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Simultaneous intraspecific facilitation and interspecific competition between native and annual grasses

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ABSTRACT

Invasive annual grasses tend to construct thinner and less dense root and leaf tissue than native perennial grasses. This allows invasive annuals to grow faster and produce more biomass in the arid grasslands of the United States. Based on these differences we tested the hypotheses that: 1) Competitive effects of the native perennial on the invasive annual will increase as plant developmental stage increases and as drought stress increases. 2) Drought stress will reduce the competitive effect of invasive annuals on native perennials proportionately more than drought stress reduces the competitive effect of native perennials on the invasive annual. 3) Facilitation among native perennial grass seedlings will decrease as developmental stage increases. Competitive effects of native squirreltail, on invasive medusahead, increased as the initial developmental stage of squirreltail increased, but not vice versa. Drought stress reduced the competitive effect of medusahead on squirreltail target biomass more than drought stress reduced the competitive effect of squirreltail on medusahead target biomass. While both squirreltail and medusahead displayed intraspecific facilitation, the net effect of their interspecific interaction was negative for both species. Habitat amelioration manifests itself differently depending on species traits, and can create conditions that simultaneously benefit one species while hindering another.

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1. Introduction

Arid ecosystems around the world provide ecological goods and services necessary for food and fiber that sustain life. Natural and human caused disturbances are continuous processes that can degrade ecological systems beyond a threshold state after which they no longer provide adequate goods and services. In arid ecosystems, these disturbances include soil erosion and desertification, invasive weeds, improper grazing, wildfires, energy development, and climate change. Maintaining and establishing healthy ecosystems is required to ensure that the natural resource base is not depleted to the point that it creates a global crisis. The ability to establish functional plant communities on degraded rangeland is fundamental to protecting and conserving our natural resource base for future generations. In many cases, once ecosystems pass a critical ecological threshold, they will not recover without active intervention (Stringham et al., 2003). Unfortunately, even with active management such as seeding, restoration of arid ecosystems is extremely difficult and restoration failure rates are high (Hardegree et al., 2011).

Competition and facilitation are central drivers of invasion resistance and restoration outcomes in invaded arid-systems (Corbin and D'Antonio, 2004a; Corbin and D'Antonio, 2004b; Gomez-Aparicio, 2009; Huston, 2004). The term competition is used in the sense of net negative interference of one plant over another (Casper and Jackson, 1997; Fowler, 1986), while the term facilitation is used when plant-plant interactions have a net positive effect (Bertness and Callaway, 1994). Both competition and facilitation can occur inter- and intra-specifically. Plant size and resource availability can strongly influence the magnitude and direction of interactions between or within invasives and natives (Callaway et al., 2002; Goldberg, 1987; Miriti, 2006; Sthultz et al., 2007). While these interactions appear linked to the success of invasive species over natives (Blumenthal and Hufbauer, 2007; Huenneke et al., 1990; Leishman et al., 2007), we know little about how initial conditions influence competitive and facilitative interactions, which is critical to our ability to manage invasion resistance and restoration of invaded systems.

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The intensity of competition and facilitation is very difficult to predict because environmental conditions interact with plant and population traits to determine outcomes. Niche-based theory suggests species with similar resource requirements compete most intensely, but it is clear that diverse plant communities exist despite nearly equivalent resource requirements among species (Leger and Espeland, 2010). Age–class variation may create size–asymmetric interactions where larger individuals preempt resources by acquiring them while they are unavailable to smaller individuals (Weiner and Damgaard, 2006). These interactions are among the strongest drivers of dynamics because they set the limits within which organisms can live and function (Lin et al., 2013). Relative plant size may be an essential factor needed to predict the outcome of plant-plant interactions when modeling vegetation dynamics.

The ability of invasives to grow faster and obtain larger biomass than native neighbors is well documented (Burns, 2004; Grotkopp et al., 2002; James and Drenovsky, 2007). Faster growth and larger size provides invasive plants an advantage in both high and low fertility systems (James et al., 2011). The mechanism that drives differences in growth rates is based on tissue economics (Diaz et al., 2004; Wright et al., 2004). Invasive annuals tend to construct thinner and less dense leaf and root tissue than natives, allowing invasives to build more leaf area and root length per unit biomass invested in these tissues and ultimately grow faster than their native counter parts (Grotkopp et al., 2002; Leishman et al., 2007; van Kleunen et al., 2010). Although competition for nutrients such as nitrogen is size symmetric, with competitive effects proportional to root system size, effects of root system size are not necessarily linear and small variation in root mass can cause large changes in competition intensity (Bartelheimer et al., 2008; Cahill and Casper, 2000). Thus, small differences in growth rates or initial plant size between natives and invasives annuals may strongly influence the degree to which natives are suppressed by invaders.

Many studies have examined how decreases in nutrient availability influence native and invasive plant interactions. This literature has failed to clearly demonstrate that native plants have a competitive advantage in low nutrient environments (Corbin and D′ Antonio, 2004b; Huddleston and Young, 2005; James et al., 2011; Mazzola et al., 2008). However, the literature has not considered how soil water content may constrain plant performance in nutrient poor soils. While the ability to construct relatively inexpensive leaf and root tissue provides invasives a growth rate and size advantage over native perennials (James et al., 2011), reduced soil water availability may constrain this advantage, particularly in nutrient poor soils. Native perennials follow an alternative tissue construction strategy. They tend to construct comparatively thicker and denser leaf and root tissue than invasives, which can increase nutrient conservation by decreasing tissue loss due to abiotic and biotic stress, thus allowing natives (but not invasives) the ability to maintain growth as soils dry. Thus, as water (and nutrient) availability decreases, the initial size advantages that invasives develop due to greater growth rate are likely to be minimized.

In addition to these negative effects of competitive interactions, plant size and resource availability may also influence facilitative interactions. The stress gradient hypothesis predicts that facilitation will increase as abiotic stress increases (Brooker et al., 2008). Ancillary data, arguments and quantitative syntheses have also suggested that facilitation may be important in a range of systems, particularly during early developmental stages (Gomez-Aparicio, 2009; Holmgren and Scheffer, 2010). However, the balance between competition and facilitation can change as plant size or densities change. As plant development and size increases, initial positive facilitative interactions may shift to negative competitive interactions, and these shifts may be more pronounced among more closely related taxa (Forrester et al., 2011; Miriti, 2006; Rousset and Lepart, 2000; Verdu et al., 2010). Therefore, any intraspecific facilitation exhibited by native perennials may be constrained to plants early in their developmental stage.

