

AN ABSTRACT OF THE DISSERTATION OF

Seema Mangla for the degree of Doctor of Philosophy in Environmental Science
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Title: Directing Ecological Succession: The Role of Competition in Restoring Semi-Arid
Grasslands Dominated by Invasive Plants.

Abstract approved: _____

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Successful ecosystem restoration requires an understanding of the ecological processes directing succession. One of the challenges in the semi-arid grasslands of western United States is replacement of native species by invasive annual grasses. Solutions to this problem require identifying and manipulating ecological processes that direct succession to favor desired vegetation. The overall objective of this research was to identify and understand processes or factors directing restoration of semi-arid grassland ecosystems dominated with invasive annual grasses. Two invasive annual (*Bromus tectorum* L. and *Taeniatherum caput-medusae* L. Nevski) and two native perennial (*Pseudoroegneria spicata* (Pursh) A) and *Poa secunda* J. Presl) grass species were used to provide a model system of semi-arid grasslands of western United States.

Plant competition is considered to be the primary ecological process limiting the success of grassland restoration. Successful restoration requires knowing the relative strength and magnitude of competition during the early stages of plant growth and how this might be impacted by nitrogen (N) availability. My research involved three experiments designed to compare competition and growth rates of native and invasive species. First, in order to understand the degree to which intra- versus inter-specific competition controls invasive and native plant growth during the early phase of establishment, I performed a diallel competition experiment with species grown either alone or in 1:1 binary combinations in a greenhouse. I hypothesized that the type and intensity of competition for invasive and native species would vary among harvest times and competitive intensity for invasive species will be higher than native species with higher N availability. My results indicated that invasive and native species are subject to both intra- and inter-specific competition; however, the dominant type differed among harvests. Invasive species also became more competitive than native species with increasing N. I suggest that opportunities to improve restoration success exist by determining the optimum combination of density, species proportion, and their spatial arrangement in various ecosystems and environments.

Second, I performed an addition series competition experiment in the field for two years to determine the intensity and importance of competition in an arid, resource poor production system. My results indicated that in resource poor environments, the intensity of competition did not significantly influence plant dominance during the first two years of plant establishment, and thus, competition was not important. I suggest that land managers may be most successful at restoration of resource poor ecosystems by

overcoming the barriers associated with plant establishment other than plant-plant interactions, such as abiotic factors.

Third, I studied growth rate and growth patterns of medusahead with bluebunch wheatgrass and cheatgrass in the field for two years. I hypothesized that medusahead would have a higher RGR, a longer period of growth, and as a consequence, more total biomass at the end of the growing season than bluebunch wheatgrass and cheatgrass. Medusahead had a longer period of growth, more total biomass and higher RGR than cheatgrass. However, bluebunch wheatgrass had more biomass and higher RGR than medusahead in 2008, but the relationship was reversed in 2009. Weather data identified that precipitation in 2008 was well below average, and this level of drought was very infrequent. Collectively, my results suggest that the continued invasion and dominance of medusahead onto native and cheatgrass dominated grasslands will continue to increase in severity because of its higher RGR and extended period of growth.

The inability to identify key ecological processes important in directing invasion and succession has limited the adoption and implementation of ecologically based invasive plant management (EBIPM). A framework that allows ecologists to identify and prioritize ecological processes most in need of repair would help overcome this barrier. I developed an initial framework that allows ecologists to prioritize the ecological processes that appear to play a dominant role in vegetation dynamics. This was accomplished by using sensitivity analysis to identify the most important transitions in the life cycle of associated species and linking those transitions with key ecological processes and their modifying factors. This method could increase land manager's ability

to implement EBIPM by allowing identification and prioritization of those ecological processes that appear to play a dominating role in vegetation dynamics.

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DIRECTING ECOLOGICAL SUCCESSION: THE ROLE OF COMPETITION IN
RESTORING SEMI-ARID GRASSLANDS DOMINATED BY INVASIVE PLANTS

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

Seema Mangla, Author

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1 General Introduction

Exotic plant invasion poses a serious global ecological and conservation threat to native plant communities (Simberloff, 2005; Vitousek et al., 1996) requires ecologically-based solutions (Davis, 2003; Krueger-Mangold et al., 2006; Weber, 2003). Invasive plants occupy over 100 million ha and are considered the second most important threat to biodiversity after habitat destruction (National Invasive Species Council, 2001). Each year, several billion dollars are spent to control plant invasions (Pimentel, 2005). In spite of major programs to address this problem, the amount of land infested by invasive plants is rapidly increasing, and the negative impacts associated with invasion are escalating at an unprecedented rate (Randall, 1996; Westbrooks, 1998).

Conversion of intact native perennial grassland to exotic annual grassland has been identified as a major threat to grassland ecosystems because it alters fire regimes, water and nutrient cycling, and erosion (D'Antonio and Vitousek, 1992). In the late 1800s, two important non-indigenous annual grasses, cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), were introduced to the United States (Mack, 1981; Turner et al., 1963). Since their introduction, these species have invaded throughout the semi-arid grasslands of the western United States and now occupy millions of hectares of once pristine plant communities. They continue to spread at a rapid rate. Medusahead dominates over 2.5 million ha (Sheley et al., 2008), while cheatgrass occupies about 22 million ha (Duncan et al., 2004). Their dominance is associated with loss of species richness, changes in structure and composition of vegetation, reduction in wildlife habitat, and potentially altered nutrient, water and fire

cycles (Harrison et al., 2003; Olson, 1999; Pellant and Hall, 1994; Pyke et al., 2003; Young, 1992). In addition, these invasive annual grasses reduce soil stability and dramatically increase fire frequency (Butler et al., 2006; Harris, 1967).

Traditional methods for controlling invasive plant species have largely relied on eliminating invasive plants, rather than understanding and manipulating the ecological processes that facilitate invasion and disrupt natural succession (Hobbs and Humphries, 1995; Sheley et al., 2006). This approach often results in reinvasion or invasion by an equally undesirable nonindigenous species (Krueger-Mangold et al., 2006; Naeem et al., 2000). Over the years, mechanisms underlying the effects of invasive species on communities have received much less attention than the impacts of the invaders on communities or ecosystems (Levine et al., 2003). For example, numerous studies have documented reductions in native species diversity following invasion, yet very few have documented whether these results are driven by resource competition, allelopathy or the alteration of ecosystem processes such as nitrogen cycling (Levine et al., 2003). To achieve sustainable management, managers need to address fundamental ecological processes and know how they promote the establishment and persistence of invasive plants (Sheley and Krueger-Mangold, 2003). Predicting and understanding invasion processes is essential for management (Gallien et al., 2010). Similarly, from a restoration standpoint, we need to know which processes must be repaired or replaced if native species are to be restored in place of exotic-dominated systems (Levine et al., 2003).

There is a basic need to identify and manipulate ecological processes that direct succession to prevent further loss to the ecosystem services provided by grasslands. In

doing so, management strategies can then be designed to target specific ecological processes that influence successional trajectories toward desirable, invasion-resistant plant communities (Krueger-Mangold et al., 2006). The goal of the research presented in this dissertation was to contribute to understanding the underlying causes of plant invasion in the semi-arid grasslands of western United States. This research uses various experimental designs to investigate competition and growth rates to explain the expansion of invasive annual grasses onto grasslands and provide new information for restoration of these invaded systems. Cheatgrass and medusahead were selected as invasive annual species for this study. Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A) and Sandberg's bluegrass (*Poa secunda* J. Presl), two native perennial species of the Intermountain West, USA, were selected because they are important subdominant plant species in the region (Zlatnik, 1999). These native species are often used in restoration efforts on sites previously infested by invasive plants.

Chapter 2 (manuscript 1) describes diallel competition experiments performed in the greenhouse at Oregon State University. The experiments were conducted to understand intra- and/or inter-specific competition influence on native plant growth. Successful restoration of invasive annual dominated grasslands requires a full understanding of the relative strength and magnitude of plant interactions during the early stages of plant growth. Therefore, understanding the type of competition (intra- or inter-specific) that influences the early stages of growth within a given system is necessary for managers to manipulate treatments to favor native species. The objective of this study was to determine how the intensity of intra- and inter-specific competition changes

during early stages of plant growth. Since the performance of an individual plant may be modified by soil nutrient availability, especially soil N, I examined these responses under two levels of N availability. I hypothesized that the type of competition and its intensity that dominate between invasive and native species would vary among harvest times during early stages of plant growth. Based on the expectation that fast growth by invasive species will allow them to acquire more N and suppress N capture by competing species during periods of rapid growth, I predicted that the competitive intensity for invasive species will be higher than native species with higher N availability.

Chapter 3 (manuscript 2) focuses on quantifying the competition intensity and importance in an arid, resource poor production system, using a two-year addition series field experiment involving manipulated densities of invasive and native species. Experimental approaches that allow the intensity and importance of competition to be determined are useful in improving our understanding of the role competition plays in stressful environments. Understanding the role of competition intensity and competition importance in directing vegetation dynamics is a useful step in allowing land managers to prioritize inputs for restoration projects. The objectives of this study were to: 1) quantify the intensity of competition among invasive annual and native perennial bunchgrasses, and 2) determine the importance of competition in influencing restoration in an arid, resource poor system. The specific hypotheses tested were 1) competition would be intense among invasive and native plant species (i.e., the effect of species density would influence biomass or survivorship and intra- and inter-specific competitive effects among invasive and native species would be significant during the two years of establishment)

but 2) competition would be unimportant in explaining variation in target plant biomass and survivorship relative to all other factors driving variation in these two parameters.

Chapter 4 (manuscript 3) describes growth dynamics of medusahead relative to bluebunch wheatgrass and cheatgrass which is central to predicting and managing medusahead invasion. Knowledge of growth rates of invasive and native species at low densities of monocultures may mimic conditions during the initial stages of invasion. The objectives of this study were to compare the growth rate and growth patterns of medusahead with that of bluebunch wheatgrass and cheatgrass in the field using frequent harvest intervals across the entire season of growth. Understanding the growth rate of medusahead relative to these other species may help explain the continued invasion and dominance of grasslands by medusahead. I hypothesized that medusahead growing in monocultures would have a higher RGR, a longer period of growth, and as a consequence, more total biomass at the end of the growing season than bluebunch wheatgrass and cheatgrass.

Chapter 5 (manuscript 4) provides an initial framework that links ecological processes with life-history model parameters. It assesses and synthesizes the associated literature, providing general annual and perennial life history models with corresponding ecological processes, and their modifying factors. It also demonstrates the use of these general models using cheatgrass and bluebunch wheatgrass. In this chapter, I present a brief description of the life history models and discuss the key ecological processes and their modifying factors that influence the various stages of annual and perennial life

history. I also provide an example demonstrating the usefulness of this method for identifying key ecological processes based on their linkages with the model parameters.

Chapter 6 provides general conclusions of the dissertation with recommendations for future research directions.

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**Intra- and inter-specific competition among invasive and native species
during early stages of plant growth**

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Intra- and inter-specific competition among invasive and native species during early stages of plant growth

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Abstract

Plant competition is an ecological process limiting grassland restoration success.

Appropriate restoration techniques require an understanding of the degree to which intra- and inter-specific competition control invasive and native plant growth. The objective of this study was to determine how the intensity of intra- and inter-specific competition changes during early stages of plant growth. Two invasive (*Bromus tectorum* L. and *Taeniatherum caput-medusae* L. Nevski) and two native (*Pseudoroegneria spicata* (Pursh) A and *Poa secunda* J. Presl) species were grown in a diallel competition experiment, either alone or in 1:1 binary combinations and exposed to two levels of N (no

N or 400 mg N·kg⁻¹ soil added) in a greenhouse. Total biomass for each species was quantified over four harvests and competitive effects were calculated. Our results show that the relative magnitude of intra- and inter-specific competition changes through time. Intra-specific competition was intense for native species at the initial harvests and therefore important in contributing to the outcome of final size of native species seedlings. Interestingly, bluebunch wheatgrass imposed inter-specific competition on annual grasses at the first two harvests and appeared to be a better competitor than Sandberg's bluegrass. We found that fast growing invasive species became more competitive compared to slow growing native species with increasing N and appear to establish a positive feedback mechanism between size and resource uptake. Opportunities to improve restoration success exist from determining the optimum combination of density, species proportion, and their spatial arrangement in various ecosystems and environments.

Keywords: Intra-specific competition, Inter-specific competition, Harvest time, Nitrogen, Restoration, Diallel design

2.1 Introduction

Exotic plant invasion poses a serious ecological and conservation threat to native plant communities (Simberloff, 2005; Vitousek et al., 1996). Conversion of perennial grassland to annual grassland has been identified as the greatest ecological threat to the native biota of the semi-arid steppe of the North America (D'Antonio and Vitousek, 1992; Germino et al., 2004). Annual grasses, particularly cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), are outstanding examples of this invasion. Since their introduction, these invasive grasses now dominate millions of hectares of arid land in the western United States, leading to loss of species diversity, livestock and wildlife habitat, and increases in fire frequency (D'Antonio and Vitousek, 1992; Pimental et al., 2005; Vitousek et al., 1996). Improved management strategies are critically needed to selectively control invasive plants, while promoting the establishment of native species (Brown et al., 2008). It is becoming increasingly clear that managers must address the underlying ecological processes and mechanisms of succession if desired vegetation dynamics are to endure (Luken, 1997; Krueger-Mangold et al., 2006; Sheley and Krueger-Mangold, 2003).

Competition among plants is a primary ecological process limiting grassland restoration success (Allen, 1995; Brown et al., 2008). The term competition is used in the sense of negative interference (i.e., any direct or indirect negative impact) of one plant over another (Casper and Jackson, 1997; Fowler, 1986) or the ability to avoid or tolerate suppression (Goldberg and Barton, 1992). Appropriate restoration techniques require an understanding of the degree to which intra- and inter-specific competition influence

invasive and native plant growth. Classical competition theory predicts intra-specific competition should be greater than inter-specific competition because individuals of the same species share similar resource requirements (Aarssen, 1983; Fowler, 1986; Goldberg and Barton, 1992; Spitters, 1983; Tilman, 1982). Reviews of the relative strength of intra- and inter-specific competition in experimental plant studies tend to find little evidence for consistently stronger intra-specific competition among interacting species (Goldberg and Barton, 1992; Gurevitch et al., 1992). However, results from recent studies not included in these reviews affirm these variable results, with some studies showing intense intra-specific competition (Sheley and Larson, 1994; Velagala et al., 1997; Wassmuth et al., 2009), while others indicate intense inter-specific competition (Blank 2010; Vasquez et al. 2008; Young and Krueger-Mangold 2008). A possible explanation for these contradictory findings may be because the interpretation of competitive interactions has been largely based on assessing individual plant biomass during a single life-history stage (Connolly et al., 1990; Farrer et al., 2010; Goldberg and Barton, 1992). Therefore, these studies may not fully capture the variation in strength and direction of plant-plant interaction which may vary considerably among life-history stages (Goldberg et al., 2001; Howard and Goldberg, 2001).

Plants pass through different physiological stages as their development progresses and competition occurs not only within species, but also within and between stages of growth of different species (Cameron et al., 2007; Connell, 1983; Schoener, 1983). Germination, emergence and initial root and shoot development may be particularly sensitive to competition (Foster and Gross 1997, 1998; Foster, 1999). It has been shown

that small seedlings are much more sensitive to competition than adult plants (Foster, 1999; Suding and Goldberg, 1999). Other research, however, indicates that competition may be relatively rare early after germination, but may be critical in determining the final plant biomass (Goldberg et al., 2001). Conflicting results concerning the differences in competitive effect among studies arise because studies have largely overlooked the value of understanding competition over sequential harvests during the early stages of plant growth. This highlights the need to explicitly investigate when during the early stages of establishment plants are most sensitive to competition.

Competitive interactions are strongly affected by resource gradients (Grime, 1977; Tilman, 1988). Grime's model predicts competition will have less influence on plant community structure in resource poor environments compared to resource rich environments (Grime, 1977) while Tilman's model predicts that competition will be similar in resource poor and resource rich environments (Tilman, 1988). However, even after decades of experimental and conceptual work, empirical data have not consistently supported either model (Goldberg et al., 1999), and the debate concerning how competitive interactions vary with productivity remains unresolved.

In semi-arid and -arid grasslands, nitrogen (N) is often the most limiting resource after water (Daehler, 2003; Vasquez et al., 2008). Research indicates that increased N favors invasive species over native species (Chambers et al., 2007; James et al., 2008) and decreased N availability favors native species (Lowe et al., 2003; McLendon and Redente, 1992). However, dominance by annual grasses has been observed even in low N environments (Vasquez et al., 2008, Young and Krueger-Mangold, 2008). Plants capture

more N during periods of high growth rate or during high plant demand for N (Collier et al., 2003). Thus, a species' ability to respond to N depends on plant growth patterns. If coexisting species differ in phenology and timing of maximum growth rate, duration of N availability may differentially impact species N acquisition (Bilbrough and Caldwell, 1997). For example, capability of fast growth by invasive species, especially during the early growth phase, allows them to capture more resources (e.g. N) than slow growing native species. This provides invasive species a competitive advantage in later stages of growth compared to native species (Lambers and Poorter, 1992; Radosevich et al., 2007). Knowledge of the plant growth stage that responds to N availability is critical to understanding the mechanisms regulating dominance of invasive species, especially in N-limited systems. Moreover, competitive interactions may vary temporally, as individuals modify the resource pool, and sequential destructive harvests are needed to investigate species interactions over time.

Successful restoration of invasive annual grass dominated grasslands requires an understanding of the relative strength and magnitude of plant interactions during the early stages of plant growth and how this is impacted by N availability. The broad objective of this study was to determine how the competition type and intensity of intra- and inter-specific competition changes during early stages of plant growth. Since the performance of an individual plant may be modified by soil nutrient availability, especially soil N, we examined these responses under two levels of N availability. We conducted competition experiments in the greenhouse because of the need to manipulate the amount of N received by plants. Although experiments under controlled environmental conditions can

rarely be directly extrapolated to field conditions, they are useful for exploring the potential for particular factors to have an impact (Novoplansky and Goldberg, 2001). We hypothesized that the type of competition and its intensity that largely dominate between invasive and native species would vary among harvest times during early stages of plant growth. Based on the expectation that fast growth by invasive species will allow them to acquire more N and suppress N capture by competing species during periods of rapid growth, we also predicted that the competitive intensity for invasive species will be higher than native species with higher N availability.

2.2 Material and Methods

2.2.1 Selection of plant species and soil

We selected two invasive and two native species that co-occur in the Intermountain West, USA. Cheatgrass and medusahead are common and widespread cool-season invasive annual grasses that have invaded much of the Intermountain West (Duncan et al., 2004; Mack, 1981; Turner et al., 1963). Native perennial species, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A) and Sandberg's bluegrass (*Poa secunda* J. Presl) are major herbaceous species in the region and widely used for restoration (Zlatnik, 1999). Seeds for this study were collected from local populations during 2006 and stored in a moisture-proof container at a cool, dry location at outside air temperatures. Seeds of cheatgrass and medusahead were de-awned prior to seeding.

Soil was collected from the Northern Great Basin Experimental Range, 16 km southeast of Riley, Oregon (28°18' 35.38" E, 48°16' 121.84" N). Soil at the site was a

fine, montmorillonitic, mesic Xeric Haplargid. The top 25 to 30 cm of the soil was collected in spring 2008. The soil was dried and sieved through a 6 mm mesh screen to create a uniform texture and thoroughly mixed. Soil analysis for nitrate N, ammonium and incubated N revealed only 0.09 μg mineralizable $\text{N}\cdot\text{g}^{-1}$ soil.

2.2.2 *Experimental design, treatments and sampling*

This greenhouse study was conducted during June through November 2008 at Oregon State University, Corvallis, OR, USA. A completely-randomized design with all the possible pairs among individuals of each species (cheatgrass, medusahead, bluebunch wheatgrass and Sandberg's bluegrass) were combined using a diallel design. The diallel design uses only one or two individuals of each species, and therefore allows study of both intra- and inter-specific competition within a framework of a substitutive experiment (Harper, 1977; Radosevich et al., 2007). Fourteen different combinations for the four species were obtained. For each combination there were two N treatments; either no N ($\text{N}-$) or 400 mg $\text{N}\cdot\text{kg}^{-1}$ soil ($\text{N}+$) added. There were ten replicates per treatment per harvest date with a total of four harvests at 15, 30, 60 and 90 days after planting (DAP). Hence, there were 14 species combinations x 2 N treatments x 10 replicates x 4 harvests = 1120 experimental units.

The performance of an individual plant can be affected by the size of its neighbor, therefore the *per capita* effect of competition must be controlled (Goldberg, 1987). This has been considered as the common problem of studies comparing intra- and inter-specific competition (Goldberg and Barton, 1992). In order to achieve uniform plant size,

seeds of each species were planted separately in liner trays and similar sized seedlings were selected and transplanted into the pots for the diallel experiments.

