Intra and interspecific competition among invasive and native species during early stages of plant growth

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Abstract Plant competition is a primary ecological process limiting grassland restoration success. Appropriate restoration techniques require an understanding of the degree to which intra and interspecific competition control invasive and native plant growth. The objective of this study was to determine how the intensity of intra and interspecific competition changes during early stages of plant growth. Two invasive (*Bromus tectorum* and *Taeniatherum caput-medusae*) and two native (*Pseudoroegneria spicata* and *Poa secunda*) 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 interspecific competition changes through time. Intraspecific 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 interspecific 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 Intraspecific competition · Interspecific competition · Harvest time · Nitrogen · Restoration · Diallel design

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Introduction

Exotic plant invasion poses a serious ecological and conservation threat to native plant communities (Vitousek et al. 1996; Simberloff 2005). 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; Vitousek et al. 1996; Pimentel et al. 2005). 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; Sheley and Mangold 2003; Mangold et al. 2006).

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 (Fowler 1986; Casper and Jackson 1997) 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 interspecific competition influence invasive and native plant growth. Classical competition theory predicts intraspecific competition should be greater than interspecific competition because individuals of the same species share similar resource requirements (Tilman 1982; Aarssen 1983; Spitters 1983; Fowler 1986; Goldberg and Barton 1992). Reviews of the relative strength of intra and interspecific competition in experimental plant studies tend to find little evidence for consistently stronger intraspecific competition among interacting species (Goldberg and Barton 1992; Gurevitch et al. 1992). However, results from more recent studies not included in these reviews affirm these variable results, with some studies showing intense intraspecific competition (Sheley and Larson 1994; Velagala et al. 1997; Wassmuth et al. 2009), while others indicating intense interspecific competition (Young and

Mangold 2008; Vasquez et al. 2008; Blank 2010). One possible explanation for these contradictory findings may be because the interpretation of competitive interactions has been largely based on assessing individual plant biomass over one life-history stages (Connolly et al. 1990; Goldberg and Barton 1992; Farrer et al. 2010). 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 different species (Connell 1983; Schoener 1983; Cameron et al. 2007). 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 may be much more sensitive to competition than adult plants (Foster 1999; Suding and Goldberg 1999). Other research, however, has indicated 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 varies 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 has indicated

that increased N favors invasive species over native species (Chambers et al. 2007; James et al. 2008) and decreased N availability favors native species (McLendon and Redente 1992; Lowe et al. 2003). However, dominance by annual grasses has been observed even in low N environments (Vasquez et al. 2008; Young and 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 that influences competition 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 a full 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 interspecific 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 time 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 predicted that the competitive intensity for invasive species will be higher than native species with higher N availability.

Materials and methods

Selection of plant species and soil

We selected two invasive and two native species that co-occur in the Intermountain West. Cheatgrass and medusahead are common and widespread cool-season invasive annual grasses that have invaded much of the Intermountain West (Turner et al. 1963; Mack 1989; Duncan et al. 2004). 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 temperature. 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 25–30 cm of the soil was collected in spring 2008. The soil was then 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 N g^{-1} soil.

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 interspecific 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 (N−) or 400 mg N kg^{-1} soil (N+) added. There were 10 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 × 2 N treatments × 10 replicates × 4 harvests = 1,120 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 interspecific 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 the 60 and 90 DAP were 15 cm diameter by 10 cm in depth. Smaller pots and larger pots were filled with 500 and 1,500 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 1,250 μmol m^{-2} s^{-1}.

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

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):

$$\ln RR = \ln (BM_{mixture}/BM_{alone}),$$

where $BM_{mixture}$ is the total biomass of target species *i* with neighbor *i* (intraspecific competition) or *j* (interspecific 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).