Although the ecological concepts of competition, facilitation, resource availability and plant size are not mutually exclusive, few studies have sought to incorporate all of these factors simultaneously. Moreover, many of the interactions between and among species are density dependent. Most studies of the interaction between native and invasive species are conducted using a single common initial stage, usually seed (Mangla et al., 2011; Vasquez et al., 2008; Young and Mangold, 2008) or do not simultaneously address a gradient of densities and proportions of species (Vila et al., 2004). We used a suite of matrices of density combinations and species proportions to evaluate how initial variation in native plant developmental stage and soil water content influences intra and interspecific interactions between a native perennial bunchgrass (bottlebrush squirreltail, *Elymus elymoides* [Raf.] Swezey) and an invasive annual grass (medusahead, *Taeniatherum caput-medusae* L.) in nutrient-poor soils. Invasion by annual grasses such as medusahead is having multi-dimensional, catastrophic effect on historically perennial-dominated ecosystems in the arid Western United States (Upadhaya et al., 1986; D'Antonio and Vitousek, 1992). Invasive winter-annual grasses emerge earlier than perennial species and thus demonstrate a strong priority effect (and corresponding size advantage) in restoration efforts where native perennials and invasive annuals establish from seed (Divittorio et al., 2007). Based on differences in growth rate and tissue construction strategies we tested the hypotheses that: 1) Competitive effects of the native perennial on the invasive annual will increase as plant developmental stage increases and this negative effect will increase as drought stress increases. 2) Drought stress will reduce the competitive effect of invasive annuals on native perennials proportionately more than drought stress reduces the competitive effect of native perennials on the invasive annual. 3) Facilitation among native perennial grass seedlings will decrease as developmental stage increases.

2. Materials and methods

2.1. Model system

Medusahead is a representative invasive annual grass. This species has evolved a variety of characteristics that facilitate invasion and dominance, including a winter-annual life cycle, high seed output, and large amounts litter accumulation, all of which form a barrier to establishment of other species (Bovey et al., 1961; Harris, 1965; Sharp et al., 1957; Young, 1992). It is very competitive with native grasses, including bottlebrush squirreltail, growing as seedlings (Young and Mangold, 2008).

Bottlebrush squirreltail represents native perennial grasses. It is a common ceaspitose grass particularly valuable for restoring medusahead-infested land (Davies, 2010; Jones, 1998) It is a competitive species against medusahead (Hironaka and Tisdale, 1973; Young and Evans, 1977), although medusahead remained two-to-seven times more competitive than squirreltail where comparison were made on even aged seedlings (Young and Mangold, 2008). However, this mid-seral species has naturally established in medusahead stands over time (Hironaka and Sindelair, 1973; Hironaka and Tisdale, 1963).

2.2. Experimental design

Varying densities and proportions of medusahead and squirreltail were arranged in several addition series matrices

(Radosevich, 1987). Squirreltail was planted at 4 densities (0, 2, 4 and 6 seedlings/pot) and medusahead seeded in 4 densities (0, 3, 20 and 40 seedlings/pot). These densities were chosen because they represent the range of combinations found under field conditions (Sheley and Larson, 1995; Young and Mangold, 2008). Each matrix was designed to have a factorial arrangement of density combinations. Densities of both matrices (squirereltail:medusahead) were 0:0, 0:3, 0:20, 0:40, 2:0, 2:3, 2:20, 2:40, 4:0, 4:3, 4:20, 4:40, 6:0, 6:3, 6:20, 6:40 plants per pot. There were a total of 8 matrices. One was comprised of both species grown simultaneously from seeds, and three other matrices were sown with varying initial plant sizes of squirreltail. The squirreltail stages were: 1 leaf stage, 3 leaf stage, and 2 tiller. The experimental pots used for the study were 30 cm (diameter) × 30 cm (depth), and filled with a 1:2 mixture of sandy loam field soil and course sand to create a nutrient-poor potting media. Soil nitrate and ammonium concentrations in the potting mixture were 1.6 ± 0.03 and 0.7 ± 0.04 μg g^{-1} (mean ± SE), respectively. Appropriate sized plants were randomly selected and carefully transplanted into the study pots on day 1. Following transplanting, medusahead was sown as seeds.

All of these matrices combinations of densities were grown at two water levels. All of the soils were initially saturated with water and allowed to equilibrate to capacity. High water content treatment pots were watered every 3 days keeping volumetric water content at 26 ± 0.5%. Low water treatments pots were allowed to dry to 9% water content and then pots were rewatered to field capacity through the 85 d study period. Average water content in the low water treatment pots was 13 ± 1%. This resulted in 16 densities × 4 phenological stages × 2 water levels = 128 treatment combinations. Each treatment was replicated three times for a total of 384 pots.

2.3. Procedures

We collected seeds of medusahead from a local field population near Burns, Oregon and purchased seeds of squirreltail from Granite Seed (Lehi, Utah USA). To achieve the 3 developmental stages of squirreltail (1 leaf stage, 3 leaf stage, and 2 tiller), we sowed seeds at different times in small cone pots and then transplanted the plants of differing sizes into larger experimental pots in spring 2010. Medusahead seeds were broadcast on the soil surface and manually arranged until a uniform distribution was achieved after squirreltail was transplanted. A small amount of dry soil was broadcast to cover the seeds. Soil was evenly misted on alternate days until emergence. We arranged the experimental pots in a completely-randomized-design outside at Burns, Oregon. Entire plants were harvested after 85 days at ground level, separated by species, and dried for 1-week at 60 °C.

2.4. Data analysis

We used multiple linear regression models to predict final plant weight for each density matrix and each replication (Spitters, 1983). Regressions predicted the per plant weight of medusahead and squirreltail as dependent variables using their densities as independent variables. The coefficient of determination (R^2) estimates the proportion of variation in the dependent variable (individual plant weight) that is accounted for by density.