Pots for the 15 and 30 DAP were 10 cm in diameter by 7.5 cm in depth while the pots for 60 and 90 DAP were 15 cm diameter by 10 cm in depth. Smaller pots and larger pots were filled with 500 g and 1500 g of soil, respectively. A preliminary study demonstrated that smaller pot sizes did not alter seedling growth compared to larger pots during the first 30 days of growth and therefore, the performance of the individual plant was not affected by the amount of space that surrounded it. After transplanting the similar sized plants to their respective pots, a one-time addition of N treatments was applied (N⁻ and N⁺). Pots without added N (N⁻) were irrigated with water, while the pots with N addition (N⁺) were irrigated with water and liquid urea (40% N) to achieve a concentration of 400 mg N·kg⁻¹ soil. Throughout the experiment the soil was irrigated daily with water using hand-held sprinklers to bring the soil to approximate field capacity. The bottoms of the pots were covered to avoid N leaching. Mid-day and night air temperature in the greenhouse ranged from 21 to 25°C and 18 to 21°C, respectively. Average solar radiation in the greenhouse was 1250 μmol m⁻² s⁻¹.

At each harvest seedlings were removed from the pots and separated. Roots were washed over a fine mesh screen. Each seedling was dried at 65 °C for 48 hours, after which total biomass was determined for each seedling.

2.2.3 Growth analysis and statistical procedures

We analyzed our data with the focus on how the relative strength and magnitude of competition changes among species over time of harvests and in response to N availability. We calculated the ln response ratio (lnRR) of each target individual on the basis of total seedling biomass (Hedges et al., 1999; Goldberg et al., 1999):

$$\lnRR = \ln (BM_{\text{mixture}}/BM_{\text{alone}})$$

where, BM_{mixture} is the total biomass of target species i with neighbor i (intra-specific competition) or j (inter-specific competition) and BM_{alone} is the mean total biomass of target species i grown as a single individual (no competition). The lnRR response ratio is a measure of competition intensity, the degree to which a neighbor plant influences target plant growth (Goldberg et al., 1999; Weigelt and Jolliffe, 2003). The statistical properties of lnRR have been examined in detail by Hedges et al. (1999) and have been shown to have major advantages over other potential indices of competition intensity. We analyzed the competition intensity of target individuals on neighbors using an ANOVA that tested the effects of target species, time of harvest, and all second-order interactions.

Comparisons between test groups were made using Tukey HSD tests at the 0.05 level of significance. We were also interested to know if competition intensity among species differed for N treatments hence N was also included in the model. Therefore, a Tukey HSD test was also performed to statistically compare the ratios of lnRR in no added N treatments to that in the added N treatments for various competition scenarios. We also presented the mean biomass of each seedling growing in different N treatments and competition scenarios. All statistical analysis was performed using S plus 7.0.2 for Microsoft windows (S plus, 2005).

2.3 Results

Overall, DAP and N had minimal effect on competition intensity but neighbor and target species had significant impacts on competition intensity (Table 2-1). Neighboring species differed significantly in their ability to suppress the growth of target species experiencing either intra- or inter-specific competition. However, neighboring species did not differ in their response to N and DAP (neighbor x N and neighbor x DAP, respectively; Table 2-1).

2.3.1 Effect of harvest time on intra- and inter-specific competitive interactions

In both N treatments, Sandberg's bluegrass had lowest intra-specific competition intensity and highest inter-specific competition intensity at every harvest. The only exception was that intra-specific competition was the dominant type for Sandberg's bluegrass at 15 DAP growing in N⁻ (Fig. 2-1 a1). Similarly, intra-specific competition was the main type of competition detected at 15 DAP in both N treatments for bluebunch wheatgrass (Fig. 2-1 b1, b2). At 30 DAP, inter-specific competition with invasive species was the dominant type and no competition was detected at 60 and 90 DAP in N⁻ (Fig. 2-1 b1). In N⁺, inter-specific competition was dominant competition type for bluebunch wheatgrass at later harvests; however, inter-specific competition with cheatgrass was detected only at 30 DAP (Fig. 2-1 b2).

In N⁻, both intra- and inter-specific competition was detected at initial harvests for cheatgrass, but minimal effect of competition was detected for later harvests (Fig. 2-1

c1). In N+, no competition was detected at 15 DAP (Fig. 2-1 c2), while at every other harvest (30, 60 and 90 DAP) addition of N resulted in intra-specific competition within this annual grasses. In N+, at 30 DAP, cheatgrass also experienced inter-specific competition from native species, but not at 60 and 90 DAP. Medusahead experienced intra-specific competition at every harvest for both N treatments (Fig. 2-1 d1, d2). Except at 15 DAP, in N–, medusahead also experienced inter-specific competition with associated species. However, in N+, minimal effect of inter-specific competition was detected at every harvest for medusahead.

2.3.2 Effect of harvest time on competition intensity

For Sandberg's bluegrass, in N–, maximum competition intensity was detected at 15 and 60 DAP and in N+, it was detected at 15 DAP (Fig. 2-1 a1, a2). Intense competition at 15 DAP in N+ resulted in a 40% decrease in Sandberg's bluegrass biomass compared to its biomass grown alone (Fig. 2-2 a2). For bluebunch wheatgrass in N–, the competition intensity was highest at initial harvest (15 DAP) resulting in 30% reduction in its biomass compared to when the species was grown alone (Figs. 2-1 b1, 2 b1). Similarly, in N+, the competition intensity was highest during initial harvests (15 and 30 DAP) for bluebunch wheatgrass; however, more intense competition was detected at 30 DAP than at 15 DAP with 72% decrease of biomass below that grown alone at 30 DAP (Figs. 2-1 b2, 2 b2).

The competition intensity was higher during initial harvests in N– for cheatgrass; however, more intense competition was detected at 30 DAP compared to 15 DAP with

50% decrease of biomass below that grown alone at 30 DAP (Figs. 2-1 c1, 2 c1). In N+, cheatgrass biomass was nearly similar between different competition scenarios at 15 DAP and consequently, competition intensity was nearly 0 at 15 DAP while competition intensity was maximum at 30 DAP and 60 DAP for this invasive grass (Figs. 2-1 c2, 2 c2). In N+, cheatgrass biomass decreased 47% and 17% at 30 and 60 DAP, respectively, below that grown in isolation (Fig. 2-2 c2). Similarly, for medusahead, in N–, the competition intensity was highest during initial harvests (Fig. 2-1 d1). But at 60 and 90 DAP, intense competition was also detected and resulted in a decrease of biomass by 38% and 30% , respectively, compared to medusahead grown alone (Figs. 2-1 d1, 2 d1). In N+, the competition intensity was highest at 30 DAP for medusahead. N addition resulted in facilitation for medusahead when competing with associated species at 60 and 90 DAP (Figs. 2-1 d2, 2 d2).

2.3.3 Comparison of competition intensity between N treatments

Competitive effect of a neighbor on a target species was not influenced by N supply ($P= 0.11$, Table 2-1), although identity of the target species were influenced differentially by N, as indicated by a significant N x target species interaction (Table 2-1).

For native species, N addition resulted in less intra-specific competition at 15 DAP compared to N–. But N addition resulted in intense inter-specific competition for Sandberg's bluegrass growing in competition with bluebunch wheatgrass at every harvest (except for 30 DAP, $P= 0.07$). On the other hand, competition with invasive species in

N⁺ resulted in greater competition intensity of Sandberg's bluegrass and bluebunch wheatgrass than in N⁻ at 15 DAP and 30 DAP, respectively ($P < 0.05$).

Except at 15 and 30 DAP, N⁺ resulted in significantly higher negative lnRR for cheatgrass grown with intra-specific competition ($P < 0.05$), i.e. intra-specific competition reduced the biomass of cheatgrass when N⁺ was compared with N⁻ at later stages (60 and 90 DAP). However, N addition resulted in reduction of intra-specific competition intensity of medusahead at 15 DAP ($P = 0.01$). At 15 and 30 DAP, cheatgrass experienced highly negative lnRR by Sandberg's bluegrass because of N addition as indicated by comparing N⁺ with N⁻. For medusahead, N⁺ resulted in greater inter-specific competition by cheatgrass at 15 DAP ($P = 0.004$). However, medusahead reduced cheatgrass growth when N⁺ was compared to N⁻ as indicated by the highly negative competition intensity at 60 and 90 DAP ($P < 0.001$).

2.4 Discussion and conclusions

Successful restoration involves identifying and modifying critical ecological processes within a complex web of interconnected processes and many collateral interactions occur to influence vegetation dynamics (Christensen et al., 1996). Plant competition is often assumed to be a primary ecological process determining the outcome of restoration efforts (Allen, 1995; Brown et al., 2008). Competition during early stages of growth can critically influence individual plant growth and determine future development patterns (Foster and Gross, 1997, 1998; Suding and Goldberg, 1999). Small differences in initial size and growth rates between individuals and species could

potentially determine long-term developmental patterns. An in-depth understanding of competitive effects among invasive and native species during early stages of plant growth can provide information helpful in altering this process to favor vegetation dynamics toward native species during restoration.

Our overall results suggest that invasive annual grasses and native perennial grasses are subject to both intra- and inter-specific competition during early growth stages; however, the type differed among harvests, lending support for the hypothesis that competition type varies among harvests during the early stages of plant growth. This finding emphasizes the need to investigate competition at several points over time (Foster and Gross, 1997, 1998; Foster 1999; Gibson et al., 1999), particularly when life-cycles differ (Gibson et al., 1999). Unfortunately, most previous studies on the effect of invasive species on associated native species are based on a single harvest, usually at the end of the growing season (Blank, 2010; Vasquez et al., 2008; Young and Krueger-Mangold, 2008). These studies have therefore overlooked changes a plant may experience when it passes through different growth stages (Cameron et al., 2007; Connell, 1983; Schoener, 1983).

A prevailing notion is that competition from invasive grasses is the primary obstacle for native grasses establishment (Allen, 1995; Brown et al., 2008). While we found inter-specific competition to be the predominant type of competition for the native species, which is in agreement with previous competition studies (Lowe et al., 2003; Vasquez et al., 2008; Young and Krueger-Mangold, 2008), intra-specific competition was also dominant within native species at the initial harvest (15 DAP). Therefore, it is

important in contributing to the outcome of final size of native species seedlings. Based on these results, there appears to be a substantial need for restoration efforts to carefully balance the seeding rate used during restoration with the number of safe site and potential for intra-specific competition by native species.

We found intra-specific competition to be dominant for invasive species as suggested by previous studies (Blank, 2010; Vasquez et al., 2008; Young and Krueger-Mangold, 2008). However, invasive species also experienced inter-specific competition by associated plant species, thus, inter-specific competition likely contributes to the final size of seedling invasive species. Bluebunch wheatgrass negatively affected annual biomass at the first two harvests as indicated by negative competition intensity. There appears to be a window of opportunity for bluebunch wheatgrass to suppress annual grasses in their seedling stage, and once established, bluebunch wheatgrass may be able to maintain itself through perennial resource allocation as suggested by Jacobs et al. (1996). Bluebunch wheatgrass also resulted in greater inter-specific competition for Sandberg's bluegrass at every harvest, while it could potentially tolerate the presence of Sandberg's bluegrass when grown in the same pot. These results suggest bluebunch wheatgrass is a better competitor than Sandberg's bluegrass and could be a more successful restoration species.

Overall, intra- and inter-specific competition intensity for native species was highest during initial harvests compared to later harvests for both N treatments, lending support for hypothesis that competition intensity would vary among harvests. In addition to intense competition at early stages of growth for invasive species, we also detected

intense competition at later stages of growth. Medusahead and cheatgrass also experienced facilitation from associated native species at later harvests in N added treatments. One mechanism to explain this pattern could be the role of native grass seedlings as nurse crops by providing greater nutrient availability to the invasive species, at least temporarily as suggested by Blank (2010).

Grime's C-S-R theory predicts competition will have a greater influence on plant community structure in resource rich environments compared to resource poor environments (Grime, 1977; 1979). Although we observed competition in both low and high N environments, we also observed an increase in competition intensity as N availability increased, supporting the predictions of Grime (Grime, 1997; 1979). Plants can have preferential uptake of, or differential needs for, particular forms of nutrients depending on their physiological efficiencies (Mckane et al., 2002). We found that annual grasses became more competitive compared to native species with increasing N, lending support for our hypothesis that increasing N would increase the competitive effects of invasives on natives. The fast growing invasive annual plant species gain more access to resources than the slower growing native plant species and appear to establish a positive feedback mechanism between size and resource uptake (Blank, 2010; Casper and Jackson, 1997).

Researchers have theorized that native perennial grasses perform better and are more competitive than invasive annual grasses under low N availability (Herron et al., 2001; Wedin and Tilman, 1990; Wilson and Gerry, 1995). For example, the CSR theory predicts that native species would perform better in low N environments (Grime, 1979).

However, we did not detect such patterns. Since some mineral N ($0.09 \mu\text{g}$ mineralized $\text{N}\cdot\text{g}^{-1}$ soil) was still present in our control N treatment, this amount of N could have been sufficient for the annuals to outperform the perennials. Therefore, low N content already presents in the soil might have been enough for a greater growth response by invasive plants. However, maintaining resource levels and minimizing the loss of previously captured resources is critical under low N availability (Berendse and Aerts, 1987). These attributes may improve the competitive ability over time of native plants over invasive plants especially under low N.

It is clear that competition between invasive and native species influence structure, pattern and dynamics of plant distributions (Crawley, 1997), but the relative role of competition may vary dramatically among different ecosystems. While we found competition type and competition intensity to vary at different harvests, caution in interpreting our findings is needed because this study was performed in a greenhouse under environmentally moderate conditions. Furthermore, our neighborhoods consisted of a single neighbor, a very unlikely situation in semi-arid grasslands. Future work with these species and other species in the field is needed to examine the generality of these findings.

Land managers have recognized the need to control competition during the initial phase of restoration (Sheley and Krueger-Mangold, 2003). Overcoming the barriers to desired species establishment is central to restoring annual grass infested ecosystems. Much literature suggests that seeding at a very high rate shifts the competitive balance in favor of desired species and maximizes the chances of a seed reaching a safe site during

restoration (Jacobs et al., 1996; Seabloom et al., 2003; Velagala et al., 1997). Our study suggests that limits to seeding rate exist because of intra-specific competition among desired species at initial stages of growth. Since density, species proportion, and their spatial arrangement determine the outcome of competition (Radosevich, 1987, 2007), these three factors could be designed to minimize intra-specific competition among desired native species and maximize inter-specific competition against annual invasive species, especially during the first few weeks after germination. Opportunities to improve restoration success exist from determining the optimum combination of these three factors in various ecosystems and environments.

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Fig.2-1 Effect of time of harvest (DAP) on intra- and inter-specific competitive interactions (lnRR) of different neighbor species on: **a.** Sandberg's bluegrass, **b.** bluebunch wheatgrass, **c.** cheatgrass and **d.** medusahead target plants under N⁻ and N⁺. Bars represent mean \pm SE (n = 10). Negative values indicate competition and positive values indicate facilitation. More negative values indicate greater competitive effects of neighbors. The dashed line indicates lnRR = 0 (i.e. no competitive effect). Bars with different letters indicate significant differences in lnRR in response to DAP within neighbor species using Tukey HSD tests ($P < 0.05$). Asterisks indicate significant differences between N treatments determined by Tukey HSD tests ($P < 0.05$), with comparisons made only between the same target species and the same neighboring species at a particular DAP.

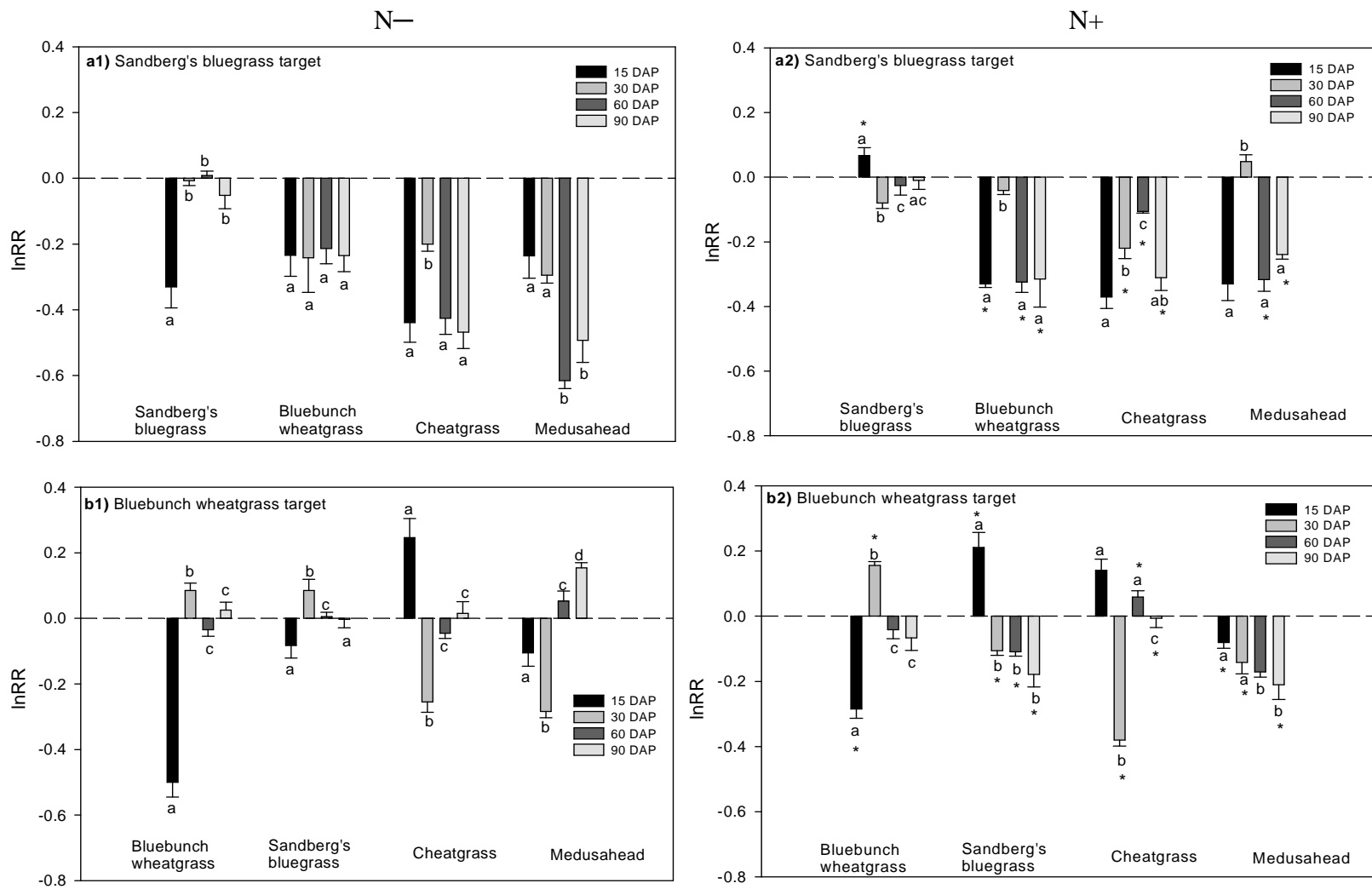


Fig. 2-1

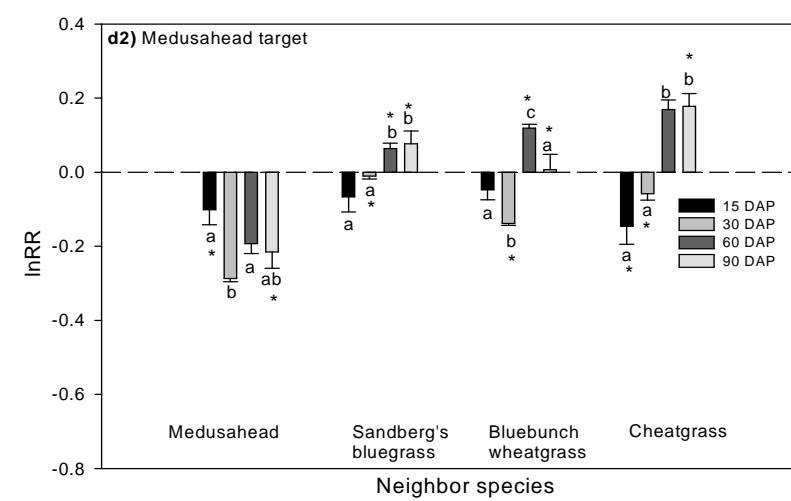
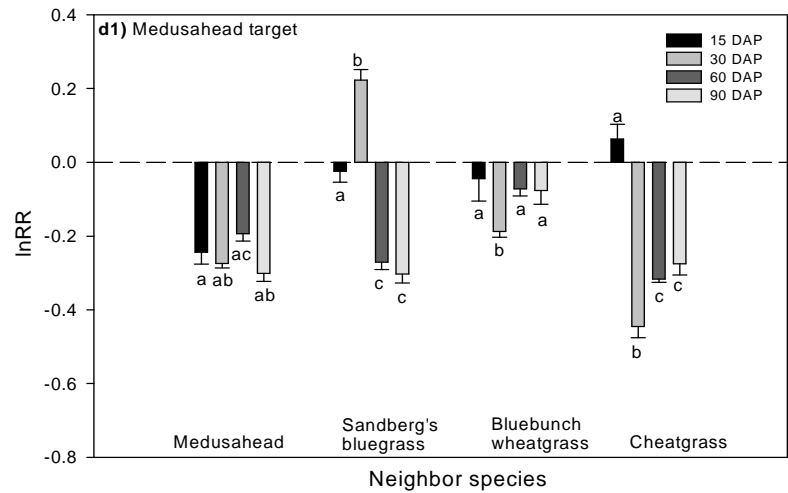
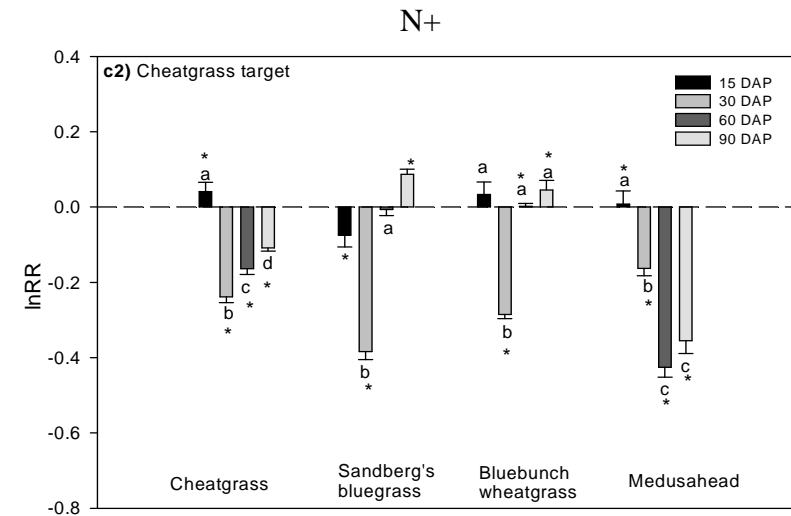
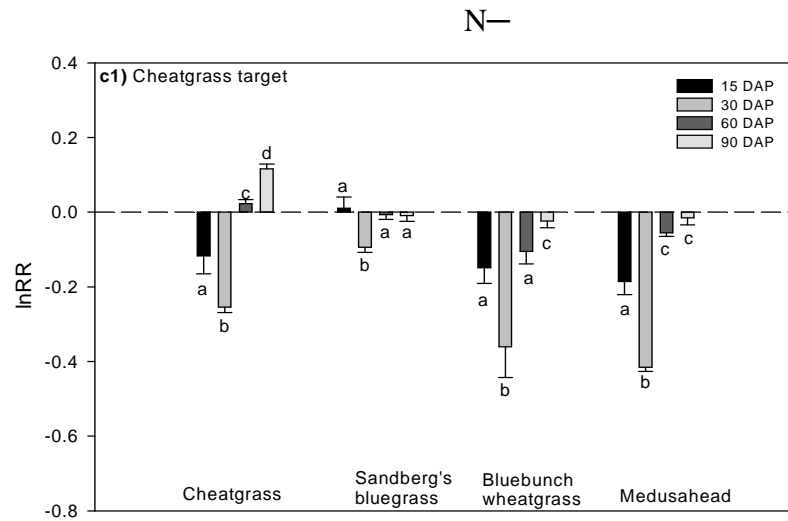


