

## Role of competition in restoring resource poor arid systems dominated by invasive grasses

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### ABSTRACT

Understanding the role competition intensity and importance play 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 variables. 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. Multiple linear regression models predicting individual plant biomass and survivorship were developed. Based on biomass, competition intensity coefficients ranged from  $-0.38$  to  $0.63$  with  $R^2 < 0.06$ . All survivorship data produced poor fitting regression models ( $R^2 < 0.05$ ). 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 abiotic barriers to plant establishment rather than focusing on plant–plant interactions.

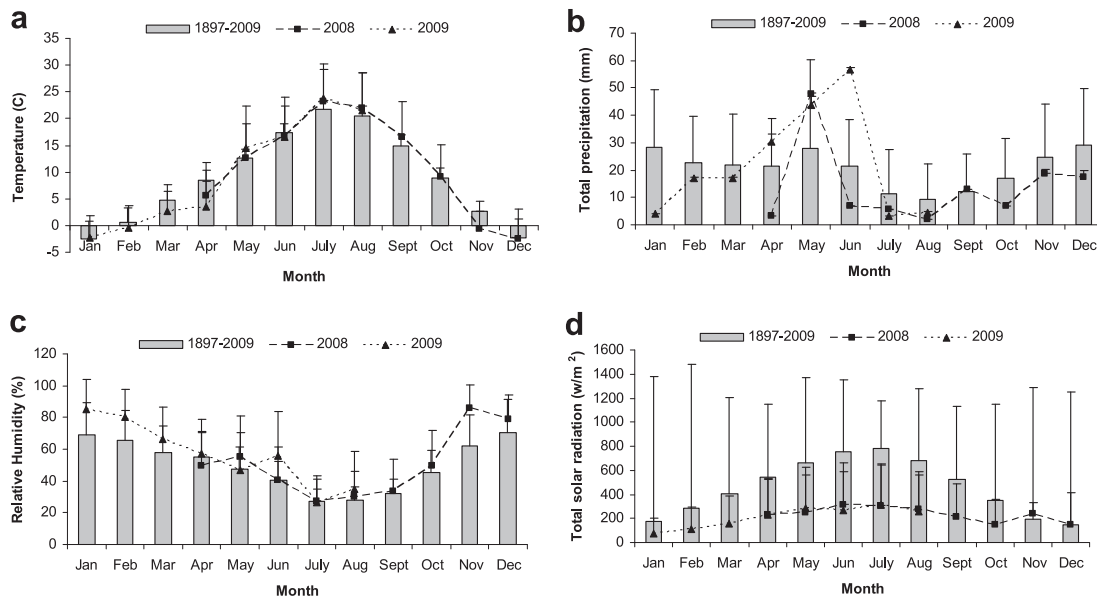
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### 1. Introduction

The role of competition in controlling plant dominance in resource poor environments remains 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). In spite of the development of refined conceptual frameworks of plant interactions occurring in varying environments (Goldberg and Novoplansky, 1997; Maestre et al., 2009) and quantitative syntheses of existing literature (Goldberg et al., 1999; Gomez-Aparicio, 2009), a unified understanding of the degree to which competitive interactions control plant dominance in resource poor environments has not emerged. This is because only limited empirical evidence exists supporting either hypothesis, and those data are not consistent.

Understanding competition intensity and importance is a central barrier to developing restoration strategies, especially in resource poor environments (Grace, 1991; Tikka et al., 2001; Sheley and Krueger-Mangold, 2003; Brooker and Kikvidze, 2008). 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 proportion of variation in target plant fitness that is accounted for by competition in relation to all other factors affecting plant fitness. A vigorous debate is occurring in the literature in an attempt to improve the concept of competition importance (Brooker and Kikvidze, 2008; Freckleton et al., 2009; Damgaard and Fayolle, 2010; Kikvidze and Brooker, 2010). Freckleton et al. (2009) argued that the definition of importance should provide an indication of long-term consequences of competition on the structuring of plant communities. This can be achieved by including the effects of plant interactions 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

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**Fig. 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, National Climate Data Centre (NCDC), 2009).

a range of approaches in determining competition importance, but should be consistent with Welden and Slauson (1986).