The regressions were of the form:

$$y_s = \beta_{0s} + \beta_{sm}N_m + \beta_{ss}N_s$$

$$y_m = \beta_{0m} + \beta_{ms}N_s + \beta_{mm}N_m$$

Where y_s and y_m are the predicted weight of squirreltail (s) and medusahead (m). β_{0s} and β_{0m} are the y-intercepts and considered the predicted maximum weight of an isolated individual, β_{ss}, and β_{mm} are intraspecific competitive coefficient, and β_{sm} and β_{ms} are the interspecific competitive coefficients. The coefficients N_s and N_m are the respective initial densities of squirreltail and medusahead. Since the data did not require transformation, a positive response denotes positive interference, while a negative response denotes negative interference. Differences in intercepts (β_{0s} and β_{0m}), competitive coefficients (β_{ss}, and β_{mm}; β_{sm} and β_{ms}), and R^2 for various squirreltail sizes and water levels were determined and comparing Beta coefficients and R^2 for medusahead with those of the squirreltail using analysis of variance (ANOVA) with three replications (Neter et al., 1989). We present P values for assessing differences in watering treatments. Separations of the means of the coefficients generated as a response to squirreltail size were achieved using a Tukey's confidence interval.

3. Results

3.1. Coefficients of determination (R^2)

Based on sums of square and R^2's, the linear regression models predicting individual plant weight using neighboring plant density provided good fits. ANOVA of the R^2 indicated that they were not affected by watering or bottlebrush squirreltail size at sowing ($P > 0.05$). R^2 for models predicting shoot ($P = 0.26$) and total weight were not different between species. R^2 for models predicting shoot weight averaged 0.67 (SE = 0.03), while the R^2 predicting total weight averaged 0.64 (SE = 0.03). R^2 from models predicting root weight depended upon the species ($P = 0.01$). R^2 predicting squirreltail root weight using density were 0.50 (SE = 0.03) and those predicting the root weight of medusahead averaged 0.62 (SE = 0.03).

3.2. Predicting bottlebrush squirreltail weight using density

Shoot weight. The maximum predicted shoot weight of an isolated individual of bottlebrush squirreltail depended upon the size of the plants sown (Fig. 1a). Plants with 3 leaves or 2 tillers produced higher maximum predicted shoot weight as isolated individuals than when sown as seeds. Smaller plants and seeds produced the lightest plants growing in isolation by the end of the study. Squirreltail interference had a positive effect on squirreltail shoot weight for all plant sizes sown. As plant size at sowing increased from seeds to plants with 2 tillers, the positive effects of interference on shoot weight increased. The effect of medusahead density on squirreltail shoot weight was negative. Each increase in medusahead density reduced squirreltail's shoot weight from about 0.01 g to 0.08 g, depending on squirreltail's initial size.

Root weight. The maximum predicted root weight of an isolated individual of bottlebrush squirreltail depended upon the size of the plants sown (Fig. 1b). Plants with 3 leaves or 2 tillers produced plants with the maximum predicted root weight as isolated individuals. Smaller plants and seeds produced the lightest plants growing in isolation. Squirreltail interference had a positive effect on squirreltail root weight for all plant sizes. Plants with 3 leaves or 2 tillers had the highest positive effects on root weight across all densities. For these larger plants, each additional plant added to the pot at sowing increased individual plant weight by about 0.75 g. The positive effect of increasing density of squirreltail at the single leaf stage on con-specific neighbors was not different than those sown as seeds. The effect of medusahead density on squirreltail root weight was negative.

Total plant weight. The maximum predicted total weight of an isolated individual of bottlebrush squirreltail depended upon the