Fig. 2-1 (Continued)

Fig.2-2 Effect of time of harvest (DAP) on biomass (g) of different neighbor species on: a. Sandberg's bluegrass, b. bluebunch wheatgrass, c. cheatgrass and d. medusahead target plants under N⁻ and N⁺. Bars represent mean \pm SE (n = 10). Biomass means were used to calculate competitive effects (lnRR) presented in Fig. 2-1.

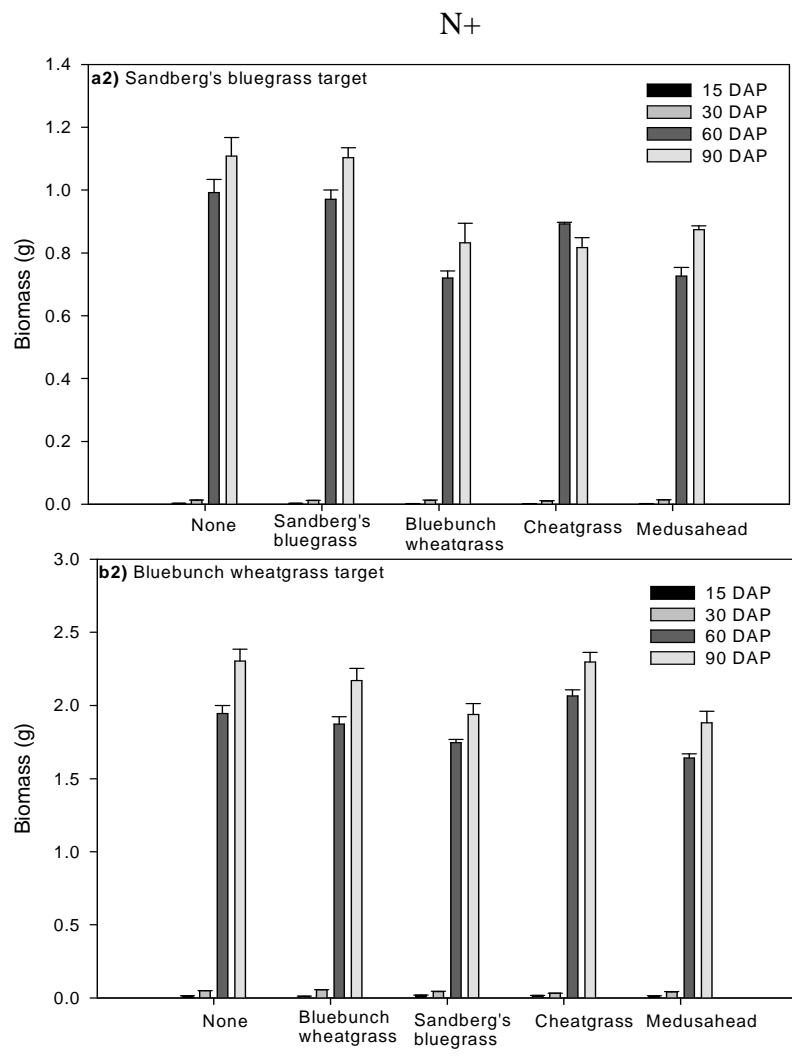
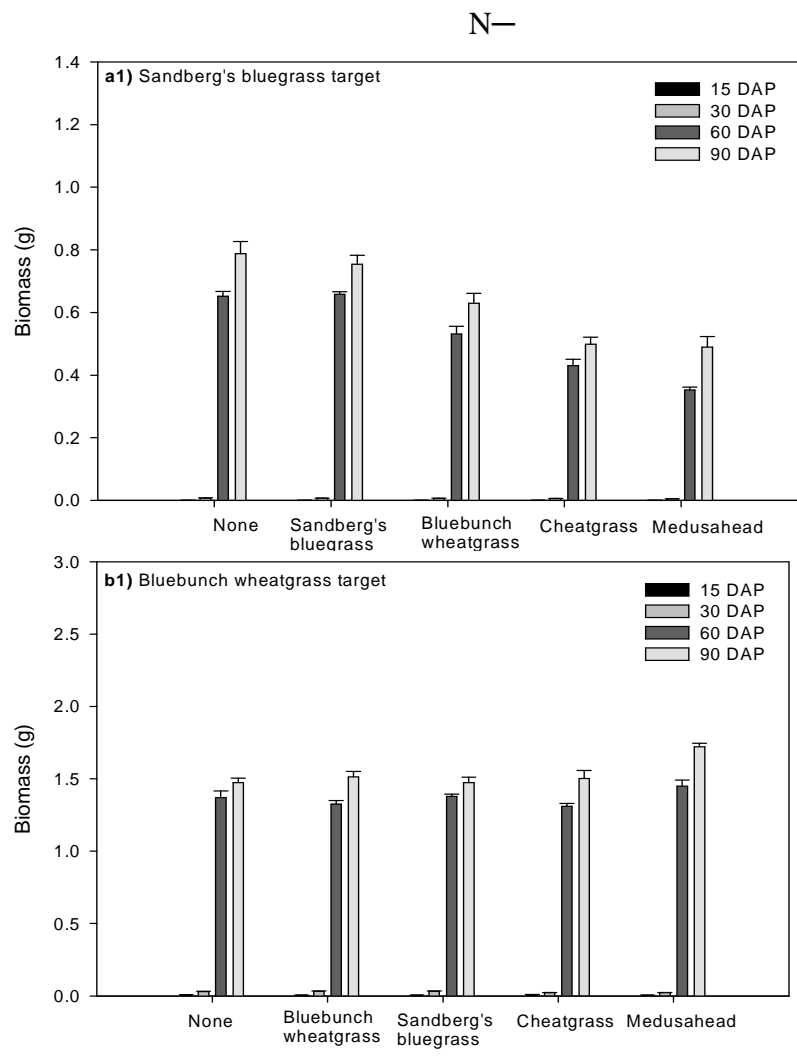


Fig. 2-2

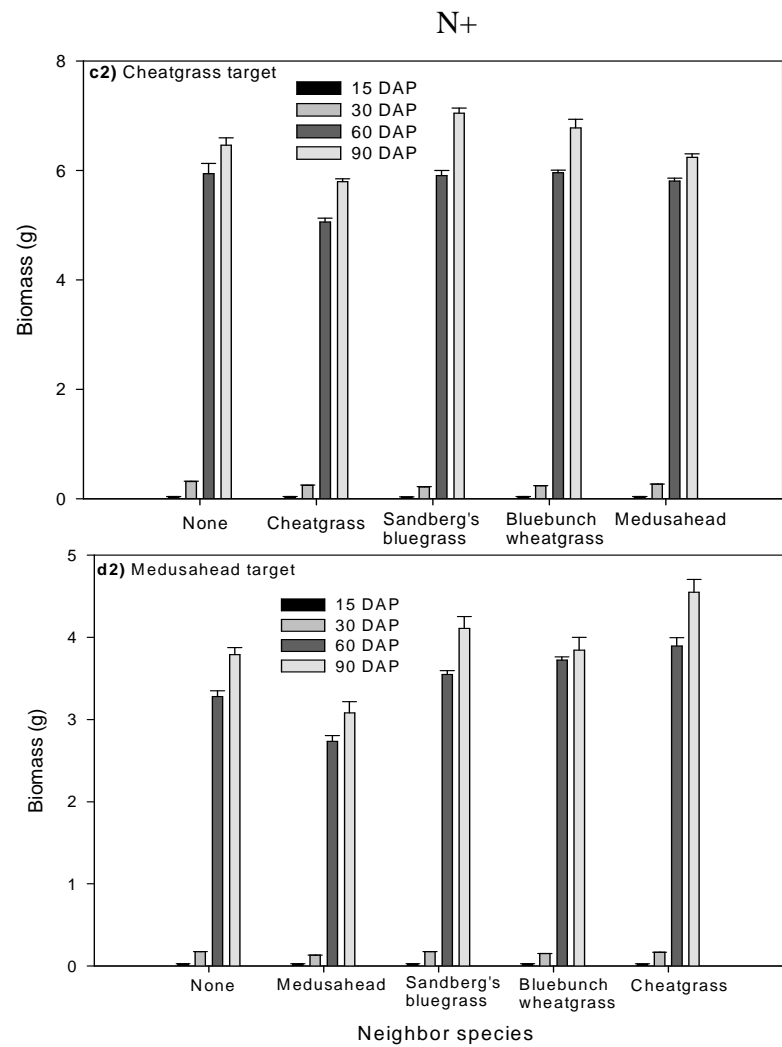
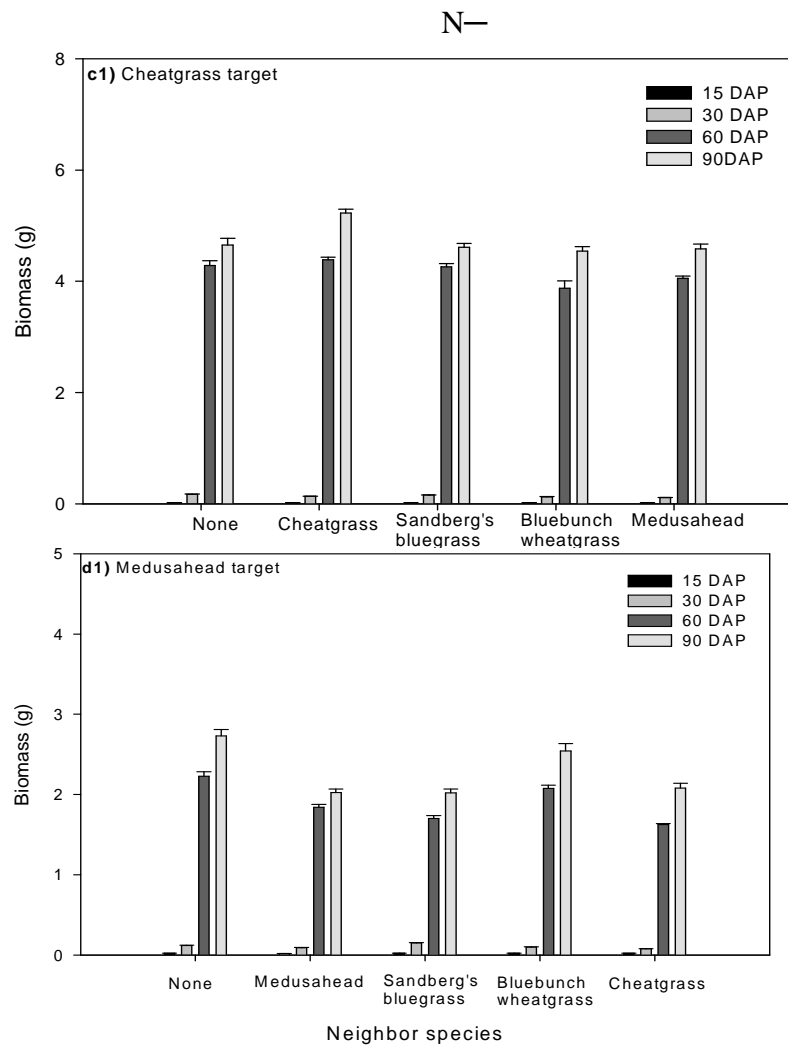


Fig. 2-2 (Continued)

Table 2-1 Results of ANOVA (*df*, *F* and *P*) testing for effects of DAP, nitrogen, target species and neighbor species on competitive effect (lnRR).

Source	lnRR		
	df	<i>F</i>	<i>P</i>
DAP	1	0.48	0.492
Nitrogen	1	2.55	0.115
Target	3	7.42	0.0002
Neighbor	3	6.31	0.0008
DAP x nitrogen	1	0.23	0.631
DAP x target	3	0.86	0.464
DAP x neighbor	3	0.81	0.492
Nitrogen x target	3	2.43	0.073
Nitrogen x neighbor	3	0.28	0.838
Target x neighbor	9	1.05	0.408
DAP x nitrogen x target	9	3.18	0.029
DAP x nitrogen x neighbor	3	1.29	0.285
DAP x target x neighbor	9	0.73	0.682
DAP x nitrogen x target x neighbor	9	1.17	0.326
Residuals	64		

**The role of competition in restoring resource poor arid production systems
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The role of competition in restoring resource poor arid production systems dominated by invasive annual grasses

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Abstract

Understanding the role that competition intensity and importance plays in directing vegetation dynamics is central to developing restoration strategies, especially in resource poor environments. We hypothesized 1) competition would be intense among invasive and native species, but 2) competition would be unimportant in explaining variation in target plant biomass and survivorship relative to other factors driving these parameters. We performed a two-year addition series field experiment to quantify competition intensity and importance. Densities of two invasive (cheatgrass and medusahead) and two native (Sandberg's bluegrass and bluebunch wheatgrass) species were arranged in

monocultures and mixtures of two, three and four species, producing varying total densities and species proportions. Total density ranged from 0 to 4000 seeds m⁻². Multiple linear regression models were developed to predict individual plant biomass and survivorship. Based on biomass, competition intensity coefficients ranged from -0.38 to 0.63 with R² <0.06. All survivorship data produced poor fitting models (R² <0.05). Our results suggest neither competition intensity nor importance influenced plant dominance in resource poor environments during the two years of establishment. Land managers may be more successful at restoration of resource poor ecosystems by overcoming the barriers associated with plant establishment such as abiotic factors rather than plant-plant interactions..

Keywords: Restoration, Competition, Importance, Intensity, Semi-arid steppe, *Bromus tectorum*, Addition series, *Taeniatherum caput-medusae*

3.1 Introduction

The role of competition in driving plant dominance in resource poor environments is poorly understood. Some authors have argued that competition is minimal or non-existent under conditions of high environmental stress (Grime, 1973, 1979), while others suggested that the strength of competition is of equal magnitude in habitats of both high and low productivity (Newman, 1973; Tilman, 1980; Wilson and Tilman, 1993). To address this debate, refined conceptual frameworks of plant interactions along environmental gradients have been proposed (Goldberg and Novoplansky, 1997; Maestre et al., 2009) and quantitative syntheses of existing literature have been performed (Goldberg et al., 1999; Gomez-Aparicio, 2009). Despite these efforts, a unified understanding of the degree to which competitive interactions control plant dominance in resource poor environments has not emerged.

Understanding competition intensity and importance is central to developing restoration strategies (Sheley and Krueger-Mangold, 2003; Tikka et al., 2001) and has been suggested as a barrier to the understanding about the role competition plays in directing vegetation dynamics, especially in resource poor environments (Brooker and Kikvidze, 2008; Grace 1991). Competition intensity refers to the degree to which resource competition by neighbors reduces target plant performance below a value when no neighbors are present (Welden and Slauson, 1986). In their original source article, Welden and Slauson (1986) indicated that importance of competition is the degree to which target plant biomass is reduced by competition intensity relative to all other abiotic and biotic factors. A vigorous debate is occurring in the literature in an attempt to

improve the concept of competition importance (Brooker and Kikvidze, 2008; Damgaard and Fayolle, 2010; Freckleton et al., 2009; Kikvidze and Brooker, 2010). Freckleton et al. (2009) argued that the definition of importance needs to provide an indication of long-term consequences of competition on the structuring of plant communities by including plant interactions effect on other indicators of fitness, especially fecundity, in plant communities at equilibrium. In response, Kikvidze and Brooker (2010) suggested that the complexity of biotic interactions invites a range of approaches, but should be backed by the original source article.

The bulk of empirical work and quantitative syntheses have focused on how the intensity of competition changes along resource gradients with the underlying assumption that intensity of competition will be proportional to the importance of competition (Grace, 1991; Mitchell et al., 2009). However, competition could be unimportant even if very intense. For example, if reductions in target plant performance by neighbors do not influence target plant survival during stress periods, competition may be intense but largely unimportant in influencing plant dominance (Goldberg and Novoplansky, 1997). Moreover, in resource poor environments, abiotic factors could have an overriding role in influencing plant survival, and be directly linked to the ability to tolerate drought and temperature extremes (Ackerman, 1979; Gutterman, 2002; Mulroy and Rundel, 1977; Went, 1949).

Experimental approaches that allow the intensity and importance of competition to be determined are useful in improving the understanding about the role competition plays in stressful environments. These approaches not only allow advancements in

understanding of ecology but are particularly important in identifying how to link ecology to management in resource poor systems. For example, invasion by exotic annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), have been identified as the greatest ecological threat to the native vegetation of the semi-arid steppe of the North America (D'Antonio and Vitousek, 1992; Duncan et al., 2004; Germino et al. 2004; Mack, 1989; Pellant, 1990; Sheley and Petroff, 1999; Sheley et al., 2008). Each year several billion dollars are spent to control invasive plant species (Pimental et al., 2005; Westbrooks, 1998), but long-term success is rare. While competition is assumed to play an important role in limiting success, harsh abiotic conditions such as drought and cold stress also influence restoration outcomes (Allen, 1989; Padilla and Pugnaire, 2006). A more complete understanding of competition intensity and competition importance is a useful step in allowing managers to understand how to prioritize inputs into restoration projects.

The objectives of this study were to: 1) quantify the intensity of competition among invasive annual grasses and native perennial bunchgrasses, and 2) determine the importance of competition in explaining variation in target plant biomass and survivorship in an arid, resource poor production system. We used an addition series competition design that allows quantification of the intensity and importance of competitive interactions (Spitters, 1983; Welden and Slauson, 1986). Intensity was measured as the slope of linear regression equations (Spitters, 1983), while importance was calculated as the percentage of the variation explained by the regression equation or as R^2 (Welden and Slauson, 1986). The specific hypotheses tested were 1) competition

would be intense among invasive and native plant species (i.e., the effect of species density would influence biomass or survivorship and intra- and inter-specific competitive effects among invasive and native species would be significant during the two years of establishment) but 2) competition would be unimportant in explaining variation in target plant biomass and survivorship relative to all other factors driving variation in these two parameters.

3.2 Material and Methods

3.2.1 Study site and environmental conditions

The study was conducted at a Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S. L. Welsh)- steppe community type in southeastern Oregon (43° 32' N, 118° 9' W), 106 km from the Eastern Oregon Agricultural Research Center, Burns, Oregon, USA. Soils at the research site were a Risley cobley loam (fine, montmorillonitic, mesic Xeric Haplargid), total soil nitrogen averaged 0.09% and our site had a 15 to 20% southerly slope. Environmental conditions (precipitation, temperature, solar radiation and relative humidity) were monitored daily from April 2008 through August 2009 using HOBO data loggers (Onset Comp. Inc., USA) installed at the research site. Daily weather data was averaged each month. Long-term weather data (1897-2009) were compiled from the Western Regional Climate Center (NCDC, 2009; Fig. 3-1). Weather data for the study site was compared with long-term weather data at different sites within the same plant community types in eastern Oregon (Krueger-Mangold et al., 2004; Sheley and Svejcar, 2009; Sheley et al., 2008).