Even though Welden and Slauson (1986) were clear that the two measures of competition are not necessarily correlated, the bulk of empirical work focuses on how intensity of competition changes along resource gradients with the underlying assumption that intensity of competition will be proportional to its importance (Grace, 1991; Mitchell et al., 2009). However, competition could range from non-existent to being intense and unimportant to being very important. For example, if the target plant biomass is affected only by competition, this interaction may have a low or high intensity but is very important (Briones et al., 1996). If the target plant biomass is determined by other factors (e.g. abiotic stress, disturbance, herbivory, parasitism) than the competition could be of low or high intensity but is unimportant (Welden and Slauson, 1986; Briones et al., 1996). In resource poor environments resources are limited and competition could be intense (Fowler, 1986), but abiotic factors could have an overriding role in influencing plant biomass and survival (Ackerman, 1979; Gutterman, 2002). This may be directly linked to the ability to tolerate drought and temperature extremes (Went, 1949; Mulroy and Rundel, 1977).

A better understanding of competition intensity and importance may allow advancements in ecology that could be particularly important in identifying how we link ecology to management and restoration of 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 (Mack, 1989; Pellant, 1990; D'Antonio and Vitousek, 1992; Sheley and Petroff, 1999; Duncan et al., 2004; Germino et al., 2004; Sheley et al., 2008). Each year several billion dollars are spent to control invasive plant species (Westbrooks, 1998; Pimentel et al., 2005), 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). Although several studies have indicated that invasive annual grasses are more competitive than grass species native to North America (Sheley and Larson, 1995;

Humphrey and Schupp, 2004; Krueger-Mangold and Sheley, 2008; Vasquez et al., 2008), most information was derived from studies conducted on relatively productive grassland sites or under optimal environmental conditions. Therefore, a more complete understanding of competition intensity and importance may be a useful step in helping managers understand how to prioritize restoration efforts in resource poor environments within the semi-arid steppe.

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 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 (i.e.,  $R^2$ ; Welden and Slauson, 1986). The analysis is confined to the natural and un-known heterogeneity of biotic and abiotic factors present at the study site. There are also possible measurement errors and genotypic differences between individuals apart from the controlled density of species in competition. The specific hypotheses tested were 1) competition would be intense among invasive and native plant species 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. Our rationale for these hypotheses was based on the theory that in resource poor environments resources are limited (by definition) and competition may be intense among species, but because there are a number of other factors determining plant fitness, competition may not be important.

## 2. Material and methods

### 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,

**Table 1**Multiple linear regression predicting individual cheatgrass shoot biomass ( $W_c$ ; g plant<sup>-1</sup>) using seeding, initial and final densities as independent variables for 2008 and 2009.

Dependent Variable	Plant Species	Year	Independent variable	$\beta_{0c}$	$\beta_{cc}$	$\beta_{cm}$	$\beta_{cb}$	$\beta_{cs}$	$R^2$
$W_c$	Cheatgrass	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

$\beta_{0c}$  is the predicted mean biomass of an individual cheatgrass plant grown in isolation;  $\beta_{cc}$  is the intra-specific interference by cheatgrass;  $\beta_{cm}$ ,  $\beta_{cb}$  and  $\beta_{cs}$  is the inter-specific interference by neighboring plants medusahead, bluebunch wheatgrass and Sandberg's bluegrass, respectively; competition coefficients ( $\beta$ ) represent the per plant weight change in response to a single plant increase in density; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived during final sampling in 2009.

118° 9' W), 106 km from the Eastern Oregon Agricultural Research Center, Burns, Oregon, USA. Soils at the research site were a Risley cobbly loam (fine, montmorillonitic, mesic Xeric Haplargid), total soil nitrogen averaged 0.09% and our site had a 15–20% 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 (National Climate Data Centre (NCDC), 2009; Fig. 1).