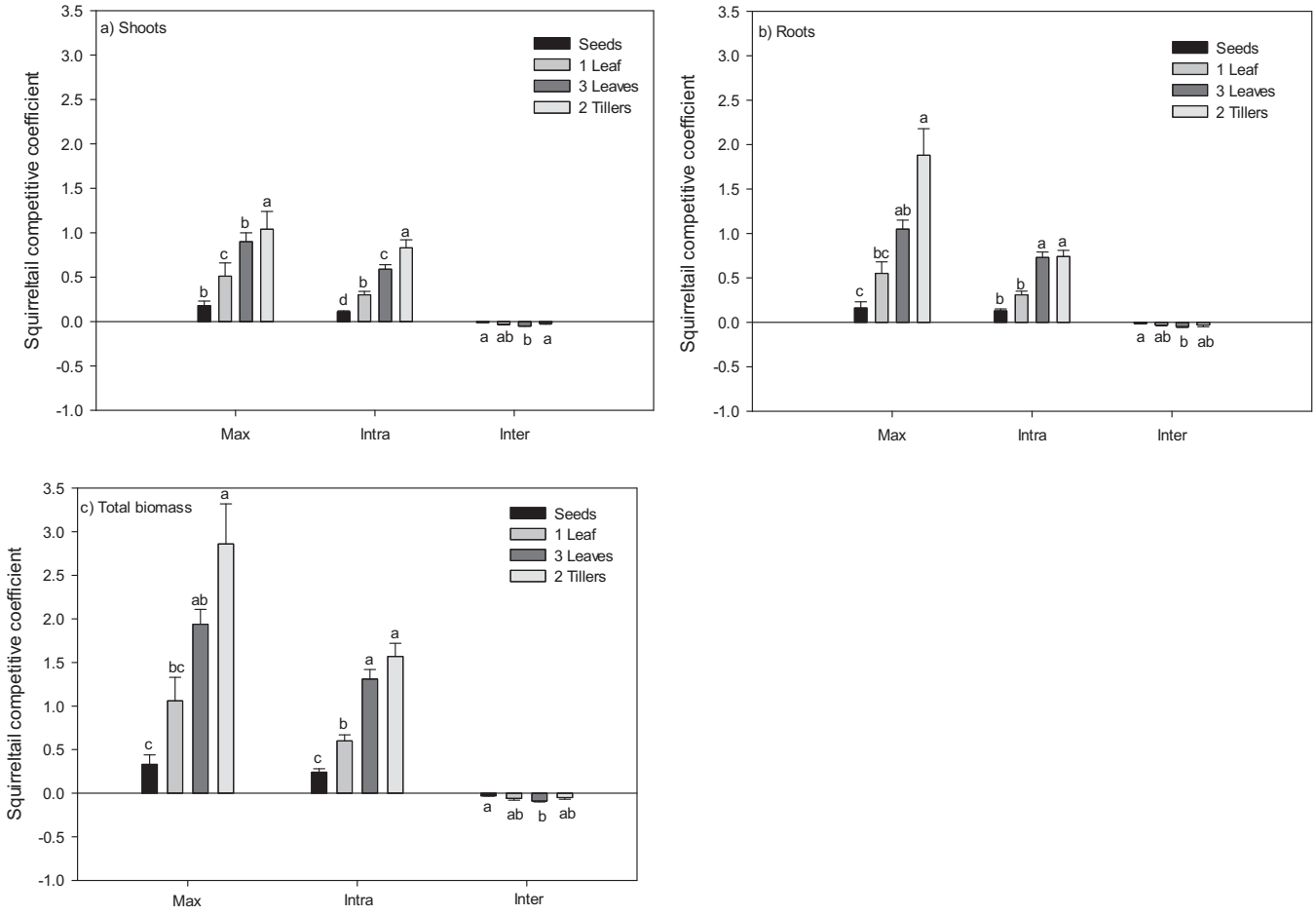

Fig. 1. Competitive coefficients predicting bottlebrush squirreltail shoot (*Elymus elymoides*) (1a), root (1b), and total (1c) biomass using plant density as the independent variable. The competitive coefficient is the amount of variation accounted for by the model. Max is the maximum size an individual can grow without neighbors. Positive coefficients show facilitation and negative competition. Intra and Inter refer to intraspecific and interspecific facilitation/competition. Bars are standard errors at $\alpha = 0.05$.

size of the plants at sowing (Fig. 1c). Plants with 3 leaves or 2 tillers produced plants with the maximum predicted total weight as isolated individuals. Smaller plants and seeds produced the lightest plants growing in isolation. Squirreltail interference had a positive effect on squirreltail's total weight for all plant sizes sown. Plants with 3 leaves or 2 tillers had the highest positive effects on plant weight across all densities. For these larger plants, each additional plant added to the pot at sowing increased individual plant weight by about 1.5 g. The positive effect of increasing density of squirreltail at the single leaf stage on con-specific neighbors was about twice that of those sown as seeds. The effect of medusahead density on squirreltail was negative.

3.3. Predicting medusahead weight using density

Shoot weight. The predicted maximum shoot weight of an isolated medusahead individual ranged from 1 g to about 1.5 g (Fig. 2a). No differences in the maximum size of medusahead in response to bottlebrush squirreltail size at sowing were detected. The effect of medusahead on its own shoot weight was positive. When squirreltail was grown from seeds, the positive benefits of intraspecific density were larger than when squirreltail was sown as a plant with 2 tillers. The effects of squirreltail density on medusahead shoot weight were negative. The strongest negative impact of squirreltail density on medusahead shoot weight was from the two largest plants at the time of sowing.

Root weight. The predicted maximum root weight of an isolated individual of medusahead plant was higher in regression models where bottlebrush squirreltail plants were sown at the 3 leaf stage than those where both species were sown as seeds (Fig. 2b). The predicted root weight of an isolated medusahead plant was about 0.55 g, when both species were sown as seeds. The predicted root weight of an isolated medusahead plant grown in pots where it was sown with squirreltail plants ranged from 1.1 g to 1.4 g. The effect of medusahead on its own root weight was positive. Each increase in medusahead density, increased its root weight by about 0.2 g when sown with squirreltail seeds, and tended to be less as the size of squirreltail sown increased. When sown from seeds, squirreltail had a slightly positive effect on medusahead root weight. However, when squirreltail was sown at any growth stage, density had a negative impact on medusahead root weight.

Total plant weight. The predicted maximum total weight of an isolated individual of medusahead plant was higher where plants of bottlebrush squirreltail were initially sown versus those where both species were sown as seeds (Fig. 2c). The predicted weight of an isolated medusahead plant was about 1.7 g, when both species were sown as seeds. The predicted weight of an isolated medusahead plant grown in pots where it was sown with squirreltail plants was about 2.6 g. The effect of medusahead on itself was positive. Each additional medusahead plant in the pot increased its total weight by about 0.3 g when sown with the two largest sizes of squirreltail plants. An additional medusahead plant increased its