This comparison indicated that our study site was very low in average precipitation and temperature over a hundred year time period, and thus, was relatively unproductive for the sagebrush-steppe region.

3.2.2 Site preparation and study species

In spring 2008, before the experiment was initiated, glyphosate [N-(phosphonomethyl) glycine] at 0.85 kg a.i. ha⁻¹ was applied to kill existing vegetation. Ten days after herbicide application, the site was rototilled to a depth of 10 cm. Large soil aggregates and dead plant material were removed to facilitate plant establishment. The site had been moderately grazed by cattle for over 50 years, but was fenced to prevent livestock grazing during the experiments.

Invasive annual species selected for this study were cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski). These plants are native to Eurasia and the Mediterranean region, respectively. They are among the most invasive plants in the Intermountain West, USA. Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A) and Sandberg's bluegrass (*Poa secunda* J. Presl), two native perennial species of the Intermountain West, were selected because they are common subdominant plant species in the region (Zlatnik, 1999). These native species are often used in restoration efforts on sites previously infested by invasive plants. All four species belong to the family Poaceae. Seeds of the four grass species were collected in the field east of Burns, Oregon (43° 22' N, 118° 22' W) during 2006 and stored in a moisture proof container at a cool, dry location. Seed germination tests were conducted prior to the experiments and >

90% seeds germinated. Awns of cheatgrass and medusahead seed were removed by hand prior to seeding.

3.2.3 Plant-plant interaction experiments

Addition series experiments were conducted in 2008 and 2009 to quantify the intensity and importance of competition among the four species. Treatments consisted of monoculture densities of each species to assess intra-specific competition, and mixtures of two, three and four species (inter-specific competition), producing varying total densities and species proportions (Radosevich, 1987; Radosevich et al., 2007; Spitters, 1983). On May 14, 2008, monocultures and mixtures of each species were planted by randomly broadcasting the seeds and lightly (< 2 mm) covering them with soil. The soil surface was kept moist until seedling emergence, after which no further water was added. The experiments were conducted as a randomized-complete-block design with three replications. Each plot was 1 m² and received a combination of the four study species ranging from 0 to 1000 seeds m⁻². Five seeding densities of each species were used (0, 1, 10, 100 and 1000 seeds m⁻²), but only one density of each species was used in a combination. Therefore, total density ranged from 0 to 4000 seeds m⁻². This density range was used because it represented the density combinations at which interactions are maximum (Young and Krueger-Mangold, 2008; Sheley and Larson, 1995).

3.2.4 Sampling

In spring 2008 (four weeks after seeding), the number of seedlings of each species that emerged were counted in each plot and recorded as initial density. Biomass was harvested on August 29, 2008 (110 days after seeding) by clipping each plant near the soil surface from a randomly located 0.1 m² circular quadrat within each 1 m² plot. Plants were separated by species and counted to determine final density. The above-ground biomass was weighed after drying for 48 hours at 60 °C. Biomass harvested from each plot was returned to the plot from which it was collected. Plants that were not harvested continued to grow and were flattened to the soil surface by snow and winter weather. The field was left undisturbed until spring 2009. The final density in 2008 was used as the initial density for 2009. A second harvest was collected on July 30, 2009 when the plants began to disperse seeds. The harvest proceeded as in 2008. However, the same quadrat sampled in 2008 was not re-sampled in 2009. Survivorship was calculated for each year as the ratio of final density over initial density.

3.2.5 Statistical analyses and model fitting

Multiple linear regression was performed using seeding, initial, and final densities (N) of each species as independent variables and shoot biomass (W) as the dependent variable (Spitters, 1983; Young and Krueger-Mangold, 2008). The following regressions equations were used to predict shoot biomass of an individual plant:

$$W_m = \beta_{m0} + \beta_{mm} N_m + \beta_{mc} N_c + \beta_{mb} N_b + \beta_{ms} N_s \text{ (medusahead)}$$

$$W_c = \beta_{c0} + \beta_{cc} N_c + \beta_{cm} N_m + \beta_{cb} N_b + \beta_{cs} N_s \text{ (cheatgrass)}$$

$$W_b = \beta_{b0} + \beta_{bb} N_b + \beta_{bm} N_m + \beta_{bc} N_c + \beta_{bs} N_s \text{ (bluebunch wheatgrass)}$$

$$W_s = \beta_{s0} + \beta_{ss} N_s + \beta_{sm} N_m + \beta_{sc} N_c + \beta_{sb} N_b \text{ (Sandberg's bluegrass)}$$

where W_m , W_c , W_b and W_s represent the average shoot biomass per plant for medusahead, cheatgrass, bluebunch wheatgrass and Sandberg's bluegrass, respectively. The regression coefficients β_{m0} , β_{c0} , β_{b0} and β_{s0} represent the y-intercept which is the estimate of maximum shoot biomass of an isolated individual. β_{mm} , β_{cc} , β_{bb} , β_{ss} represent intra-specific competition in the medusahead, cheatgrass, bluebunch wheatgrass and Sandberg's bluegrass models, respectively. Inter-specific competition was estimated by β_{mc} , β_{mb} , β_{ms} , β_{bc} , β_{bs} , β_{cs} . The data were normally distributed, except in a few cases, where the distribution appeared to deviate slightly. In those cases various transformations were attempted, but did not improve the distribution and did not help model fitness. Thus, the equations presented were calculated using non-transformed data. A positive response denotes facilitation, whereas a negative response denotes competition. Similarly, multiple regression equations were used to predict survivorship using seeding density as the independent variable because initial and final densities were used to calculate survivorship. The coefficient of determination (R^2) estimates the proportion of variation in the dependent variable (shoot biomass or survivorship) that is described by the regression model. R^2 value from each regression was used to determine the importance of

competition in explaining variation in target plant biomass and survivorship (Spitters, 1983; Weldon and Slauson, 1986). T-tests ($P \leq 0.05$) were used to determine the significance of the regression coefficients. Statistical computations were performed using S-Plus (S-Plus, 2005) software.

3.3 Results

3.3.1 Environmental Conditions

Average monthly temperature and relative humidity at the study site were consistent with the long-term average for the area (Figs. 3-1a and 3-1c). Months with the lowest and highest maximum temperatures were December (-2.5 °C for 2009) and July (23.2 °C for 2008; 23.8 °C for 2009), respectively. The monthly precipitation for 2008 and 2009 deviated from the long-term precipitation pattern (Fig. 3-1b). Precipitation for 2008 was 121 mm with most precipitation falling in May. In 2009, precipitation was 176 mm with the largest amount falling in April-June. At the start of the experiment (April 2008) there was a dramatic decrease in precipitation (3 mm) as compared to the long-term precipitation pattern (21 mm). However in 2009, monthly springtime precipitation exceeded the historical range (Fig. 3-1b). Large variation in solar radiation was also observed during the study (Fig. 3-1d). Average solar radiation for the study period was similar for both years with an average solar radiation for the years 2008 and 2009 ranging from 146.0 to 311.2 and 70.2 to 308.1 wm^{-2} , respectively.

3.3.2 Competition Intensity

3.3.2.1 Seeding density versus target plant biomass: For 2008, the maximum predicted biomass of an isolated individual was 0.18 and 0.28 g plant⁻¹ for cheatgrass and medusahead, respectively (Tables 3-1 and 3-2) which increased to 12 and 23 times for respective species in 2009. However, models for predicting biomass per plant were non-significant ($P > 0.05$) for both species. Both cheatgrass and medusahead biomass was not influenced by intra- or inter-specific competition ($P > 0.05$, Tables 3-1 and 3-2). Similarly for perennial species, the models resulted in non-significant regression coefficients ($P > 0.05$) for predicting maximum biomass per plant. Similar trends were observed for both 2008 and 2009. However, Sandberg's bluegrass plants died and no seedlings survived to 2009. For both years, addition of intra- or inter-specific competition had no influence on biomass of bluebunch wheatgrass or Sandberg's bluegrass ($P > 0.05$, Tables 3-3 and 3-4).

3.3.2.2 Initial seedling density versus target plant biomass: Both annual species showed a greater increase in maximum predicted biomass for 2009 compared to 2008 with cheatgrass resulting in an increase of 2.03 g plant⁻¹. Intra- or inter-specific competition had no influence on biomass of both annuals ($P > 0.05$, Tables 3-1 and 3-2) or perennials ($P > 0.05$, Tables 3-3 and 3-4) in 2008. During 2009, similar results were found for both annuals and bluebunch wheatgrass (no Sandberg's bluegrass seedlings survived).

3.3.2.3 Final seedling density versus target plant biomass: In 2009, cheatgrass and medusahead biomass per plant were 15 and 35 times greater ($P < 0.05$) than compared to

2008. Intra-specific competition coefficients for cheatgrass increased from 0.0009 in 2008 to 0.1 in 2009 while they increased from 0.0008 to 0.33 for medusahead (Tables 3-1 and 3-2). However, as with seeding and initial density, for both years, cheatgrass and medusahead biomass was not affected by either intra- or inter-specific competition ($P > 0.05$). Similarly, competition did not influence biomass of either native plant species.

3.3.3 Survivorship

3.3.3.1 Seeding density versus survivorship: Both annual species and bluebunch wheatgrass showed an increase in maximum predicted survivorship for 2009 compared to 2008 (Table 3-5). However, the models for predicting survivorship were non-significant for both annual and perennial species for both years ($P > 0.05$). Similarly, intra- or inter-specific competition had no influence on survivorship of both annual and perennial species in 2008 and both annual species and bluebunch wheatgrass in 2009 ($P > 0.05$, no Sandberg's bluegrass seedlings survived in 2009).

3.3.4 Competition Importance and Survivorship R^2

Biomass of cheatgrass, medusahead, bluebunch wheatgrass, and Sandberg's bluegrass was not significantly influenced by either seeding density, initial density or final density in any year (Tables 3-1 to 3-4). The highest R^2 observed in any of the models was less than 0.06. Similarly, survivorship was not significantly influenced by seeding density in any year and all R^2 were less than 0.05 (Table 3-5).

3.4 Discussion and conclusions

Contrary to our first hypothesis, we found no evidence to suggest that intra- or inter-specific competition were significant at our study site for the first two years that species were establishing, regardless of the density (seeding, initial or final density) used as the independent variable. Lack of competition in our study is in agreement with research showing no net plant-plant interactions for available water and nutrients with desert shrubs (Donovan and Richards, 2000). However, other studies of plant-plant interactions in resource poor systems support the expectation that plants compete with each other for resources (Fowler, 1986; Keddy, 1989; Whitford, 2002). We believe site specific variability may largely control the effects of intra- and inter-specific competition.

We accepted our hypothesis that competition would be unimportant among invasive and native species in our study system. Since our R^2 's were below 0.06, we found little, if any evidence that competitive interactions were important in influencing target plant biomass and survivorship within the range of environmental conditions encountered in the current study. Given the lack of competition intensity observed, it was predictable that competition importance would not be detectable either. A possible explanation for these results could be due to the harsh and fluctuating environmental conditions at our study site. Such stressful environments could potentially influence establishment, survival and growth of plant species (Ackerman, 1979; Gutterman, 2002; Mulroy and Rundel, 1977; Went, 1949). For instance, Sandberg's bluegrass did not survive to the second year of the study and had a very low seedling survival during the first year. Dry and hot weather conditions coupled with the shallow roots of Sandberg's

bluegrass may have led to very low moisture availability for the first year. We speculate that our study site is stressful within the sagebrush/steppe ecosystem and abiotic factors could potentially dominate plant establishment and survivorship and eventually plant dominance for the first two years.

Goldberg and Novoplansky (1997) hypothesized that competition will be unimportant in stressful environments (i) when individual plant survival is primarily determined by conditions between resources pulses and (ii) soil resource availability during interpulse intervals is largely independent of plant density, i.e. abiotically driven. This scenario has been observed for juvenile plants from a saline desert habitat site (Donovan and Richards, 2000). This scenario also may apply to our site, where plant survival is largely linked to plant ability to tolerate drought and temperature extremes. We speculate that environmental conditions in our system are more important than competition in determining plant establishment and dominance. Support for our speculation can be found in other ecosystems experiencing extremely stressful abiotic environments. In the semi-arid mountain range of Spain, Armas et al. (2009) experimentally tested the effect of shrub competition on a perennial tussock grass (*Stipa tenacissima* L.) along a gradient of aridity. They found that environmental severity largely influenced the performance of the perennial tussock grass and concluded that abiotic conditions were more important towards the harsher abiotic end of the gradient, where the selective force of habitat conditions was proportionally most important. Similar work in a high-latitude system demonstrated that abiotic conditions rather than

competition were most important in determining tussock tundra species distributions (Hobbie et al., 1999).

Taken together, our results suggest that in our study system neither the intensity of competition nor the importance of competition was an important variable in explaining variation in target plant biomass and survivorship for the first two years plants were establishing. Instead abiotic factors may have an overriding influence on plant biomass and survivorship. We propose three scenarios which might apply to stressful environments that can be used by land managers to prioritize restoration efforts. First, competition may be both intense and important if competition with neighbors negatively influences plant biomass and thus, plant survival (Goldberg and Barton, 1992). Second, competition may be intense but not necessarily important in structuring plant communities if reductions in target plant performance by neighbors do not influence target plant survival during stress periods (Lamb et al. 2009; Mitchell et al., 2009). Third, competition is neither intense nor an important variable in structuring plant communities when plant survival is largely linked to plant ability to tolerate drought and temperature extreme, i.e. abiotically driven (Armas et al., 2009; Hobbie et al., 1999). In resource poor systems, we suggest that land managers will be more successful at restoration by overcoming the barriers associated with plant establishment other than competition, such as abiotic factors, rather than focusing on treatments aimed at controlling invasive plants.

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Fig 3-1 Monthly precipitation (a), temperature (b), solar radiation (c) and relative humidity (d) at the study site. Long-term monthly precipitation, temperature, solar radiation and relative humidity also were determined at a weather station near the study site (monitored daily, NCDC 2009).

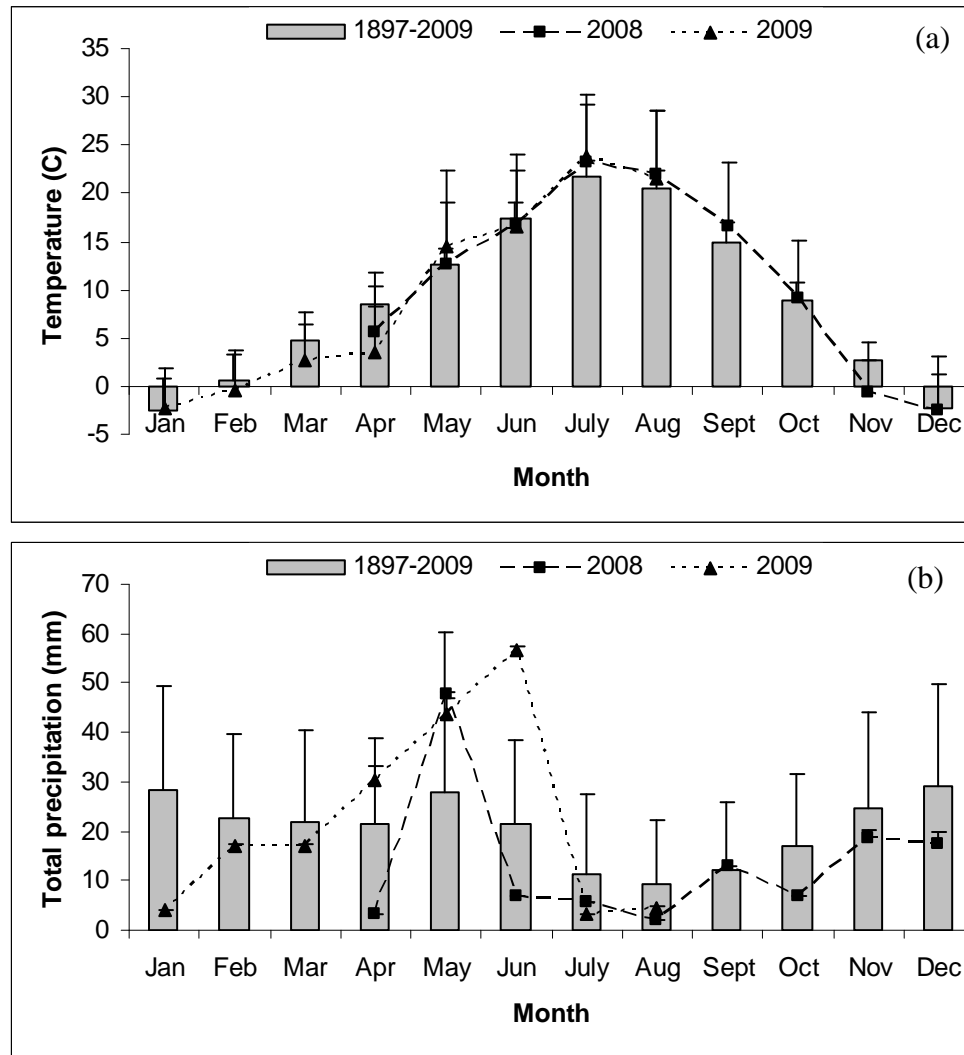


Fig. 3-1

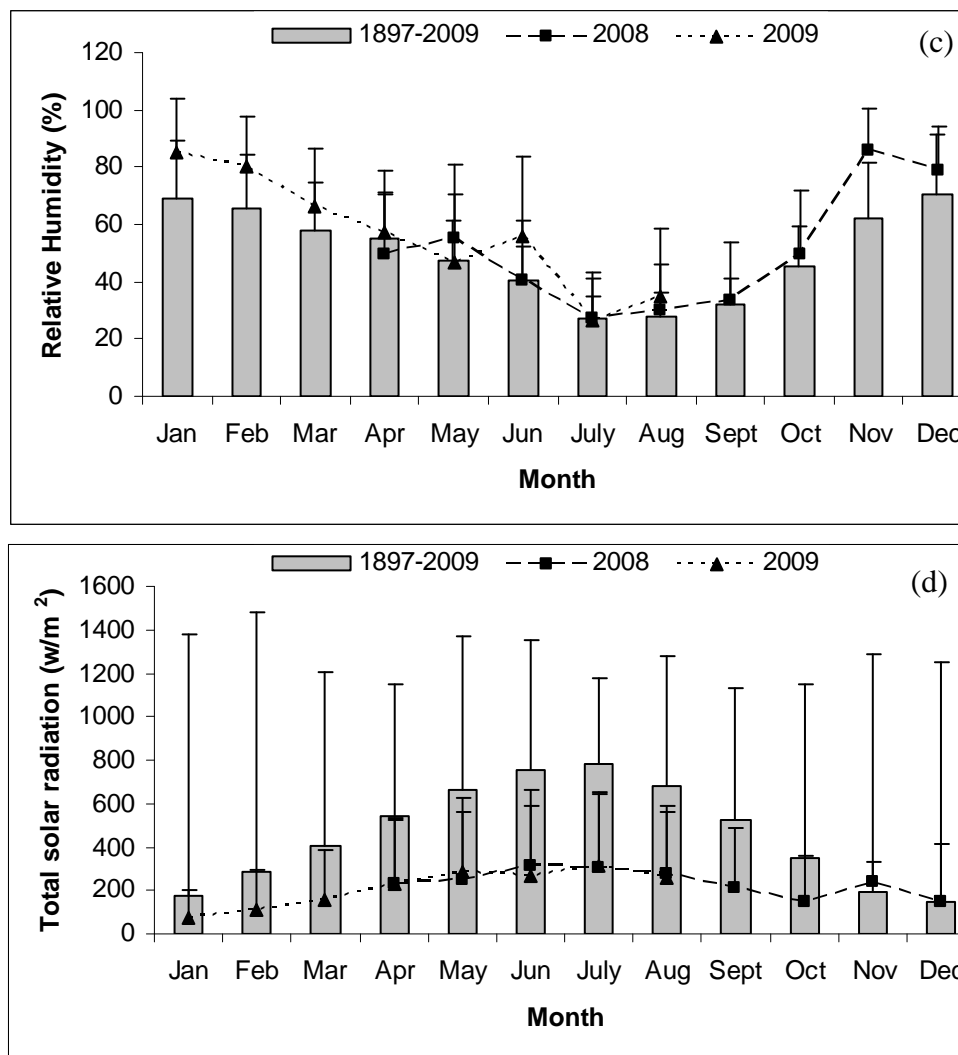


Fig. 3-1 (Continued)

Table 3-1 Multiple linear regression predicting individual cheatgrass shoot biomass (W_c ; g plant⁻¹) using seeding, initial and final densities as independent variables for 2008 and 2009.