Average monthly temperature and relative humidity at the study site were consistent with the long-term average for the area (Fig. 1a, c). 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. 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. 1b). Large variation in solar radiation was also observed during the study (Fig. 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 w m<sup>-2</sup>, respectively. 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 et al., 2008; Sheley and Svejcar, 2009). 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 of the region.

## 2.2. Site preparation and study species

In spring 2008, before the experiment was initiated, we applied glyphosate [N-(phosphonomethyl) glycine] at 0.85 kg a.i. ha<sup>-1</sup> 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 (*B. tectorum* L.) and medusahead (*T. 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. 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 annual grasses. All four species belongs to the family Poaceae. Seeds of the four species were field-collected east of Burns, Oregon (43° 22' N, 118° 22' W) during 2006 and stored in a moisture proof container at a cool, dry location. During the seed cleaning process, awns were inadvertently removed with chaff. Seed germination tests were conducted prior to the experiments and >90% seeds germinated.

## 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 (Spitters, 1983; Radosevich, 1987; Radosevich et al., 2007). Five seeding densities

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

Dependent Variable	Plant species	Year	Independent variable	$\beta_{0m}$	$\beta_{mm}$	$\beta_{mc}$	$\beta_{mb}$	$\beta_{ms}$	$R^2$
$W_m$	Medusahead	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

$\beta_{0m}$  is the predicted mean biomass of an individual medusahead plant grown in isolation;  $\beta_{mm}$  is the intra-specific interference by medusahead;  $\beta_{mc}$ ,  $\beta_{mb}$  and  $\beta_{ms}$  is the inter-specific interference by neighboring plants cheatgrass, bluebunch wheatgrass and Sandberg's bluegrass, respectively; competition coefficients ( $\beta$ ) represent the per plant weight change in response to a single plant increase in density; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived during final sampling in 2009.

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

Dependent variable	Plant species	Year	Independent variable	$\beta_{0b}$	$\beta_{bb}$	$\beta_{bm}$	$\beta_{bc}$	$\beta_{bs}$	$R^2$
$W_b$	Bluebunch wheatgrass	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

$\beta_{0b}$  is the predicted mean biomass of an individual bluebunch wheatgrass plant grown in isolation;  $\beta_{bb}$  is the intra-specific interference by bluebunch wheatgrass;  $\beta_{bm}$ ,  $\beta_{bc}$  and  $\beta_{bs}$  is the inter-specific interference by neighboring plants medusahead, cheatgrass and Sandberg's bluegrass, respectively; competition coefficients ( $\beta$ ) represent the per plant weight change in response to a single plant increase in density; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived during initial and final sampling in 2009.

of each of the four species were arranged in all possible combinations of 0, 1, 10, 100 and 1000 seeds m<sup>-2</sup> for a total of 625 plots (5 seeding densities; raised to the power of 4 species = 625) in each replication. Therefore, total density ranged from 0 seeds m<sup>-2</sup> to 4000 seeds m<sup>-2</sup>. Density combinations were completely randomized and replicated three times (625 × 3 reps = 1875 plots). 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 on 1 m<sup>2</sup> plots. The soil surface was kept moist until seedling emergence, after which no further water was added. These densities were used because they represent the range of combinations found in field situations on these resource poor sites (Sheley and Larson, 1995; Young and Krueger-Mangold, 2008).

#### 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 m<sup>2</sup> circular quadrat within each 1 m<sup>2</sup> plot. Plants were separated by species and counted to determine final density. The above-ground biomass of each individual was weighed after drying for 48 h 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. Since final density in 2008 may not be a good predictor of initial density in 2009, we emphasize using caution in interpreting these data. 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.