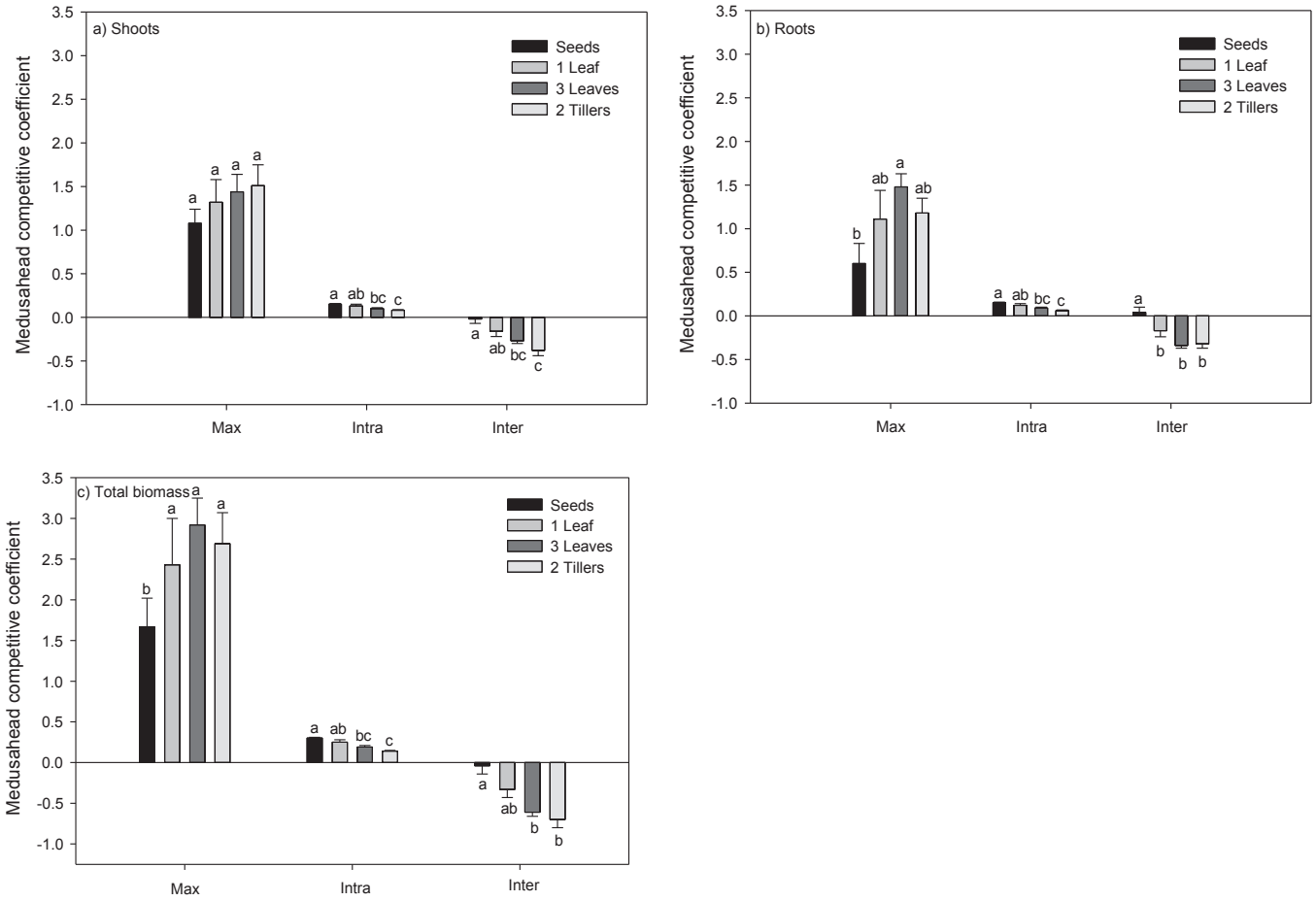

Fig. 2. Competitive coefficients predicting medusahead (*Taeniatherum caput-medusae*) shoot (1a), root (1b), and total (1c) biomass using plant density as the independent variable. The competitive coefficient is the amount of variation accounted for by the model. Max is the maximum size an individual can grow without neighbors. Positive coefficients show facilitation and negative competition. Intra and Inter refer to intraspecific and interspecific facilitation/competition. Bars are standard errors at $\alpha = 0.05$.

own weight by about 0.2 g when it was sown with small squirreltail plants or squirreltail seeds. The effect of squirreltail density on medusahead weight was negative. The strongest negative impact of squirreltail density was from those sown as plants. For each increase in squirreltail density, the reduction in medusahead per plant was 0.35, 6.0, and 7.5 g for squirreltail plant sown at 1 leaf, 3 leaves, and 2 tillers, respectively. However, the reduction in medusahead weight by squirreltail sown at the single leaf stage was not different than larger plants or those sown from seeds.

3.4. Predicting bottlebrush squirreltail weight using plant density with added water

The maximum predicted weight of an isolated bottlebrush squirreltail plant was greater with added water (Table 1). Across all three weight variables, water increased the predicted weight of an isolated squirreltail plant by about 33%. Adding water also increased the positive effects of intraspecific facilitation. For example, for each increase in squirreltail density, total weight increased from 0.78 g to 108 g per plant. The negative effects of medusahead on squirreltail doubled with added water.

3.5. Predicting medusahead weight using plant density with added water

The maximum predicted root and total weight of an isolated medusahead plant was greater with added water (Table 1), whereas the maximum shoot weight was not different between watering treatments. Intraspecific interference was unaffected by watering for medusahead. The influence of squirreltail density on medusahead root and shoot weight became more intense with watering. For example, each additional increase in squirreltail density reduced the total weight of medusahead by 0.33 g without water and 0.51 g with water.

Table 1
ANOVAs comparing competitive coefficients between low and high water levels from regression models predicting individual plant bottlebrush squirreltail and medusahead biomass using plant density as the independent variable. Max is the maximum size an individual can grow without neighbors. Intra and inter refer to intra- and inter-specific competitive coefficients, with positive values showing facilitation and negative values competition.

	Level of water	Max	*P*	Intra	*P*	Inter	*P*
Squirreltail							
Root	High	1.08	0.053	0.54	0.006	−0.04	0.113
	Low	0.73		0.41		−0.02	
Shoot	High	0.85	0.002	0.54	0.002	−0.04	0.004
	Low	0.46		0.37		−0.02	
Total	High	1.89	0.01	1.08	0.002	−0.08	0.02
	Low	1.2		0.78		−0.04	
Medusahead							
Root	High	1.35	0.008	0.11	0.54	−0.25	0.04
	Low	0.83		0.1		−0.15	
Shoot	High	1.48	0.09	0.12	0.09	−0.22	0.29
	Low	1.89		0.11		−0.18	
Total	High	2.83	0.02	0.23	0.23	−0.51	0.04
	Low	2.03		0.21		−0.33	

4. Discussion

Competition can be very intense as plant struggle to acquire resources in limited supply. In unproductive and/or harsh environments competition, even though intense, may not be a major factor determines the relative ability of plants to accumulate biomass (Goldberg and Novoplansky, 1997; Mangla et al., 2011). Other abiotic and biotic factors may have a stronger influence on plant growth than competition, such as extreme temperatures, drought and/or herbivory. Analyzing addition series designs, Weldon and Slauson (1986) suggest the importance of competitive interference is the proportion of variation accounted for by coefficient of determination (R^2). This simple interpretation of R^2 does not consider an indication of the long-term consequences of plant-plant interactions on structuring plant communities, only on individual plant performance (Brooker and Kikvidze, 2008; Damgaard and Fayolle, 2010; Freckleton et al., 2009). However, it does provide some indication of the importance of interference relative to all other factors in the environment and time period in which the experiment was conducted. In this study, about 60% of the variation in final biomass was accounted for by plant density. These R^2 are consistent with those found by Young and Mangold (2008), while studying interactions between bottlebrush squirreltail and medusahead seedlings sown as seeds. Given the complexity of biotic interactions, this provides some evidence that interference can be an important determinant of plant biomass in these systems, and may be an important factor influencing vegetation dynamics.