Year	Independent variable	β_{0c}	β_{cc}	β_{cm}	β_{cb}	β_{cs}	R ²
2008	Seeding density	0.18(0.03)	-0.0001(0.0001)	0.0001(0.0001)	-0.0001(0.0001)	0.0(0.0001)	0.009
	Initial density	0.17(0.03)	0.0001(0.0006)	-0.0002(0.0006)	0.0001(0.001)	0.006(0.009)	0.003
	Final density	0.18(0.03)	0.0009(0.001)	-0.001(0.0006)	0.01(0.004)	-0.02(0.06)	0.059
2009	Seeding density	2.34(0.41)	-0.0008(0.001)	-0.002(0.001)	-0.0011(0.001)	0.002(0.001)	0.042
	Initial density	2.21(0.47)	-0.002(0.02)	-0.01(0.009)	-0.04(0.06)	0.63(1.05)	0.009
	Final density	2.71(0.54)	0.1(0.09)	-0.13(0.04)	-0.02(0.01)		0.039

β_{0c} is the predicted mean biomass of an individual cheatgrass plant grown in isolation; β_{cc} is the intra-specific interference by cheatgrass; β_{cm} , β_{cb} and β_{cs} is the inter-specific interference by neighboring plants medusahead, bluebunch wheatgrass and Sandberg's bluegrass, respectively; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived during final sampling in 2009.

Table 3-2 Multiple linear regression predicting individual medusahead shoot biomass (W_m ; g plant⁻¹) using seeding, initial and final densities as independent variables for 2008 and 2009.

Year	Independent variable	β_{0m}	β_{mm}	β_{mc}	β_{mb}	β_{ms}	R ²
2008	Seeding density	0.28(0.02)	0.0001(0.00)	-0.0001(0.00)	0.0001(0.00)	0.00(0.00)	0.038
	Initial density	0.28(0.02)	-0.001(0.0004)	-0.0005(0.0004)	0.0(0.001)	0.01(0.006)	0.036
	Final density	0.27(0.02)	-0.0008(0.0004)	0.0003(0.0008)	-0.004(0.003)	-0.05(0.05)	0.028
2009	Seeding density	6.55(1.16)	-0.002(0.003)	-0.001(0.003)	-0.003(0.003)	-0.0001(0.003)	0.019
	Initial density	5.80(1.29)	-0.01(0.03)	-0.02(0.04)	-0.12(0.17)	-0.75(2.92)	0.004
	Final density	9.27(1.49)	-0.32(0.12)	-0.38(0.24)	-0.06(0.041)		0.047

β_{0m} is the predicted mean biomass of an individual medusahead plant grown in isolation; β_{mm} is the intra-specific interference by medusahead; β_{mc} , β_{mb} and β_{ms} is the inter-specific interference by neighboring plants cheatgrass, bluebunch wheatgrass and Sandberg's bluegrass, respectively; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived during final sampling in 2009.

Table 3-3 Multiple linear regression predicting individual bluebunch wheatgrass shoot biomass (W_b ; g plant⁻¹) using seeding, initial and final densities as independent variables for 2008 and 2009.

Year	Independent variable	β_{0b}	β_{bb}	β_{bm}	β_{bc}	β_{bs}	R ²
2008	Seeding density	0.04(0.03)	0.0(0.0001)	0.0(0.0001)	0.0(0.0001)	0.0(0.0001)	0.0009
	Initial density	-0.008(0.03)	0.003(0.002)	0.0005(0.0006)	0.0002(0.0006)	0.005(0.009)	0.022
	Final density	0.04(0.03)	0.008(0.004)	-0.0001(0.0006)	-0.0002(0.001)	-0.009(0.07)	0.015
2009	Seeding density	0.42(0.21)	0.0(0.0005)	-0.0003(0.0005)	0.0(0.0005)	-0.0001(0.0005)	0.002
	Initial density	0.52(0.23)	-0.002(0.03)	-0.004(0.005)	-0.005(0.009)		0.004
	Final density	0.48(0.27)	-0.002(0.007)	-0.012(0.02)	-0.009(0.04)		0.002

β_{0b} is the predicted mean biomass of an individual bluebunch wheatgrass plant grown in isolation; β_{bb} is the intra-specific interference by bluebunch wheatgrass; β_{bm} , β_{bc} and β_{bs} is the inter-specific interference by neighboring plants medusahead, cheatgrass and Sandberg's bluegrass, respectively; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived during initial and final sampling in 2009.

Table 3-4 Multiple linear regression predicting individual Sandberg’s bluegrass shoot biomass (W_s ; g plant⁻¹) using seeding, initial and final densities as independent variables for 2008 and 2009.

Year	Independent variable	β_{0s}	β_{ss}	β_{sm}	β_{sc}	β_{sb}	R^2
2008	Seeding density	0.001(0.0007)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.004
	Initial density	0.001(0.0008)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0002)	0.006
	Final density	-0.0002(0.0004)	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.02(0.001)	0.06
2009	Seeding density						
	Initial density						
	Final density						

β_{0s} is the predicted mean biomass of an individual Sandberg’s bluegrass plant grown in isolation; β_{ss} is the intra-specific interference by Sandberg’s bluegrass; β_{sm} , β_{sc} and β_{sb} is the inter-specific interference by neighboring plants medusahead, cheatgrass and bluebunch wheatgrass, respectively; Numbers in parentheses are standard errors for coefficients. No Sandberg’s bluegrass survived in 2009.

Table 3-5 Multiple linear regression predicting survivorship of cheatgrass (S_c), medusahead (S_m), bluebunch wheatgrass (S_b) and Sandberg's bluegrass (S_s) using seeding density as the independent variable for 2008 and 2009.

Dependent Variable	Year	β_0	β_c	β_m	β_b	β_s	R^2
S_c	2008	0.46(0.14)	0.0004(0.0003)	-0.0006(0.0003)	0.0000(0.0003)	0.0003(0.0003)	0.019
	2009	0.53(0.11)	0.0001(0.0003)	0.000(0.0003)	0.000(0.0003)	-0.0002(0.000)	0.003
S_m	2008	1.03(0.23)	-0.0006(0.0006)	-0.0005(0.0005)	0.0012(0.0006)	-0.0003(0.000)	0.022
	2009	1.17(0.22)	-0.0005(0.0005)	-0.0006(0.0005)	-0.0004(0.0005)	0.002(0.0005)	0.021
S_b	2008	0.05(0.04)	-0.0001(0.0001)	-0.0001(0.0001)	0.0003(0.0001)	-0.0001(0.000)	0.044
	2009	0.44(0.23)	-0.0002(0.0006)	-0.0004(0.0005)	0.0004(0.0006)	-0.0002(0.000)	0.005
S_s	2008	0.02(0.01)	0.0000(0.0000)	0.0000(0.0000)	0.0000(0.0000)	0.0000(0.0000)	0.002
	2009						

β_0 is the predicted survivorship of each species; β_c , β_m , β_b and β_s , is the change in survivorship in response to density of cheatgrass, medusahead, bluebunch wheatgrass and Sandberg's bluegrass, respectively; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived in 2009.

**Field growth comparisons of medusahead versus bluebunch wheatgrass and
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4 Third Manuscript

Field growth comparisons of medusahead versus bluebunch wheatgrass and cheatgrass in monocultures

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Abstract

Medusahead is rapidly invading native grassland and cheatgrass dominated grassland throughout the western United States. Understanding medusahead growth dynamics relative to native grasses and cheatgrass is central to predicting and managing medusahead. We hypothesized that medusahead would have a higher relative growth rate (RGR), a longer period of growth, and as a consequence, more total biomass at the end of the growing season than the native bluebunch wheatgrass and cheatgrass. In 2008 (dry conditions), 250 seeds and in 2009 (wet conditions), 250 and 100 seeds of each species were sown in 1 m² plots with 5 replicates. Shoots were harvested on 3 to 25 day intervals throughout the growing season. Bluebunch wheatgrass had more biomass and higher

RGR than medusahead in the dry year, but the relationship was reversed in the wet year. Precipitation in 2008 was well-below average and this level of drought is very infrequent based on historical weather data. Medusahead had a longer period of growth and more total biomass than cheatgrass for both years. We expect that medusahead will continue to invade grassland ecosystems because of its higher RGR and extended period of growth.

Keywords: Taeniatherum caput-medusae, Relative growth rate, Shoot weight, Bromus tectorum, Pseudoroegneria spicata

4.1 Introduction

Throughout the western United States, the exotic annual grasses, cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), are expanding and dominating expansive areas once dominated by native perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A) (D'Antonio and Vitousek, 1992; Germino et al., 2004). Annual grass invasion is driving one of the largest changes in vegetation structure ever documented (D'Antonio and Vitousek, 1992; Upadhyaya et al., 1986). Vegetation dynamics involve deterioration of healthy intact shrub-steppe plant communities into annual grass monocultures. This conversion has major negative impacts on ecosystem function, wildlife, and fire regimes (Randall, 1996; Stohlgren et al., 1999; Vitousek et al., 1996; Whisenant, 1990). For example, conversion of shrub-steppe ecosystems to annual grass dominated systems replaces structurally complex, diverse communities with complementary patterns of resource use, with a single monoculture of annual grass that grows for a limited time in early spring (Rosentrater, 1994).

In the Intermountain West, the exponential increase in dominance by medusahead has largely been at the expense of other annual grasses, especially cheatgrass (Bovey et al., 1961; Harris, 1977; Turner, 1963; Young and Evans, 1970). In this scenario, medusahead either joins, replaces or displaces cheatgrass (Hironaka, 1989; Miller et al., 1999). From an agricultural and restorative perspective, conversion of cheatgrass rangeland to predominantly medusahead rangeland represents further deterioration beyond that of cheatgrass alone. Invasion by medusahead substantially reduces forage

quality and amount, alters timing of forage availability, and increases year to year variation in forage production on rangeland (Murray et al., 1978). The high silica content in medusahead can reduce forage production for livestock in invaded areas by 80% (Hironaka, 1961). Mature medusahead seeds have long, stiff awns that often puncture the mouth and throat tissue of livestock, reducing feed intake and subsequent weight gain (Currie et al., 1987). The rapid spread of medusahead is a serious management concern (Dahl and Tisdale, 1975; Monaco et al., 2005), especially because most restoration efforts in the Intermountain West fail (Young, 1992; Young et al., 1999).

Invasive plants are hypothesized to share a host of specific plant traits that contribute to their invasiveness (Grotkopp and Rejmánek, 2007). One trait that seems to be particularly important for invasive species is high relative growth rate (Burns, 2004, 2006; Grotkopp et al., 2002). A high relative growth rate (RGR, plant weight increase per unit of biomass per unit of time) allows invasive plants to occupy space and capture resources quickly and reduces the time between vegetative growth and reproduction (Poorter, 1989). Higher RGR provides an initial size advantage that allows invasive plants to capture more resources than natives, thus minimizing their exposure to drought stress as upper soils dry during the growing season (Grotkopp and Rejmánek, 2007). High RGR is one of the major factors responsible for successful invasion of native grasslands by cheatgrass (Arredondo et al., 1998; Humphrey and Schupp, 2004; James, 2008; Sheley and Larson, 1994a).

While the potential for cheatgrass to achieve high RGR is well documented, less is known about RGR of medusahead compared to native species and cheatgrass. Only a

few greenhouse studies provide evidence that differences exist in RGR between medusahead and co-occurring species (Arredondo et al., 1998; James, 2008). In spite of the importance of studying growth related traits under natural conditions (Garnier and Freijssen, 1994; Villar et al., 2005), no field experiment has been conducted comparing RGR of medusahead with other co-occurring species. Furthermore, studies comparing invasive and native species from the Intermountain West have focused on RGR's of species growing in isolation, an unlikely situation during the invasion process (Radosevich et al., 2007). Knowledge of growth rates of invasive and native species at low densities of monocultures may mimic conditions during the initial stages of invasion.

The objectives of this study were to compare the growth rate and growth patterns of medusahead with that of bluebunch wheatgrass and cheatgrass in the field using frequent harvest intervals across the entire season of growth. As RGR is the most ecologically significant plant growth index and is very sensitive to plant growth response to environment (Grime and Hunt, 1975; Hunt, 1978, 1982; Lambers et al., 1998), frequent RGR comparisons throughout the growing season could lead to better predictions of growth conditions under which medusahead might dominate over native species and cheatgrass. Understanding the growth rate of medusahead relative to these species may help explain the continued invasion and dominance of rangeland by medusahead. We hypothesized that medusahead growing in monocultures would have a higher RGR, a longer period of growth, and as a consequence, more total biomass at the end of the growing season than bluebunch wheatgrass and cheatgrass.

4.2 Material and Methods

4.2.1 Study site and site preparation

The study was conducted in 2008 and 2009 within a Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S.L. Welsh)-steppe community type in southeastern Oregon (43° 32' N, 118° 9' W), about 106 km from Burns, Oregon, USA. Elevation at the study site was 1229 m, with long term annual average precipitation between 200 and 250 mm (NCDC, 2009). Soils at the research site were a Risley copley loam (fine, montmorillonitic, mesic Xeric Haplargid) with total soil nitrogen of 0.09 μg mineralized N g^{-1} soil and had a 15 to 20% southerly slope. Environmental conditions (precipitation, temperature, solar radiation) were monitored daily from January 2008 through December 2009 using HOBO (Onset Comp. Inc., USA) data loggers located at the research site (Fig. 4-1). The solar radiation was similar for two years of the study ranging from 6 to 8 KW-hr m^{-2} day^{-1} (data not shown). Long-term monthly precipitation data (1897-2009) was compiled from the Western Regional Climate Center (NCDC, 2009; Fig. 4-1).

In spring 2008, before the experiment was initiated, glyphosate [N-(phosphonomethyl) glycine] was applied at the rate of 0.85 kg active ingredient per hectare to kill existing vegetation. Ten days after herbicide application, the site was rototilled to a depth of 10 cm. Large soil aggregates and dead plant material were removed to facilitate plant establishment. The site had been moderately grazed (50% utilization) in the summer by cattle for over 50 years, but was fenced to prevent livestock grazing during the experiments.

4.2.2 Experimental design

On May 14, 2008, 250 individual seeds of medusahead, cheatgrass and bluebunch wheatgrass were sown in completely-randomized 1 x 1 m² plots. A total of 5 replicates of each species were established separately providing a total of 15 plots spaced 200 mm apart. Seeds of each species were randomly broadcasted and were lightly (< 2mm) covered with soil. Each seed was separated from the nearest neighbor to avoid clustering and provide uniform distribution among seeds. The surface soil was kept moist until emergence. No further water was added. This experiment was repeated in 2009. Additionally, in 2009, a similar experiment using 100 seeds of each species in 1 x 1 m² plots were sown to compare plant weight and RGR of plant species at a slightly lower monoculture density.

4.2.3 Sampling

Seedlings of each species were harvested by randomly hand-removing 5 seedlings from each plot at an interval of 7 to 25 days for 126 days beginning 18 days after planting (DAP) for 2008. For 2009, seedlings were harvested for 131 days beginning 22 DAP by randomly harvesting 5 seedlings from each plot at an interval of 3 to 7 days. Therefore, the densities declined over time as harvests continued and the days between harvests increased as the season progressed. Roots could not be retrieved intact given the rocky nature of the soil; therefore only shoots of each seedling were collected. Shoots were oven-dried at 65 °C for 48 hours before weighing.

4.2.4 Growth analysis and statistical procedures

Mean shoot weight and standard deviation were calculated at each harvest and plotted against DAP to determine the differences in growth for each species. We calculated RGR over all harvest intervals using the classical plant growth analysis for ungraded and unpaired harvests (Causton and Venus, 1981). The excel file published in Hunt et al. (2002) (http://people.exeter.ac.uk/rh203/growth_analysis.html) was used to perform the calculations. As there were a series of successive harvests, fitted growth analysis (functional plant growth analysis) was also used to derive RGR for each harvest (Hunt and Parson, 1974). For this purpose, HP curves were used (http://people.exeter.ac.uk/rh203/growth_analysis.html). The results were very similar to those obtained with the classical approach, and therefore, only the functional growth analysis is presented. Without roots it was impossible to calculate the total plant weight, therefore the RGR calculated is shoot RGR (referred to as RGR throughout this manuscript). All data were subjected to ANOVA, and Tukey's tests were used for pairwise comparisons ($\alpha = 0.05$). All statistical analysis was performed using S-plus 7.0.2 for Microsoft windows (S plus, Insightful corp. 2005).

4.3 Results

4.3.1 Environmental conditions

Ambient air temperature was lower early in the growing season than during the middle and later portions of the growing season (Fig.4-1a, b). The lowest temperature in

2008 was nearly 7 °C but was 2 °C in 2009. The highest temperatures in 2008 and 2009 were similar, 21 °C and 23 °C in 2008 and 2009, respectively. Based upon long-term monthly precipitation data, precipitation in 2008 was 30% less than the long-term average, whereas it was similar to the long-term average in 2009. In early spring, the site received 103 mm of precipitation in 2008, which was 30% greater than the long-term average but 50% less than the 2009 for the same time period. In early summer 2008, precipitation was 50% less than that received in 2009 and the long-term average during that period (Fig. 4-1c). The highest total precipitation (81.2 ± 5.7 mm) was recorded in 2008 at 18 DAP. But after 18 DAP, total precipitation was below 10 mm with none recorded during the last two harvest times. In 2009, the highest total precipitation was recorded in the middle of the growing season during the 70 (28.9 ± 5.9 mm) and 77 (37.1 ± 5.9 mm) DAP periods of growth. There were few days in the growing season without precipitation in 2009 (Fig. 4-1b). Total precipitation was less than the long-term average in 2008 (NCDC, 2009).

4.3.2 Shoot weight: medusahead vs. bluebunch wheatgrass and cheatgrass

In 2008, medusahead had greater shoot weight than cheatgrass for most harvests ($P < 0.05$, Fig. 4-2a); however, bluebunch wheatgrass was greater in shoot weight than medusahead during all harvests ($P < 0.01$, Fig. 4-2a). During the last harvest (126 DAP), seedlings of bluebunch wheatgrass dried and were not harvestable; therefore, no comparisons were possible during the last harvest. Averaged across all harvests excluding 126 DAP, bluebunch wheatgrass had 2 times higher shoot weight than medusahead ($P <$

0.01). Both medusahead (554.6 ± 137.8 mg) and bluebunch wheatgrass (705.5 ± 96.9 mg) had highest shoot weight at 101 DAP.

In 2009, no differences in shoot weight of medusahead, bluebunch wheatgrass and cheatgrass resulted when 250 (Fig. 4-2b) and 100 (Fig. 4-2c) individual seeds of each species were sown and therefore results from only 250 seeds per m^2 are presented. Medusahead (539.7 ± 233.7 mg) had greater shoot weight at the end of the growing season compared to bluebunch wheatgrass (236.8 ± 180.7 mg) and cheatgrass (405.3 ± 273.6 mg). Averaged across all harvests, medusahead (396.3 ± 295.2 mg) maintained greater shoot weight compared to bluebunch wheatgrass (83.6 ± 54.9 mg) and cheatgrass (287.5 ± 249.8 mg). The maximum shoot weight was observed at 117 DAP for medusahead (1720.1 ± 1380.7 mg) and bluebunch wheatgrass (369.4 ± 258.8 mg) while for cheatgrass (977.1 ± 746.4 mg) maximum shoot weight was observed at 110 DAP (Fig. 4-2b).

4.3.3 RGR: medusahead vs. bluebunch wheatgrass and cheatgrass

In 2008, during the first two harvests (18 and 28 DAP, $P < 0.01$); medusahead had a higher RGR than bluebunch wheatgrass. However, during the mid-period of growth (48-77 DAP); bluebunch wheatgrass experienced a tremendous increase in its RGR compared to medusahead. During the last two harvests (94 and 101 DAP), a negative RGR for bluebunch wheatgrass was recorded, which was significantly lower than the RGR for medusahead ($P < 0.01$, Fig. 4-3a). Comparing medusahead with cheatgrass, medusahead had significantly lower RGR than cheatgrass during the first two harvests

($P < 0.01$) while medusahead had higher RGR hereafter ($P < 0.01$) except at 48 and 101 DAP. At 126 DAP, both medusahead and cheatgrass had negative RGR.

In 2009, trends of RGR of all species when grown with 250 individual seeds per m^2 (Fig. 4-3b) were consistent with the experiment performed with lower monoculture densities of 100 individual seeds per m^2 (Fig. 4-3c). Therefore, only data from experiments planted with 250 seeds per m^2 are discussed. Medusahead had greater RGR than bluebunch wheatgrass during the earliest periods of growth (22-62 DAP, $P < 0.01$). During the mid-periods of growth (70-91 DAP, $P > 0.01$) no significant differences in RGR between the two species were observed, while during the late periods of growth (97-131 DAP), medusahead had a lower RGR than bluebunch wheatgrass. During the last two harvests (124 and 131 DAP), both species had negative RGR. Averaged across all harvests, medusahead ($0.066 \pm 0.008 \text{ mg mg}^{-1} \text{ d}^{-1}$) maintained a greater RGR than bluebunch wheatgrass ($0.049 \pm 0.007 \text{ mg mg}^{-1} \text{ d}^{-1}$). Medusahead had a lower RGR than cheatgrass from 22 DAP to 50 DAP ($P < 0.01$) while from 56 to 110 DAP, medusahead had the greater RGR. No differences in RGR were recorded at 56 and 62 DAP ($P > 0.01$). Averaged across all harvests, medusahead ($0.066 \pm 0.008 \text{ mg mg}^{-1} \text{ d}^{-1}$) had higher RGR than cheatgrass ($0.052 \pm 0.004 \text{ mg mg}^{-1} \text{ d}^{-1}$). From 117 to 131 DAP, negative RGR for both the species were recorded (Fig. 4-3c).

