

AN ABSTRACT OF THE THESIS OF

Kert R. Young for the degree of Master of Science in Rangeland Ecology and Management presented on July 21, 2006.

Title: Influence of Nitrogen and Phosphorus on Interference between Medusahead and Squirreltail.

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Abstract approved: _____

Jane M. Mangold

Restoration of invaded aridlands is required to reduce the exorbitant ecological and monetary losses related to noxious weeds. An understanding of how reduced and increased levels of soil N and P influence interference between medusahead and squirreltail is imperative to understanding how squirreltail may be used in restoration of medusahead infested rangelands. Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) is an invasive, nonnative, annual grass that is rapidly displacing desirable rangeland plants in western North America. Evidence suggests that the native, perennial bunchgrass squirreltail (*Elymus elymoides* (Raf.) Swezey) may be able to displace medusahead under certain conditions, but the role of soil nutrients in this process is not well understood. I performed interference and growth analysis studies in a greenhouse to determine if soil nitrogen (N) and phosphorus (P) alter interference between medusahead and squirreltail. In both studies, plants were grown in pots containing a one-to-one mixture of sand and field soil from a site containing medusahead and squirreltail. In the interference experiment, medusahead and squirreltail were

planted in density combinations of 0, 1, 5, 25, and 125 seeds per species per pot at four levels of N and P (loNloP, loNhiP, hiNloP, hiNhiP). Results indicated that medusahead and squirreltail competed for N. Increased soil N reduced medusahead and squirreltail's relative competitive abilities largely due to reductions in the intensity of intraspecific interference. High N also reduced the effect of medusahead density on squirreltail biomass. Soil P levels had little influence on predicted species aboveground growth or relative competitive ability. In the growth analysis experiment, plant growth, growth rates, and relative growth rates for above- and belowground biomass, total biomass, leaf area, total root length, and depth of root penetration of isolated individuals were recorded for harvested plants at 2-week intervals over a 70-day period. Results indicated that medusahead produced more absolute belowground biomass, aboveground biomass, total biomass, leaf area, and root length and had higher growth rates for these parameters than squirreltail. Squirreltail allocated more of its acquired resources to belowground growth endowing it with greater root:shoot ratios. Medusahead relative growth rates decreased in belowground biomass, aboveground biomass, total biomass, leaf area, and root length over the course of the study period, while squirreltail's relative growth rate for leaf area remained constant; however, medusahead still maintained higher relative leaf area growth rates during the experiment.

Results from the growth analysis study matched results from the interference study in that medusahead was found to be a superior competitor over squirreltail for environmental resources. In order to understand the full benefits of squirreltail's relatively higher allocation of biomass to belowground growth, a long-term study would be necessary. A long-term study would allow for the differences in perennial versus

annual resource allocation patterns to manifest themselves to their fullest extent. Over time and with consistently low nutrient availability, squirreltail might increase in medusahead infested rangelands. The maintenance of continually low levels of nutrient availability combined with a reduction of medusahead competition are prerequisites for reclamation of medusahead infested rangelands. Maintaining soil N at very low levels, over the long term, may diminish medusahead seed banks to low enough levels that squirreltail can increase and slowly replace medusahead. Competition between medusahead and squirreltail seedlings will likely be won by medusahead, but seedling-to-mature plant competition may be won by squirreltail. It appears that management inputs, e.g., seed drilling, herbicides, and best management practices that maintain low N availability, will be required to allow native perennials to firmly establish in invasive annual weed infested rangelands.

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Influence of Nitrogen and Phosphorus on Interference between
Medusahead and Squirreltail

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Kert R. Young

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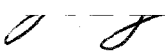
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CONTRIBUTIONS OF AUTHORS

Dr. Jane M. Mangold was involved in experimental development, funding, data collection and analysis, statistical guidance, facilities coordination, and thesis revisions. Dr. Michael M. Borman was involved in experimental development, academic guidance, program review, and thesis editing. Dr. Michael F. Carpinelli initiated the project and was involved in experimental design, funding, and facilities coordination. Dr. Jennifer G. Kling was involved in statistical guidance and thesis editing.

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INFLUENCE OF NITROGEN AND PHOSPHORUS ON INTERFERENCE
BETWEEN MEDUSAHEAD AND SQUIRRELTAIL

CHAPTER 1: INTRODUCTION

Weeds occur throughout the world and more species have gone extinct as a result of biological invasions than from climate change related to human activity (D'Antonio and Vitousek 1992). Some biological invasions can modify ecosystem composition, function, processes, environmental conditions, resource availability, and threaten indigenous populations (Braithwaite et al 1989, D'Antonio and Vitousek 1992, Hobbs and Mooney 1986, Vitousek et al. 1987). More particularly, weed populations have the ability to diminish soil moisture and nutrients, water quality, wildlife habitat, plant diversity, and endanger sensitive species, modify fire intervals, and accelerate erosion (DiTomaso 2000, BLM 1996).

Even though there is not one life cycle that represents the average weed (DiTomaso 2000), exotic plants have invaded all continents (D'Antonio and Vitousek 1992). Plants introduced from other countries are often released from the natural controls of their native habitat that prevented them from becoming as aggressive as they can become in new countries (BLM 1996). In 2001, 40 million U.S. hectares were estimated to be infested with invasive weeds spreading at an estimated one million hectares annually (NISC 2001). This onslaught from exotic weeds costs the U.S. agricultural economy an estimated \$26 billion annually (Pimentel et al. 2000).

Restoration of noxious weed infested rangelands through the use of desirable species that meet land use objectives is critical to stemming future monetary and ecological damages from weeds. Competition studies conducted simultaneously with growth analysis studies are important in creating weed management plans (Radosevich et al. 1997) and identifying the most effective time for weed control practices (Patterson

1980). Identifying determinants of competitive plant interactions and their associated effects on plant growth facilitates ecosystem management in favor of desirable species (Radosevich et al. 1997). Furthermore, evaluation of plant growth traits during non-competitive and competitive situations improves our understanding of the specific mechanisms by which plants interfere with each other while verifying that competitive plant traits identified in growth analysis still endow competitive ability when species are grown together (Radosevich et al. 1997). Identification of competitive mechanisms used by invasive weeds may allow land managers to influence ecological processes in a way that shifts the competitive edge away from invasive weeds and towards desirable species. Restoration of degraded rangelands is essential to return proper ecological functioning to millions of hectares and socioeconomic values to thousands of citizens across the U.S.

CHAPTER 2: LITERATURE REVIEW

LIFE HISTORY STRATEGIES

A species life history strategy influences its growth rate, resource allocation, and response to resource availability. For example, annuals and short-lived perennials with high maximum relative growth rates allow for quick life cycle completion and the opportunity to preempt resources necessary for growth in productive environments (Grime and Hunt 1975). Arredondo et al. (1998) found that annual plants had higher belowground biomass, aboveground biomass, and leaf area growth rates than perennials, and the annual species aboveground growth rates were higher than belowground growth rates. Annual and perennial grasses can also employ different root growth schemes (Arredondo et al. 1998). Arredondo et al. (1998) found that annual grasses developed root systems with greater length, whereas the perennial grasses developed thicker roots. Korner and Renhardt (1987) suggested that production of many thin roots may be a more efficient use of carbon than the production of thicker perennial roots thought to be important in sustaining perennial plant life (Arredondo et al. 1998, Hironaka and Sindelar 1975).

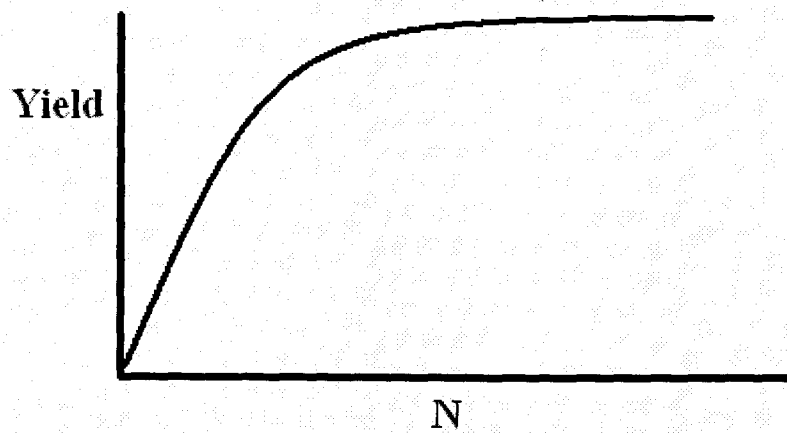
Nitrogen (N) use efficiency is another distinguishing characteristic between annual and perennial grasses. Monaco et al. (2003) found that invasive annual grasses were at least as efficient in N uptake as native perennial grasses, but that native perennial grasses used their absorbed N more efficiently. Native perennial grasses invest a larger portion of their acquired N and developing biomass in belowground biomass structures, which endows them with greater root:shoot ratios than invasive annual grasses and should increase nutrient uptake (Monaco et al. 2003). Additionally, perennials lost less

of their acquired nutrients over time by maintaining leaves longer and reabsorbing nutrients from senescing leaves (Monaco et al. 2003).

PLANT DENSITY AFFECTS GROWTH

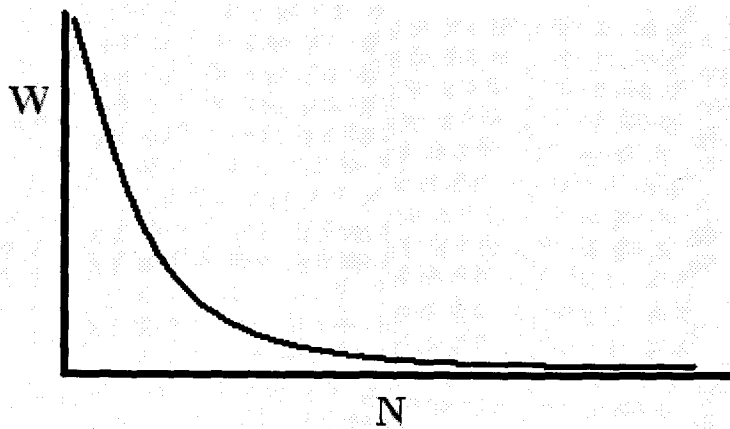
In addition to life history strategies influencing plant growth, species density affects the biomass of each species grown together (Radosevich et al. 1997). According to Radosevich et al. (1997), this effect can be estimated by systematically planting each species over a range of relative and total densities in an addition series design while assuming the effect of spatial arrangement to be constant. Planting seeds of potentially competing species in an addition series design allows for the evaluation of species performance over the hyperbolic relationship between plant density and plant yield. As plant density increases, yield increases until the ability of the environment to supply additional resources for plant growth can no longer increase, which is referred to as the "law of constant final yield" (Shinozaki and Kira 1956) (Figure 2.1). As density increases, weight per individual plant decreases (Figure 2.2). The inverse of weight across increasing density is a linear relationship known as the reciprocal yield law (Radosevich et al. 1997) (Figure 2.3). Spitters (1983) extended the reciprocal yield law to include multiple species to help explain the plant-to-plant interactions between species grown in proximity (Radosevich et al. 1997). Multiple linear regression analysis of species densities and biomass for two or more species planted in an addition series design allows for separation and estimation of intra- and interspecific interference (Radosevich et al. 1997).

Figure 2.1. Law of constant final yield.



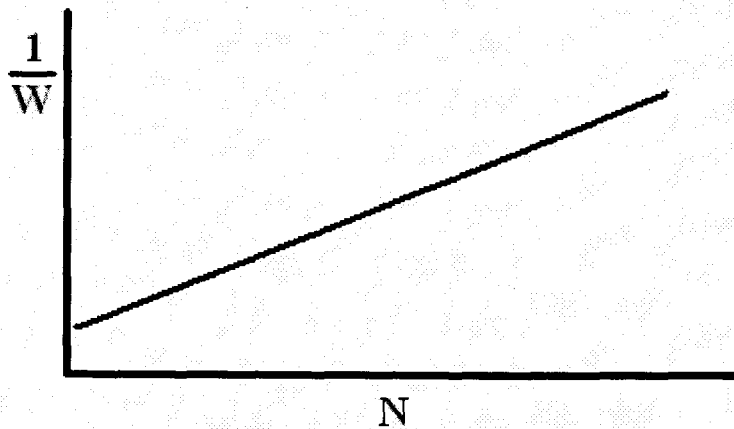
Yield=biomass production per unit area. N =plant density.

Figure 2.2. Hyperbolic relationship between individual plant weight and density.



W =individual plant weight. N =plant density.

Figure 2.3. Reciprocal yield law.



W =individual plant weight. N =plant density.

RESOURCE AVAILABILITY ALTERS PLANT GROWTH AND INTERFERENCE

Plant growth is dependent upon a plant's ability to obtain resources necessary for growth, and plants must acquire resources to increase in size and perpetuate their species (Radosevich et al. 1997). As current plant growth is dependent on previous plant growth (Evans 1972), the increase in biomass and photosynthetically active shoot material are crucial to evaluating vegetative growth (Radosevich et al. 1997). Evaluation of plant growth includes the measuring and analysis of biomass accumulated as leaves, stems, reproductive organs, and roots (Radosevich et al. 1997). Growth analysis conducted with plants grown individually under environmentally uniform conditions can predict the competitive mechanisms and performance of species grown in mixed stands and can serve as an indicator of future competitive success (Radosevich et al. 1997). The mechanisms by which plants compete include the effects of plants on environmental resources and the way they react to altered resource availability (Goldberg 1990). For example, exotic, invasive species have been found to benefit from and be more

responsive to abundant nitrogen (N) availability than native species (Herron et al. 2001, Mangold 2004, Krueger-Mangold et al. 2006, Monaco et al. 2003).

Measurements of absolute plant growth and growth rate may help explain why some species display competitive superiority over other species. Because plant growth is directly related to the amount of resources sequestered from the environment, a species potential competitive ability when grown in mixed stands is indicated by a plant's mean relative growth rate, which is the amount of plant growth over a time interval relative to plant size at the beginning of the time interval. These measurements can increase our understanding of the effects of the environment, resource limitations, and other plants on plant growth (Radosevich et al. 1997). For example, Holt and Orcutt (1991) combined a growth analysis and competition study and found in the growth analysis study that the weeds produced greater leaf area, biomass, and relative growth rates than cotton. These findings identified plant characteristics that may have endowed the weeds with competitive superiority over cotton as found in the competition study (Holt and Orcutt 1991).

Maximum relative growth rates for dominant plant species are different between productive and unproductive sites, and plants with low maximum relative growth rates are less competitive on productive sites (Grime and Hunt 1975). Grime and Hunt (1975) suggested that traits that endow plants with the ability to grow rapidly under situations of high resource availability can reduce a plant's ability to thrive under high stress situations where nutrient availability is very low. However, in semiarid plant communities, where nutrient availability is presumed low, competition exists (Fowler

1986, Redente 1992), and early seral and annual grass species, known for rapid growth rates, are usually very successful (Arredondo et al. 1998).

Plants grown in proximity often compete for nutrients (Radosevich et al. 1997) and N and phosphorus (P) have been shown to greatly affect biomass production (Redente et al. 1992). Nitrogen is the macronutrient most intensely competed for and additions of soil N can increase interference between weeds and crops likely due to luxuriant nutrient uptake by weeds (Radosevich et al. 1997, Vengris et al. 1955). Blackshaw et al. (2004) found that above- and belowground biomass for 22 weeds increased with increased soil P, and they suggested that P may influence weed populations over long periods of time and alter interference between plants. In addition, Redente et al. (1992) and Vitousek and White (1981) indicated that both soil N and P concentrations influence the intensity of interference between plants grown in mixed plant communities. More specifically, Redente et al. (1992) found that both N and P influenced early seral species growth, growth rates, and aboveground tissue nutrient concentrations. They concluded that early successional species should be less dominant in areas that are low in soil N.

The availability and acquisition of resources required for growth greatly influences interference between plants (Radosevich et al. 1997). The plant that acquires optimal levels of all resources required for plant growth should out-compete other nearby plants (Radosevich et al. 1997). Thereby, species that grow more quickly have the opportunity to preempt limited resources to the detriment of slower growing species, which is a form of competitive superiority (Radosevich et al. 1997). Additionally, a plant that can establish before, increase in size more quickly, or that has more access to

resources should have at least partial competitive superiority over a nearby plant (Radosevich et al. 1997).

Nitrogen and P have been shown to greatly influence resource allocation (Dakheel et al. 1993). Native perennials generally produce greater root:shoot ratios and allocate more N to roots across nutrient gradients than annual plants; however, annuals are more responsive to nutrient additions than native perennials (Monaco et al. 2003). According to Radosevich et al. (1997), plants growing in low nutrient environments commonly allocate large amounts of biomass to belowground growth and increase specific root length. When soil resources are ample or aboveground competition is greater than belowground competition, low root:shoot ratios should be beneficial and vice versa (Parrish and Bazzaz 1982). The root:shoot ratios for four of the five species studied by Redente et al. (1992) were roughly equivalent at the extreme levels of soil N and P availability. Squirreltail (*Elymus elymoides* (Raf.) Swezey), however, produced its lowest root:shoot ratios when soil P was reduced, suggesting its belowground biomass was affected by changes in soil P levels more so than changes in soil N levels (Redente et al. 1992). Squirreltail's large investment into perennial root systems should improve its nutrient uptake (Monaco et al. 2003).

INFLUENTIAL SPECIES

The invasion of exotic species into ecosystems endangers natural plant communities (Heywood 1989). Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) is an invasive, winter-annual grass that invades native plant communities, altering biological and physical site potential (Young 1992). Medusahead has the potential to quickly spread, dominate, and permanently injure many plant

communities (BLM 1996). Medusahead was introduced to North America around the late 1800s from Eurasia (McKell et al. 1962a), probably via livestock importation (Hilken and Miller 1980). It has disseminated from Roseburg, Oregon, to Washington, Idaho, California (McKell et al. 1962a), Nevada (Young et al. 1968), and Utah (Horton 1991) and may infest hundreds of thousands of hectares (Young 1992).