Results

Overall, DAP and N had minimal effect on competition intensity, but neighbor and target species identity had significant impacts on competition

Table 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	F	P
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 × nitrogen	1	0.23	0.631
DAP × target	3	0.86	0.464
DAP × neighbor	3	0.81	0.492
Nitrogen × target	3	2.43	0.073
Nitrogen × neighbor	3	0.28	0.838
Target × neighbor	9	1.05	0.408
DAP × nitrogen × target	9	3.18	0.029
DAP × nitrogen × neighbor	3	1.29	0.285
DAP × target × neighbor	9	0.73	0.682
DAP × nitrogen × target × neighbor	9	1.17	0.326
Residuals	64		

intensity (Table 1). Neighbor species differed significantly in their ability to suppress the growth of target species experiencing either intra or interspecific competition. However, neighbor species did not differ in their response to N and DAP (neighbor × N and neighbor × DAP, respectively; Table 1).

Effect of harvest time on intra and interspecific competitive interactions

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

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

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. 1a1, 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. 2a2). For bluebunch wheatgrass in N−, the competition intensity was highest at initial harvest (15 DAP) resulting in 30% reduction in its biomass compared to where grown alone (Figs. 1b1, 2b1). 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. 1b2, 2b2).

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. 1c1, 2c1). 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. 1c2, 2c2). In N+, cheatgrass biomass decreased 47 and 17% at 30 and 60 DAP, respectively, below that grown in isolation (Fig. 2c2). Similarly, for medusahead, in N−, the competition intensity was highest during initial harvests (Fig. 1d1). However, at 60 and 90
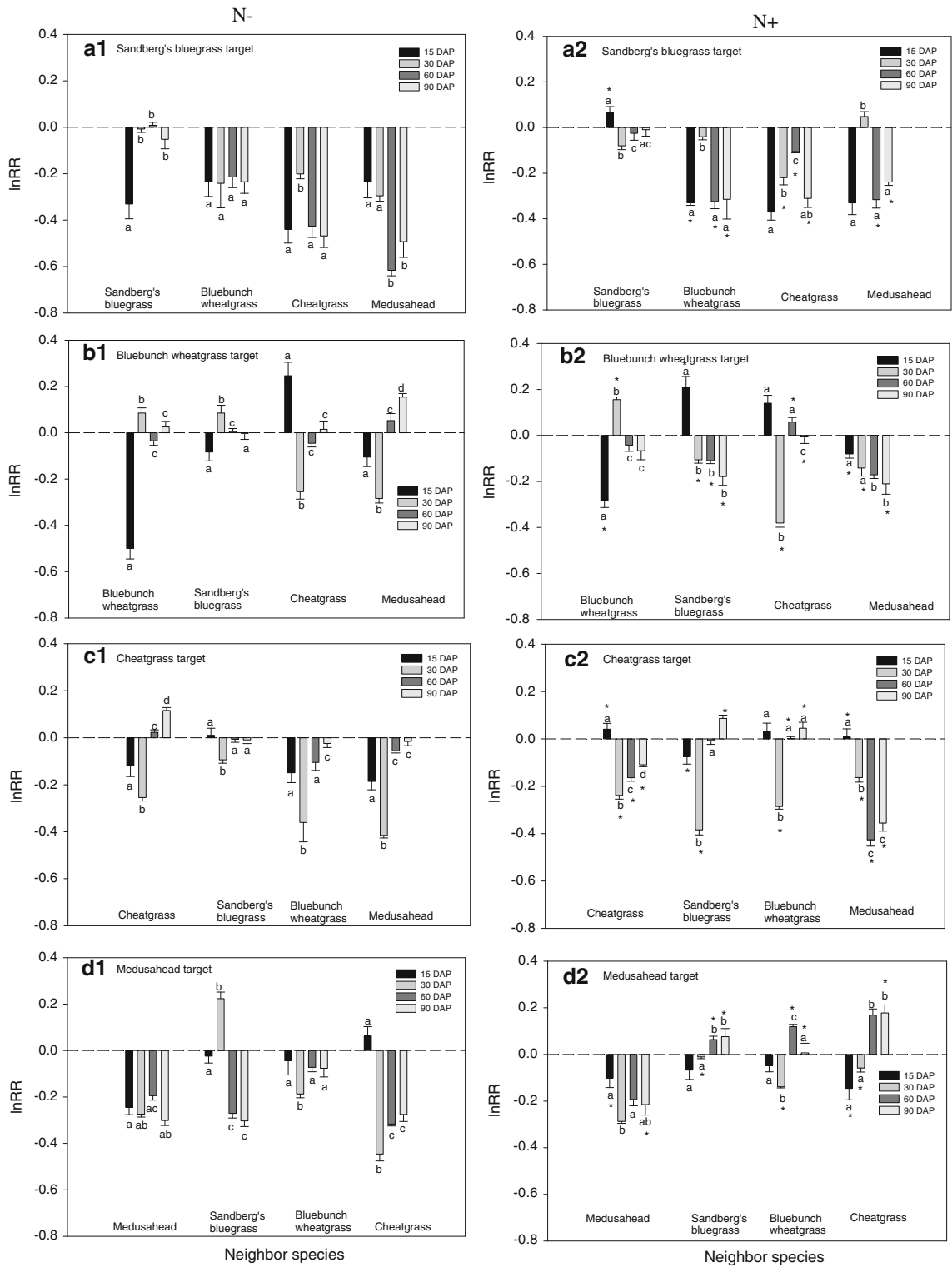
◄**Fig. 1** Effect of time of harvest (DAP) on intra and interspecific competitive interactions (lnRR) of different neighbor species on **a** Sandberg's bluegrass, **b** bluebunch wheatgrass, **c** cheatgrass, and **d** medusahead target plants under N− and N+. *Bars* represent mean ± SE ($n = 10$). 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 same target species and same neighbor species at a particular DAP