4.4 Discussion and conclusions

Annual grass invasion is having a multi-dimensional, catastrophic effect on agriculture in the West that extends well beyond the direct economic impacts on livestock

production. The exotic annual grass, medusahead, is an example of this problem in the Intermountain region of the western United States (D'Antonio and Vitousek, 1992; Germino et al., 2004). Medusahead has invaded millions of hectares of rangeland and continues to spread rapidly. The spread and increase in dominance of medusahead in plant communities of semi-arid grasslands has been largely at the expense of other annual grasses, especially cheatgrass (Miller et al., 1999; Young and Evans, 1970). Knowledge about the growth dynamics of medusahead relative to co-occurring species under natural conditions is central to understanding and predicting medusahead invasion.

Plant species may differ considerably in biomass production. Production can be influenced by the relative ability of a plant to capitalize on resources, differences in length of the growing period, and environmental conditions (Poorter and Remkes, 1990; Williamson, 1996). Duration of growth and greater biomass accumulation by invasive species has been identified as important factors contributing to their successful invasion (Feng et al., 2007; Grotkopp and Rejmánek, 2007; Jacobs and Sheley, 1998). Over the two years of this study, our hypothesis that medusahead would have a longer period of growth than bluebunch wheatgrass, and as a consequence more total biomass at the end of the growing season was partially supported. In 2008, bluebunch wheatgrass had greater total shoot weight than medusahead, but did not have a longer growing period. In 2009, medusahead had a slightly longer growing period and produced more biomass than bluebunch wheatgrass. We believe that differences in year to year precipitation patterns may explain such contrasting growth (Fig. 4-1). Environmental variability is a ubiquitous feature of arid systems, of which precipitation is a major driver of growth (Chambers et

al., 2007). In our study, 2008 was drier than 2009 with most precipitation arriving during the very early portion (May) of the growing season. This is consistent with the work of Kiemnec et al. (2003) who reported that warm, dry conditions resulted in a slower growth rate of diffuse knapweed (*Centaurea diffusa* L). The slow growth rate lessened soil depth penetration by diffuse knapweed and favored bluebunch wheatgrass. Conversely, the invasive plant grew rapidly and substantially increased soil depth penetration by roots in cool, wet conditions (Kiemnec et al. 2003). This suggests that biomass dynamics between study species is likely to be oscillatory based on the amount and timing of precipitation. Oscillatory dynamics was predicted between cheatgrass and yellow starthistle (*Centaurea solstitialis* L), but in this case, yellow starthistle growth increased after wet summers (Sheley and Larson, 1994b).

We believe that more biomass accumulated by bluebunch wheatgrass in 2008 and medusahead in 2009 is associated with their high RGR during the year that favored one species over the other. In 2008, bluebunch wheatgrass had higher RGR than medusahead during the middle part of the growing season and therefore, more total shoot biomass was produced by bluebunch wheatgrass. In 2009, medusahead had higher RGR than bluebunch wheatgrass throughout the growing season and subsequently more biomass at the end of the growing season (Fig. 4-3). These contrasting results between the two years of the study provided only partial evidence for our hypothesis that medusahead growing in monocultures will have higher RGR than bluebunch wheatgrass for both years. Variation in RGR amongst species could be achieved by having higher rates of photosynthesis and/or lower rates of respiration (high NAR, net assimilation rate),

allocating more biomass to leaves (high LMR, leaf mass ratio), or producing thinner or less dense leaves resulting in more leaf area per unit leaf biomass (high SLA, specific leaf area) (Causton and Venus, 1981; Evans, 1982). SLA is usually considered most important in determining differences in RGR amongst species (Grotkopp et al., 2002; Villar et al., 2005). In this present study, although we were not able to identify the components of RGR driving the differences, we speculate that year to year variation in environmental conditions change the relative contribution of SLA or NAR to RGR as suggested by Loveys et al. (2002).

Medusahead matures 2 to 3 weeks later than cheatgrass (Miller et al., 1999; Sharp et al., 1957). Recently, James et al. (2008) measured leaf biomass over the growing season and found that medusahead maintained vegetative growth later in the growing season than cheatgrass. Consistent with those findings, data from this study supports the hypothesis that medusahead has a longer period of growth and more total biomass than that of cheatgrass. Possible explanations may be related to the ability of medusahead to deplete soil moisture, and its adaptation to higher temperatures compared to co-occurring species, especially cheatgrass (Harris, 1977). Cheatgrass roots have a relatively poorly developed endodermis layer to insulate against hot, dry surface soils, while medusahead roots have thicker cell walls, which allow the conduction of water throughout very dry soil horizons (Harris, 1977). Cheatgrass roots develop a more fragile root system than medusahead and this fragility increases later in the growing season as the roots become older (Hironaka, 1961). Our findings support the speculations of Hironaka (1989) that the

sequence of species replacement among invasive annuals in the western United States would be from early maturing cheatgrass to later maturing medusahead.

It is possible that differences in RGR between medusahead and cheatgrass could be a major factor for replacement of cheatgrass by medusahead. Consistent with our hypothesis, we found significantly higher RGR by medusahead compared to cheatgrass for both years of the study. However, the degree of differences in RGR between species varied between years (Fig. 4-3). This contrasts with earlier work reporting a comparable RGR among medusahead and cheatgrass in a greenhouse experiment (James, 2008). This discrepancy may be related to the differences in importance of particular RGR component for a particular species. For example, cheatgrass maintained a higher NAR than medusahead, while medusahead maintained higher SLA than cheatgrass, ultimately resulting in comparable RGR among the two annual species (James, 2008). In another greenhouse experiment, medusahead had similar SLA to cheatgrass and equal RGR (Arredondo et al., 1998). Contrasting growth condition between the present study and greenhouse experiments could affect RGR values as suggested by Villar et al. (2005).

The RGR of annual and perennial grasses reached an inflection point when seedlings were young and then decreased over time (Fig. 4-3). The general trend of decline in RGR with time for invasive and native species is consistent with the findings of several other studies (Causton and Venus, 1981; Grotkopp et al., 2002; Hunt, 1982; Villar et al., 2005). Ontogenic changes, higher allocation to low-efficiency tissues and self-shading are the possible explanation of this reduction. However, both invasive and native species had negative RGR towards the end of the growing season for both years of

the study (Fig. 4-3). Typically, species demonstrate a greater reduction in RGR with time without reaching negative values. We believe that fluctuating environmental conditions might have constrained plant growth in this system. For both years, absence of precipitation coupled with high temperatures could have resulted in leaf desiccation and leaf senescence. For example, on days with very high temperatures, leaf water potentials drop rapidly, and apparently cheatgrass roots cannot move water fast enough (from deep soil layers where it is available) to keep the leaves from becoming desiccated (Harris, 1977). Support for our results could be found in other ecosystems with deciduous invasive species experiencing drought, burning and other treatments resulting in negative RGR (Bellingham et al., 2004). RGR of the invasive forbs from the Hawaiian Islands had lower and negative RGR as determined by change in their total biomass under highly stressful condition of minimum water and light availability (Baruch et al., 2000). Similarly, water limitation considerably reduced RGR of faba beans (*Vicia faba* L.) and was negative at the end of the growing season (Golezani et al., 2009).

Recent modeling and empirical work suggests that seasonal patterns of precipitation input and temperature are key factors determining regional variation in the growth, seed production, and spread of annual invasive species (Bradford and Lauenroth, 2006). Establishment of annual grasses is heavily influenced by year-to-year variation in precipitation timing and amounts (Mack and Pyke, 1983; Miller et al., 2006; Schwinning and Ehleringer, 2001). In our study, medusahead produced two times higher RGR in 2009 than in 2008 and consequently produced three times more biomass during the second growing season because precipitation was substantially higher that year.

Precipitation in 2008 was well below average and this level of drought is infrequent based on historical data. Collectively, our results suggest that the continued invasion and dominance of medusahead into native grasslands and cheatgrass infested grasslands will continue to increase in severity because conditions that favor bluebunch wheatgrass over medusahead are rare.

4.5 Acknowledgments

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Fig. 4-1 Total precipitation (mm) and temperature (C) at the study site for year 2008 (a) and 2009 (b) during the studied period of growth. Additionally, monthly average precipitation for 2008, 2009 and long-term (1890-2009) are also shown (c).

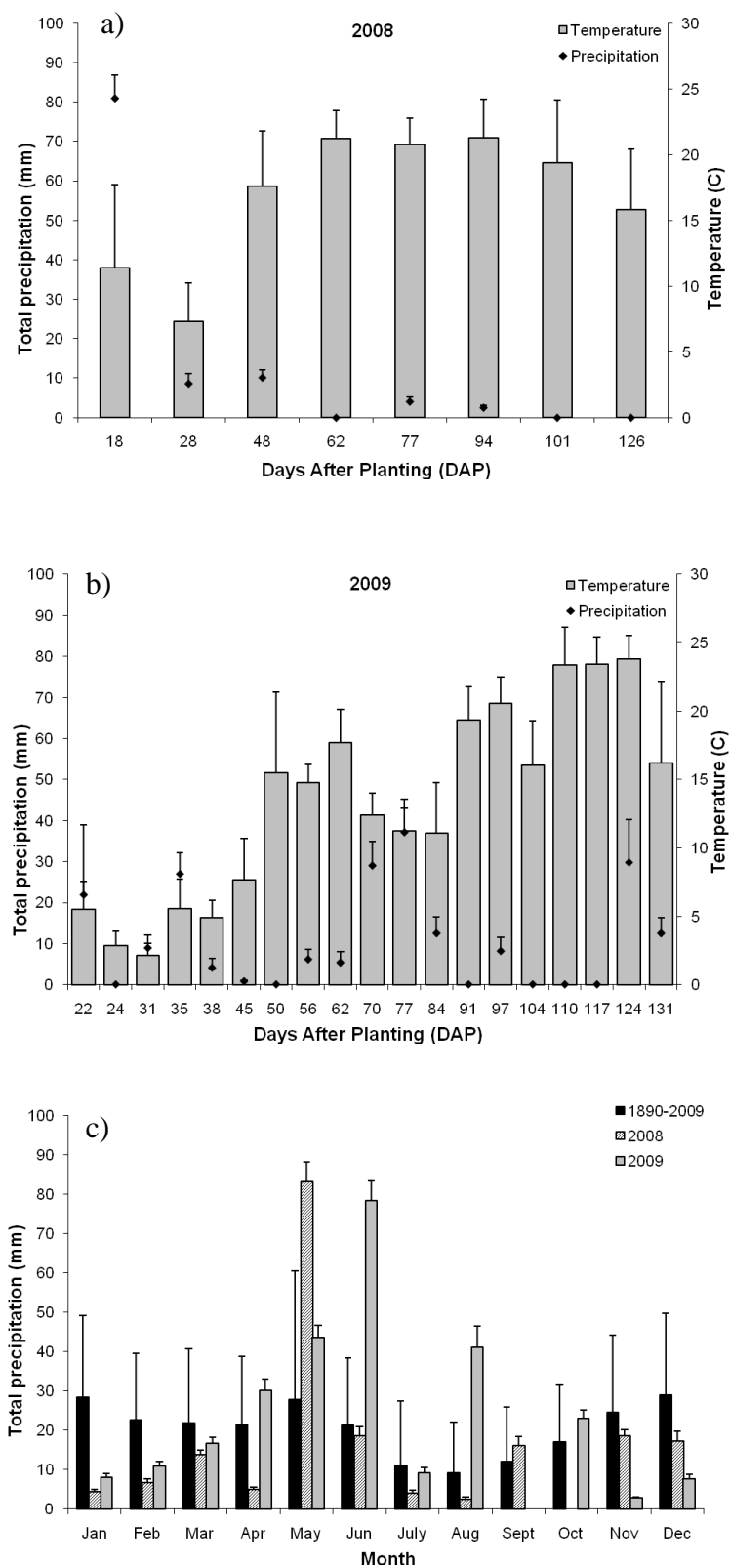


Fig. 4-1

Fig. 4-2 Shoot weight (mg) for cheatgrass, medusahead and bluebunch wheatgrass over all harvest intervals during the studied period of growth for 2008 (a) and 2009 (b, c). Bars represent mean \pm SD (n = 25).

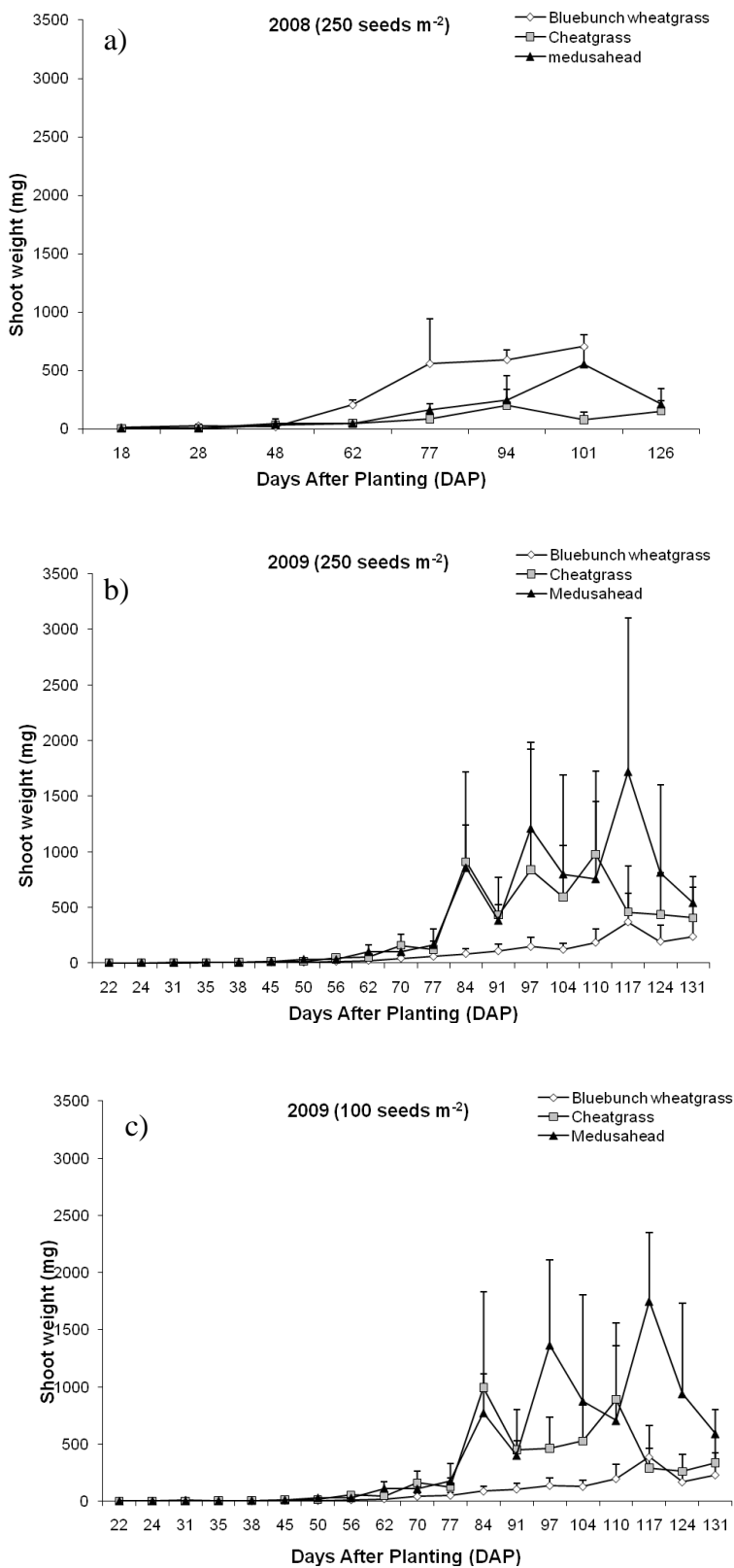


Fig. 4-2

Fig. 4-3 Relative growth rate (RGR, $\text{mg mg}^{-1} \text{d}^{-1}$) for cheatgrass, medusahead and bluebunch wheatgrass over all harvest intervals during the studied period for 2008 (a) and 2009 (b, c). Bars represent mean \pm SD ($n = 25$).

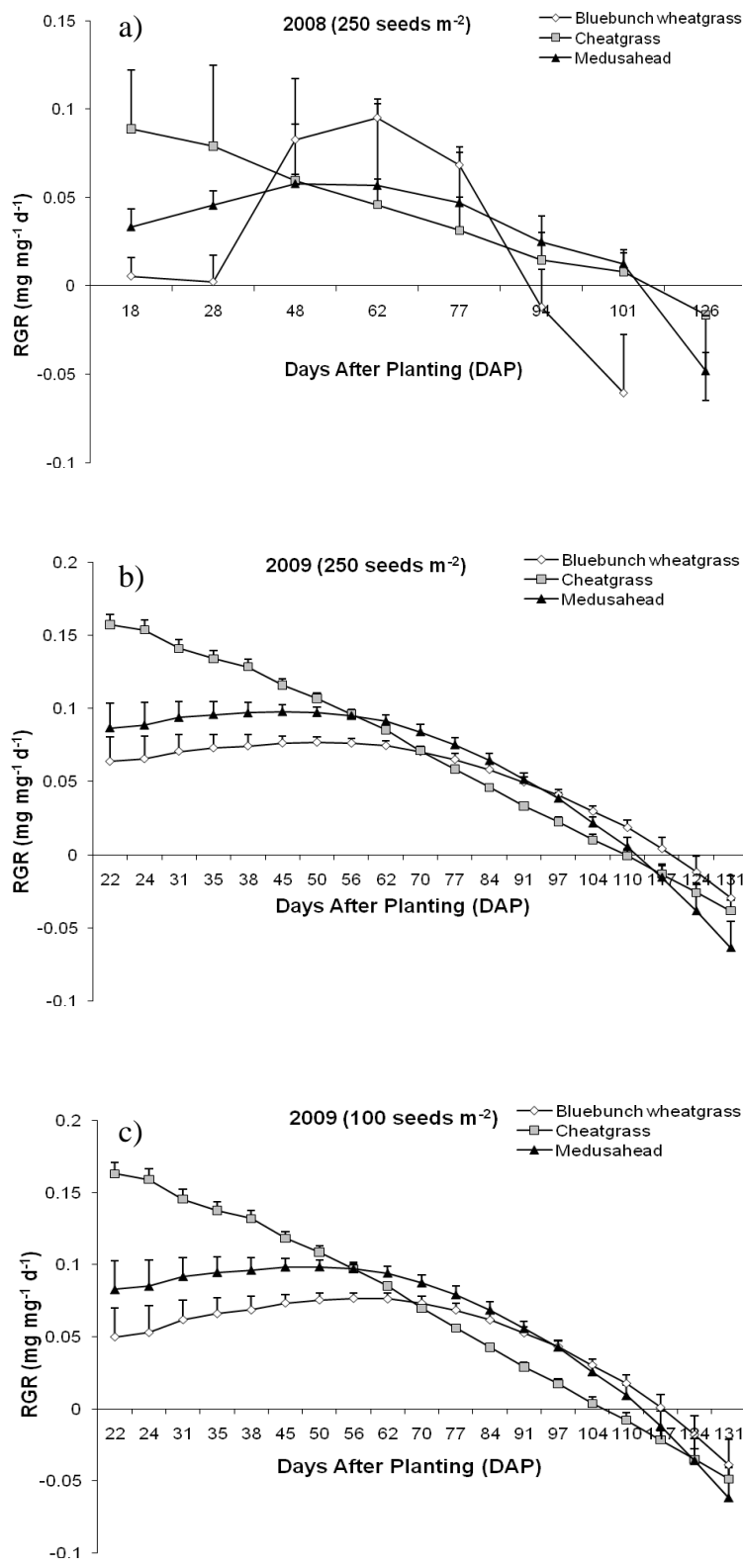


Fig. 4-3

**Using plant life-histories to determine relative importance of key processes for
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Using plant life-histories to determine relative importance of key processes for ecologically based invasive plant management

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Abstract

Ecologically based invasive plant management (EBIPM) is a decision-tool to move restoration away from strategies focused heavily on controlling invasive plant species and towards strategies for repair of damaged ecological processes that facilitate invasion. The ability to identify the most influential individuals or suite of ecological processes driving the plant population dynamics to guide implementation of EBIPM is substantial and unmet. Life-history simulation models are an important tool to identify the vulnerable parameters in the life cycle of plants. A major weakness of this approach is that it lacks a clear framework that links model parameters with ecological processes. The purposes of this article were to provide an initial framework that links ecological processes with life-

history model parameters by assessing and synthesizing the associated literature, providing a general annual and perennial life history model with corresponding ecological processes and their modifying factors. To demonstrate the usefulness of this framework, an example from the semi-arid grasslands steppe using cheatgrass and bluebunch wheatgrass as model system is provided. Sensitivity analysis indicated fall germination and the proportion of juveniles converting to mature cheatgrass were the most sensitive parameters directing cheatgrass population dynamics, whereas the proportion of vegetative ramets converting to flowering ramets were most sensitive parameters of the bluebunch wheatgrass. Our framework suggests that germination, emergence, stress and resource acquisition are critical ecological processes for cheatgrass, whereas ontogeny, environmental signals and resource acquisition dominated for bluebunch wheatgrass. We believe this framework provides a foundation for using life history models to determine the relative importance of various processes occurring throughout the life cycle of plants and could advance the ability to implement EBIPM by providing an indication of key processes needing modification to shift vegetation dynamics towards species that are desired.