Medusahead has many aggressive characteristics that allow it to invade and dominate many native ecosystems. Medusahead has a short life span and high seed production, typical of a ruderal (*sensu* Grime 1979) species. On good soil in dense stands, Sharp et al. (1957) observed 1,500 to 2,000 plants per square foot with an average of 8.7 seed heads per plant, while on poor soil they observed 500 plants per square foot with an average of 5.6 seed heads per plant. Medusahead germinates in the fall and grows rapidly in the spring with seed heads appearing in May (Murphy and Turner 1959), and plants maturing in June/July (Sharp et al. 1957). Medusahead seeds require cold temperatures prior to germination. Young et al. (1968) found optimal germination with treatments of 10 and 15°C. Medusahead requires soil moisture availability later into the spring than cheatgrass (*Bromus tectorum* L.) (Hironaka 1961) and commonly occupies clay soils that maintain moisture later into the growing season (Fosberg 1965). However, medusahead is also capable of growing in coarser textured soils with an argillic horizon (Young 1992) and even has the capacity to encroach on native shrub-steppe plant communities with loam soils (Miller 1996).

Because of medusahead's high silica content, its litter decomposes slowly (Bovey et al. 1961), allowing litter to accumulate and stifle the growth of other plants (Harris 1965). Medusahead litter is unpalatable (Bovey et al. 1961), very susceptible to burning

(McKell et al. 1962b), and reduces germination of other species by preventing their seeds from touching the soil (Young 1992). However, medusahead seeds can germinate without soil as the litter layer provides the right humidity for its germination (Young 1992). Furthermore, a new root may emerge when moisture becomes available following the desiccation of the initial root (Young 1992). Medusahead is also able to sustain root growth in cool temperatures and acquire soil moisture and nutrients earlier in the season than bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), a native perennial grass common to semiarid western rangeland (Harris and Wilson 1970). When a seed source is available, medusahead is more likely to invade disturbed sites where competition from other plants has been reduced (Miller 1996). With medusahead's high seed production, litter accrual, cool season root growth, and fall germination, it can efficiently compete with desirable forage species (Hilken and Miller 1980) and develop dense monocultures.

Healthy, perennial vegetation is the most effective form of control against medusahead encroachment (Turner et al. 1963). Hironaka and Tisdale (1963) suggest that over time squirreltail may establish in medusahead stands as manifest in the western Great Basin (Young 1992). Hironaka and Sindelar (1973) demonstrated that squirreltail could establish in medusahead stands without first reducing competition. Additionally, Jones (1998) stated that squirreltail may be useful in restoration of medusahead infested rangeland. However, Young (1992) cautioned that successful squirreltail establishment may not lead to occupation by longer-lived perennial grasses over time.

Squirreltail is an early to mid seral, cool-season, native, short-lived perennial grass that germinates in the fall and has the ability to establish in land dominated by

annual plants (Arredondo et al. 1998, Hironaka and Sindelar 1973, Hironaka and Tisdale 1963). Squirreltail can germinate across a range of temperatures (Young and Evans 1977). The most favorable soil temperature for seedling growth is 25°C while root growth continues at 5 °C (Hironaka and Tisdale 1972). Cool season root growth may help explain squirreltail's ability to compete with annual grasses (Hironaka and Tisdale 1972). Squirreltail has a variety of other attributes that may help it compete with medusahead including self-pollination, wide ecotypic variations, and seed dispersal mechanisms (Jensen et al. 1990, Jones 1998, Arredondo et al. 1998). In addition, with squirreltail's perennial structure, greater nutrient retention, and higher root:shoot ratios than medusahead's, squirreltail may increase in relative competitive ability as long as N availability remains low, disturbance is minimal, and soil P remains sufficiently available (Monaco et al. 2003, Miller 1996, Redente et al. 1992). Therefore, squirreltail may be a good restoration species for medusahead infested plant communities in the Great Basin.

CHAPTER 3: QUANTIFYING INTERFERENCE BETWEEN SQUIRRELTAIL AND MEDUSAHEAD AT DIFFERENT LEVELS OF NITROGEN AND PHOSPHORUS

INTRODUCTION

Plant growth depends upon a plant's ability to obtain resources necessary for growth, and plants must acquire resources to increase in size and perpetuate their species (Radosevich et al. 1997). The availability and acquisition of resources required for growth greatly influences interference between plants (Radosevich et al. 1997). The plant that acquires optimal levels of all resources required for plant growth should out-compete other nearby plants (Radosevich et al. 1997). Thereby, species that grow more quickly have the opportunity to preempt limited resources to the detriment of slower growing species (Radosevich et al. 1997). Monaco et al. (2003) found that invasive annual grasses were at least as efficient in nitrogen (N) uptake as native perennial grasses, but that native perennial grasses used their absorbed N more efficiently. Native perennial grasses invest a larger portion of their acquired N and developing biomass in belowground structures, which endows them with greater root:shoot ratios than invasive annual grasses and should increase their nutrient uptake (Monaco et al. 2003). Additionally, perennials lose less of their acquired nutrients over time by maintaining leaves longer and reabsorbing nutrients from senescing leaves (Monaco et al. 2003).

Plants grown in proximity often compete for nutrients (Radosevich et al. 1997). In semiarid plant communities, where nutrient availability is presumed low, competition exists (Fowler 1986, Redente 1992), and early seral and annual grass species, known for rapid growth rates, are usually very successful (Arredondo et al. 1998). The mechanisms by which plants compete include the effects of plants on environmental resources and the

way they react to altered resource availability (Goldberg 1990). For example, exotic, invasive species have been found to benefit from and be more responsive to abundant nutrient availability than native species (Herron et al. 2001, Mangold 2004, Krueger-Mangold et al. 2006, Monaco et al. 2003). Additionally, a plant that can establish before, increase in size more quickly, or that has more access to resources should have at least partial competitive superiority over a nearby plant (Radosevich et al. 1997).

Nitrogen is the macronutrient most intensely competed for and additions of N can increase interference between weeds and crops, likely due to luxuriant nutrient uptake by weeds (Radosevich et al. 1997, Vengris et al. 1955). Blackshaw et al. (2004) found that above- and belowground biomass for 22 weeds increased with increased soil phosphorus (P), suggesting that P may influence weed populations over long periods of time and alter interference between plants. Some native species are also greatly influenced by P, for example, squirreltail (*Elymus elymoides* (Raf.) Swezey) produced its lowest root:shoot ratios when soil P was reduced (Redente et al. 1992). In addition, Redente et al. (1992) and Vitousek and White (1981) indicated that both soil N and P concentrations influence the level of interference between plants grown in mixed plant communities. More specifically, Redente et al. (1992) found that both N and P influenced early seral species growth, growth rates, and aboveground tissue nutrient concentrations. They concluded that early successional species should be less able to dominate areas that are low in soil N.

The invasion of exotic species threatens native plant communities (Heywood 1989). Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) is an invasive, winter-annual grass that invades native plant communities, altering biological

and physical site potential (Young 1992). Medusahead has the potential to quickly spread, dominate, and permanently injure many plant communities (BLM 1996). Medusahead was introduced to North America around the late 1800s from Eurasia (McKell et al. 1962a), probably via livestock importation (Hilken and Miller 1980). It has disseminated from Roseburg, Oregon, to Washington, Idaho, California (McKell et al. 1962a), Nevada (Young et al. 1968), and Utah (Horton 1991) and may infest hundreds of thousands of hectares (Young 1992).

Medusahead has many aggressive characteristics that allow it to invade and dominate many native ecosystems. Medusahead has a short life span and high seed production, typical of a ruderal (*sensu* Grime 1979) species. On good soil in dense stands, Sharp et al. (1957) observed 1,500 to 2,000 plants per square foot with an average of 8.7 seed heads per plant, while on poor soil they observed 500 plants per square foot with an average of 5.6 seed heads per plant. Medusahead germinates in the fall and grows rapidly in the spring with seed heads appearing in May (Murphy and Turner 1959), and plants maturing in June/July (Sharp et al. 1957). Medusahead seeds require cold temperatures prior to germination. Young et al. (1968) found optimal germination with treatments of 10 and 15°C. Medusahead requires soil moisture availability later into the spring than cheatgrass (*Bromus tectorum* L.) (Hironaka 1961) and commonly occupies clay soils that maintain moisture later into the growing season (Fosberg 1965). However, medusahead is also capable of growing in coarser textured soils with an argillic horizon (Young 1992) and even has the capacity to encroach on native shrub-steppe plant communities with loam soils (Miller 1996).

Because of medusahead's high silica content, its litter decomposes slowly (Bovey et al. 1961), allowing litter to accumulate and stifle the growth of other plants (Harris 1965). Medusahead litter is unpalatable (Bovey et al. 1961), very susceptible to burning (McKell et al. 1962b), and reduces germination of other species by preventing their seeds from touching the soil (Young 1992). However, medusahead seeds can germinate without soil because the litter layer provides ideal humidity for germination (Young 1992). Furthermore, a new root may emerge when moisture becomes available following the desiccation of the initial root (Young 1992). Medusahead is also able to sustain root growth in cool temperatures and acquire soil moisture and nutrients earlier in the season than bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), a native perennial grass common to semiarid western rangeland (Harris and Wilson 1970). When a seed source is available, medusahead is more likely to invade disturbed sites where competition from other plants has been reduced (Miller 1996). With medusahead's high seed production, litter accrual, cool season root growth, and fall germination, it can efficiently compete with desirable forage species (Hilken and Miller 1980) and develop dense monocultures.

Healthy, perennial vegetation is the most effective form of control against medusahead encroachment (Turner et al. 1963). Hironaka and Tisdale (1963) suggest that over time squirreltail may establish in medusahead stands as manifest in the western Great Basin (Young 1992). Hironaka and Sindelar (1973) demonstrated that squirreltail could establish in medusahead stands without first reducing competition. Additionally, Jones (1998) stated that squirreltail may be useful in restoration of medusahead infested

rangeland. However, Young (1992) cautioned that successful squirreltail establishment may not lead to occupation by longer-lived perennial grasses over time.

Squirreltail is an early to mid seral, cool-season, native, short-lived perennial grass that germinates in the fall and has the ability to establish in land dominated by annual plants (Arredondo et al. 1998, Hironaka and Sindelar 1973, and Hironaka and Tisdale 1963). Squirreltail can germinate across a range of soil temperatures (Young and Evans 1977). The most favorable temperature for seedling growth is 25°C while root growth continues at 5 °C (Hironaka and Tisdale 1972). Cool season root growth may help explain squirreltail's ability to compete with annual grasses (Hironaka and Tisdale 1972). Squirreltail has a variety of other attributes that may help it compete with medusahead including self-pollination, wide ecotypic variations, and seed dispersal mechanisms (Jensen et al. 1990, Jones 1998, and Arredondo et al. 1998). In addition, with squirreltail's perennial structure, greater nutrient retention, responsiveness to P, and higher root:shoot ratios than medusahead's, squirreltail may increase in relative competitive ability as long as N availability remains low, disturbance is minimal, and soil P remains sufficiently available (Monaco et al. 2003, Miller 1996, Redente et al. 1992).

Even though an extensive understanding has been acquired regarding the effects of nutrients on plant growth, usually related to crop production, knowledge of how N and P availability influences the relationship between species in a semiarid ecosystem, especially between medusahead and squirreltail, is lacking. A greater understanding of nutrient related plant interactions would improve a land manager's ability to potentially use native species in restoration of annual weed infested rangelands. As suggested by Arredondo et al. (1998), more studies are required to more fully understand how

colonization of annual dominated lands by squirreltail can occur. This study evaluated the effects of N, P, and plant density on the interference relationship between medusahead and squirreltail. This research attempted to further our understanding of squirreltail recolonization of medusahead infested rangelands and its potential use as a candidate species for restoration of medusahead infested rangelands to healthy and functioning native ecosystems.

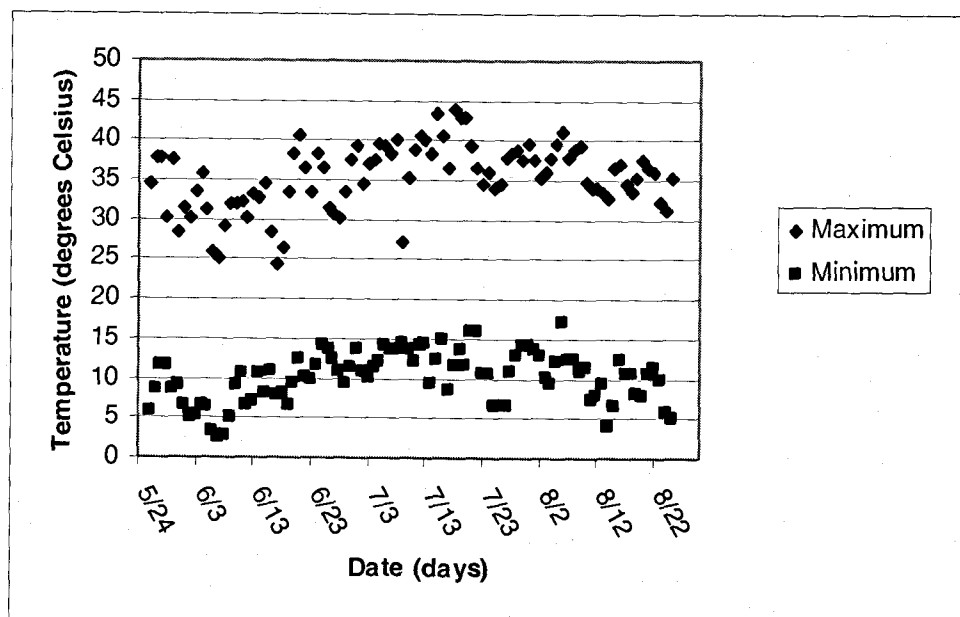
OBJECTIVES

The overall objective of this study was to quantify interference between medusahead and squirreltail under varying levels of soil N and P. More specifically, the objective was to measure intra- and interspecific interference, relative competitive ability, and niche differentiation of medusahead and squirreltail at high and low levels of N and P. I hypothesized that high soil N and P would increase medusahead growth and competitive ability relative to squirreltail.

METHODS

This study was conducted in a greenhouse at the Eastern Oregon Agricultural Research Center in Burns, Oregon, from May 25-August 25, 2005. Burns is 1,265 meters above sea level and located at latitude 43°35'N and longitude 119°03'W. Average annual temperature is 7.8°C, average annual precipitation is 279 mm, and annual average growing degree-days (base 10°C) is 1,881 (WRCC 2004). Average daily temperature in the greenhouse during the experiment was 22.0°C (Figure 4). Photosynthetically active radiation between 11 am and 2 pm averaged about 700 $\mu\text{mol s}^{-1}\text{m}^{-2}$.

Figure 3.1. Maximum and minimum greenhouse temperatures.



Medusahead seed was locally collected by hand during the summer of 2003. Seed was cleaned and partially de-awned with a rubbing board and Ferrell-Ross seed cleaner during summer 2004. Squirreltail seed was purchased from L and H Seed in southeastern Washington in the spring of 2004. Germination tests in June 2004 yielded 66% squirreltail germination and 87% medusahead germination. Later germination tests conducted in March 2005 yielded 70% squirreltail germination and 99% medusahead germination. Seeding densities were increased to account for the lower percent germination.

The study was conducted in pots (polyvinyl chloride pipe) with a surface area of 0.018 m^2 and depth of 0.5 m. Weed barrier fabric covered the bottoms of pots and was secured with tape and/or perforated (five holes at 0.6 cm) PVC end caps. Native soil that had supported squirreltail and medusahead was collected from two sites near John Day, Oregon, and sieved through a 0.6 cm screen to remove rocks and large roots. The potting

medium consisted of soil mixed with concrete grade sand in a one to one ratio by volume. Potting medium was saturated prior to planting with approximately 2,300 ml of tap water. Pots were allowed to drain to column capacity, then seeds were uniformly scattered across the surface of each pot and covered with approximately two mm of native soil. Medusahead and squirreltail were planted in an addition series design (Spitters 1983). Density matrices consisted of 0:0, 0:1, 0:5, 0:25, 0:125, 1:0, 1:1, 1:5, 1:25, 1:125, 5:0, 5:1, 5:5, 5:25, 5:125, 25:0, 25:1, 25:5, 25:25, 25:125, 125:0, 125:1, 125:5, 125:25, 125:125 pure live seeds per pot. Four matrices constituted a block with 100 pots per block and three blocks totaling one replication. Pots were arranged in a completely randomized block design (CRBD) and replicated in time with trial 2 beginning 20 days following the planting of trial 1. Each trial lasted approximately 70 days with trial 1 running May 26-August 4 and trial 2 running June 14-August 23, 2005.

Following planting, nutrient treatments applications were begun and pots were covered with clear plastic for six to seven days to maintain humidity conducive to germination. Each planting matrix received one of four nutrient treatments weekly. The low N low P treatment (loNloP) was the control with no N or P added to the pots. The low N high P treatment (loNhiP) added 250 ml of a 600 μ M P solution in the form of calcium phosphate. The high N low P treatment (hiNloP) added 250 ml of an 8,400 μ M N solution in the forms of calcium nitrate and potassium nitrate. The high N high P treatment (hiNhiP) added 250 ml of an 8,400 μ M N and 600 μ M P solution in the forms of calcium nitrate, potassium nitrate, and potassium phosphate. The high N and P treatments were roughly equivalent to 60% strength modified Hoagland's solution. Essential macro- and micro-nutrients (K, Ca, Mg, S, Fe, Cl, Mn, Zn, Cu, B, and Mo)

were applied in a 10-20% 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 3.1). The pots were misted twice daily as needed throughout the study to prevent water stress.

Volunteer seedlings of undesired species were removed as necessary. After 70 days, the density per pot of each species was counted and aboveground biomass clipped approximately five mm above the soil surface. Aboveground biomass was dried for 72 hours at 50°C and weighed.

Table 3.1. Nutrient treatment concentrations (μM) in solution added weekly to potting medium.