DAP, intense competition was also detected and resulted in a decrease of biomass by 38 and 30%, respectively, compared to medusahead grown alone (Figs. 1d1, 2d1). 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. 1d2, 2d2).

Comparison of competition intensity between N treatments

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

For native species, N addition resulted in less intraspecific competition at 15 DAP compared to N−. However, N addition resulted in intense interspecific 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 and 30 DAP, respectively ($P < 0.05$).

Except at 15 and 30 DAP, N+ resulted in significantly higher negative lnRR for cheatgrass grown with intraspecific competition ($P < 0.05$), i.e., intraspecific competition reduced the biomass of cheatgrass when N+ was compared with N− at later stages (60 and 90 DAP). However, N addition resulted in the reduction of intraspecific 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 interspecific competition by cheatgrass at 15 DAP ($P = 0.004$). However, medusahead reduced cheatgrass growth when N+ was compared to N− as indicated by highly negative competition intensity at 60 and 90 DAP ($P < 0.001$).

Discussion

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 may 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 interspecific 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 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 (Vasquez et al. 2008; Young and Mangold 2008; Blank 2010). These studies have therefore largely overlooked changes a plant may experience when it
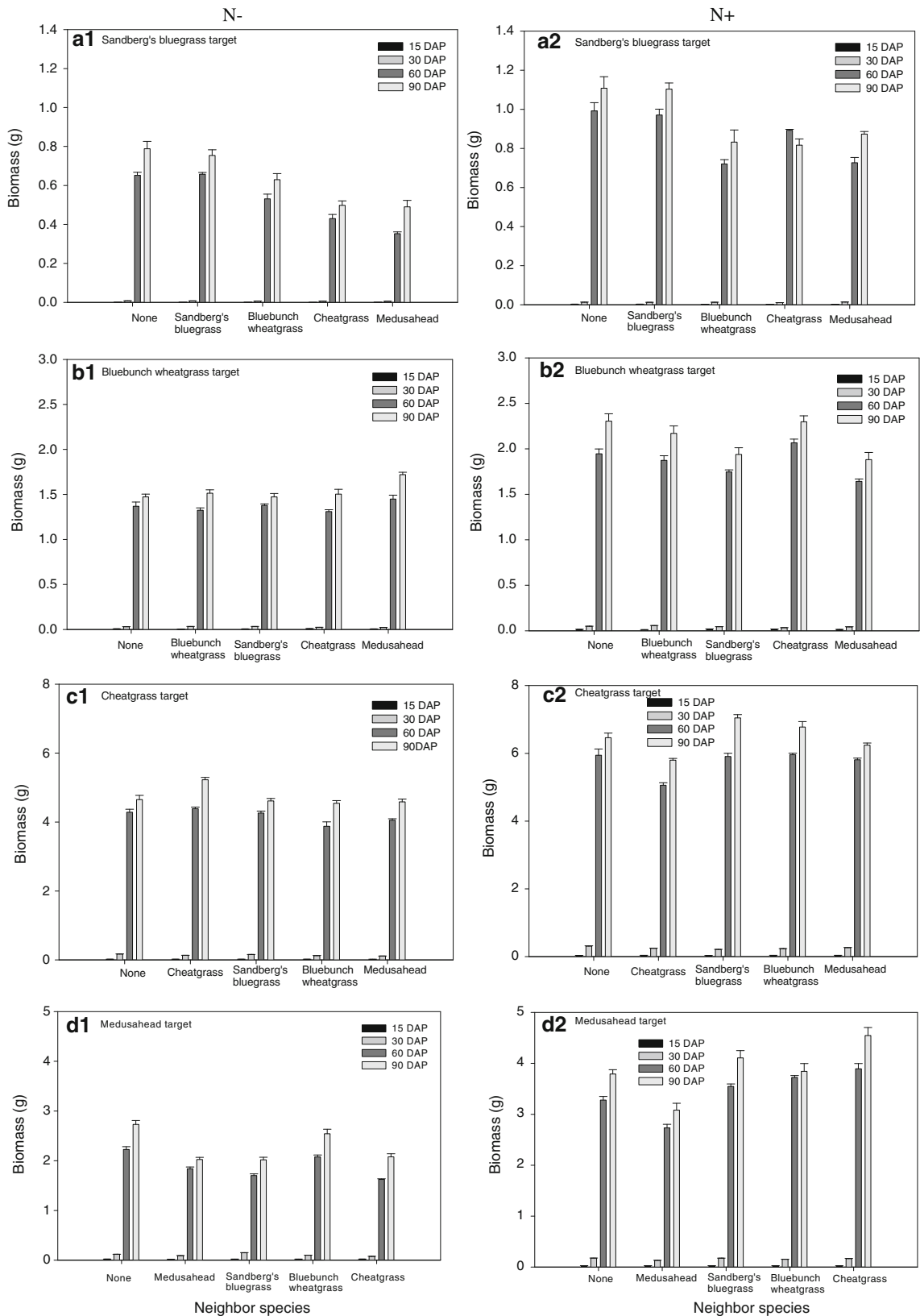
Fig. 2 Effect of time of harvest (DAP) on biomass (g) of different neighbor species on **a** Sandberg's bluegrass, **b** bluebunch wheatgrass, **c** cheatgrass, and **d** medusahead target plants under N− and N+. *Bars* represent mean ± SE ($n = 10$). Biomass means were used to calculate competitive effects (lnRR) presented in Fig. 1

passes through different growth stages (Connell 1983; Schoener 1983; Cameron et al. 2007).

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 did find interspecific 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 Mangold 2008), intraspecific competition was also dominant within native species at the initial harvest (15 DAP) and therefore, 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 intraspecific competition by native species.

We found intraspecific competition to be dominant for invasive species as suggested by previous studies (Vasquez et al. 2008; Young and Mangold 2008; Blank 2010). However, invasive species also experienced interspecific competition by associated plant species, thus, interspecific 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 interspecific 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 interspecific 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 did observe 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 (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 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 (Casper and Jackson 1997; Blank 2010).

Researchers have theorized that native perennial grasses perform better and are more competitive than invasive annual grasses under low N availability (Wedin and Tilman 1990; Wilson and Gerry 1995; Herron et al. 2001). 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 µg mineralized N g^{-1} soil) was still present in our control N treatment, this amount of N may 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 of native plants over invasive plants especially under low N over time.

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 did find 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 in 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 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; Velagala et al. 1997; Seabloom et al. 2003). Our study suggests that limits to seeding rate exist because of intraspecific 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 intraspecific competition among desired native species and maximize interspecific 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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