Keywords: Ecological process, Restoration, Population dynamics, Plant life-histories, Cheatgrass, Bluebunch wheatgrass

5.1 Introduction

Successful restoration of invasive plant infested wildlands requires addressing the underlying causes of vegetation dynamics (Gallien et al. 2010, Sheley et al. 1996, Sheley and Krueger-Mangold 2003). These underlying causes are driven by various ecological processes that direct succession, retrogression, and invasion dynamics (Krueger-Mangold et al. 2006, Luken 1997). Ecologically based invasive plant management (EBIPM) is a decision-tool to move restoration away from strategies focused on controlling the abundance of invasive species and towards strategies focused on repairing damaged ecological processes that facilitate invasion (James et al. 2010, Sheley and Krueger-Mangold 2003, Sheley et al. 2010). However in a review of over 150 ecological studies, Levine et al. (2003) found that while the majority of studies documented reductions in native species, less than 5% tested the processes or pathways by which management altered ecological processes. This lack of scientific knowledge of how various mechanisms and processes contribute to successional dynamics limits the application of EBIPM by land managers (Sheley et al. 2010). Determining priorities for effective management action and restoration depends on having a basic understanding of the processes that are most important in directing a particular plant community on a desired trajectory (Bennett et al. 2009, Levine et al. 2003). Land managers must have techniques to identify ecological processes that are most in need of repair before EBIPM can be fully implemented (Hobbs and Harris 2001, Hobbs and Norton 1996, Sheley et al. 2010).

Discussion of naturally occurring processes dominate the ecological literature (Bennett et al. 2009, Levine et al. 2003, Richardson and Pysek 2006), but few

publications attempt to construct frameworks for implementing process-based natural resource management (Bennett et al. 2009, Pickett et al. 1989, Temperton et al. 2004). The exploration of a single process perceived as most important is common, but the knowledge of interacting processes that direct vegetation dynamics is increasing (Higgins and Richardson 1998, Levine et al. 2003, Richardson and Pyšek 2006, Thuiller et al. 2006, Whelan et al. 2002). To improve these efforts and to be most useful to management, investigations should focus on ecological processes that are most important in determining the magnitude and direction of vegetation dynamics (Bennett et al. 2009, Levine et al. 2003, Sebert-Cuvillier et al. 2010). When this occurs, managers can consider modifying the key processes or processes that influence change. This is critical because a suite of key factors generally interact to create successional patterns, therefore multiple factors often need amending to direct positive plant community trajectories (Cannas et al. 2003, Sheley et al. 2010). The need to identify the most influential individual or suite of ecological processes dictating dynamics prior to management is substantial.

Life history simulation models are an important tool to identify the vulnerable parameters in the life cycle of plants (Buckley et al. 2003, Harper and Sagar 1953, Maxwell et al. 1988, Sagar and Mortimer 1976). Historically, various processes have been studied and the results incorporated into life history models to improve their accuracy in predicting vegetation dynamics (Higgins et al. 1996, Sebert-Cuvillier et al. 2010). It is significant that life history models can be used to identify the key ecological processes directing plant population and community dynamics (Ghersa et al. 2000, Jacobs and Sheley 1997, Kriticos et al. 1999, Maxwell et al. 1988, Sagar and Mortimer

1976). For example, the life history of cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) indicated that adult survivorship and seed production are critical parameters influencing cheatgrass. Therefore dispersal and the propagule pool are the important processes directing dynamics of these species (Sheley and Larson 1994). Similarly, life history analysis of spotted knapweed (*Centaurea stoebe* L.) identified juvenile and adult survivorship, and transition from juvenile to adult, as critical phases in the life cycle; competition, growth rate, duration of growth, and reproduction allocation were critical processes associated with these life stages (Jacobs and Sheley 1997).

A major weakness of this approach is that it lacks a clear framework that links model parameters with ecological processes. This framework would provide a foundation for using life history models to determine the relative importance of various processes occurring throughout the life cycle and would promote more consistent interpretation of life history models. There is a substantial need for a framework to identify critical processes directing vegetation dynamics that provides information necessary to fully implementing EBIPM. The purposes of this article are to provide an initial framework that links ecological processes with life-history model parameters by assessing and synthesizing the associated literature, providing a general annual and perennial life history model with corresponding ecological processes and their modifying factors, and demonstrating the use of these general models using cheatgrass and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A). Our goal was to provide a framework which allows ecologists to prioritize ecological processes that play a dominant role in

vegetation dynamics in a manner in which factors can be modified if dynamics are to be shifted toward species that are desired.

5.2 Life history models

Life history stages (state variables) of an annual (e.g. invasive) and a perennial (e.g. native) species is the core of the model used in this study. Figures 5-1a and 5-1b represent the basic model components for annual and perennial plant species, respectively. Spring and fall seed banks, spring and fall seedlings, juvenile, mature plants, and seed produced which returned to the fall seed bank are the state variables present in simulations for annual population (Table 5-2). Seed bank, seedlings, flowering and vegetative ramets, and seed produced are the state variables present in simulations for perennial population (Table 5-2). The demographic parameters that regulate the transition between state variables over a one-year time period are provided in Table 5-1.

The model predicts the number of individual plants per unit area (density) at each life history stage every year (generation) for a selected number of years. The number of individuals at each life history stage depends on the rate new individual's graduate into a stage and the rate at which already existing individuals graduate to another stage or die. A standard approach to make population dynamics model more realistic is to add density-dependence. This means as the population gets larger the mortality rates increase and the fecundity rates decline. This model allows the user to add intra- and inter-specific density-dependent regulation and a competitive coefficient. Therefore, it allows integration of two populations using a competitive coefficient. The model is provided

with default values for starting the population dynamic simulations at $t = 0$ (starting time). However, the model allows users to change any parameter value. The model is not parameterized for any particular species. It can be reparameterized to simulate any invasive or native plant of interest. Hence, it is easy to incorporate values that are available from the scientific literature or direct research. Mathematical models can be generated from the diagrammatic models in Figures 5-1a and 5-1b through a series of equations representing each demographic process (arrows) in the model. The equations are presented in Maxwell and Sheley (1997).

5.2.1 Plant Population Model Behavior and Sensitivity

To determine which life-history stage has greatest impact on population dynamics, a sensitivity analysis was performed. The process involves repeated simulation in which each parameter is increased or decreased by 10%, keeping all other parameters constant. A sensitivity value (SV) which gives a measure of greatest proportional change in the output associated with a change in the selected parameters was used to identify the parameter with greatest impact. In order to calculate the sensitivity values, a model simulation for t generations using all the default values for demographic parameters was run. It gives the original output ($OP0_t$) value which is used to compare with all the changed output values. Varying one parameter i by a fixed population (p_c) and holding all other parameters at the default mean value and then running the simulation and recording the selected output value after t generations provides the changed output value. The process was continued until all the parameters were used. The greatest proportional

change in the output associated with a change in a selected parameter indicates the most sensitive parameter. The following is the formula used to calculate the sensitivity value:

$$SV = \frac{|\Delta OP_t| / OP_0_t}{\Delta parm_i / parm_i} \text{ or } SV = \frac{|OP_0_t - OP_t| / OP_0_t}{P_c}$$

where SV is the sensitivity value, $parm_i$ is the selected mean demographic parameter value, OP_t is the selected output value corresponding to simulation with the changed parameter value. For example, the relative effect of 10% reduction on seed output is determined as:

$$SV = \frac{\Delta \textit{seed output} / \textit{seed output}}{\Delta \textit{transition parameter} / \textit{transition parameter}}$$

5.3 Ecological processes and their linkages with life-history parameters

Ecological process is a broadly defined term that can be applied in a number of ways (Bennett et al. 2009, SERI 2004). Although ecological processes can be spatially and/or temporally scale dependent and complex, many processes consistently exert their influence on plant populations and communities at various stages within the life cycle (Harper 1977). For the purposes of this paper, we defined ecological processes as sequences of changes in the biotic and abiotic environment that affect plant population dynamics and manifest themselves during specific growth stages of a plant population's life cycle. The framework presented here focuses on population or community-level processes that can be linked to the relative abundance of invasive and native species. We also emphasized ecological processes that can be modified by land managers, such as those discussed by Krueger-Mangold et al. (2006). It is recognized that these processes

and their influence on vegetation dynamics vary widely across ecosystems, but enough data exists to begin to categorize ecological processes by the growth stage in which they exert their influence on vegetation dynamics.

Table 5-3 provides a framework that links life history model transitions to ecological processes for both annual and perennial species. The modifying factors influencing each ecological process at a particular transition are also listed with references documenting their association with a particular ecological process. The sensitivity analysis calculated using life history models helps identify the transitions having the greatest influence on plant population dynamics. This allows ecologists to prioritize ecological processes that appear to play a dominate role in the dynamics of species and suggests which factors might require modification if the dynamics are to be shifted toward species that are desired (Hobbs and Harris 2001, Hobbs and Norton 1996, Sheley et al. 1996, Sheley and Krueger-Mangold 2003, Sheley et al. 2010). This framework improves the ability to implement EBIPM by addressing underlying causes of vegetation change by identifying ecological processes in need of repair (James et al. 2010, Sheley and Krueger-Mangold 2003, Sheley et al. 2010).

5.4 Identifying important life-history parameters and ecological processes in a perennial-annual grass ecosystem

The models for invasive annual species, cheatgrass (*Bromus tectorum* L.) and native perennial species, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A) were constructed using population dynamics models for annual (Fig. 5-1a) and perennial species (Fig. 5-1b), respectively. We base this species selection on the continuous spread

of cheatgrass throughout the Intermountain West and a need to implement successful management that controls its spread (Duncan et al. 2004, Olson 1999, Pellant and Hall 1994) and increases the population size of native perennial species, especially bluebunch wheatgrass (Luken 1997, Krueger-Mangold et al. 2006, Sheley and Krueger-Mangold 2003). Model transition parameters, state variables and defaults values necessary to parameterize the model for cheatgrass were obtained from Sheley and Larson (1994) and are listed in Table 5-1. For bluebunch wheatgrass, data was obtained from James et al. (unpublished data, Table 5-1); a study conducted in 2008 at the Northern Great Basin Experimental Range (NGBER), in the southeastern Oregon (43° 29' N, 119° 43' W) about 56 km west of Burns, Oregon, USA. A summary of output for cheatgrass and bluebunch wheatgrass is displayed in Figs.5-2 and 5-3. These figures show rosette and flowering plant densities at each year for a 10-year simulation time.

A 10% sensitivity analysis was conducted on the life history model of cheatgrass and bluebunch wheatgrass for a 10-year simulation time by changing the value of a parameter in the model that describes a particular transition, while keeping all other transition parameters constant. The highest sensitivity values (SV) resulting in the largest change in the model output were recorded.

5.4.1 Parameters and process assessment

For cheatgrass, the highest sensitivity values were associated with SBf (SV = 9.9), JS (SV = 9.6), MP (SV = 9.6) and SP (SV = 9.6) when a 10% reduction in fall germination rate occurred. JS (SV = 9.5) and MP (SV = 9.7) also resulted in highest sensitivity values with a 10% reduction in *flw*. Therefore, the fall germination rate (*gmrf*) and the

proportion of juvenile plant converting to mature cheatgrass (*flw*) were the most sensitive transition parameters for cheatgrass population (Table 5-4). The processes associated with these transitions are germination, emergence, stress and resource acquisition. Rate, timing and requirements for germination are the factors influencing the process of germination (Baskin and Baskin 1981, Benech-Arnold et al. 2000, Gurevitch et al. 2006, Probert 1992, Radosевич et al. 2007). Litter accumulation, microbial population and availability of nutrients and water in the soil significantly influence the germination of seedlings (Eldridge and Greene 1994, Facelli and Pickett 1991, Harper 1977, Johansen 1993, Reinhert and Callaway 2006, Tilman 1982, Wardle 2002). Nematodes and fungal plant population could also significantly modify germination (Gurevitch et al. 2006, Harper 1977). The environmental conditions such as freezing and drought also influences germination (Fenner 1985, 1994, Silvertown and Charlesworth 2001) and availability of safe site is critical for effective germination (Bernal-Lugo and Leopold 1998, Harper 1977). From juvenile to mature plant transition, small or large ungulates are the major herbivores having major impacts. Insect predation or pathogen attack could also influence the transition of juvenile plants to mature plants (Crawley 1983, Gurevitch et al. 2006, Radosевич et al. 2007). Photosynthetic rate, respiration, nutrient assimilation rate, rate and timing of plant growth and biomass allocation could potentially the major modifying factor influencing the process of resource acquisition (DiTomaso 1999, Gedroc et al. 1996, Grime 1977, 1979, Grime and Hunt 1975, Grotkopp et al. 2002, Poorter 1989, Poorter and Remkes 1990, Rice 1999, Tilman 1982, 1988).

For bluebunch wheatgrass, vegetative ramets ($SV = 1.42$) were found to be the most sensitive to v_s while flowering ramets ($SV = 2.08$) showed maximum sensitivity to v_f . Moreover for seed production ($SV = 1.45$), v_f was the most sensitive parameter (Table 5-5). Therefore, the proportion of vegetative ramets converting to flowering ramets was the most sensitive parameter for bluebunch wheatgrass population. The processes associated with this transition are ontogeny, environmental signals and resource acquisition (Table 5-3). Availability of resources, plant genetics and environmental conditions largely influence the process of ontogeny while photoperiod has great impact on environmental signals (Gatsuk et al. 1980, Koornneef et al. 1998, Mc Connaughay and Coleman 1999, Samach et al. 2000). Nutrient assimilation rate, plant growth pattern and biomass allocation are the major factors responsible for modifying resource acquisition (DiTomaso 1999, Gedroc et al. 1996, Grime 1977, 1979, Poorter 1989, Rice 1999, Tilman 1982, 1988).

5.5 Summary

EBIPM offers a promising decision-tool to move management towards repairing the ecological processes that have the greatest impact on vegetation dynamics. The inability to identify key ecological processes most important in directing invasion and successional dynamics has limited the adoption and implementation of EBIPM. A framework allowing ecologist to identify and prioritize ecological processes most in need of repair would help overcome this barrier. In this paper, we provided an initial framework that allows ecologists to prioritize those ecological processes that appear to

play a dominant role in vegetation dynamics in a manner that suggests those factors needing modification if dynamics are to be shifted toward species that are desired. We have linked key ecological processes and their modifying factors to the various stages of annual and perennial's life histories as a framework useful to ecologists and land managers studying any invasive or native plant species of concern. This linkage could increase manager's ability to implement EBIPM by allowing identification and prioritization of those ecological processes that appears to play a dominating role in vegetation dynamics. The life history model provided by Maxwell and Sheley (1997) was used to demonstrate the usefulness of the approach, and an example from the grassland ecosystem using cheatgrass and bluebunch wheatgrass as model species was provided. By performing the sensitivity analysis, we identified fall germination rate and the proportion of juveniles converting to mature cheatgrass as the most sensitive parameters for cheatgrass population dynamics while the proportion of vegetative ramets converting to flowering ramets as most sensitive parameters for bluebunch wheatgrass populations. Using the Table 5-3, we then identified the corresponding ecological processes and their modifying factors for the most sensitive parameters and transitions. Our framework suggested germination, emergence, stress and resource acquisition as the critical ecological processes for cheatgrass, whereas ontogeny, environmental signals and resource acquisition were the dominating ecological processes for bluebunch wheatgrass. We believe that this framework provides the ability to use life history models to determine the relative importance of various processes occurring throughout the life cycle of plants. This knowledge should advance the ability to implement EBIPM by providing

an indication of key processes needing modification to shift vegetation dynamics towards species that are desired.

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5.7 References

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Fig. 5-1 Diagrammatic model of an annual (a) and perennial (b) species. The unfilled white boxes indicate the state variables and the filled gray boxes indicate the processes that link state variables. The arrows represent the transition parameters. A description of symbols used is provided in the text and in Table 5-1 and 5-2.

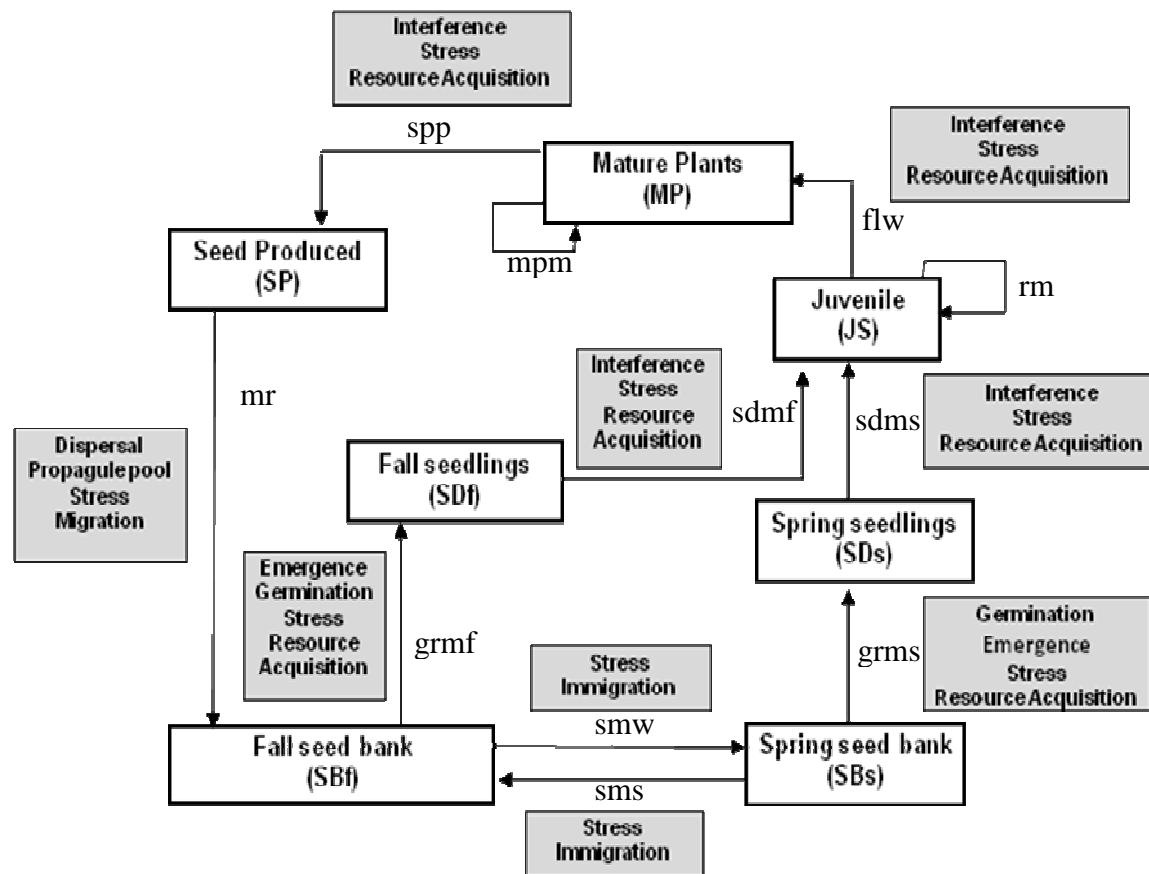


Fig. 5-1

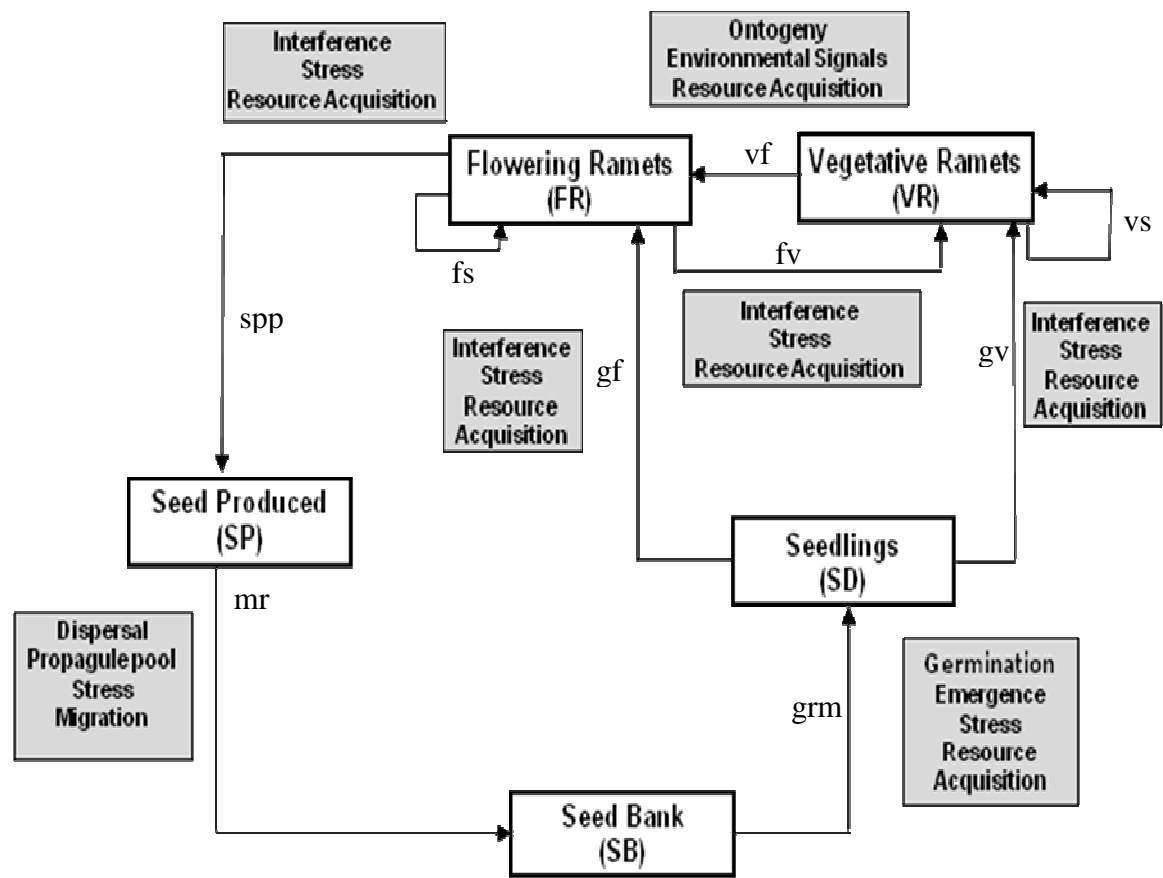


Fig. 5-1 (Continued)

