecast long-term dynamics between medusahead and squirreltail in the field.

Our study suggests that interference between medusahead and squirreltail seedlings will most likely be dominated by medusahead. Based on our results and those of others (Sheley and Carpinelli 2005), we suspect that revegetation of medusahead-infested rangeland will require a large quantity of resources and time. Aggressive and comprehensive prevention programs that include early detection and eradication are critical for conserving rangeland that is currently relatively medusahead-free (Sheley et al. 1999; Zamora and Thill 1999).

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