Nutrients	Nutrient Treatments			
	loNloP	loNhiP	hiNloP	hiNhiP
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

Multiple linear regression predicted biomass for medusahead and squirreltail as influenced by species densities (Spitters 1983). The inverse of medusahead individual aboveground biomass per plant was predicted using medusahead and squirreltail final densities per pot as independent variables. The inverse of squirreltail individual

aboveground biomass per plant was predicted using squirreltail and medusahead final densities per pot as independent variables.

Models were of the 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^{-1} and y_s^{-1} were the predicted inverse average aboveground biomass per plant for medusahead and squirreltail, respectively. The regression coefficients β_{m0} and β_{s0} predicted the inverse of maximum aboveground biomass for a medusahead and squirreltail plant grown in isolation, respectively. A smaller inverse number means greater biomass. β_{mm} and β_{ss} measured the effect of species density upon its own biomass (intraspecific interference) from the medusahead and squirreltail models, respectively. β_{ms} and β_{sm} measured 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 pot of medusahead and squirreltail, respectively.

Slopes from the regression models for each nutrient treatment with high N and/or high P were compared with the slope of the regression model from the loNloP (control) treatment using the extra sums of squares method (Snedecor and Cochran 1980). In this procedure slopes of the regression models are compared using variance ratios of the form:

$$\text{Variance Ratio}_i = \text{VR}_i = [(RSS_i - RSS_1) / (df_i - df_1)] / (RSS_1 / df_1)$$

where RSS_i equals the pooled residual sum of squares, RSS_1 equals the residual sum of squares of each treatment being compared added together, df_i equals the pooled error degrees of freedom, and df_1 equals error degrees of freedom of each treatment being

compared added together. The null hypothesis that the slopes of the regression lines are similar was rejected when the variance ratio was greater than the critical

$F_{(\alpha, df_{\text{numerator}}, df_{\text{denominator}})}$ value.

The relative competitive ability for each species under each nutrient treatment was calculated by dividing the intraspecific competition coefficient by the interspecific competition coefficient (Spitters 1983). For example, if $\beta_{\text{mm}}/\beta_{\text{ms}}$ equaled 2, then medusahead density had twice the influence of squirreltail density on medusahead's average biomass per plant. By multiplying together the relative competitive abilities from both models $[(\beta_{\text{mm}} / \beta_{\text{ms}}) * (\beta_{\text{ss}} / \beta_{\text{sm}})]$, niche differentiation was determined, which is a measure of resource partitioning (Spitters 1983). The farther the niche differentiation value was from unity (1), the greater the resource partitioning between species. An extreme niche differentiation value suggested that competition between species for the same resource was minimal.

Percent N (total N on Leco CNS-2000 Macro Analyzer) and %P (dry ash acid digest on Perkin Elmer Optima 3000DV ICP spectrometer) in aboveground biomass were determined by Central Analytical Lab at Oregon State University. Percent N and %P were compared separately between nutrient treatments for medusahead and squirreltail using analysis of variance and Fisher's least significant difference ($\text{LSD}_{\alpha=0.05}$). Soil nitrate-nitrogen ($\text{NO}_3\text{-N}$) (KCl extraction on Alpkem RFA 300 auto-analyzer), ammonium-nitrogen ($\text{NH}_4\text{-N}$) (KCl extraction on Alpkem RFA 300 auto-analyzer), and P (sodium bicarbonate on Alpkem RFA 300 auto-analyzer) concentrations were determined by Central Analytical Lab at Oregon State University from adjusted random soil samples taken from 35 pots per nutrient treatment from each trial. Soil $\text{NO}_3\text{-}$

N, NH₄-N, and P concentrations were compared separately between pre- and post treatment conditions and between the nutrient treatments after harvesting plants.

Comparisons were made using analysis of variance and Fisher's least significant difference ($LSD_{\alpha=0.05}$).

RESULTS

Extra sums of squares F-tests identified multiple linear regression models that were significant. In trials 1 and 2, all models predicting medusahead or squirreltail aboveground biomass were highly significant (Table 3.2).

Table 3.2. Model P-values for multiple linear regression models predicting medusahead or squirreltail aboveground biomass for each treatment in trials 1 and 2.

Species	Trial 1				Trial 2			
	hiNloP	loNloP	hiNhiP	loNhiP	hiNloP	loNloP	hiNhiP	loNhiP
Medusahead	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Squirreltail	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

In the models for trial 1 predicting medusahead aboveground biomass, the high N treatments were different from the low N treatments, but the high and low P treatments were not different from each other (Table 3.3). The predicted maximum aboveground biomass for a medusahead plant without competition (i.e. β_{m0}) was 0.3 g (low P or high P) for the two low N treatments and the predicted inverse maximum aboveground biomass for a medusahead plant with high N was not significant. In each of these models, intraspecific interaction was more intense than interspecific interaction. With the low N treatments, the effect of medusahead density on medusahead biomass was 5.8 (low P) and 8.6 (high P) times greater than the effect of squirreltail density on medusahead biomass. The influence of squirreltail density on medusahead biomass was

insignificant with the low N treatments. With the high N treatments, the effect of medusahead density on medusahead biomass was 1.9 (high P) and 2.6 (low P) times greater than the effect of squirreltail density on medusahead biomass. Intraspecific competition coefficients decreased from approximately 0.35 with low N treatments to 0.1 with high N treatments. All of the relative competitive ratios for medusahead were greater than one. The coefficients of determination (R^2) for the medusahead model ranged from 0.83 (loNhiP) to 0.97 (hiNhiP). Additionally, the R^2 values were 11.6 (low P) and 16.8% (high P) greater with the high N treatments than with the low N treatments.

Table 3.3. Trial 1 multiple linear regression analysis with medusahead and squirreltail pot density predicting the inverse of individual medusahead biomass (g plant^{-1}).

Treatment	β_{m0}	β_{mm}	β_{ms}	β_{mm}/β_{ms}	R^2
loNloP	3.16 (1.25)	0.34 (0.02)	0.06 (NS)	5.82 (a)	0.86
hiNloP	0.33 (NS)	0.11 (0.00)	0.04 (0.01)	2.57 (b)	0.96
loNhiP	3.47 (1.52)	0.37 (0.02)	0.04 (NS)	8.61 (a)	0.83
hiNhiP	0.16 (NS)	0.11 (0.00)	0.06 (0.01)	1.92 (b)	0.97
Comparing Nutrient Treatments:					
hiNloP vs loNloP – VR 115.98, critical $F_{(0.05, 3, 111)} < 2.69$ for accepting null hypothesis, F test p-value <0.01					
loNhiP vs loNloP – VR 0.58, critical $F_{(0.05, 3, 110)} < 2.69$ for accepting null hypothesis, F test p-value 0.63					
hiNhiP vs loNloP – VR 113.66, critical $F_{(0.05, 3, 110)} < 2.69$ for accepting null hypothesis, F test p-value <0.01					
hiNloP vs hiNhiP – VR 1.91, critical $F_{(0.05, 3, 113)} < 2.68$ for accepting null hypothesis, F test p-value 0.13					
hiNhiP vs loNhiP – VR 87.19, critical $F_{(0.05, 3, 112)} < 2.69$ for accepting null hypothesis, F test p-value <0.01					
loNhiP vs hiNloP – VR 90.12, critical $F_{(0.05, 3, 113)} < 2.68$ for accepting null hypothesis, F test p-value <0.01					

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 competitive ability of the two species and R^2 =coefficient of determination. Numbers in parentheses are standard errors for coefficients significantly different from zero ($P=0.05$). NS=not significant and VR=Variance Ratio.

For the multiple linear regression models of trial 1 predicting squirreltail aboveground biomass, the hiNloP and hiNhiP treatments were not different from each other but were different than the loNloP treatment, while the loNhiP treatment was not different than the loNloP treatment (Table 3.4). The predicted maximum aboveground biomass for a squirreltail plant without competition was 0.1 g for the loNloP nutrient treatment while the other nutrient treatment models did not significantly predict squirreltail inverse maximum aboveground biomass per plant to be different than zero. For each of these models, interspecific interaction was more intense than intraspecific interaction. With the low N treatments, the effect of squirreltail density on squirreltail biomass was 0.6 (high P) and 0.8 (low P) times the effect of medusahead density on squirreltail biomass. For the high N treatments, the effect of squirreltail density on squirreltail biomass was 0.3 (low P or high P) times the effect of medusahead density on squirreltail biomass. Under the high N high P treatment, the effect of squirreltail density on its own biomass was insignificant. Intraspecific competition coefficients decreased from 0.4 with low N treatments to 0.1 with high N treatments. All of the relative competitive ratios for squirreltail were less than one. The coefficients of determination (R^2) for the squirreltail model ranged from 0.43 (loNloP) to 0.82 (hiNloP). In addition, the R^2 values were 40.9 (high P) to 90.7% (low P) greater for the high N treatments than for the low N treatments. Niche differentiation in trial 1 between medusahead and squirreltail for nutrient treatments loNloP, hiNloP, loNhiP, and hiNhiP was 4.6, 0.7, 8.0, and 0.5, respectively.

Table 3.4. Trial 1 multiple linear regression analysis with squirreltail and medusahead pot density predicting the inverse of individual squirreltail biomass (g plant^{-1}).

Treatment	B_{s0}	B_{ss}	B_{sm}	B_{ss}/β_{sm}	r^2
loNloP	15.02 (5.30)	0.41 (0.13)	0.52 (0.10)	0.80 (a)	0.43
hiNloP	1.89 (NS)	0.12 (0.04)	0.43 (0.03)	0.26 (b)	0.82
loNhiP	16.13 (NS)	0.42 (0.20)	0.76 (0.14)	0.55 (a)	0.44
hiNhiP	3.61 (NS)	0.10 (NS)	0.40 (0.05)	0.26 (b)	0.62
Comparing Nutrient Treatments:					
hiNloP vs loNloP – VR 11.97, critical $F_{(0.05, 3, 97)} < 2.70$ for accepting null hypothesis, F test p-value < 0.01					
loNhiP vs loNloP – VR 1.19, critical $F_{(0.05, 3, 94)} < 2.70$ for accepting null hypothesis, F test p-value 0.32					
hiNhiP vs loNloP – VR 10.01, critical $F_{(0.05, 3, 97)} < 2.70$ for accepting null hypothesis, F test p-value < 0.01					
hiNloP vs hiNhiP – VR 0.14, critical $F_{(0.05, 3, 96)} < 2.70$ for accepting null hypothesis, F test p-value < 0.94					
hiNhiP vs loNhiP – VR 10.87, critical $F_{(0.05, 3, 93)} < 2.70$ for accepting null hypothesis, F test p-value < 0.01					
loNhiP vs hiNloP – VR 11.60, critical $F_{(0.05, 3, 93)} < 2.70$ for accepting null hypothesis, F test p-value < 0.01					

B_{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. B_{ss}/β_{sm} =relative competitive ability of the two species and R^2 =coefficient of determination. Numbers in parentheses are standard errors for coefficients significantly different from zero ($P=0.05$). NS=not significant and VR=Variance Ratio.

In the multiple linear regression models for trial 2 predicting medusahead aboveground biomass, the results were generally similar to trial 1. In contrast to trial 1, the predicted maximum aboveground biomass for a medusahead plant without competition was not significantly different from zero for any nutrient treatment (Table 3.5). In addition, the influence of squirreltail density on medusahead biomass was significant for all nutrient treatments.

Table 3.5. Trial 2 multiple linear regression analysis with medusahead and squirreltail pot density predicting the inverse of individual medusahead biomass (g plant^{-1}).

Treatment	β_{m0}	β_{mm}	β_{ms}	β_{mm}/β_{ms}	r^2
loNloP	1.39 (NS)	0.29 (0.01)	0.06 (0.02)	4.74 (a)	0.92
hiNloP	-0.03 (NS)	0.11 (0.00)	0.04 (0.00)	2.87 (b)	0.98
loNhiP	1.30 (NS)	0.31 (0.01)	0.04 (0.02)	7.05 (a)	0.89
hiNhiP	0.03 (NS)	0.11 (0.00)	0.04 (0.00)	2.98 (b)	0.96
Comparing Nutrient Treatments:					
hiNloP vs loNloP – VR 154.07, critical $F_{(0.05, 3, 115)} < 2.68$ for accepting null hypothesis, F test p-value < 0.01					
loNhiP vs loNloP – VR 0.50, critical $F_{(0.05, 3, 113)} < 2.68$ for accepting null hypothesis, F test p-value 0.68					
hiNhiP vs loNloP – VR 137.89, critical $F_{(0.05, 3, 114)} < 2.68$ for accepting null hypothesis, F test p-value < 0.01					
hiNloP vs hiNhiP – VR 0.09, critical $F_{(0.05, 3, 115)} < 2.68$ for accepting null hypothesis, F test p-value 0.96					
hiNhiP vs loNhiP – VR 103.50, critical $F_{(0.05, 3, 113)} < 2.68$ for accepting null hypothesis, F test p-value < 0.01					
loNhiP vs hiNloP – VR 114.36, critical $F_{(0.05, 3, 114)} < 2.68$ for accepting null hypothesis, F test p-value < 0.01					

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 competitive ability of the two species and R^2 =coefficient of determination. Numbers in parentheses are standard errors for coefficients significantly different from zero ($P=0.05$). NS=not significant and VR=Variance Ratio.

For the multiple linear regression model of trial 2 predicting squirreltail aboveground biomass, the majority of the results were similar to trial 1. In contrast to trial 1, all nutrient treatments produced significantly different results from that of the loNloP treatment (Table 3.6). Not only were the high N treatments different from the low N treatments, but the high P treatment was different from the low P treatment while N was low but not when N was high. In trial 2, the predicted maximum aboveground biomass for a squirreltail plant without competition was 0.15 g (low P or high P) with the low N treatments while the high N treatment models did not predict a significant

maximum aboveground biomass for squirreltail individuals. With the high N treatments, the effect of squirreltail density on squirreltail biomass was 0.5 (low P) and 0.7 (high P) times the effect of medusahead density on squirreltail biomass. The effect of squirreltail density on its own biomass was significant for all treatments. The R^2 values were 10.8 (high P) to 17.8% (low P) lower for the high N treatments than for the low N treatments. Niche differentiation between medusahead and squirreltail in trial 2 was 3.5, 1.3, 3.8, and 2.2 for nutrient treatments loNloP, hiNloP, loNhiP, and hiNhiP, respectively.

Table 3.6. Trial 2 multiple linear regression analysis with squirreltail and medusahead pot density predicting the inverse of individual squirreltail biomass (g plant^{-1}).

Treatment	B_{s0}	B_{ss}	B_{sm}	B_{ss}/β_{sm}	r^2
loNloP	6.71 (2.86)	0.33 (0.05)	0.44 (0.04)	0.75 (a)	0.73
hiNloP	3.62 (NS)	0.12 (0.04)	0.26 (0.03)	0.45 (b)	0.60
loNhiP	6.81 (2.68)	0.31 (0.05)	0.58 (0.04)	0.54 (b)	0.83
hiNhiP	0.92 (NS)	0.18 (0.03)	0.24 (0.02)	0.73 (b)	0.74
Comparing Nutrient Treatments:					
hiNloP vs loNloP – VR 19.32, critical $F_{(0.05, 3, 110)} < 2.69$ for accepting null hypothesis, F test p-value < 0.01					
loNhiP vs loNloP – VR 2.89, critical $F_{(0.05, 3, 109)} < 2.69$ for accepting null hypothesis, F test p-value 0.04					
hiNhiP vs loNloP – VR 23.41, critical $F_{(0.05, 3, 110)} < 2.69$ for accepting null hypothesis, F test p-value < 0.01					
hiNloP vs hiNhiP – VR 0.89, critical $F_{(0.05, 3, 112)} < 2.69$ for accepting null hypothesis, F test p-value 0.45					
hiNhiP vs loNhiP – VR 52.67, critical $F_{(0.05, 3, 111)} < 2.69$ for accepting null hypothesis, F test p-value < 0.01					
loNhiP vs hiNloP – VR 41.13, critical $F_{(0.05, 3, 111)} < 2.69$ for accepting null hypothesis, F test p-value < 0.01					

B_{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. B_{ss}/β_{sm} =relative competitive ability of the two species and R^2 =coefficient of determination. Numbers in parentheses are standard errors for coefficients significantly different from zero ($P=0.05$). NS=not significant and VR=Variance Ratio.

Aboveground plant tissue for medusahead plants in trial 1 treated with nutrient treatments hiNloP (2.17%) and hiNhiP (2.14%) had greater %N than plants treated with loNloP (1.12%) (Table 3.7). The loNhiP (1.12%) nutrient treatment resulted in less %N in medusahead aboveground tissue than the hiNloP (2.17%) treatment. The hiNhiP (2.14%) treatment had twice the tissue N of the loNhiP (1.12%) treatment. Percent P in medusahead aboveground biomass was lower for the hiNloP (0.14%) treatment than for the loNloP (0.17%) treatment, but the hiNhiP (0.21%) treatment was higher than loNloP (0.17%) treatment. Treatments loNhiP (0.18%) and hiNhiP (0.21%) both had greater %P than treatment hiNloP (0.14%). The hiNhiP (0.21%) treatment was greater in %P than the loNhiP (0.18%) treatment.

Trial 1 %N in aboveground biomass for squirreltail plants under the hiNloP (1.84%) and hiNhiP (1.65%) treatments had nearly twice the %N as the loNloP (1.05%) treatment (Table 3.7). The loNhiP (1.01%) treated plants had about half the %N of the hiNloP (1.84%) and hiNhiP (1.65%) treated plants. Percent P in squirreltail aboveground biomass was greater for plants treated with loNloP (0.22%) than for plants treated with hiNloP (0.12%) or hiNhiP (0.19%). The loNhiP (0.26%) treated plants contained more %P than the loNloP (0.22%) treated plants. Percent P in squirreltail aboveground tissue was greater when treated with loNhiP (0.26%) or hiNhiP (0.19%) than %P in plants treated with hiNloP (0.12%). The hiNhiP (0.19%) treatment resulted in aboveground tissue containing less %P than plants treated with loNhiP (0.26%).