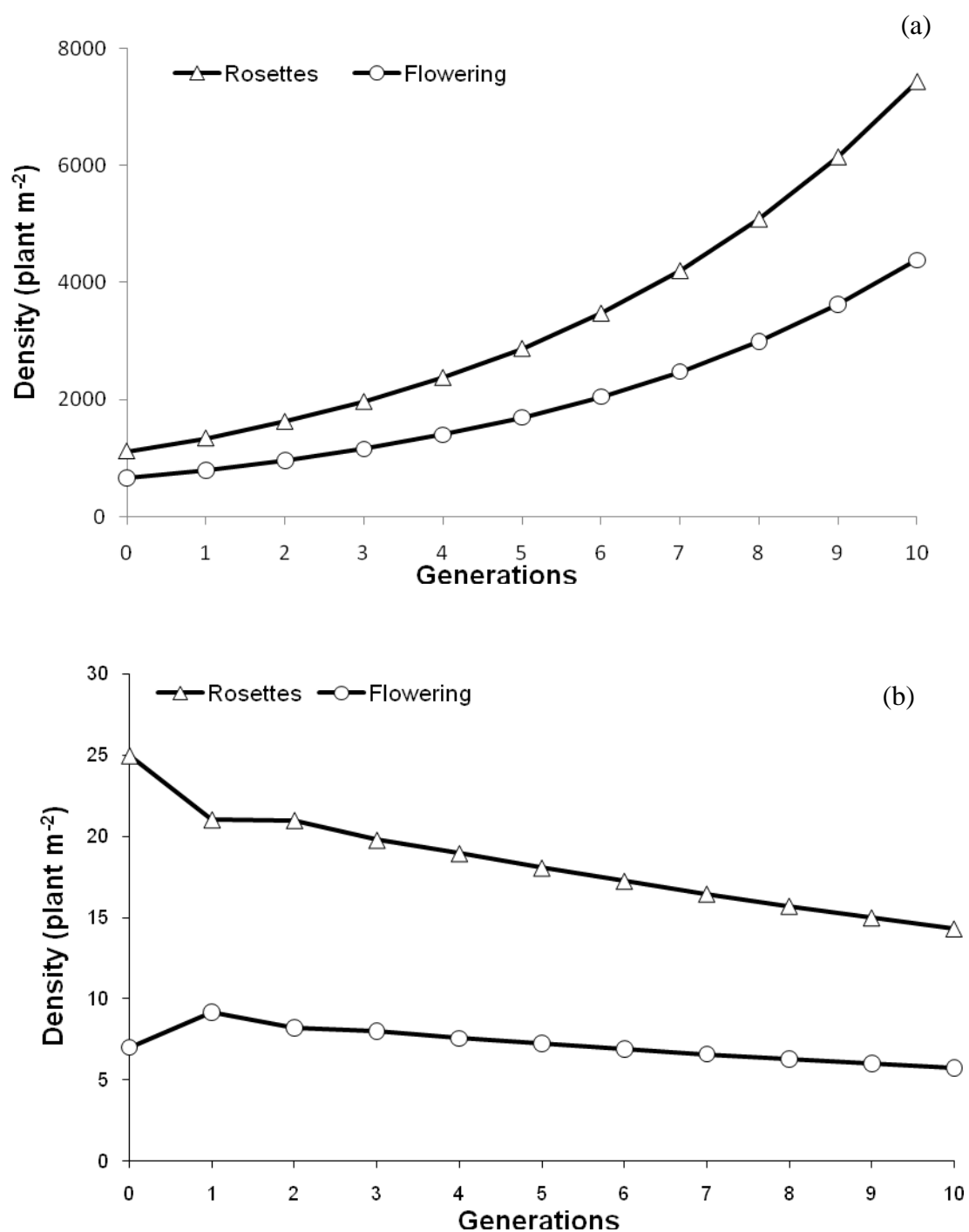


Fig. 5-2 Simulations of average cheatgrass (a) and bluebunch wheatgrass (b) rosette and flowering density over 10 generations with *spp* equals 10.7 and 200 for cheatgrass and bluebunch wheatgrass, respectively.

Table 5-1 List of model transition parameters with their description and mean default values for cheatgrass and bluebunch wheatgrass.

Parameters	Description	Default values
Cheatgrass^a:		
grms	Spring germination rate	0.13
grmf	Fall germination rate	0.9
smw	Seed mortality rate over winter	0.53
sms	Seed mortality rate over summer	0.13
sdms	Seedling mortality rate over winter	0.12
sdmf	Seedling mortality rate over summer	0.3
rm	Juvenile mortality rate over winter	1
flw	Juvenile to flowering plant transition rate	0.77
mpm	Mature mortality over winter	1
spp	Seed produced per plant	10.7
mr	Proportion of seed that migrates away	0.04
Bluebunch wheatgrass^b:		
grm	Germination rate	0.13
gf	Proportion of seedling growing into flowering plants	0.08
gv	Proportion of seedling growing into vegetative plants	0.34
vf	Proportion of vegetative plant converting to flowering	0.3
fv	Proportion of flowering plant converting to vegetative	0.81
vs	Proportion of vegetative plant that survive	0.45
fs	Proportion of flowering plant that survive	0.1
spp	Seed produced per plant	200
mr	Proportion of seed that migrates away	0.05

Source: ^aSheley, R.L., Larson, L.L. 1994. Observation: comparative life histories of cheatgrass and yellow starthistle. *Journal of Range Management* 47, 450–456. ^bJames et al. (*unpublished data*).

Table 5-2 List of state variable with their description and mean default values for starting population of cheatgrass and bluebunch wheatgrass at $t = 0$ (starting time). The population is defined as a 1 m^2 area.

State Variable	Description	Default values
Cheatgrass^a:		
SBf	Fall seed bank	298
SBs	Spring seed bank	158
SDf	Fall seedlings	2900
SDs	Spring seedlings	20
JS	Juveniles	850
MP	Mature Plants	660
SP	Seed Produced	7000
Bluebunch wheatgrass^b:		
SB	Seed bank	500
SD	Seedlings	65
VR	Vegetative ramets	25
FR	Flowering ramets	7
SP	Seed Produced	1400

Source: ^aSheley, R.L., Larson, L.L. 1994. Observation: comparative life histories of cheatgrass and yellow starthistle. *Journal of Range Management* 47, 450–456.

^bJames et al. (*unpublished data*).

Table 5-3 List of key ecological processes at each transition for the annual and perennial life history models. Modifying factors influencing each transition with relevant scientific literature citations are provided.

Transition		Ecological	Modifying factors	References
Annual plants	Perennial plants	Processes		
spring seed bank	seed bank	Germination	Germination time	Radosevich et al. (2007) page 171-172
to spring seedlings	to seedlings		Germination rate	Baskin and Baskin (1998), Benech-Arnold et al. (2000), Probert (1992)
			Germination requirements	Gurevitch et al. (2006) page 195
or				
fall seed bank		Emergence	Litter accumulation	Facelli and Pickett (1991), Wardle (2002)
to fall seedlings			Soil microbial populations	Johansen (1993), Harper (1977), Eldridge and Greene (1994)
			Soil nutrients and water contents	Reinhert and Callaway (2006), Tilman (1982, 1988)
		Stress	Predation/diseases	Gurevitch et al. (2006), Harper (1977)
			(nematode and fungal population dynamics)	
			abiotic stress (freezing, drought)	Fenner (1985, 1994), Silvertown and Charlesworth (2001)
			Safe sites	Bernal-Lugo and Leopold (1998), Harper (1977)
		Resource acquisition	Space capture	Radosevich et al. (2007) page 190
			Nutrient assimilation rates	Grime (1977, 1979), Tilman (1982, 1988)
			Plant growth pattern	DiTomaso (1999), Rice (1999)
			(rate and timing of plant growth)	
			Biomass allocation	Gedroc et al. (1996), Poorter (1989), Poorter and Remkes (1990)

Table 5-3 (Continued)

Transition		Ecological	Modifying factors	References
Annual plants	Perennial plants	Processes		
spring seedling to juveniles	seedlings to vegetative ramets	Interference	Competition, Facilitation, Allelopathy	Goldberg (1990), Harper (1977), Vandermeer (1989)
or	or	Stress	Herbivory	
			1. Type of herbivory (small or large ungulates)	Pickett et al. (1987), Radosevich et al. (2007) page 244
			2. Timing, intensity and frequency	Radosevich et al. (2007) page 248
			Plant Diseases (insect predation, pathogen attack)	Crawley (1983), Gurevitch et al. (2006)
juveniles to mature plants	seedlings to flowering ramets	Resource	Photosynthetic rate	Grime and Hunt (1975), Grotkopp et al. 2002
	or	acquisition	Respiration	Poorter and Remkes (1990)
			Nutrient assimilation rates	Grime (1977, 1979), Tilman (1982, 1988)
	flowering ramets to vegetative ramets		Plant growth pattern (rate and timing of plant growth)	DiTomaso (1999), Rice (1999)
			Biomass allocation	Gedroc et al. (1996), Poorter (1989), Poorter and Remkes (1990)

Table 5-3 (Continued)

Annual plants	Transition Perennial plants	Ecological Processes	Modifying factors	References
	vegetative ramets to flowering ramets	Ontogeny	Resource availability Plant genetics Environmental conditions	Gatsuk et al. (1980), McConnaughay and Coleman (1999) Koornneef et al. (1998), Samach et al. (2000)
		Environmental signals	Photoperiod	Smith and Whitelam (1990)
		Resource acquisition	Nutrient assimilation rates Plant growth pattern (rate and timing of plant growth) Biomass allocation	Grime (1977, 1979), Tilman (1982, 1988) DiTomaso (1999), Rice (1999) Gatsuk et al. (1980), McConnaughay and Coleman (1999)
mature plant to seed produced	flowering ramets to seed produced	Interference	Competition, Facilitation, Allelopathy	Goldberg (1990), Harper (1977), Vandermeer (1989)
		Stress	Herbivory 1. Type of herbivory (grazing animals) 2. Timing, intensity and frequency	Pickett et al. (1987), Radosevich et al. (2007) page 244 Radosevich et al. (2007) page 248
		Resource acquisition	Respiration Senescence Resorption	Poorter and Remkes (1990) Noy-Meir (1973) Eckstein et al. (1998), Killingbeck (1996), van Heerwaarden et al. (2003)

Table 5-3 (Continued)

Transition		Ecological	Modifying factors	References
Annual plants	Perennial plants	Processes		
seed produced to fall seed bank	seed produced to seed bank	Dispersal	Seed dispersal vectors	Crawley (1983) page 76-79, Harper (1977)
			Rate and frequency of dispersal	Booth and Swanton (2002)
fall seed bank to spring seed bank		Propagule pool	Seed production	Connell and Slayter (1977), Egler (1954)
			Dormancy	Grime (1979) page 95, Harper (1977)
			Seed viability	Radosevich et al. (2007) Page 93, Williamson (1996)
			Seed Longevity in soil	Auld et al. (2000), Lewis (1973)
		Migration	Wind velocity, vectors	Crawley (1983) page 144, Harper (1977)
			Stress	Seed predation (seeds eaten by rodents, insects)
		Seed pathogens		Coombs et al. (2004), Packer and Clay (2000), Spencer (2000)
		Stress	Winter hardiness	Harper (1977), Silvertown and Charlesworth (2001)
			Seed predation (seeds eaten by rodents, insects)	Crawley (1992), Harper (1977), Ostfeld et al. (1997) Westerman et al. (2003)
			Soil disturbance, depth of seed burial	Baskin and Baskin (1989), Cook (1980), Wilson (1988)
Immigration	Wind velocity, vectors	Crawley (1983) page 144, Harper (1977)		

Table 5-3 (Continued)

Transition		Ecological	Modifying factors	References
Annual plants	Perennial plants	Processes		
spring seed bank		Stress	Frost and heating	Harper (1977), Silvertown and Charlesworth (2001)
to fall seed bank			Seed predation (seeds eaten by rodents, insects)	Crawley (1992), Harper (1977), Ostfeld et al. (1997) Westerman et al. (2003)
			Soil disturbance, depth of seed burial	Baskin and Baskin (1989), Cook (1980), Wilson (1988)
		Immigration	Wind velocity, vectors	Crawley (1983) page 144, Harper (1977)

Table 5-4 Sensitivity values calculated for cheatgrass population size (plant m⁻²) resulting from a 10% decrease in each transition parameter after a 10-year simulation.

Parameters	Species						
	Cheatgrass						
	SBf	SBs	SDf	SDs	JS	MP	SP
grmf	9.9*	0.3	5.9	0.3	9.6*	9.6*	9.6*
grms	0.2	2.1	0.1	0.7	9.0	9.1	0.9
smw	0.4	3.6	0.4	3.6	0.4	9.0	1.1
sms	0.2	2.0	0.2	2.0	9.0	9.0	0.9
sdmf	8.5	7.4	4.8	7.4	8.5	8.6	6.5
sdms	0.2	2.0	0.2	2.0	9.0	9.0	1.0
rm	0.7	2.4	0.6	2.4	8.9	9.0	1.4
flw	6.4	5.3	6.0	5.3	9.5*	9.7*	6.2
mpm	2.2	4.0	1.9	4.0	8.8	8.9	3.1
spp	0.2	2.0	0.2	2.0	9.0	9.0	0.9
mr	0.7	2.5	0.6	2.5	8.9	9.0	1.4

*highest sensitivity values. Parameters description is provided in Table 5-1.

Table 5-5 Sensitivity values calculated for bluebunch wheatgrass population size (plant m⁻²) resulting from a 10% decrease in each transition parameter after a 10-year simulation.

Parameters	Species				
	Bluebunch wheatgrass				
	SB	SDL	VR	FR	SP
grm	0.42	1.38	0.77	0.80	0.46
gv	0.24	0.24	0.59	0.52	0.26
gf	0.19	0.19	0.19	0.30	0.20
vs	0.63	0.63	1.42*	1.28	0.68
vf	1.38	1.38	1.20	2.08*	1.45*
fs	0.18	0.18	0.19	0.29	0.19
spp	1.36	1.36	0.74	0.77	1.39
mr	0.46	0.46	1.10	0.97	0.50

*highest sensitivity values. Parameters description is provided in Table 5-1.

6 General Conclusion

6.1 Summary of main dissertation findings

On landscapes dominated by invasive plants, restoration is central to fostering desired vegetation composition and structure (Christensen et al., 1996). Restoration requires replacing and/or repairing ecological processes and mechanisms that direct vegetation dynamics (SERI, 2004). However, restoration involves identifying and modifying critical ecological processes within a complex web of interconnected processes and many collateral interactions occur to influence vegetation dynamics (Christensen et al., 1996). Successful ecosystem restoration requires a fundamental understanding of ecological processes that direct vegetation dynamics, together with the knowledge of how they promote the establishment and persistence of invasive plants (Christensen et al., 1996; Sheley and Krueger-Mangold, 2003). One of the grand challenges in the semi-arid grasslands of western United States is to identify and manipulate the ecological processes directing successional dynamics to restore annual grass infested ecosystems. The research presented in this dissertation uses various experimental approaches to investigate processes influencing the establishment and growth of invasive annual grasses and desired perennial grasses and provide new information for restoration of these invaded systems.

Plant competition is often assumed to be a primary ecological process determining the outcome of restoration efforts (Allen, 1995; Brown et al., 2008). Land managers have recognized the need to control competition during the initial phase of restoration and dedicate resources to reduce invasive plants (Sheley and Krueger-

Mangold, 2003). However, the paucity of success in restoration has caused ecologists to question the fundamental role of competition as a barrier to plant establishment. In Chapter 2, I used a diallel-greenhouse competition experiment to examine competitive effects among invasive and native species during early stages of growth at two levels of N availability. Diallel experiments use one or two individuals of each species, and therefore provided us an opportunity to study both intra- and inter-specific competition within a framework of a substitutive experiment (Harper, 1977; Radosovich et al., 2007; Spitters, 1983). The overall results suggest that invasive annual grasses and native perennial grasses are subject to both intra- and inter-specific competition during the early stages of plant growth. I found that fast growing invasive species became more competitive compared to slow growing native species with increasing N and establish a positive feedback mechanism between size and resource uptake. Opportunities to improve restoration success exist by determining the optimum combination of density, species proportion, and their spatial arrangement in various ecosystems and environments. This work represents a step forward in understanding the relative strength and magnitude of competition during early stages of plant growth, and if N availability influences it. I suggest that plant competition studies evaluate the type of competition and competition intensity at several points over time during early stages of plant establishment when plants are most sensitive to competition.

In Chapter 3, I performed an additional series field experiment for two years to quantify the intensity and importance of competition between invasive annual grasses and native perennial grasses. I found that competition intensity, and thus its importance did

not influence the target plant biomass and survivorship during the first two years of plants establishment. I speculate that at resource poor study site, abiotic factors dominate plant establishment and survivorship and eventually plant dominance. In stressful systems, land managers would be more successful at restoration by overcoming the barriers associated with plant establishment other than competition, such as abiotic factors, rather than focusing on treatments aimed at controlling invasive plants.

In Chapter 4, I studied the mechanism for the exponential increase in dominance by medusahead onto native grassland and cheatgrass dominated grassland throughout the western United States. Comparing the growth rate and growth patterns of medusahead with bluebunch wheatgrass and cheatgrass in the field for two years, I found that medusahead had a longer period of growth, more total biomass and higher RGR than cheatgrass for both years. Bluebunch wheatgrass had more biomass and higher RGR than medusahead in 2008, but the relationship was reversed in 2009. Weather data identified that precipitation in 2008 was well below average and this level of drought is infrequent. Collectively, the results suggest that the continued invasion and dominance of medusahead onto native grasslands will continue to increase in severity because conditions that favor bluebunch wheatgrass over medusahead are rare. I expect that medusahead will continue to invade both grassland ecosystems because of its higher RGR and extended period of growth.

In Chapter 5, I presented a framework which could allow ecologists to prioritize the ecological processes that play a dominate role in vegetation dynamics in a manner that indicates which factors need to be modified if dynamics are to be shifted toward

species that are desired. Using cheatgrass and bluebunch wheatgrass as a model system to demonstrate a method of identifying key ecological processes and their linkages with the model parameters, I identified germination, emergence, stress and resource acquisition as the critical ecological processes for cheatgrass population dynamics, whereas ontogeny, environmental signals and resource acquisition were the dominating ecological processes for bluebunch wheatgrass. The identification of processes that direct successional dynamics should enhance application of ecologically based invasive plant management (EBIPM) by land managers (Hobbs and Harris, 2001; Hobbs and Norton, 1996; Sheley et al., 2010).

6.2 Future research

A general concept for future research is to use the life history models to guide the identification of key processes, and to investigate how these processes can be modified to stimulate desired vegetation dynamics. Once this information is known, research must synthesize it into ecological principles for EBIPM. Principles provide “rules of thumbs” about how managers can repair or modify ecological processes that have the highest probability to propel the vegetation trajectory toward desired species within a plant community. This effort has been initiated and described in a recent review by James et al. (2010), but is still underdeveloped and requires much expansion, modification and improvement.

There are a host of ecological processes that need to be repaired for successful restoration and competition is one of them. Specifically, with respect to competition, my studies highlight a need to understand what combination of density, species proportions,

and their spatial arrangements are optimum for establishment of desired species to improve restoration success at systems where competition is a primarily dominating process. However, I identified that competition is not a dominating process in resource poor or highly stressful environments. There is a need to understand what factors other than competition, such as abiotic factors, are limiting the establishment of desired species in resource poor systems. For effective management of medusahead, there is substantial need to identify desired species with comparable RGR and extended period of growth so that the desired species can capture the resources otherwise utilized by medusahead.

6.3 References

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