In partial support of our first hypothesis, the *competitive effects* of the squirreltail, the native perennial grass, on medusahead, the invasive annual grass, was large and increased with developmental stage of squirreltail. In contrast, the *competitive response* of squirreltail to medusahead was small and largely unaffected by initial squirreltail stage. In terms of competitive effect of squirreltail on medusahead, the impact of developmental stage was only evident between the two youngest stages (seed to one leaf), but then did not yield further increases in competitive effects. This result is contrary to the theoretic expectation that competition is size symmetric (i.e., competition increases with size), and exemplifies disproportional competitive effects early (compared to later) in development, as is demonstrated in other studies (Bartelheimer et al., 2008; Cahill and Casper, 2000; Schwinning and Weiner, 1998). This could be due to reduced resource uptake efficiency or increased competition as root systems age (Berntson, 1994; Krannitz et al., 1991). In terms of competitive response, there was an even larger departure from theoretic expectations of increased competition with stage, as we observed that squirreltail stage had no influence on the competitive response of squirreltail to competition by medusahead. Thus, our study provides clear evidence that plant size exerts a larger influence on competitive effect than on competitive response. If this is true, then future work examining the role of plant size on competitive ability may benefit by examining the role of plant size on competitive effect and response.

In support of our second hypothesis, drought stress reduced the competitive effect of medusahead on squirreltail target biomass more than drought stress reduced the competitive effect of squirreltail on medusahead target biomass. While we did not measure tissue construction and morphology in this experiment, these results are broadly consistent with the differences in tissue economics reported for annual and perennial grasses. In general, annuals construct thinner and less dense leaf and root tissue (Garnier, 1992; Roumet et al., 2006). Construction of thinner and less dense tissue allows invasives to grow faster (Grotkopp and Rejmanek, 2007; Leishman et al., 2007) this comes at a cost in terms of decreased tissue life span and a lower ability to maintain physiological function under drought stress (Dale and Causton, 1992; Ramirez-Valiente et al., 2010; Scheepens et al., 2010). Success of invasive plants has been widely attributed to increases in resource availability (Davis et al., 2000), although evidence is equivocal and has not considered the influence of concurrent stressors such as drought. A number of studies have examined how decreases in nutrient availability influence native and invasive plant interactions. In general, most of this literature has failed to demonstrate that native plants have a competitive advantage in low nutrient environments (James et al., 2011). The bulk of the literature has not considered how soil water content may constrain plant performance in nutrient poor soils. One recent study examining native and invasive plant competition in low nutrient soils found that natives had a greater competitive ability under pulsed versus continuous water supply (Firn and Buckley, 2010). Taken together with the results from our study, this suggests that competitive interactions between native and invasive plants in low nutrient soils may only be likely to shift when factors such as drought, herbivory or wind abrasion that impose a relatively greater cost on fast growing species compared to slow growing species are considered (Fraser and Grime, 1999). Interestingly, the shift in the competitive balance under water stress was applicable across the different squirreltail stages.

We found that intraspecific facilitation by squirreltail seedlings increased 3-fold as plant stage increased, which was contrary to our third hypothesis and to previous related studies. Research examining how plant interactions shift with ontogeny of size has mostly focused on changes in interactions over multiple years. These studies generally suggest that as plants grow and develop interactions typically shift from positive to negative (Forrester et al., 2011; Miriti, 2006; Rousset and Lepart, 2000), particularly among phylogenetically related taxa because they share similar niche requirements (Verdu et al., 2010). We suspect that habitat amelioration from conspecific neighbors outweighed negative effects of competition, as has been observed in other systems as well (e.g., during tree seedling establishment; Fajardo and McIntire, 2011). If restoration and community assembly outcomes are largely driven by processes occurring at the seedling stage (Grubb, 1977), then it might be valuable to focus future work on short-term intraspecific facilitation.

The outcome of plant-plant interference is considered to be the net effect of sometimes complex negative and positive interactions (Bertness and Callaway, 1994). Theoretically, intraspecific competition would be stronger than interspecific competition because conspecific species possess the same requirements for and ability to sequester nutrients (Connell, 1983; Schoener, 1983). However, evidence and examples of facilitation are increasingly prevalent in the literature, especially for K-strategist, like bottlebrush squirreltail (Golubski et al., 2010). Leger and Espeland (2010) saw facilitative, neutral and competitive interactions in the California annual grassland depending upon species. In our study, both squirreltail and medusahead responded positively to association with neighbors of their own species. This supports the small amount of evidence provided by Fajardo and McIntire (2011) studying tree seedlings that under strong niche overlap conspecifics do not compete, but help each other succeed at least during establishment. This study extends this finding to grassland systems that are being invaded by annual grasses and supports the ongoing shift in our understanding of density-dependent interactions in arid grasslands under invasion (Fajardo and McIntire, 2011; Mangla et al., 2011).

Net positive interactions among conspecific seedlings are inconsistent with predictions using the niche concepts of

competition. The benefits are likely due to habitat amelioration (Bertness and Callaway, 1994; Callaway, 2007). Bertness and Callaway (1994) suggested that facilitation is warranted much more attention because benefits from neighboring plants could outweigh the simultaneously occurring competitive interactions. Mangla et al. (2011) suggested that abiotic factors have an overriding influence on bluebunch wheatgrass and medusahead plant biomass in environments characterized by extreme conditions. In that study, perennial seedlings and medusahead growing in isolation had slow growth rates, and in the case of Sandberg's bluegrass, had 100% mortality. Sheley and James (2010) were unable to establish isolated plants of medusahead on cleared surfaces within the sagebrush steppe ecosystem of Oregon. Amelioration can occur in several ways. For example, water stress is reduced by neighbors that create cooler air and soil temperatures, as well as higher air humidity (Holmgren, 2000; Larcher, 2001; Quero et al., 2006). Although neighbors may also decrease light and soil moisture, the net effects are positive, especially during seedling competition where their effects on light may be low (Valladares et al., 2008). In general, intraspecific facilitation was greater for bottlebrush squirreltail than for medusahead. In addition, within the size classes of this experiment, the net benefits of habitat amelioration increased as the size of interacting bottlebrush squirreltail plants increased.

One of the most unique and important findings of this study was that while both bottlebrush squirreltail and medusahead displayed intraspecific facilitation, the net effect of their interspecific interaction was negative for both species. The ecological advantage of this simultaneous intraspecific facilitation and interspecific competition could be profoundly influential in plant establishment and the structuring of plant communities. The notion that a species can ameliorate its own local habitat for itself and for conspecific neighbors without benefiting other neighboring species is of significant ecological value. Amelioration of the stress factor and differential species ecophysiological requirements and tolerances interact to determine the net outcome of the interference (Maestre et al., 2005). Therefore, changes in the environment may manifest themselves differently depending on species traits, and create conditions that simultaneously favor one species and favor a nearby associated species less or even disfavor it.