Table 3.7. Trial 1 percent nitrogen (%N) and percent phosphorus (%P) compared between nutrient treatments for medusahead and squirreltail separately.

Medusahead				Squirreltail				
N%		P%		N%		P%		
loNloP	hiNloP	loNloP	hiNloP	loNloP	hiNloP	loNloP	hiNloP	
1.12	2.17	0.17	0.14	1.05	1.84	0.22	0.12	
(0.04)	(0.05)	(0.01)	(0.00)	(0.06)	(0.10)	(0.01)	(0.01)	
loNloP	loNhiP	loNloP	loNhiP	loNloP	loNhiP	loNloP	loNhiP	
1.12	1.12	0.17	0.18	1.05	1.01	0.22	0.26	
(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	(0.01)	(0.01)	
loNloP	hiNhiP	loNloP	hiNhiP	loNloP	hiNhiP	loNloP	hiNhiP	
1.12	2.14	0.17	0.21	1.05	1.65	0.22	0.19	
(0.04)	(0.05)	(0.01)	(0.01)	(0.06)	(0.07)	(0.01)	(0.01)	
hiNloP	loNhiP	hiNloP	loNhiP	hiNloP	loNhiP	hiNloP	loNhiP	
2.17	1.12	0.14	0.18	1.84	1.01	0.12	0.26	
(0.05)	(0.04)	(0.00)	(0.01)	(0.10)	(0.05)	(0.01)	(0.01)	
hiNloP	hiNhiP	hiNloP	hiNhiP	hiNloP	hiNhiP	hiNloP	hiNhiP	
2.17	2.14	0.14	0.21	1.84	1.66	0.12	0.19	
(NS)	(NS)	(0.00)	(0.01)	(NS)	(NS)	(0.01)	(0.01)	
loNhiP	hiNhiP	loNhiP	hiNhiP	loNhiP	hiNhiP	loNhiP	hiNhiP	
1.12	2.14	0.18	0.21	1.01	1.65	0.26	0.19	
(0.04)	(0.05)	(0.01)	(0.01)	(0.05)	(0.07)	(0.01)	(0.01)	
1.98		1.98		1.99		1.99		LSD CP
<0.01		<0.01		<0.01		<0.01		95%
								P-value

Numbers in parentheses are standard errors for parameters significantly different between nutrient treatments ($P=0.05$). CP=critical point.

In trial 2, %N in aboveground tissue of medusahead plants was greater with hiNloP (2.32%) and hiNhiP (2.41%) treatments than with loNloP (1.31%) treatments (Table 3.8). Plants treated with loNhiP (1.38%) had less %N in aboveground biomass than plants treated with hiNloP (2.32%) while plants treated with hiNhiP (2.41%) had more %N than plants under loNhiP (1.38%) treatment. Medusahead aboveground biomass %P was greater for plants treated with hiNloP (0.13%) or hiNhiP (0.13%) than for plants treated with loNloP (0.09%).

Squirreltail aboveground biomass %N in trial 2 for plants treated with hiNloP (2.14%) and hiNhiP (1.94%) was greater than for plants treated with loNloP (1.07%) (Table 3.8). Aboveground biomass %N was lower in squirreltail plants treated with loNhiP (1.13%) versus plants treated with hiNloP (2.14%). In addition, %N was greater for plants treated with hiNhiP (1.94%) than for plants treated with loNhiP (1.13%).

Percent P in squirreltail aboveground biomass was not different between nutrient treatments.

Table 3.8. Trial 2 percent nitrogen (N%) and percent phosphorus (P%) compared between nutrient treatments for medusahead and squirreltail separately.

Medusahead				Squirreltail				
N%		P%		N%		P%		
loNloP	hiNloP	loNloP	hiNloP	loNloP	hiNloP	loNloP	hiNloP	
1.31	2.32	0.09	0.13	1.07	2.14	0.13	0.17	
(0.04)	(0.05)	(0.01)	(0.01)	(0.06)	(0.13)	(NS)	(NS)	
loNloP	loNhiP	loNloP	loNhiP	loNloP	loNhiP	loNloP	loNhiP	
1.31	1.38	0.09	0.11	1.07	1.13	0.13	0.17	
(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	
loNloP	hiNhiP	loNloP	hiNhiP	loNloP	hiNhiP	loNloP	hiNhiP	
1.31	2.41	0.09	0.13	1.07	1.94	0.13	0.17	
(0.04)	(0.06)	(0.01)	(0.01)	(0.06)	(0.12)	(NS)	(NS)	
hiNloP	loNhiP	hiNloP	loNhiP	hiNloP	loNhiP	hiNloP	loNhiP	
2.33	1.38	0.13	0.11	2.14	1.13	0.17	0.17	
(0.05)	(0.05)	(NS)	(NS)	(0.13)	(0.07)	(NS)	(NS)	
hiNloP	hiNhiP	hiNloP	hiNhiP	hiNloP	hiNhiP	hiNloP	hiNhiP	
2.33	2.41	0.13	0.13	2.14	1.94	0.17	0.17	
(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	
loNhiP	hiNhiP	loNhiP	hiNhiP	loNhiP	hiNhiP	loNhiP	hiNhiP	
1.38	2.41	0.11	0.13	1.13	1.94	0.17	0.17	
(0.05)	(0.06)	(NS)	(NS)	(0.07)	(0.12)	(NS)	(NS)	
1.98		1.98		1.99		1.99		LSD CP
<0.01		<0.01		<0.01		0.17		95%
								P-value

Numbers in parentheses are standard errors for parameters significantly different between nutrient treatments ($P=0.05$). CP=critical point.

Potting medium in trial 1 pots treated with loNloP had 11.6 ppm less $\text{NO}_3\text{-N}$ and 0.8 ppm less $\text{NH}_4\text{-N}$ at the end of the experiment than pretreatment levels (Table 3.9).

With the hiNloP treatments, potting medium was 11.9 ppm lower in $\text{NO}_3\text{-N}$ and 1.8 ppm lower in P than pretreatment levels. Pots treated with loNhiP had 10.9 ppm less $\text{NO}_3\text{-N}$ while pots treated with hiNhiP had 11.6 ppm less $\text{NO}_3\text{-N}$ than pretreatment concentrations.

Table 3.9. Trial 1 mean nitrate-nitrogen ($\text{NO}_3\text{-N}$), ammonium-nitrogen ($\text{NH}_4\text{-N}$), and phosphorus (P) potting medium concentrations compared between pre- and post nutrient treatments.

Nutrients	Pretreatment (ppm)	Post Treatments (ppm)			
		loNloP	hiNloP	loNhiP	hiNhiP
$\text{NO}_3\text{-N}$	12.4	0.8	0.5	1.5	0.8
	NA	(0.1)	(0.1)	(0.2)	(0.3)
P-value		<0.01	<0.01	<0.01	<0.01
$\text{NH}_4\text{-N}$	1.9	1.1	1.6	1.4	1.8
	NA	(0.0)	(NS)	(NS)	(NS)
P-value		<0.01	0.67	0.49	0.89
P	5.0	4.4	3.2	7.3	5.6
	NA	(NS)	(0.1)	(NS)	(NS)
P-value		0.57	0.03	0.43	0.71

ppm=parts per million. NA=no standard error because there was one representative datum. Numbers in parentheses are standard errors for parameters significantly different between pre- and post nutrient treatments ($P=0.05$).

In trial 1, potting medium $\text{NO}_3\text{-N}$ concentrations were not significantly different between nutrient treatments (Table 3.10). Ammonium-nitrogen potting medium concentrations for the hiNloP, loNhiP, and hiNhiP treatments were 0.5, 0.4, and 0.7 ppm greater than the loNloP treatment. Phosphorus potting medium concentrations were different between every nutrient treatment including the loNloP treatment. The hiNloP treatment had 1.1 ppm lower P than the loNloP treatment, while the loNhiP and hiNhiP treatments had 2.9 and 1.2 ppm greater P, respectively, than the loNloP treatment. The

loNhiP and hiNhiP treatments were 4.0 and 2.3 ppm greater in P, respectively, than the hiNloP treatment. Phosphorus concentration with the hiNhiP treatment was 1.7 ppm lower than the loNhiP treatment.

Table 3.10. Trial 1 mean nitrate-nitrogen ($\text{NO}_3\text{-N}$), ammonium-nitrogen ($\text{NH}_4\text{-N}$), and phosphorus (P) potting medium concentrations compared between nutrient treatments.

$\text{NO}_3\text{-N}$ (ppm)		$\text{NH}_4\text{-N}$ (ppm)		P (ppm)		
loNloP	hiNloP	loNloP	hiNloP	loNloP	hiNloP	
0.96	1.16	1.09	1.61	4.60	3.49	
(NS)	(NS)	(0.04)	(0.11)	(0.19)	(0.23)	
loNloP	loNhiP	loNloP	loNhiP	loNloP	loNhiP	
0.96	1.70	1.09	1.54	4.60	7.52	
(NS)	(NS)	(0.04)	(0.14)	(0.19)	(0.48)	
loNloP	hiNhiP	loNloP	hiNhiP	loNloP	hiNhiP	
0.96	1.12	1.09	1.76	4.60	5.81	
(NS)	(NS)	(0.04)	(0.12)	(0.19)	(0.30)	
hiNloP	loNhiP	hiNloP	loNhiP	hiNloP	loNhiP	
1.16	1.70	1.61	1.54	3.49	7.52	
(NS)	(NS)	(NS)	(NS)	(0.23)	(0.48)	
hiNloP	hiNhiP	hiNloP	hiNhiP	hiNloP	hiNhiP	
1.16	1.12	1.61	1.76	3.49	5.81	
(NS)	(NS)	(NS)	(NS)	(0.23)	(0.31)	
loNhiP	hiNhiP	loNhiP	hiNhiP	loNhiP	hiNhiP	
1.70	1.12	1.54	1.76	7.52	5.81	
(NS)	(NS)	(NS)	(NS)	(0.48)	(0.31)	
1.98		1.98		1.98		LSD CP
0.44		<0.01		<0.01		95%
						P-value

ppm=parts per million. Numbers in parentheses are standard errors for parameters significantly different between nutrient treatments ($P=0.05$). CP=critical point.

In Trial 2, $\text{NO}_3\text{-N}$ potting medium concentrations were not different for pretreatment and post treatment comparisons (Table 3.11). Ammonium-nitrogen potting medium concentrations for loNhiP, hiNloP, loNhiP, and hiNhiP nutrient treatments were 3.2, 2.9, 3.0, and 3.0 ppm less than pretreatment concentrations. Phosphorus concentrations were not different between pre- and post nutrient treatments.

Table 3.11. Trial 2 mean nitrate-nitrogen ($\text{NO}_3\text{-N}$), ammonium-nitrogen ($\text{NH}_4\text{-N}$), and phosphorus (P) potting medium concentrations compared between pre- and post nutrient treatments.

Nutrients	Pretreatment (ppm)	Post Treatments (ppm)			
		loNloP	hiNloP	loNhiP	hiNhiP
$\text{NO}_3\text{-N}$	1.7	1.0	1.0	1.1	0.8
	NA	(NS)	(NS)	(NS)	(NS)
P-value		0.09	0.66	0.28	0.40
$\text{NH}_4\text{-N}$	4.6	1.4	1.7	1.6	1.6
	NA	(0.1)	(0.1)	(0.1)	(0.1)
P-value		<0.01	<0.01	<0.01	<0.01
P	13.0	12.0	10.8	16.9	14.3
	NA	(NS)	(NS)	(NS)	(NS)
P-value		0.60	0.22	0.14	0.58

ppm=parts per million. NA=no standard error because there was one representative datum. Numbers in parentheses are standard errors for parameters significantly different between pre- and post nutrient treatments ($P=0.05$).

Similar to trial 1, trial 2 $\text{NO}_3\text{-N}$ potting medium concentrations did not differ between nutrient treatments (Table 3.12). Ammonium-nitrate potting medium concentrations for nutrient treatments hiNloP and hiNhiP were 0.3 and 0.2 ppm greater, respectively, than loNloP concentrations. Phosphorus levels differed between every nutrient treatment including the loNloP treatment. Phosphorus potting medium concentrations for hiNloP were 1.4 ppm lower than for the loNloP nutrient treatment and the loNhiP and hiNhiP treated pots had 4.7 and 2.1 ppm greater P, respectively, than the loNloP treated pots. The loNhiP treated pots had 6.1 ppm greater P than the hiNloP pots. Pots treated with hiNhiP had 3.5 ppm more P than pots treated with hiNloP while hiNhiP pots had 2.6 ppm less P than the loNhiP pots.

Table 3.12. Trial 2 mean nitrate-nitrogen ($\text{NO}_3\text{-N}$), ammonium-nitrogen ($\text{NH}_4\text{-N}$), and phosphorus (P) potting medium concentrations compared between nutrient treatments.

$\text{NO}_3\text{-N}$ (ppm)		$\text{NH}_4\text{-N}$ (ppm)		P (ppm)		
loNloP	hiNloP	loNloP	hiNloP	loNloP	hiNloP	
1.11 (NS)	1.76 (NS)	1.40 (0.05)	1.67 (0.07)	12.17 (0.36)	10.83 (0.29)	
loNloP	loNhiP	loNloP	loNhiP	loNloP	loNhiP	
1.11 (NS)	1.24 (NS)	1.40 (NS)	1.52 (NS)	12.17 (0.36)	16.90 (0.43)	
loNloP	hiNhiP	loNloP	hiNhiP	loNloP	hiNhiP	
1.11 (NS)	1.22 (NS)	1.40 (0.05)	1.57 (0.06)	12.17 (0.36)	14.30 (0.37)	
hiNloP	loNhiP	hiNloP	loNhiP	hiNloP	loNhiP	
1.76 (NS)	1.24 (NS)	1.67 (NS)	1.52 (NS)	10.83 (0.29)	16.90 (0.43)	
hiNloP	hiNhiP	hiNloP	hiNhiP	hiNloP	hiNhiP	
1.76 (NS)	1.22 (NS)	1.67 (NS)	1.57 (NS)	10.83 (0.29)	14.30 (0.37)	
loNhiP	hiNhiP	loNhiP	hiNhiP	loNhiP	hiNhiP	LSD CP 95% P-value
1.24 (NS)	1.22 (NS)	1.52 (NS)	1.57 (NS)	16.90 (0.43)	14.30 (0.37)	
1.98	1.98	1.98	1.98	1.98	1.98	
0.61	0.02	0.02	0.02	<0.01	<0.01	

ppm=parts per million. Numbers in parentheses are standard errors for parameters significantly different between nutrient treatments ($P=0.05$). CP=critical point.

DISCUSSION AND CONCLUSIONS

The overall objective of this study was to quantify interference between medusahead and squirreltail under different levels of soil N and P. All regression models were significant ($p<0.05$). In both trials, the high N treatments for medusahead and squirreltail were significantly different from the respective low N treatments, and the only difference between P levels occurred in trial 2 for squirreltail where the loNhiP treatment was different from the loNloP.

By conducting an addition series experiment, I was able to separate the various components of species-to-species interference into intra- and interspecific interference,

predict the inverse maximum aboveground biomass for a plant grown in isolation, and calculate relative competitive ratios for each species. Predictions for the inverse of maximum aboveground biomass for an individual plant were usually insignificant, especially for the high N models, which failed to find any inverse predictions different from zero. These non-significant predictions suggest that the reciprocal of these inverse predictions, i.e., the actual predicted maximum aboveground biomass per plant, increased in biomass with increased N almost without limits. My observations support Dakheel et al. (1993) and Redente et al. (1992) who found that medusahead and squirreltail biomass production were greatly influenced by soil N and P levels.

Intraspecific interactions were always significant for medusahead and squirreltail models except for the hiNhiP treatment for the squirreltail model in trial 1. In this case, nutrient availability may have been sufficient to eliminate squirreltail intraspecific interaction; however, medusahead density still significantly impacted squirreltail aboveground biomass. This result suggests that medusahead has a greater ability to absorb N than squirreltail or that squirreltail exhibits less luxuriant N uptake. Weeds have been found capable of luxuriant nutrient uptake (Vengris et al. 1955). For the medusahead and squirreltail models in both trials, intraspecific interaction was less intense in high N treatments compared to low N treatments.

Interspecific interactions for the medusahead models in either trial did not increase or decrease with increased N availability, which indicates that the effect of squirreltail interference may have been undetectable given medusahead's stronger competitive ability. However, interspecific interference decreased for the squirreltail models with increased soil N availability, which contradicts the claim by Radosevich et

al. (1997) that increased soil N can increase negative interference. Increased N availability reduced intraspecific interaction more so than interspecific interaction, as expected. When nutrient availability increases, competition for that abundant resource should decrease. This reduction in intraspecific interference should occur because plants of the same species usually have more identical resource requirements than plants from different species. Plants of different species should have at least slight differences in root morphology, root length, timing of maximum nutrient uptake, absorption ability, or nutrient requirements. Therefore, intraspecific competition should be more intense than interspecific competition because plants of the same species should have more niche overlap than plants from different species (Barbour et al. 1987).

In general, the reduced relative competitive ability of medusahead or squirreltail comparing low to high N treatments was largely a result of reduced intraspecific interaction. For the prediction of medusahead aboveground biomass, intraspecific competition was always more intense than interspecific interaction, which means that squirreltail density had very little effect on medusahead biomass. Therefore, medusahead competed with itself for nutrients more strongly than with squirreltail, and medusahead competed with squirreltail more strongly than squirreltail competed with itself for nutrient uptake. For squirreltail, this contradicts the theory described above that intraspecific competition should be greater than interspecific competition. Fowler (1986) clarifies this contradiction by explaining that intra- or interspecific interference can be stronger depending upon the particular situation. Furthermore, all of the relative competitive ratios for medusahead were greater than one, and all of the relative competitive ratios for squirreltail were less than one, which further indicates that

medusahead was a stronger competitor for resources than squirreltail. Interspecific interference is a significant influence on plant community structure and dynamics (Aerts 1999), and this attribute of relatively intense interspecific interference may help explain medusahead's competitiveness on disturbed landscape.