**Table 4**  
Multiple linear regression predicting individual Sandberg's bluegrass shoot biomass ( $W_s$ ; g plant<sup>-1</sup>) using seeding, initial and final densities as independent variables for 2008 and 2009.

Dependent variable	Plant species	Year	Independent variable	$\beta_{0s}$	$\beta_{ss}$	$\beta_{sm}$	$\beta_{sc}$	$\beta_{sb}$	$R^2$	
$W_s$	Sandberg's bluegrass	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							

$\beta_{0s}$  is the predicted mean biomass of an individual Sandberg's bluegrass plant grown in isolation;  $\beta_{ss}$  is the intra-specific interference by Sandberg's bluegrass;  $\beta_{sm}$ ,  $\beta_{sc}$  and  $\beta_{sb}$  is the inter-specific interference by neighboring plants medusahead, cheatgrass and bluebunch wheatgrass, respectively; competition coefficients ( $\beta$ ) represent the per plant weight change in response to a single plant increase in density; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived in 2009.

#### 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:

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

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

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

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

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  $\beta_{m0}$ ,  $\beta_{c0}$ ,  $\beta_{b0}$  and  $\beta_{s0}$  represent the y-intercept which is the estimate of maximum shoot biomass of an isolated individual.  $\beta_{mm}$ ,  $\beta_{cc}$ ,  $\beta_{bb}$ ,  $\beta_{ss}$  represent intra-specific competition in the medusahead, cheatgrass, bluebunch wheatgrass and Sandberg's bluegrass models, respectively. Inter-specific competition was estimated by  $\beta_{mc}$ ,  $\beta_{mb}$ ,  $\beta_{ms}$ ,  $\beta_{bc}$ ,  $\beta_{bs}$ ,  $\beta_{cs}$ . 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 fit. 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



**Table 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	Plant species	Year	Independent variable	$\beta_0$	$\beta_c$	$\beta_m$	$\beta_b$	$\beta_s$	$R^2$
$S_c$	Cheatgrass	2008	Seeding density	0.46(0.14)	0.0004(0.0003)	-0.0006(0.0003)	0.0000(0.0003)	0.0003(0.0003)	0.019
		2009	Seeding density	0.53(0.11)	0.0001(0.0003)	0.000(0.0003)	0.000(0.0003)	-0.0002(0.000)	0.003
$S_m$	Medusahead	2008	Seeding density	1.03(0.23)	-0.0006(0.0006)	-0.0005(0.0005)	0.0012(0.0006)	-0.0003(0.000)	0.022
		2009	Seeding density	1.17(0.22)	-0.0005(0.0005)	-0.0006(0.0005)	-0.0004(0.0005)	0.002(0.0005)	0.021
$S_b$	Bluebunch wheatgrass	2008	Seeding density	0.05(0.04)	-0.0001(0.0001)	-0.0001(0.0001)	0.0003(0.0001)	-0.0001(0.000)	0.044
		2009	Seeding density	0.44(0.23)	-0.0002(0.0006)	-0.0004(0.0005)	0.0004(0.0006)	-0.0002(0.000)	0.005
$S_s$	Sandberg's bluegrass	2008	Seeding density	0.02(0.01)	0.0000(0.0000)	0.0000(0.0000)	0.0000(0.0000)	0.0000(0.0000)	0.002
		2009	Seeding density						

$\beta_0$  is the predicted survivorship of each species;  $\beta_c$ ,  $\beta_m$ ,  $\beta_b$  and  $\beta_s$  is the change in survivorship in response to density of cheatgrass, medusahead, bluebunch wheatgrass and Sandberg's bluegrass, respectively; competition coefficients ( $\beta$ ) represent the change in survivorship in response to a single plant increase in density; Numbers in parentheses are standard errors for coefficients. No Sandberg's bluegrass survived in 2009.

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; Welden and Slauson, 1986). Statistical computations were performed using S-Plus (S-Plus (Computer Program), 2005) software.