References

Bartelheimer, M., Steinlein, T., Beyschlag, W., 2008. 15N-nitrate-labelling demonstrates a size symmetric competitive effect on belowground resource uptake. Plant Ecol. 199, 243–253.

Berntson, G.M., 1994. Modeling root architecture – are there tradeoffs between efficiency and potential of resource acquisition. New Phytol. 127, 483–493.

Bertness, M.D., Callaway, R., 1994. Positive interaction in communities. Trends Ecol. Evol. 9, 191–193.

Blumenthal, D.M., Hufbauer, R.A., 2007. Increased plant size in exotic populations, a common-garden test with 14 invasive species. Ecology 88, 2758–2765.

Bovey, R.W., Le Tourneau, D., Erickson, L.C., 1961. The chemical composition of medusahead and downy brome. Weeds 9, 307–311.

Brooker, R.W., Kikvidze, Z., 2008. Importance, an overlooked concept in plant interaction research. J. Ecol. 96, 703–708.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Justin, M., Travis, J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. J. Ecol. 96, 18–34.

Burns, J.H., 2004. A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. Divers. Distrib. 10, 387–397.

Cahill, J.F., Casper, B.B., 2000. Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. Oikos 90, 311–320.

Callaway, R.M., 2007. Positive Interactions and Interdependence in Plant Communities. Springer, Dordrecht, The Netherlands, p. 415.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–848.

Casper, B.B., Jackson, R.B., 1997. Plant competition underground. Annu. Rev. Ecol. Syst. 28, 545–570.

Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition, evidence from field experiments. Am. Nat. 12, 661–696.

Corbin, J.D., D'Antonio, C.M., 2004a. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85, 1273–1283.

Corbin, J.D., D'Antonio, C.M., 2004b. Can carbon addition increase competitiveness of native grasses? A case study from California. Restor. Ecol. 12, 36.

Dale, M.P., Causton, D.R., 1992. The ecophysiology of veronica-chamaedrys, v-montana and v-officinalis. 2. The interaction of irradiance and water regime. J. Ecol. 80, 493–504.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.

Damgaard, C., Fayolle, A., 2010. Measuring the importance of competition, a new formulation of the problem. J. Ecol. 98, 1–6.

Davies, K.W., 2010. Revegetation of medusahead-invaded sagebrush steppe. Rangel. Ecol. Manag. 63, 564–571.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88, 528–534.

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci. 15, 295–304.

Divittorio, C.T., Corbin, J.D., D'antonio, C.M., 2007. Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. Ecol. Appl. 17, 311–316.

Fajardo, A., McIntire, E.J.B., 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. J. Ecol. 99, 642–650.

Firn, J., MacDougall, A., Schmidt, S., Buckley, Y.M., 2010. Early emergence and resource availability can competitively favour natives over a functionally similar invader. Oecologia 163, 775–784.

Forrester, D.I., Vanclay, J.K., Forrester, R.I., 2011. The balance between facilitation and competition in mixtures of Eucalyptus and Acacia changes as stands develop. Oecologia 166, 265–272.

Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions. Annu. Rev. Ecol. Syst. 17, 89–110.

Fraser, L.H., Grime, J.P., 1999. Interacting effects of herbivory and fertility on a synthesized plant community. J. Ecol. 87, 514–525.

Freckleton, R.P., Watkinson, A.R., Rees, M., 2009. Measuring the importance of competition in plant communities. J. Ecol. 97, 379–384.

Garnier, E., 1992. Growth analysis of congeneric annual and perennial grass species. J. Ecol. 80, 665–675.

Goldberg, D.E., 1987. Neighborhood competition in an old field plant community. Ecology 68, 1211–1223.

Goldberg, D., Novoplansky, A., 1997. On the relative importance of competition in unproductive environments. J. Ecol. 85, 409–418.

Golubski, A.J., Gross, K.L., Mittelbach, G.G., 2010. Recycling-mediated facilitation and coexistence based on plant size. Am. Nat. 176, 588–600.

Gomez-Aparicio, L., 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. J. Ecol. 97, 1202–1214.

Grotkopp, E., Rejmanek, M., 2007. High seedling relative growth rate and specific leaf area are traits of invasive species, phylogenetically independent contrasts of woody angiosperms. Am. J. Bot. 94, 526–532.

Grotkopp, E., Rejmanek, M., Rost, T.L., 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. Am. Nat. 159, 396–419.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. Camb. Philos. 52, 107–145.

Hardegree, S.P., Jones, T.A., Roundy, B.A., Shaw, N.L., Monaco, T.A., 2011. Assessment of rage planting as a conservation practice. In: Briske, D.D. (Ed.), Conservation Benefits of Rangeland Practices, Assessment, Recommendations, and Knowledge Gaps. Allen Press, Lawrence, KS, USA, pp. 171–212.

Harris, G.A., 1965. Medusahead competition. In: Proceedings of the Cheatgrass Symposium, Vale, Oregon. Bureau of Land Management, Portland, Oregon, pp. 66–69.

Hironaka, M., Sindelair, B.W., 1973. Reproductive success of squirreltail in medusahead infested range. J. Range Manage. 26, 219–221.

Hironaka, M., Tisdale, E.W., 1973. Growth and Development of Sitanion Hystrix and Poa Sandbergii. Desert Biome. U.S. International Biological Program, Desert Biome, UT. RM 73–16.

Hironaka, M.T., Tisdale, E.W., 1963. Secondary succession in annual vegetation in southern Idaho. Ecology 44, 810–812.