All of the models had high R^2 values, which indicated that the explanatory variables of medusahead and squirreltail density accounted for a large portion of variation in medusahead and squirreltail predicted aboveground biomass. R^2 is a measure of the importance of competition (Welden and Slauson 1986). In the medusahead and squirreltail models in trial 1 and in the medusahead model in trial 2, the R^2 values increased when high N treatments were applied in comparison to low N treatments suggesting that competition for N was an especially important factor in the relationship between medusahead and squirreltail. However, in the squirreltail model in trial 2, the R^2 values decreased when high N treatments were applied compared to low N treatments. Perhaps, another factor that had a large impact on plant growth was not accounted for in this case. Nevertheless, R^2 values were relatively high compared to similar studies (Heron et al. 2001, Mangold 2004).

As the product of the double ratio for niche differentiation approaches unity (1.0), plant partitioning of environmental resources decreases, and species are increasingly competing for similar resources (Spitters 1983). In all four nutrient treatments in both trials, niche differentiation was not far from 1.0 (0.5 to 8.0). Therefore, medusahead and squirreltail largely occupied the same ecological niche and mainly competed for the same environmental resources. This is in contrast to bluebunch wheatgrass and spotted knapweed that exhibited extreme niche differentiation and resource partitioning

(Mangold 2004). As expected, greater niche differentiation should occur between species with different growth forms than between species of similar growth forms. Furthermore, N was a major resource for which medusahead and squirreltail competed, as evidenced by increased niche differentiation with decreased soil N. Therefore, medusahead and squirreltail may compete for N more similarly than they compete for P, perhaps due to plant and soil microorganism associations.

Redente et al. (1992) stated that tissue nutrient concentrations could serve as an indicator of species competitive success for soil nutrients when grown in proximity. They found that increased soil N and P levels increased aboveground biomass concentrations of N and P for every plant in their study. The results from my study concur with the results from Redente et al. (1992), in that for trials one and two, the high N treatments increased aboveground biomass N concentrations in medusahead and squirreltail. In addition, the high P treatments increased the concentration of P in medusahead aboveground biomass in both trials. However, the high P treatments increased squirreltail aboveground biomass P concentrations only in trial 1, especially when combined with low N treatments. In trial 2, squirreltail aboveground biomass P concentration was not different between nutrient treatments. This lack of tissue P concentration increase was probably due to aboveground biomass production being influenced to a greater degree by N than by P and as N availability increased, aboveground plant growth increased leaving aboveground biomass P concentration diluted even though soil P levels increased. In support of this argument, Dakheel et al. (1993) found medusahead to be more responsive to N than to P reductions and that medusahead accumulated the greatest biomass at high N and medium P soil levels.

At the beginning of the study, trial 1 potting medium appeared to have more $\text{NO}_3\text{-N}$ and less $\text{NH}_4\text{-N}$ than trial 2. This may be due to trial 1 potting medium having been mixed and saturated eight months prior to being re-saturated and planted, possibly allowing nitrification to occur, thereby converting $\text{NH}_4\text{-N}$ to $\text{NO}_3\text{-N}$. Nitrification may also help explain why trial 1 pretreatment levels of $\text{NO}_3\text{-N}$ were higher than any post treatment level. In trial 2, there were no differences between pre- and post treatment $\text{NO}_3\text{-N}$ levels, which suggests that N additions roughly matched the amount of N extracted by plants. In trials one and two, $\text{NH}_4\text{-N}$ levels may have decreased between pre- and post treatment levels due to nitrification. Ammonium-nitrogen was not added during the course of the study, yet plants likely took up $\text{NH}_4\text{-N}$ in addition to $\text{NO}_3\text{-N}$. In trial 1, the P remaining in the potting medium following the low P treatments was less than pretreatment levels, but P levels remaining following high P treatments were not different from pretreatments levels. This suggests that the high P treatments supplied ample P for near optimum plant growth and the low P treatments supplied less than optimal levels of P.

Concentrations of $\text{NO}_3\text{-N}$ in the potting medium did not change between nutrient treatments for trials one or two. Ammonium-nitrate concentrations were higher after high N treatments than after low N treatments in both trials. Soil P levels differed between every nutrient treatment and P concentrations remaining in the potting medium following the study were greater for high P treatments than for low P treatments in trials one and two. In addition, soil P levels decreased with increased soil N supplementation. I believe this result is due to plant growth being more responsive to N additions and thereby larger plants took up more P from the soil leaving soil P levels lower when high

N treatments were applied than when low N treatments were applied. These results only show the approximate nutrient levels at the time the soil samples were taken, i.e., before and after the experiment, and not during the course of the study. Sampling soil nutrients periodically over the course of the experiment may have revealed different results.

I hypothesized that increased soil N and P would increase medusahead's competitive ability relative to squirreltail. Based on the results from this study, the hypothesis was rejected for N. Intraspecific competition for both species decreased as N increased, and the effect of medusahead density on squirreltail biomass decreased as N increased. However, there was little change in the effect of squirreltail density on medusahead aboveground biomass under different N and P additions. The weak influence of squirreltail density on medusahead biomass at low or high N levels was probably due to medusahead's strong competition with itself for nutrients, masking the effect of squirreltail density on medusahead biomass. The effect of P on the competitive relationship between medusahead and squirreltail was difficult to find amid the greater impact of N. Perhaps a lengthier study would help to realize the effects of P on interference between medusahead and squirreltail. Blackshaw et al. (2004) suggested that soil P concentrations might influence populations of weeds over long periods of time.

Hironaka and Sindelar (1973) demonstrated that squirreltail could establish in medusahead stands without first reducing competition. However, the results from my study suggest that squirreltail cannot effectively compete with medusahead in the short-term. In order to establish squirreltail in medusahead dominated rangelands, competition would need to be reduced and disturbance managed to minimize N availability. 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. Restoring medusahead infested rangeland with squirreltail may hold the most potential in environments with low nutrient availability, because root morphology and root allocations are often more influential in the long-term than are the dynamics of nutrient uptake in the competition for nutrients (Aerts 1999).

CHAPTER 4: GROWTH ANALYSIS OF MEDUSAHEAD AND SQUIRRELTAIL

INTRODUCTION

Plant growth is dependent upon a plant's ability to obtain resources necessary for growth, and plants must acquire resources to increase in size and perpetuate their species (Radosevich et al. 1997). Because current plant growth is dependent on previous plant growth (Evans 1972), the increase in biomass and photosynthetically active shoot material are crucial to evaluating vegetative growth (Radosevich et al. 1997). Evaluation of plant growth includes measuring and analyzing biomass accumulated as leaves, stems, reproductive organs, and roots (Radosevich et al. 1997). Growth analysis conducted with plants grown individually under environmentally uniform conditions can predict the competitive mechanisms and performance of species grown in mixed stands and serve as an indicator of future competitive success (Radosevich et al. 1997).

Measurements of absolute plant growth and growth rate may help explain why some species are competitively superior to other species. Because plant growth is directly related to the amount of resources sequestered from the environment, a species potential competitive ability is indicated by its mean relative growth rate, which is the amount of plant growth over a time interval relative to plant size at the beginning of the time interval. These measurements can increase our understanding of the effects of the environment, resource limitations, and other plants on plant growth (Radosevich et al. 1997). For example, Holt and Orcutt (1991) combined a growth analysis and competition study and found that the weeds in their study produced greater leaf area, biomass, and relative growth rates than cotton. Their findings identified plant

characteristics that may have endowed the weeds with the competitive superiority over cotton that was found in the competition study (Holt and Orcutt 1991).

A species life history strategy also influences its growth rate, resource allocation, and response to resource availability. For example, annuals and short-lived perennials have high maximum relative growth rates, which allows for quick life cycle completion and the opportunity to preempt available resources necessary for growth (Grime and Hunt 1975). Arredondo et al. (1998) found that annual plants had higher belowground biomass, aboveground biomass, and leaf area growth rates than perennials, and the annual species aboveground biomass growth rates were higher than belowground growth rates. Annual and perennial grasses can also employ different root growth schemes (Arredondo et al. 1998). Arredondo et al. (1998) found that annual grasses developed root systems with greater length, whereas the perennial grasses developed thicker roots. Korner and Renhardt (1987) suggested that production of many thin roots may be a more efficient use of carbon than the production of thicker perennial roots believed to be important in sustaining perennial plant life (Arredondo et al. 1998, Hironaka and Sindelar 1975).

The invasion of exotic species into ecosystems endangers natural plant communities (Heywood 1989). Medusahead (*Taeniatherum caput-medusae* ssp. *asperum* (Simk.) Melderis) is an invasive, winter-annual grass that invades native plant communities, altering biological and physical site potential (Young 1992). Medusahead has the potential to quickly spread, dominate, and permanently injure many plant communities (BLM 1996). Medusahead was introduced to North America around the late 1800s from Eurasia (McKell et al. 1962a), probably via livestock importation

(Hilken and Miller 1980). It has disseminated from Roseburg, Oregon, to Washington, Idaho, California (McKell et al. 1962a), Nevada (Young et al. 1968), and Utah (Horton 1991) and may infest hundreds of thousands of hectares (Young 1992).

Medusahead has many aggressive characteristics that allow it to invade and dominate many native ecosystems. Medusahead has a short life span and high seed production, typical of a ruderal (*sensu* Grime 1979) species. On good soil in dense stands, Sharp et al. (1957) observed 1,500 to 2,000 plants per square foot with an average of 8.7 seed heads per plant, while on poor soil they observed 500 plants per square foot with an average of 5.6 seed heads per plant. Medusahead germinates in the fall and grows rapidly in the spring with seed heads appearing in May (Murphy and Turner 1959), and plants maturing in June/July (Sharp et al. 1957). Medusahead seeds require cold temperatures prior to germination. Young et al. (1968) found optimal germination with treatments of 10 and 15°C. To complete its life cycle, medusahead requires soil moisture availability later into the spring than cheatgrass (*Bromus tectorum* L.) (Hironaka 1961) and commonly occupies clay soils that maintain moisture for a longer period of time (Fosberg 1965). However, medusahead is also capable of growing in coarser textured soils with an argillic horizon (Young 1992) and even has the capacity to encroach on native shrub-steppe plant communities with loam soils (Miller 1996).

Because of medusahead's high silica content, its litter decomposes slowly (Bovey et al. 1961), allowing litter to accumulate and stifle the growth of other plants (Harris 1965). Medusahead litter is unpalatable (Bovey et al. 1961), very susceptible to burning (McKell et al. 1962b), and reduces germination of other species by preventing their seeds from touching the soil (Young 1992). However, medusahead seeds can germinate within

the litter layer because it provides the right humidity for germination (Young 1992). Furthermore, if the initial root becomes desiccated, a new root may emerge when moisture becomes available (Young 1992). Medusahead is also able to sustain root growth in cool temperatures and acquire soil moisture and nutrients earlier in the season than bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), a native perennial grass common to semi-arid western rangeland (Harris and Wilson 1970). When a seed source is available, medusahead is more likely to invade disturbed sites where competition from other plants has been reduced (Miller 1996). With medusahead's high seed production, litter accrual, cool season root growth, and fall germination, it can efficiently compete with desirable forage species (Hilken and Miller 1980) and develop dense monocultures.

Healthy, perennial vegetation is the most effective form of control against medusahead encroachment (Turner et al. 1963). Hironaka and Tisdale (1963) suggested that over time squirreltail may establish in medusahead stands as manifest in the western Great Basin (Young 1992). Hironaka and Sindelar (1973) demonstrated that squirreltail could establish in medusahead stands without first reducing competition. Additionally, Jones (1998) stated that squirreltail may be useful in restoration of medusahead infested rangeland. However, Young (1992) cautioned that successful squirreltail establishment may not lead to occupation by longer-lived perennial grasses over time.

Squirreltail is an early to mid seral, cool-season, native, short-lived perennial grass that germinates in the fall and has a strong ability to establish in land dominated by annual plants (Arredondo et al. 1998, Hironaka and Sindelar 1973, and Hironaka and Tisdale 1963). Squirreltail can germinate across a range of temperatures (Young and

Evans 1977). The most favorable soil temperature for seedling growth is 25°C while root growth continues at 5 °C (Hironaka and Tisdale 1972). Cool season root growth may help explain squirreltail's ability to compete with annual grasses (Hironaka and Tisdale 1972). Squirreltail has a variety of other attributes that may help it compete with medusahead including self-pollination, wide ecotypic variations, and seed dispersal mechanisms (Jensen et al. 1990, Jones 1998, and Arredondo et al. 1998).

Growth analysis measurements are useful in explaining the mechanisms by which species compete. Even though extensive understanding has been acquired in reference to growth analysis and interference between plants, often related to crop production, knowledge of which specific growth characteristics enable invasive annual weeds and native perennials to compete for resources is insufficient. A greater understanding of plant growth habits and their effect on interference relationships would improve a land manager's ability to use native species in restoration of annual weed infested rangelands. As suggested by Arredondo et al. (1998), more studies are required to more fully understand how colonization of annual dominated lands by squirreltail occurs. This study evaluated the individual growth habits of medusahead and squirreltail in an attempt to understand invasion of rangeland by medusahead, squirreltail recolonization of medusahead infested rangelands, and the feasibility of restoring medusahead infested rangelands to healthy and functioning native ecosystems using squirreltail.

OBJECTIVES

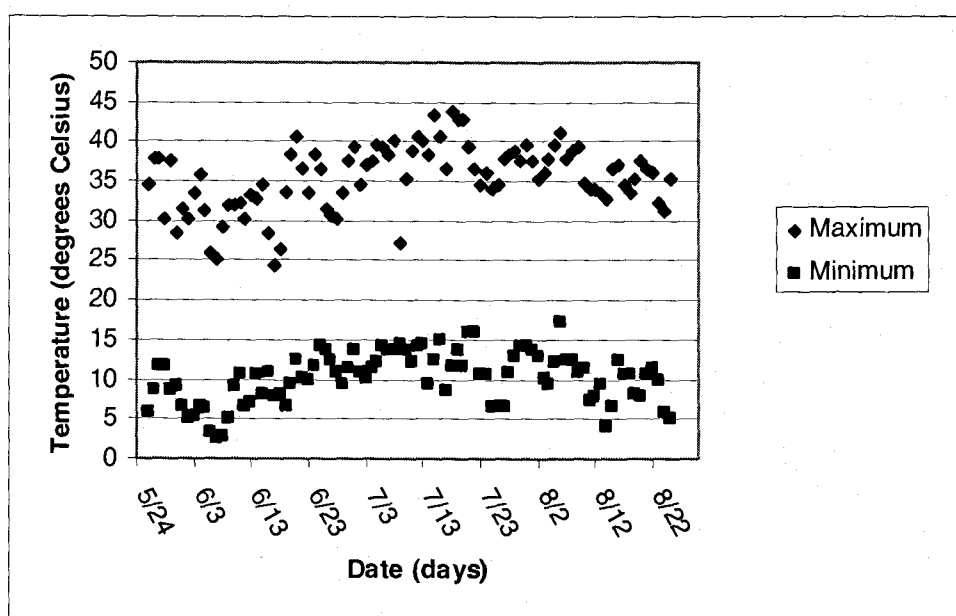
The overall objective of this study was to measure growth analysis parameters to help explain interference between medusahead and squirreltail across low and high soil N and P levels. More specifically, the objective included comparing belowground biomass,

aboveground biomass, total biomass, root:shoot ratios, leaf area, and root length of medusahead and squirreltail grown individually. I hypothesized that medusahead would exhibit higher growth rates than squirreltail, especially for aboveground biomass, and that squirreltail would allocate more of its biomass to belowground growth.

METHODS

This study was conducted in a greenhouse at the Eastern Oregon Agricultural Research Center in Burns, Oregon, from May 25-August 25, 2005. Burns is 1,265 meters above sea level and located at latitude 43°35'N and longitude 119°03'W. The average annual temperature is 7.8°C, average annual precipitation is 279.4 mm, and annual average growing degree-days (base 10°C) is 1,881 (WRCC 2004). The average daily temperature in the greenhouse during the experiment was 22.0°C (Figure 4.1). Photosynthetically active radiation between 11 am and 2 pm averaged $703 \mu\text{mol s}^{-1}\text{m}^{-2}$.

Figure 4.1. Maximum and minimum greenhouse temperatures



Medusahead seed was locally collected by hand during the summer of 2003. The medusahead seed was cleaned and partially de-awned with a rubbing board and Ferrell-Ross seed cleaner during the summer of 2004. Cleaned squirreltail seed was purchased from L and H Seed in southeastern Washington in the spring of 2004.

The study was conducted in pots (polyvinyl chloride pipe) with a surface area of 0.018 m^2 and depth of 0.98 m. Weed barrier fabric covered the bottoms of pots and was secured with tape or perforated (five holes at 0.5953 cm) PVC end caps.

Field soil that had supported squirreltail and medusahead was collected from John Day, Oregon, and sieved through a 0.6 cm screen to remove rocks and large roots. The potting medium consisted of soil mixed with concrete grade sand in a one to one ratio by volume. Potting medium was saturated with approximately 4,600 ml of tap water prior to planting. Pots were allowed to drain to column capacity, then seeds were uniformly scattered across the surface of each pot. Five seeds of medusahead or squirreltail were planted in 40 separate pots (20 pots for each species), and covered with approximately two mm of field soil. Pots were arranged in a completely randomized design (CRD). Pots were covered with clear plastic for six to seven days following planting to maintain humidity conducive to germination. The pots were misted twice daily as needed throughout the study to prevent water stress. Volunteer seedlings of undesired species were pulled as necessary. The density of each pot was reduced to one vigorous seedling following establishment. The CRD was replicated in time with trial 2 beginning 20 days following the planting of trial 1. Each trial lasted approximately 70 days with trial 1 running May 26-August 4 and trial 2 running June 14-August 23, 2005. No nutrient treatments were applied.