### 3. Results

#### 3.1. Competition intensity

##### 3.1.1. Seeding density predicting target plant biomass

For 2008, the maximum predicted biomass of an isolated individual was 0.18 and 0.28 g plant<sup>-1</sup> for cheatgrass and medusahead, respectively (Tables 1 and 2) and it increased to 12 and 23 times for cheatgrass and medusahead, respectively 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 1 and 2). Similarly for perennial species, the models resulted in non-significant regression coefficients ( $P > 0.05$ , Tables 3 and 4) for predicting maximum biomass per plant. Similar trends were observed for both 2008 and 2009 for bluebunch wheatgrass. 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 and 4).

##### 3.1.2. Initial seedling density predicting 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<sup>-1</sup>. Intra- or inter-specific competition had no influence on biomass of both annuals ( $P > 0.05$ , Tables 1 and 2) or perennials ( $P > 0.05$ , Tables 3 and 4) in 2008. During 2009, similar results were found for both annuals and bluebunch wheatgrass (no Sandberg's bluegrass seedlings survived).

##### 3.1.3. Final seedling density predicting 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 1 and 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.

#### 3.2. Survivorship

##### 3.2.1. Seeding density predicting survivorship

Both annual species and bluebunch wheatgrass showed an increase in maximum predicted survivorship for 2009 compared to 2008 (Table 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. 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 1–4). 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 5).

### 4. Discussion and conclusions

Contrary to our first hypothesis, we found no evidence that intensity of intra- or inter-specific competition were significant at our study site for the first two years 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). Even within resource poor systems, it appears that site specific variability may control the intensity of intra- or inter-specific competition and managers will struggle to infer competition intensity from environmental conditions.

We accepted our hypothesis that competition would be unimportant among invasive and native species in relation to other sources of variation in individual fitness at our study site. 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 the harsh and fluctuating environmental conditions at our study site. Such stressful environments can influence establishment, survival and growth of plant species (Went, 1949; Mulroy and Rundel, 1977; Ackerman, 1979; Gutterman, 2002). 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 may have made it difficult for these shallow rooted Sandberg's bluegrass to reach soil moisture that is increasingly deeper as the summer progresses. It appears that at our study site, factors other than competition could potentially dominate plant establishment, 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 may apply to our site, where plant survival is largely linked to plant tolerance of 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 indicate that neither the intensity of competition nor the importance of competition explained variation in target plant biomass and survivorship for the first two years plants were establishing in resource poor environments within the semi-arid steppe. Instead abiotic factors may have an overriding influence on plant biomass and survivorship. We propose four scenarios which apply to semi-arid environments that can be used by land managers to determine the necessity of employing techniques to minimize competition during the initial phase of restoration. 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 not be intense but important if target plant biomass is affected only by competition (Briones et al., 1996). In these two situations, which are unlikely to occur in resource poor environments, managers will likely need to minimize competition. Third, competition may be intense, but not necessarily important if the amount of overall variation in fitness it accounted for is low (Sheley and Larson, 1995). Fourth, competition is neither intense nor an important variable when plant survival is largely linked to plant tolerance of drought and temperature extremes, i.e. when survivorship is abiotically driven (Hobbie et al., 1999; Armas et al., 2009). The last two scenarios are likely to occur in resource poor systems. In these situations, competition can range from non-existent to intense, but will not likely be important. This suggests

that land managers may be more successful at restoration by overcoming the barriers associated with plant establishment other than competition in resource poor systems, such as abiotic factors, rather than focusing on treatments aimed at controlling invasive plants. To clearly determine which factors limit the plants' fitness, additional studies are needed, comprising a range of those biotic and abiotic factors under question. Improved methods manipulating the abiotic environment in ways that enhance the performance of native species over invasive species are needed to overcome obstacles to restoration success. For example, using cover crops/bridge species (Blumenthal et al., 2003; Krueger-Mangold and Sheley, 2008) and plant litter management (Sheley et al., 2009) during restoration could potentially manipulate the abiotic environment.

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