Holmgren, M., 2000. Combined effects of shade and drought on tulip poplar seedlings: trade-off in tolerance or facilitation? OIKOS 90, 67–78.
Holmgren, M., Scheffer, M., 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. J. Ecol. 98, 1269–1275.
Huddleston, R.T., Young, T.P., 2005. Weed control and soil amendment effects on restoration plantings in an Oregon grassland. West. N. Am. Nat. 65, 507–515.
Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71, 478–491.
Huston, M.A., 2004. Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Divers. Distrib. 10, 167–178.
James, J.J., Drenovsky, R.E., 2007. A basis for relative growth rate differences between native and invasive forb seedlings. Rangel. Ecol. Manag. 60, 395–400.
James, J.J., Drenovsky, R.E., Monaco, T.A., Rinella, M.J., 2011. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? Ecol. Appl. 21, 490–502.
Jones, T.A., 1998. Viewpoint, the present status and future prospects of squirreltail research. J. Range Manage. 51, 326–331.
Krannitz, P.G., Aarssen, L.W., Lefebvre, D.D., 1991. Correction for nonlinear relationships between root size and short-term pi uptake in genotype comparisons. Plant Soil. 133, 157–167.
Larcher, W., 2001. Ökophysiologie der Pflanzen. Ulmer, Stuttgart, Germany, p. 408.
Leger, E.A., Espeland, E.K., 2010. The shifting balance of facilitation and competition affects the outcomes of intra- and interspecific interactions over the life history of California grassland annuals. Plant Ecol. 208, 333–345.
Leishman, M.R., Haslehurst, T., Ares, A., Baruch, Z., 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. New Phytol. 176, 635–643.
Lin, Y., Berger, U., Grimm, V., Huth, F., Weiner, J., 2013. Plant interactions alter the predictions of metabolic scaling theory. PLoS ONE 8, e57612.
Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. J. Ecol. 93, 748–757.
Mangla, S., Sheley, R.L., James, J.J., 2011. Field growth comparisons of invasive alien annual and native perennial grasses in monocultures. J. Arid. Environ. 75, 206–210.
Mazzola, M.B., Allcock, K.G., Chambers, J.C., Blank, R.R., Schupp, E.W., Doescher, P.S., Nowak, R.S., 2008. Effects of nitrogen availability and cheatgrass competition on the establishment of Vavilov Siberian Wheatgrass. Rangel. Ecol. Manag. 61, 475–484.
Miriti, M.N., 2006. Ontogenetic shift from facilitation to competition in a desert shrub. J. Ecol. 94, 973–979.
Neter, J., Wasserman, W., Kutner, M., 1989. Applied Linear Regression Models. Irwin, Inc, Boston, Mass, p. 667.
Quero, J.L., Villar, R., Maranon, T., Zamora, R., 2006. Interactions of drought and shade effects on seedlings of four Quercus species, physiological and structural leaf responses. New Phytol. 1170, 819–834.
Radosevich, S.R., 1987. Methods to study interactions among crops and weeds. Weed Technol. 1, 190–198.
Ramirez-Valiente, J.A., Sanchez-Gomez, D., Aranda, I., Valladares, F., 2010. Phenotypic plasticity and local adaptation in leaf ecophysiological traits of 13 contrasting cork oak populations under different water availabilities. Tree Physiol. 30, 618–627.
Roumet, C., Urcelay, C., Diaz, S., 2006. Suites of root traits differ between annual and perennial species growing in the field. New Phytol. 170, 357–368.
Rousset, O., Lepart, J., 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). J. Ecol. 88, 401–412.
Scheepens, J.F., Frei, E.S., Stocklin, J., 2010. Genotypic and environmental variation in specific leaf area in a widespread Alpine plant after transplantation to different altitudes. Oecologia 164, 141–150.
Schoener, T.W., 1983. Field experiments on interspecific competition. Am. Nat. 122, 240–285.
Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113, 447–455.
Sharp, L.A., Hironaka, M., Tisdale, E.W., 1957. Viability of Medusa-head (*Elymus caput-medusae* L.) seed collected in Idaho. J. Range Manage. 10, 123–126.
Sheley, R.L., James, J.J., 2010. Resistance of native plant functional groups to invasion by medusahead. Invasive Plant Sci. Manage. 3, 294–300.
Sheley, R.L., Larson, L.L., 1995. Interference between cheatgrass and yellow starthistle at 3 soil depths. J. Range Manage. 48, 392–397.
Spitters, C.J.T., 1983. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. Neth. J. Agric. Sci. 31, 1–11.
Stringham, T.K., Krueger, W.C., Shaver, P.L., 2003. State and transition modeling: an ecological process approach. J. Range Manage. 56, 106–113.
Sthultz, C.M., Gehring, C.A., Whitham, T.G., 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. New Phytol. 173, 135–145.
Upadhaya, M.K., Turkington, R., McIlyride, D., 1986. The biology of Canadian weeds. Can. J. Plant Sci. 66, 689–709.
Valladares, F., Zaragoza-Castells, J., Sanchez-Gomez, D., Matesanz, S., Alonso, B., Portsmuth, A., Delgado, A., Atkin, O.K., 2008. Is shade beneficial for mediterranean shrubs experiencing periods of extreme drought and late-winter frosts? Ann. Bot. Lond. 102, 923–933.
van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol. Lett. 13, 235–245.
Verdu, M., Jordano, P., Valiente-Banuet, A., 2010. The phylogenetic structure of plant facilitation networks changes with competition. J. Ecol. 98, 1454–1461.
Vasquez, E., Sheley, R., Svejcar, T., 2008. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. Invasive Plant Sci. Manage. 1, 287–295.
Vila, M., Willamson, M., Lonsdale, M., 2004. Competition experiments on alien weeds with crops, lessons for measuring plant invasion impact? Biol. Invasions 6, 59–69.
Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navis, M., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.
Weiner, J., Damgaard, C., 2006. Size-asymmetric competition and size asymmetric growth in a spatially explicit zone-of-influence model of plant competition. Ecol. Restor. 21, 702–712.
Weldon, C.W., Slauson, W.L., 1986. The intensity of competition versus its importance, an overlooked distinction and some implications. Q. Rev. Biol. 61, 23–44.
Young, J.A., 1992. Ecology and management of medusahead (*Taeniatherum caput-medusae* SSP. Asperum [Simk.] Melderis). Gt. Basin Nat. 52, 245–252.
Young, J.A., Evans, R.A., 1977. Squirreltail seed germination. J. Range Manage. 30, 33–66.
Young, K., Mangold, J., 2008. Medusahead (*Taeniatherum caput-medusae*) outperforms squirreltail (*Elymus elymoides*) through interference and growth rate. Invasive Plant Sci. Manage. 1, 73–81.