On 14 day intervals, four squirreltail and four medusahead plants were randomly sampled throughout the 70-day trials with the following two exceptions from trial 1: 1) growth period (GP) 2 between sample dates (SD) 28 and 35 days post planting (dpp) was seven days and GP 3 between SD 35 and 56 dpp was 21 days long, whereas all other GPs in trial 1 and trial 2 were approximately 14 days long; and 2) only two plants of each species were measured 14 dpp and six plants of each species were measured 28 dpp in trial 1. After rinsing soil from roots, root penetration was measured, above- and belowground biomass separated, leaf area quantified (Licor-3100 with conveyor belt, LICOR, Inc. Lincoln, Neb.), root length determined (WinRHIZO 2005 Reg. with LC4800 scanner, Regent Instruments, Inc. Sainte-Foy, Qc, Canada), and above- and belowground biomass dried (72 hours at 50°C) and weighed. Depth of root penetration, belowground biomass, aboveground biomass, leaf area, and root length were measured directly and root:shoot ratio and total biomass were calculated from the direct measurements for each SD.

Data collected from each trial were analyzed separately because soils for the two trials were collected at different sites and times and the biomass accumulation was greater in trial 2. Growth, growth rates, and relative growth rates were calculated using the following equations:

Growth = plant weight at a specified point in time.

$$\text{Growth Rate} = \frac{W_2 - W_1}{t_2 - t_1}$$

where W_1 equals initial plant weight at the beginning of a growth period (t_1) and

W_2 equals plant weight at the end of a growth period (t_2).

$$\text{Relative Growth Rate} = \bar{R} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_1 equals initial plant weight at the beginning of a growth period (t_1), and

W_2 equals plant weight at the ending of a growth period (t_2) (Evans 1972).

Growth, growth rates, and relative growth rates were analyzed using ANOVA and means were compared between species within SDs and within species between SDs using Fisher's least significant difference ($\text{LSD}_{\alpha=0.05}$).

RESULTS

In trial 1, biomass increased for both species over time with medusahead producing more below- and aboveground biomass than squirreltail at SD 28 (61 and 157%), SD 56 (105 and 170%), and SD 70 (57 and 76%, respectively) (Table 4.1). Medusahead root:shoot ratios ranged from 0.6 to 1.2 and squirreltail root:shoot ratios ranged from 0.8 to 1.1. The only significant difference between medusahead and squirreltail root:shoot ratios occurred at SD 28 when squirreltail allocated 60% more of its resources to roots than medusahead. Total biomass and leaf area increased for both species over time with medusahead producing more biomass and leaf area than squirreltail at SD 28 (110, 126%), SD 56 (136, 135%), and SD 70 (91, 91%, respectively). Root length increased for both species over time with medusahead producing more root length at each sample date after SD 14 (135% average increase). Depth of root penetration is not reported because medusahead roots reached the bottom of the pots soon after SD 28.

Table 4.1. Trial 1 comparison of plant growth parameter means between medusahead and squirreltail for respective sample dates.

Sample Date (dpp)	Belowground biomass (g)		Aboveground biomass (g)		Root:shoot ratio		Total biomass (g)		Leaf area (cm ²)		Root length (cm)	
	M	S	M	S	M	S	M	S	M	S	M	S
14	0.005 (NS)	0.004 (NS)	0.004 (NS)	0.004 (NS)	1.214 (NS)	0.837 (NS)	0.009 (NS)	0.008 (NS)	1.6 (NS)	1.4 (NS)	352 (NS)	155 (NS)
P-value	0.47		0.87		0.09		0.68		0.50		0.15	
28	0.029 (0.003)	0.018 (0.002)	0.050 (0.006)	0.019 (0.002)	0.591 (0.025)	0.947 (0.051)	0.079 (0.009)	0.038 (0.003)	12.8 (1.7)	5.7 (0.7)	1656 (122)	932 (119)
P-value	0.01		<0.01		<0.01		<0.01		<0.01		<0.01	
35	0.059 (NS)	0.032 (NS)	0.090 (NS)	0.041 (NS)	0.662 (NS)	0.818 (NS)	0.149 (NS)	0.073 (NS)	16.7 (NS)	12.0 (NS)	3591 (729)	1698 (183)
P-value	0.10		0.06		0.22		0.07		0.33		0.05	
56	0.522 (0.022)	0.255 (0.065)	0.622 (0.034)	0.231 (0.043)	0.842 (NS)	1.063 (NS)	1.144 (0.05)	0.485 (0.10)	127.5 (9.5)	54.3 (10.3)	27386 (1340)	8466 (1686)
P-value	0.01		<0.01		0.26		<0.01		<0.01		<0.01	
70	1.099 (0.036)	0.698 (0.092)	1.185 (0.110)	0.673 (0.120)	0.949 (NS)	0.897 (NS)	2.285 (0.110)	1.196 (0.305)	231.2 (38.9)	120.8 (18.9)	49101 (2967)	22534 (4956)
P-value	0.01		0.02		0.64		0.02		0.04		0.01	

dpp=days post planting, M=medusahead, and S=squirreltail. Numbers in parentheses are standard errors for parameters significantly different between medusahead and squirreltail for identical sample dates ($P=0.05$).

For trial 1, medusahead belowground biomass, aboveground biomass, total biomass, leaf area, and root length, compared between SDs, did not increase until SD 56 (Table 4.2). Medusahead belowground and aboveground biomass increased by 1.09 and 1.18 g, respectively, between SDs 14 and 70. Medusahead root:shoot ratios decreased from SD 14 to SDs 28, 35, 56, and 70 by 0.62, 0.55, 0.37, and 0.26, respectively. However, medusahead root:shoot ratios increased when comparing SDs 28-56, 28-70, 35-70, and 56-70 by 0.25, 0.36, 0.29, and 0.11, respectively. Total biomass increased by 2.28 g from SD 14 to SD 70. Medusahead leaf area was 230.0 cm² greater by SD 70 than at SD 14, while root length increased by 48,700 cm during the same time.

Trial 1 squirreltail growth parameter differences between SDs for belowground biomass, aboveground biomass, leaf area, and root length did not increase until SD 56 when compared with earlier SDs (Table 4.2). Squirreltail belowground and aboveground biomass increased for SD comparison 14-70 by 0.70 and 0.67 g, respectively. Squirreltail root:shoot ratios did not change between SDs. Squirreltail total biomass increased 1.19, 0.45, 1.16, 1.12, and 0.71 g from SDs 14-70, 28-56, 28-70, 35-70, and 56-70, respectively. Leaf area increased by 119.0 cm² between SD 14 and 70. When comparing SDs 14 and 70, root length increased by 22,400 cm.

For trial 2, medusahead belowground biomass was greater than squirreltail belowground biomass for SD 44 (117%) and 72 (81% greater) (Table 4.3). Medusahead aboveground biomass was greater than squirreltail aboveground biomass for every sampling date (144% average) with increasing disparity over time. Root:shoot ratios for medusahead and squirreltail ranged from 0.3 to 0.6 and 0.5 to 0.7, respectively. Squirreltail root:shoot ratios were always higher than medusahead ratios except for SD 17. Total biomass and leaf area for medusahead were greater than for squirreltail at SD 30 (37, 59%), 44 (180, 215%), 58 (198, 273%), and 72 (113, 140%). Medusahead root length was 192, 252, and 297% greater than squirreltail root length for SD 44, 58, and 72, respectively. Depth of root penetration is not reported because medusahead roots reached the bottom of the pots soon after SD 17.

Table 4.2. Trial 1 plant growth parameter differences between sampling dates for medusahead and squirreltail.

Medusahead						
Sample Dates (dpp)	Belowground Biomass (g)	Aboveground Biomass (g)	Root:Shoot Ratio	Total Biomass (g)	Leaf Area (cm ²)	Root Length (cm)
14-28	0.024 (NS)	0.046 (NS)	-0.622 (0.103)	0.070 (NS)	11.2 (NS)	1300 (NS)
14-35	0.054 (NS)	0.086 (NS)	-0.551 (0.109)	0.140 (NS)	15.1 (NS)	3240 (NS)
14-56	0.517 (0.035)	0.618 (0.091)	-0.372 (0.109)	1.140 (0.099)	126.0 (31.2)	27000 (2590)
14-70	1.090 (0.035)	1.180 (0.091)	-0.264 (0.109)	2.280 (0.099)	230.0 (31.2)	48700 (2590)
28-35	0.030 (NS)	0.040 (NS)	0.071 (NS)	0.070 (NS)	3.9 (NS)	1940 (NS)
28-56	0.493 (0.026)	0.572 (0.068)	0.250 (0.082)	1.070 (0.074)	115.0 (23.3)	25700 (1930)
28-70	1.070 (0.026)	1.140 (0.068)	0.358 (0.082)	2.210 (0.074)	218.0 (23.3)	47400 (1930)
35-56	0.462 (0.028)	0.533 (0.074)	0.179 (NS)	0.995 (0.081)	111.0 (25.5)	23800 (2110)
35-70	1.040 (0.28)	1.100 (0.074)	0.287 (0.089)	2.140 (0.081)	214.0 (25.5)	45500 (2110)
56-70	0.577 (0.28)	0.563 (0.074)	0.107 (0.089)	1.140 (0.081)	104.0 (25.5)	21700 (2110)
LSD CP						
95%	2.131	2.131	2.131	2.131	2.131	2.131
P-value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Squirreltail						
Sample Dates (dpp)	Belowground Biomass (g)	Aboveground Biomass (g)	Root:Shoot Ratio	Total Biomass (g)	Leaf Area (cm ²)	Root Length (cm)
14-28	0.015 (NS)	0.015 (NS)	0.109 (NS)	0.030 (NS)	4.2 (NS)	777 (NS)
14-35	0.028 (NS)	0.036 (NS)	-0.019 (NS)	0.065 (NS)	10.5 (NS)	1540 (NS)
14-56	0.251 (0.074)	0.226 (0.099)	0.225 (NS)	0.477 (NS)	52.8 (16.8)	8310 (3130)
14-70	0.695 (0.078)	0.668 (0.099)	0.060 (NS)	1.190 (0.249)	119.0 (16.8)	22400 (3290)
28-35	0.014 (NS)	0.021 (NS)	-0.129 (NS)	0.035 (NS)	6.3 (NS)	766 (NS)
28-56	0.237 (0.055)	0.211 (0.074)	0.116 (NS)	0.447 (0.186)	48.6 (12.5)	7530 (2330)
28-70	0.680 (0.061)	0.653 (0.074)	-0.050 (NS)	1.160 (0.186)	115.0 (12.5)	21600 (2550)
35-56	0.223 (0.061)	0.189 (0.081)	0.245 (NS)	0.412 (NS)	42.3 (13.7)	6770 (2550)
35-70	0.666 (0.065)	0.632 (0.081)	0.079 (NS)	1.120 (0.204)	109.0 (13.7)	20800 (2760)
56-70	0.444 (0.065)	0.442 (0.081)	-0.166 (NS)	0.712 (0.204)	66.5 (13.7)	14100 (2760)
LSD CP						
95%	2.145	2.131	2.145	2.131	2.131	2.145
P-value	<0.01	<0.01	0.45	<0.01	<0.01	<0.01

dpp=days post planting. Numbers in parentheses are standard errors for parameters significantly different between sampling dates (SDs) for medusahead and squirreltail, separately (P=0.05). CP=Critical Point.

Table 4.3. Trial 2 comparison of plant growth parameter means between medusahead and squirreltail for respective sample dates.

Sample Date (dpp)	Belowground biomass (g)		Aboveground biomass (g)		Root:shoot ratio		Total biomass (g)		Leaf area (cm ²)		Root length (cm)	
	M	S	M	S	M	S	M	S	M	S	M	S
17	0.006 (NS)	0.005 (NS)	0.011 (0.001)	0.008 (0.001)	0.539 (NS)	0.689 (NS)	0.016 (NS)	0.013 (NS)	3.9 (NS)	4.1 (NS)	319 (NS)	316 (NS)
P-value	0.56		0.01		0.06		0.05		0.95		0.95	
30	0.040 (NS)	0.038 (NS)	0.95 (0.006)	0.060 (0.003)	0.416 (0.017)	0.640 (0.059)	0.135 (0.010)	0.099 (0.003)	23.2 (1.6)	14.6 (1.2)	2097 (NS)	1668 (NS)
P-value	0.74		<0.01		0.01		0.01		0.01		0.21	
44	0.288 (0.030)	0.132 (0.011)	0.778 (0.072)	0.248 (0.012)	0.370 (0.017)	0.532 (0.034)	1.065 (0.099)	0.380 (0.021)	164.4 (15.4)	52.0 (2.3)	14363 (1147)	4916 (487)
P-value	<0.01		<0.01		0.01		<0.01		<0.01		<0.01	
58	0.809 (NS)	0.465 (NS)	2.702 (0.355)	0.712 (0.163)	0.317 (0.053)	0.605 (0.074)	3.511 (0.338)	1.177 (0.301)	527.3 (120.5)	141.2 (32.4)	34912 (4895)	9921 (2476)
P-value	0.07		<0.01		0.02		<0.01		0.02		<0.01	
72	2.130 (0.158)	1.174 (0.268)	3.869 (0.336)	1.646 (0.263)	0.554 (NS)	0.694 (NS)	5.998 (0.487)	2.819 (0.526)	673.3 (21.7)	280.7 (50.3)	85760 (5496)	21608 (4390)
P-value	0.02		<0.01		0.06		<0.01		<0.01		<0.01	

dpp=days post planting, M=medusahead, and S=squirreltail. Numbers in parentheses are standard errors for parameters significantly different between medusahead and squirreltail for identical sample dates (P=0.05).

Trial 2 medusahead belowground biomass, aboveground biomass, total biomass, leaf area, and root length were different between every SD comparison except 17-30 (Table 4.4). Medusahead belowground and aboveground biomass growth increased by 2.12 and 3.86 g, respectively, for SD comparison 17-72. Root:shoot ratios decreased from SD 17 to SDs 30, 44, and 58 by 0.12, 0.17, and 0.22, respectively, then increased by 0.14, 0.18, and 0.24 between SDs 30-72, 44-72, and 58-72. However, beginning and ending root:shoot ratios were not different. Medusahead total biomass increased by 5.98 g for SD comparisons 17-72. For this same SD comparisons, leaf area increased by 669.0 cm². Root length increased by 85400 cm between the first and last SDs.

Trial 2 plant growth parameter differences between SDs for squirreltail belowground biomass, aboveground biomass, total biomass, leaf area, and root length did not increase until SD 58 when compared with earlier SDs (Table 4.4). Squirreltail belowground and aboveground biomass increased by 1.17g and 1.64 g, respectively, between SDs 17 and 72. Squirreltail root:shoot ratios were not different between any SD comparisons. Total biomass increased by 2.81 g, leaf area increased by 277.0 cm², and root length increased by 21,300 cm between SDs 17 and 72.

Mean growth rates in trial 1 for aboveground biomass, total biomass, and leaf area in GP 1 (GP=14 days) were 335.0, 215.9, and 495.2% greater for medusahead than for squirreltail (Table 4.5). Medusahead rates of increase for belowground biomass, aboveground biomass, total biomass, leaf area, and root length in GP 3 were 107.5, 180.7, 141.7, 161.9, and 251.6% greater than squirreltail rates of increase. Other plant growth rate comparisons between species were not different within GPs.

Trial 1 medusahead belowground and aboveground biomass increased by 0.02, 0.04, 0.02, and 0.04 g day⁻¹ for GP comparisons 1-3, 1-4, 2-3, and 2-4, respectively, while belowground biomass increased by 0.02 and aboveground biomass increased by 0.01 g day⁻¹ for GP comparison 3-4 (Table 4.6). Medusahead total biomass increased by 0.04, 0.08, 0.04, 0.07, and 0.03 g day⁻¹ for GP comparisons 1-3, 1-4, 2-3, 2-4, and 3-4, respectively. Leaf area increased 6.3 cm² day⁻¹ for GP comparison 1-4 and 7.0 cm² day⁻¹ for GP comparison 2-4. Root length increased by 1,020, 1,440, 858, 1,280, and 418 cm day⁻¹ for GP comparisons 1-3, 1-4, 2-3, 2-4, and 3-4.

Table 4.4. Trial 2 plant growth parameter differences between sampling dates for medusahead and squirreltail.

Medusahead						
Sample Dates (dpp)	Belowground Biomass (g)	Aboveground Biomass (g)	Root:Shoot Ratio	Total Biomass (g)	Leaf Area (cm ²)	Root Length (cm)
17-30	0.034 (NS)	0.085 (NS)	-0.123 (0.050)	0.119 (NS)	19.3 (NS)	1780 (NS)
17-44	0.282 (0.112)	0.767 (0.312)	-0.169 (0.050)	1.050 (0.380)	160.0 (58.4)	14000 (4710)
17-58	0.804 (0.112)	2.690 (0.312)	-0.222 (0.050)	3.490 (0.380)	523.0 (63.1)	34600 (4710)
17-72	2.120 (0.112)	3.860 (0.312)	0.014 (NS)	5.980 (0.380)	669.0 (58.4)	85400 (4710)
30-44	0.248 (0.112)	0.682 (0.312)	-0.046 (NS)	0.930 (0.380)	141.0 (58.4)	12300 (4710)
30-58	0.769 (0.112)	2.610 (0.312)	-0.099 (NS)	3.380 (0.380)	504.0 (63.1)	32800 (4710)
30-72	2.090 (0.112)	3.770 (0.312)	0.137 (0.050)	5.860 (0.380)	650.0 (58.4)	83700 (4710)
44-58	0.522 (0.112)	1.920 (0.312)	-0.053 (NS)	2.450 (0.380)	363.0 (63.1)	20500 (4710)
44-72	1.840 (0.112)	3.090 (0.312)	0.184 (0.050)	4.930 (0.380)	509.0 (58.4)	71400 (4710)
58-72	1.320 (0.112)	1.170 (0.312)	0.236 (0.050)	2.490 (0.380)	146.0 (63.1)	50800 (4710)
LSD CP 95%	2.131	2.131	2.131	2.131	2.145	2.131
P-value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Squirreltail						
Sample Dates (dpp)	Belowground Biomass (g)	Aboveground Biomass (g)	Root:Shoot Ratio	Total Biomass (g)	Leaf Area (cm ²)	Root Length (cm)
17-30	0.033 (NS)	0.053 (NS)	-0.049 (NS)	0.086 (NS)	10.6 (NS)	1350 (NS)
17-44	0.127 (NS)	0.240 (NS)	-0.156 (NS)	0.367 (NS)	48.1 (NS)	4600 (NS)
17-58	0.460 (0.191)	0.704 (0.196)	-0.084 (NS)	1.160 (0.384)	137.0 (37.9)	9610 (3200)
17-72	1.170 (0.191)	1.640 (0.196)	0.005 (NS)	2.810 (0.384)	277.0 (37.9)	21300 (3200)
30-44	0.094 (NS)	0.188 (NS)	-0.107 (NS)	0.282 (NS)	37.5 (NS)	3250 (NS)
30-58	0.427 (0.191)	0.652 (0.196)	-0.035 (NS)	1.080 (0.384)	127.0 (37.9)	8250 (3200)
30-72	1.140 (0.191)	1.590 (0.196)	0.054 (NS)	2.720 (0.384)	266.0 (37.9)	19900 (3200)
44-58	0.333 (NS)	0.464 (0.196)	0.073 (NS)	0.80 (NS)	89.1 (37.9)	5010 (NS)
44-72	1.040 (0.191)	1.400 (0.196)	0.162 (NS)	2.440 (0.384)	229.0 (37.9)	16700 (3200)
58-72	0.709 (0.191)	0.933 (0.196)	0.089 (NS)	1.640 (0.384)	140.0 (37.9)	11700 (3200)
LSD CP 95%	2.131	2.131	2.131	2.131	2.131	2.131
P-value	<0.01	<0.01	0.27	<0.01	<0.01	<0.01

dpp=days post planting. Numbers in parentheses are standard errors for parameters significantly different between sampling dates (SDs) for medusahead and squirreltail, separately (P=0.05). CP=Critical Point.

Table 4.5. Trial 1 comparison of mean growth rates between medusahead and squirreltail for respective growth periods.

Growth Period	Belowground biomass (g day ⁻¹)		Aboveground biomass (g day ⁻¹)		Total biomass (g day ⁻¹)		Leaf area (cm ² day ⁻¹)		Root length (cm day ⁻¹)	
	M	S	M	S	M	S	M	S	M	S
1	0.002 (NS)	0.001 (NS)	0.004 (0.000)	0.001 (0.000)	0.007 (0.001)	0.002 (0.000)	1.1 (0.2)	0.2 (0.0)	111 (NS)	53 (NS)
P-value	0.18		0.02		0.04		0.04		0.16	
2	0.004 (NS)	0.002 (NS)	0.005 (NS)	0.003 (NS)	0.009 (NS)	0.004 (NS)	0.4 (NS)	0.9 (NS)	275 (NS)	88 (NS)
P-value	0.27		0.44		0.35		0.49		0.10	
3	0.022 (0.001)	0.011 (0.003)	0.025 (0.001)	0.009 (0.002)	0.047 (0.002)	0.020 (0.005)	5.3 (0.6)	2.0 (0.5)	1133 (67)	322 (83)
P-value	0.01		<0.01		<0.01		0.01		<0.01	
4	0.041 (NS)	0.019 (NS)	0.040 (NS)	0.032 (NS)	0.081 (NS)	0.051 (NS)	7.4 (NS)	4.8 (NS)	1551 (NS)	602 (NS)
P-value	0.23		0.45		0.27		0.43		0.13	

M=medusahead and S=squirreltail. Numbers in parentheses are standard errors for parameters significantly different between medusahead and squirreltail for identical growth periods ($P=0.05$).

Trial 1 squirreltail aboveground biomass increased during GP comparisons 1-4, 2-4, and 3-4 by 0.03, 0.03, and 0.02 g day⁻¹, respectively, and total biomass increased by 0.05 g day⁻¹ during GP comparison 2-4 (Table 4.6). Squirreltail leaf area increased by 4.6, 3.9, and 2.7 cm² day⁻¹ between GPs 1 and 4, 2 and 4, and 3 and 4, respectively. Squirreltail growth rates did not change between GPs for belowground biomass or root length.

Table 4.6. Trial 1 comparison of mean growth rates between growth periods for medusahead and squirreltail.

Medusahead					
Growth Periods	Belowground Biomass (g day ⁻¹)	Aboveground Biomass (g day ⁻¹)	Total Biomass (g day ⁻¹)	Leaf Area (cm ² day ⁻¹)	Root Length (cm day ⁻¹)
1-2	0.002 (NS)	0.001 (NS)	0.002 (NS)	-0.7 (NS)	164 (NS)
1-3	0.020 (0.004)	0.021 (0.007)	0.041 (0.008)	4.2 (NS)	1020 (206)
1-4	0.039 (0.004)	0.036 (0.007)	0.075 (0.008)	6.3 (2.8)	1440 (206)
2-3	0.018 (0.003)	0.020 (0.006)	0.038 (0.007)	4.9 (NS)	858 (168)
2-4	0.037 (0.003)	0.035 (0.006)	0.072 (0.007)	7.0 (2.3)	1280 (168)
3-4	0.019 (0.003)	0.015 (0.006)	0.034 (0.007)	2.1 (NS)	418 (168)
LSD CP					
95%	2.228	2.228	2.228	2.228	2.228
P-value	<0.01	<0.01	<0.01	0.05	<0.01
Squirreltail					
Growth Periods	Belowground Biomass (g day ⁻¹)	Aboveground Biomass (g day ⁻¹)	Total Biomass (g day ⁻¹)	Leaf Area (cm ² day ⁻¹)	Root Length (cm day ⁻¹)
1-2	0.001 (NS)	0.002 (NS)	0.002 (NS)	0.7 (NS)	35 (NS)
1-3	0.010 (NS)	0.008 (NS)	0.018 (NS)	1.8 (NS)	269 (NS)
1-4	0.018 (NS)	0.031 (0.008)	0.049 (NS)	4.6 (1.4)	549 (NS)
2-3	0.009 (NS)	0.006 (NS)	0.015 (NS)	1.2 (NS)	234 (NS)
2-4	0.018 (NS)	0.029 (0.007)	0.046 (0.019)	3.9 (1.2)	514 (NS)
3-4	0.009 (NS)	0.028 (0.007)	0.031 (NS)	2.7 (1.2)	280 (NS)
LSD CP					
95%	2.228	2.228	2.228	2.228	2.228
P-value	0.52	0.01	0.12	0.02	0.57

Numbers in parentheses are standard errors for parameters significantly different between growth periods for medusahead and squirreltail, separately (P=0.05). CP=Critical Point.

The mean growth rate in trial 2 for medusahead belowground biomass in GP 2 was 164% greater than for squirreltail (Table 4.7). Medusahead growth rates for aboveground biomass were 62, 263, and 314 % greater during GP 1, 2, and 3 while total biomass growth rates were 39, 230, and 207% greater, respectively, than for squirreltail. Leaf area growth rates for medusahead in GP 1 and 2 were 82 and 277% greater, respectively, than for squirreltail. Medusahead growth rates for root length in GP 2, 3,

and 4 were 278, 311, and 804% greater, respectively, than for squirreltail. Other growth rate comparisons between species were not different for corresponding GPs.

Table 4.7. Trial 2 comparison of mean growth rates between medusahead and squirreltail for respective growth periods.

Growth Period	Belowground biomass (g day ⁻¹)		Aboveground biomass (g day ⁻¹)		Total biomass (g day ⁻¹)		Leaf area (cm ² day ⁻¹)		Root length (cm day ⁻¹)	
	M	S	M	S	M	S	M	S	M	S
1	0.003 (NS)	0.003 (NS)	0.007 (0.000)	0.004 (0.000)	0.009 (0.001)	0.007 (0.000)	1.5 (0.2)	0.8 (0.1)	137 (NS)	104 (NS)
P-value	0.80		<0.01		0.02		0.02		0.24	
2	0.018 (0.002)	0.007 (0.001)	0.049 (0.006)	0.013 (0.001)	0.066 (0.008)	0.020 (0.002)	10.1 (1.2)	2.7 (0.1)	876 (88)	232 (39)
P-value	0.01		<0.01		<0.01		<0.01		<0.01	
3	0.037 (NS)	0.024 (NS)	0.137 (0.021)	0.033 (0.011)	0.175 (0.019)	0.057 (0.021)	16.5 (NS)	6.4 (NS)	1468 (370)	358 (155)
P-value	0.28		0.01		0.01		0.37		0.03	
4	0.094 (NS)	0.051 (NS)	0.083 (NS)	0.067 (NS)	0.178 (NS)	0.117 (NS)	19.8 (NS)	10.0 (NS)	3632 (577)	835 (348)
P-value	0.13		0.72		0.38		0.47		0.01	

M=medusahead and S=squirreltail. Numbers in parentheses are standard errors for parameters significantly different between medusahead and squirreltail for identical growth periods ($P=0.05$).

For trial 2, medusahead belowground biomass increased during GP comparisons 1-3, 1-4, 2-3, 2-4 and 3-4 by 0.04, 0.09, 0.02, 0.08, and 0.06 g day⁻¹, respectively (Table 4.8). During GP comparisons 1-3, 1-4, and 2-3, aboveground biomass increased by 0.13, 0.08, and 0.09 g day⁻¹, respectively. Total biomass increased by 0.17 g day⁻¹ during both GP comparisons 1-3 and 1-4 and increased by 0.11 g day⁻¹ during GP comparisons 2-3 and 2-4. Medusahead leaf area growth rates did not change between GP comparisons. Root length increased by 1,330, 3,500, 2,760, and 2,160 cm day⁻¹ for GP comparisons 1-3, 1-4, 2-4, and 3-4, respectively.

For trial 2, squirreltail below- and aboveground biomass increased by 0.05 and 0.06 g day⁻¹ during GP comparison 1-4 and 0.04 and 0.05 g day⁻¹ during GP comparison 2-4, respectively (Table 4.8). Total biomass increased by 0.11 and 0.10 g day⁻¹ during GP comparisons 1-4 and 2-4. Squirreltail leaf area increased by 9.2 cm² day⁻¹ during GP comparison 1-4. Root length increased by 731 and 603 cm day⁻¹ during GP comparisons 1-4 and 2-4, respectively.

Table 4.8. Trial 2 comparison of mean growth rates between growth periods for medusahead and squirreltail.

Medusahead					
Growth Periods	Belowground Biomass (g day ⁻¹)	Aboveground Biomass (g day ⁻¹)	Total Biomass (g day ⁻¹)	Leaf Area (cm ² day ⁻¹)	Root Length (cm day ⁻¹)
1-2	0.015 (NS)	0.042 (NS)	0.057 (NS)	8.6 (NS)	739 (NS)
1-3	0.035 (0.009)	0.131 (0.032)	0.166 (0.036)	15.0 (NS)	1330 (489)
1-4	0.092 (0.009)	0.077 (0.032)	0.169 (0.036)	18.4 (NS)	3500 (489)
2-3	0.020 (0.009)	0.089 (0.032)	0.108 (0.036)	6.4 (NS)	592 (NS)
2-4	0.077 (0.009)	0.035 (NS)	0.111 (0.036)	9.8 (NS)	2760 (489)
3-4	0.057 (0.009)	-0.054 (NS)	0.003 (NS)	3.3 (NS)	2160 (489)
LSD CP					
95%	2.179	2.179	2.179	2.179	2.179
P-value	<0.01	0.01	<0.01	0.41	<0.01
Squirreltail					
Growth Periods	Belowground Biomass (g day ⁻¹)	Aboveground Biomass (g day ⁻¹)	Total Biomass (g day ⁻¹)	Leaf Area (cm ² day ⁻¹)	Root Length (cm day ⁻¹)
1-2	0.004 (NS)	0.009 (NS)	0.014 (NS)	1.9 (NS)	128 (NS)
1-3	0.021 (NS)	0.029 (NS)	0.050 (NS)	5.6 (NS)	253 (NS)
1-4	0.048 (0.017)	0.063 (0.017)	0.111 (0.034)	9.2 (3.7)	731 (271)
2-3	0.017 (NS)	0.020 (NS)	0.037 (NS)	3.7 (NS)	126 (NS)
2-4	0.044 (0.017)	0.053 (0.017)	0.097 (0.034)	7.3 (NS)	603 (271)
3-4	0.027 (NS)	0.034 (NS)	0.060 (NS)	3.6 (NS)	477 (NS)
LSD CP					
95%	2.179	2.179	2.179	2.179	2.179
P-value	0.06	0.02	0.03	0.12	0.09

Numbers in parentheses are standard errors for parameters significantly different between growth periods for medusahead and squirreltail, separately (P=0.05). CP=Critical Point.

The mean relative growth rates for trial 1 in GP 1 for aboveground biomass and leaf area were between 93 and 127% greater, respectively, for medusahead than for squirreltail (Table 4.9). The relative rate of increase for root length in GP 4 for squirreltail was 88% greater than for medusahead. Other relative growth rate comparisons between species were not different for corresponding GPs.

Table 4.9. Trial 1 comparison of mean relative growth rates between medusahead and squirreltail for respective growth periods.

Growth Period	Belowground biomass ($\text{g g}^{-1} \text{day}^{-1}$)		Aboveground biomass ($\text{g g}^{-1} \text{day}^{-1}$)		Total biomass ($\text{g g}^{-1} \text{day}^{-1}$)		Leaf area ($\text{cm}^2 \text{cm}^{-2} \text{day}^{-1}$)		Root length ($\text{cm cm}^{-1} \text{day}^{-1}$)	
	M	S	M	S	M	S	M	S	M	S
1	0.144 (NS)	0.119 (NS)	0.199 (0.022)	0.103 (0.003)	0.174 (NS)	0.111 (NS)	0.168 (0.020)	0.074 (0.003)	0.121 (NS)	0.130 (NS)
P-value	0.57		0.05		0.15		0.04		0.81	
2	0.081 (NS)	0.060 (NS)	0.067 (NS)	0.085 (NS)	0.073 (NS)	0.073 (NS)	0.022 (NS)	0.102 (NS)	0.099 (NS)	0.065 (NS)
P-value	0.60		0.62		0.99		0.07		0.36	
3	0.108 (NS)	0.094 (NS)	0.096 (NS)	0.082 (NS)	0.101 (NS)	0.088 (NS)	0.101 (NS)	0.071 (NS)	0.101 (NS)	0.074 (NS)
P-value	0.47		0.48		0.49		0.21		0.18	
4	0.053 (NS)	0.094 (NS)	0.046 (NS)	0.077 (NS)	0.049 (NS)	0.060 (NS)	0.040 (NS)	0.059 (NS)	0.042 (0.004)	0.079 (0.012)
P-value	0.07		0.17		0.77		0.42		0.02	

M=medusahead and S=squirreltail. Numbers in parentheses are standard errors for parameters significantly different between medusahead and squirreltail for identical growth periods ($P=0.05$).

For trial 1, medusahead mean relative growth for belowground biomass differed between GPs 1 and 4 with a $0.09 \text{ g g}^{-1} \text{day}^{-1}$ decrease (Table 4.10). Aboveground biomass decreased by 0.13, 0.10, and $0.15 \text{ g g}^{-1} \text{day}^{-1}$ while total biomass decreased by 0.10, 0.07, and $0.13 \text{ g g}^{-1} \text{day}^{-1}$ for GP comparisons 1-2, 1-3, and 1-4, respectively. Leaf area decreased by 0.15 and $0.13 \text{ cm}^2 \text{cm}^{-2} \text{day}^{-1}$ between GP comparison 1-2 and 1-4,

although it increased by $0.08 \text{ cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$ between GP 2-3. Root length relative growth decreased ($0.08 \text{ cm cm}^{-1} \text{ day}^{-1}$) between growth periods 2 and 3.

For trial 1, squirreltail mean relative growth rates for belowground biomass, aboveground biomass, total biomass, and leaf area did not differ between growth periods (Table 4.10). Root length relative growth decreased for GP comparisons 1-2, 1-3, and 1-4 by 0.07, 0.06, and $0.05 \text{ cm cm}^{-1} \text{ day}^{-1}$, respectively.

Table 4.10. Trial 1 comparison of mean relative growth rates between growth periods for medusahead and squirreltail.

Medusahead					
Growth Periods	Belowground Biomass ($\text{g g}^{-1} \text{ day}^{-1}$)	Aboveground Biomass ($\text{g g}^{-1} \text{ day}^{-1}$)	Total Biomass ($\text{g g}^{-1} \text{ day}^{-1}$)	Leaf area ($\text{cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$)	Root Length ($\text{cm cm}^{-1} \text{ day}^{-1}$)
1-2	-0.063 (NS)	-0.132 (0.030)	-0.101 (0.029)	-0.147 (0.037)	-0.022 (NS)
1-3	-0.036 (NS)	-0.104 (0.030)	-0.074 (0.029)	-0.068 (NS)	-0.020 (NS)
1-4	-0.090 (0.035)	-0.154 (0.030)	-0.125 (0.029)	-0.129 (0.037)	-0.080 (0.035)
2-3	0.027 (NS)	0.028 (NS)	-0.028 (NS)	0.079 (0.030)	0.002 (NS)
2-4	-0.028 (NS)	-0.022 (NS)	-0.024 (NS)	0.018 (NS)	-0.057 (NS)
3-4	-0.055 (NS)	-0.050 (NS)	-0.051 (NS)	-0.061 (NS)	-0.059 (NS)
LSD CP					
95%	2.228	2.228	2.228	2.228	2.228
P-value	0.11	<0.01	0.01	0.01	0.12
Squirreltail					
Growth Periods	Belowground Biomass ($\text{g g}^{-1} \text{ day}^{-1}$)	Aboveground Biomass ($\text{g g}^{-1} \text{ day}^{-1}$)	Total Biomass ($\text{g g}^{-1} \text{ day}^{-1}$)	Leaf area ($\text{cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$)	Root Length ($\text{cm cm}^{-1} \text{ day}^{-1}$)
1-2	-0.058 (NS)	-0.019 (NS)	-0.038 (NS)	0.029 (NS)	-0.065 (0.019)
1-3	-0.025 (NS)	-0.021 (NS)	-0.023 (NS)	0.003 (NS)	-0.056 (0.019)
1-4	-0.024 (NS)	-0.026 (NS)	-0.051 (NS)	-0.015 (NS)	-0.050 (0.021)
2-3	0.033 (NS)	0.002 (NS)	0.015 (NS)	-0.031 (NS)	0.009 (NS)
2-4	0.034 (NS)	-0.007 (NS)	-0.013 (NS)	-0.041 (NS)	0.014 (NS)
3-4	0.001 (NS)	-0.005 (NS)	-0.028 (NS)	-0.012 (NS)	0.005 (NS)
LSD CP					
95%	2.262	2.228	2.228	2.228	2.262
P-value	0.26	0.84	0.64	0.32	0.05

Numbers in parentheses are standard errors for parameters significantly different between growth periods for medusahead and squirreltail, separately ($P=0.05$). CP=Critical Point.

Mean relative growth rates in trial 2 were only different between medusahead and squirreltail in GP 2 (Table 4.11). In GP 2, belowground biomass, aboveground biomass, total biomass, leaf area, and root length for medusahead were 59.6, 47.9, 52.8, 52.5, and 79.0% greater than for squirreltail. Other relative growth rate comparisons between species were not different for corresponding GPs.

Table 4.11. Trial 2 comparison of mean relative growth rates between medusahead and squirreltail for respective growth periods.

Growth Period	Belowground biomass ($\text{g g}^{-1} \text{ day}^{-1}$)		Aboveground biomass ($\text{g g}^{-1} \text{ day}^{-1}$)		Total biomass ($\text{g g}^{-1} \text{ day}^{-1}$)		Leaf area ($\text{cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$)		Root length ($\text{cm cm}^{-1} \text{ day}^{-1}$)	
	M	S	M	S	M	S	M	S	M	S
1	0.151 (NS)	0.152 (NS)	0.170 (NS)	0.158 (NS)	0.163 (NS)	0.156 (NS)	0.140 (NS)	0.104 (NS)	0.144 (NS)	0.128 (NS)
P-value	0.92		0.29		0.41		0.18		0.44	
2	0.141 (0.015)	0.088 (0.011)	0.149 (0.011)	0.101 (0.001)	0.147 (0.012)	0.096 (0.005)	0.139 (0.011)	0.091 (0.005)	0.138 (0.012)	0.077 (0.012)
P-value	0.03		0.01		0.01		0.01		0.01	
3	0.074 (NS)	0.076 (NS)	0.088 (NS)	0.068 (NS)	0.085 (NS)	0.072 (NS)	0.076 (NS)	0.065 (NS)	0.062 (NS)	0.043 (NS)
P-value	0.95		0.32		0.55		0.67		0.40	
4	0.069 (NS)	0.075 (NS)	0.027 (NS)	0.064 (NS)	0.039 (NS)	0.068 (NS)	0.021 (NS)	0.052 (NS)	0.066 (NS)	0.059 (NS)
P-value	0.87		0.17		0.31		0.39		0.78	

M=medusahead and S=squirreltail. Numbers in parentheses are standard errors for parameters significantly different between medusahead and squirreltail for identical growth periods ($P=0.05$).

For trial 2 mean relative growth rates, medusahead below- and aboveground biomass decreased for GP comparisons 1-3, 1-4, 2-3, and 2-4 by 0.08 and 0.08, 0.08 and 0.14, 0.07 and 0.06, and 0.07 $\text{g g}^{-1} \text{ day}^{-1}$ and 0.12 $\text{g g}^{-1} \text{ day}^{-1}$, respectively (Table 4.12). Additionally, aboveground biomass decreased by 0.06 $\text{g g}^{-1} \text{ day}^{-1}$ between GPs 3 and 4. Total biomass and leaf area relative growth decreased for GP comparisons 1-3, 1-4, 2-3, 2-4, and 3-4 by 0.08 and 0.06, 0.13 and 0.12, 0.06 and 0.06, 0.11 and 0.12, and 0.05 g g^{-1}

day⁻¹ and 0.06 cm² cm⁻² day⁻¹, respectively. Relative root length decreased 0.08 cm cm⁻¹ day⁻¹ during GP comparison 1-3, 0.08 cm cm⁻¹ day⁻¹ during GP comparison 1-4, 0.08 cm cm⁻¹ day⁻¹ during GP comparison 2-3, and 0.07 cm cm⁻¹ day⁻¹ during GP comparison 2-4.

Table 4.12. Trial 2 comparison of mean relative growth rates between growth periods for medusahead and squirreltail.

Medusahead					
Growth Periods	Belowground Biomass (g g ⁻¹ day ⁻¹)	Aboveground Biomass (g g ⁻¹ day ⁻¹)	Total Biomass (g g ⁻¹ day ⁻¹)	Leaf Area (cm ² cm ⁻² day ⁻¹)	Root Length (cm cm ⁻¹ day ⁻¹)
1-2	-0.010 (NS)	-0.020 (NS)	-0.016 (NS)	-0.001 (NS)	-0.006 (NS)
1-3	-0.077 (0.016)	-0.082 (0.013)	-0.078 (0.013)	-0.064 (0.022)	-0.082 (0.018)
1-4	-0.081 (0.016)	-0.143 (0.013)	-0.125 (0.013)	-0.120 (0.022)	-0.078 (0.018)
2-3	-0.067 (0.016)	-0.061 (0.013)	-0.062 (0.013)	-0.064 (0.022)	-0.076 (0.018)
2-4	-0.072 (0.016)	-0.123 (0.013)	-0.108 (0.013)	-0.119 (0.022)	-0.073 (0.018)
3-4	0.005 (NS)	-0.062 (0.013)	-0.047 (0.013)	-0.055 (0.023)	0.004 (NS)
LSD					
CP 95%	2.179	2.179	2.179	2.179	2.179
P-value	<0.01	<0.01	<0.01	<0.01	<0.01
Squirreltail					
Growth Periods	Belowground Biomass (g g ⁻¹ day ⁻¹)	Aboveground Biomass (g g ⁻¹ day ⁻¹)	Total Biomass (g g ⁻¹ day ⁻¹)	Leaf Area (cm ² cm ⁻² day ⁻¹)	Root Length (cm cm ⁻¹ day ⁻¹)
1-2	-0.064 (NS)	-0.057 (0.020)	-0.060 (0.024)	-0.012 (NS)	-0.051 (0.023)
1-3	-0.076 (0.032)	-0.090 (0.020)	-0.084 (0.024)	-0.039 (NS)	-0.085 (0.023)
1-4	-0.077 (0.032)	-0.094 (0.020)	-0.088 (0.024)	-0.051 (NS)	-0.069 (0.023)
2-3	-0.012 (NS)	-0.033 (NS)	-0.025 (NS)	-0.027 (NS)	-0.034 (NS)
2-4	-0.013 (NS)	-0.037 (NS)	-0.028 (NS)	-0.039 (NS)	-0.019 (NS)
3-4	0.001 (NS)	0.004 (NS)	-0.003 (NS)	-0.012 (NS)	0.016 (NS)
LSD					
CP 95%	2.179	2.179	2.179	2.179	2.179
P-value	0.10	<0.01	0.01	0.22	0.01

Numbers in parentheses are standard errors for parameters significantly different between growth periods for medusahead and squirreltail, separately (P=0.05). CP=Critical Point.

In trial 2, relative growth for squirreltail belowground biomass decreased by 0.08 g g⁻¹ day⁻¹ between GP comparisons 1-3 and 1-4 while aboveground biomass relative growth decreased by 0.06, 0.09, and 0.09 g g⁻¹ day⁻¹ between GP comparisons 1-2, 1-3, and 1-4, respectively (Table 4.12). Squirreltail relative total biomass decreased by 0.06,

0.08, and 0.09 g g⁻¹ day⁻¹ for GP comparisons 1-2, 1-3, and 1-4, respectively. Relative root length decreased for GP comparisons 1-2, 1-3, and 1-4 by 0.05, 0.08, and 0.07 cm cm⁻¹ day⁻¹, respectively while relative leaf area did not change between GPs.

DISCUSSION AND CONCLUSIONS

Growth analysis can help elucidate the mechanisms by which plants compete and how they might perform under competitive environments (Radosevich et al. 1997). Measurements of growth analysis parameters in this study helped explain the interference relationship between medusahead and squirreltail. In general, medusahead had greater growth, growth rates, and relative growth rates than squirreltail, which supports findings from the interference study. In the interference study between medusahead and squirreltail at high and low levels of N and P, medusahead was competitively superior at preempting environmental resources to the detriment of squirreltail.

In trials one and two of the growth analysis study, medusahead produced more biomass, leaf area, and root length than squirreltail. However, in trial 1, squirreltail allocated a greater portion of its accumulated biomass to belowground growth than medusahead at SD 28. Furthermore, in trial 2, squirreltail always had higher root:shoot ratios following SD 17. These findings agree with Monaco et al. (2003) who found that, in general, annuals produced smaller root:shoot ratios and allocated more N to shoots than perennials, and that native perennials produced greater root:shoot ratios and allocated more N to roots across nutrient gradients. Results from a competition study between medusahead and squirreltail conducted by Hironaka and Sindelar (1975) further support these findings. At the end of 85 days, they found that medusahead had acquired more aboveground biomass than squirreltail plants when the two species were grown

together. They also found that belowground biomass was greater for squirreltail than medusahead, which contradicts my results; my results suggest medusahead always produces greater belowground biomass, but squirreltail allocates more of its acquired resources to belowground biomass.

Annual and perennial grasses may employ different root growth schemes. Arredondo et al. (1998) found that medusahead had higher specific root length whereas perennial grasses, including squirreltail, developed thicker roots. In this study, root thickness was not measured, but medusahead always had greater root length than squirreltail. Arredondo et al. (1998) and Korner and Renhardt (1987) suggested that longer thinner root systems may make more efficient use of carbon allocations, but the development of thicker roots signifies a greater carbon investment and may help perennials survive from year to year. Hironaka and Sindelar (1975) suggested that the ability to live through the high temperatures and moisture deficiencies of summer is related to root reserve quantity and that squirreltail seems better able than many other perennial grasses to store sufficient root reserves when faced with competition from annual plants.

As expected, both species increased in all aspects of growth over time. In trial 1, medusahead root:shoot ratios decreased from the first SD through the second SD but appeared to increase thereafter. However, squirreltail root:shoot ratios did not change over time. In trial 2, medusahead root:shoot ratios declined over a longer period of time than in trial 1 and did not increase again until the last SD, which resulted in root:shoot ratios similar to the first SD. In contrast to medusahead's more dynamic root:shoot ratios, Lowe et al. (2002) found that exotic, weedy species did not increase in root:shoot

ratios. Hironaka and Sindelar (1975) found squirreltail root:shoot ratios to be 3 to 8 times greater than medusahead's which is in agreement with my findings that squirreltail root:shoot ratios were approximately 1.5 times greater than medusahead root:shoot ratios in trial 2.

In general, medusahead had belowground biomass, aboveground biomass, total biomass, leaf area, and root length growth rates higher than squirreltail. These findings support results by Arredondo et al. (1998) who also found that annual plants had higher belowground biomass, aboveground biomass, and leaf area growth rates than perennials. In general, my findings agreed with Redente et al. (1992) who found early seral species to have low root:shoot ratios and high growth rates.

Overall, medusahead relative growth rates for belowground biomass, aboveground biomass, total biomass, leaf area, and root length decreased during the study. In trial 1, the only relative growth rate that changed for squirreltail was a decrease in relative root length; however, squirreltail's relative root length growth rate was greater than medusahead's for GP 4 in trial 1. This anomaly may suggest that squirreltail can demonstrate faster relative root length growth later in the season than medusahead under certain conditions, even though medusahead had greater relative aboveground biomass and leaf area growth rates than squirreltail. In trial 2, relative growth rates for belowground biomass, aboveground biomass, total biomass, and root length decreased for squirreltail. The only relative growth rate parameter that did not decrease was leaf area, which remained constant while medusahead relative leaf area growth rate declined; however, medusahead still maintained higher relative leaf area growth rates over the course of the study. Squirreltail's continued relative root and leaf area growth suggests

that squirreltail may be able to grow later into the growing season. Greater leaf longevity and perennial allocation of resources to roots suggests squirreltail may utilize N more efficiently than medusahead. Monaco et al. (2003) supported this notion by indicating that perennial plants maintained nutrients longer than annual plants through leaf retention and nutrient reabsorption.

I hypothesized that medusahead would exhibit higher growth rates than squirreltail, especially for aboveground biomass, and that squirreltail would allocate more of its biomass to belowground growth. I accepted this hypothesis based on the results of this study. I found that medusahead grew faster than squirreltail in many aspects and squirreltail usually allocated more of its acquired resources to belowground growth. Overall, medusahead growth was superior to that of squirreltail in the parameters that were measured in this study. An advantage squirreltail may have over medusahead is the allocation of more of its resources to belowground biomass. Monaco et al. (2003) found that native perennials invested more of their biomass into their root systems, thereby increasing root:shoot ratios above that of invasive annual grasses, which may increase nutrient uptake and retention over time. I believe that a long-term study would be required to fully evaluate the ramifications of this potential advantage in squirreltail.

The maintenance of continually low levels of nutrient availability and reduction of medusahead competition are obvious prerequisites for restoration of medusahead infested rangelands given the characteristics of squirreltail and medusahead. Because medusahead seedlings will rapidly utilize available resources before perennial grass seedlings, any management practice that will help squirreltail establish and achieve a few

years' worth of growth so that it can compete more effectively against medusahead will be beneficial to the restoration process. Competition between seedlings of medusahead and squirreltail will likely be won by medusahead, but seedling-to-mature plant competition may be won by squirreltail. It appears that management inputs, e.g., seed drilling, herbicides, and best management practices that maintain low N availability, will be required to allow native perennials to firmly establish in medusahead infested rangelands.

CHAPTER 5: GENERAL CONCLUSIONS

Weeds occur throughout the world, and more species have gone extinct as a result of biological invasions than from climate change related to human activity (D'Antonio and Vitousek 1992). Weed populations have the ability to diminish soil moisture and nutrients, water quality, wildlife habitat, and plant diversity, and endanger sensitive species, modify fire intervals, and accelerate erosion (DiTomaso 2000, BLM 1996). Exotic weeds, including medusahead, cost the U.S. agricultural economy an estimated \$26 billion annually (Pimentel et al. 2000).

Restoration of invaded plant communities is required to reduce the substantial ecological and monetary losses related to noxious weeds. A critical component was lacking from our understanding of how squirreltail may be used in the restoration of medusahead infested rangelands, that being a knowledge of how soil N and P levels influence interference between medusahead and squirreltail seedlings.

The two objectives of this research were to determine if soil N and P levels alter interference between medusahead and squirreltail and to compare growth characteristics of the two species. The interference study determined whether soil N and P levels influenced interference between medusahead and squirreltail. I hypothesized that high soil N and P would increase medusahead growth and competitive ability relative to squirreltail. I concluded that medusahead and squirreltail competed for N. Increased soil N reduced medusahead and squirreltail's relative competitive abilities largely due to reductions in the intensity of intraspecific interference. High N also reduced the effect of medusahead density on squirreltail biomass. Soil P levels had little influence on predicted species aboveground growth or interference, at least at the levels used in this

study. In addition, medusahead and squirreltail largely occupied the same ecological niche and mainly competed for the same environmental resources, particularly N.

The objective of the growth analysis portion of my research was to measure plant growth parameters to identify the mechanisms by which medusahead and squirreltail interfere with each other. I hypothesized that medusahead would exhibit higher growth rates than squirreltail, especially for aboveground biomass, and that squirreltail would allocate more of its biomass to belowground growth. I concluded that medusahead grew faster than squirreltail and that squirreltail allocated a greater proportion of its resources to belowground growth than medusahead.

In general, during the growth analysis study, medusahead produced more biomass, leaf area, and root length than squirreltail, while squirreltail allocated more of its acquired resources to belowground growth. In addition, medusahead growth rates for biomass, leaf area, and root length were greater than squirreltail's, while squirreltail partitioned resources to belowground growth to a greater extent than medusahead did. Rates of increase of root:shoot ratios for medusahead and squirreltail did not differ between species over the course of the study. Medusahead relative growth rates decreased for biomass, leaf area, and root length, while squirreltail's relative growth rate for leaf area remained constant; however, medusahead still maintained higher relative leaf area growth rates during the study.

Relative growth rate can serve as a predictor of competitive success, while absolute changes in biomass and comparisons between growth rates can help explain differences in relative growth rates (Radosevich et al. 1997). Results from growth analysis helped to explain results from the interference study. The growth analysis and

the interference study found medusahead to be a superior competitor over squirreltail for environmental resources. Interference studies conducted simultaneously with growth analysis studies are important for creating weed management plans (Radosevich et al. 1997). Identifying determinants of competitive plant interactions and their effects on plant growth facilitates ecosystem management in favor of desirable species (Radosevich et al. 1997).

On landscapes limited in nutrient availability, root allocation and morphology are more critical than nutrient uptake dynamics in deciding success in nutrient competition (Aerts 1999). Aerts (1999) suggested that plants adapted to low nutrient loss rates are naturally favored on nutrient limited landscapes over plants predisposed to be highly competitive for nutrient absorption. To further understand squirreltail's apparent relatively high allocation of biomass to belowground growth, a long-term study would be necessary. A multi-year study would allow for the differences in perennial versus annual resource allocation patterns to manifest themselves. Over time and under consistently low nutrient availability, squirreltail might increase in medusahead infested rangelands. Long term maintenance of soil N at very low levels may diminish medusahead seedbanks to low enough levels that squirreltail can increase and slowly replace medusahead (Monaco et al. 2003).

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