

Role of Size and Nitrogen in Competition between Annual and Perennial Grasses

L. Noelle Orloff, Jane M. Mangold, and Fabian D. Menalled*

Differing life histories contribute to difficulties establishing perennial grasses on lands dominated by exotic annual grasses. In a greenhouse study, we investigated to what extent allowing the perennial grass bluebunch wheatgrass to emerge before the exotic annual grass downy brome would increase its competitive ability and whether modifying nitrogen (N) would affect competition. We conducted an addition-series factorial experiment. In three cohort treatments, the two species were seeded concurrently or bluebunch wheatgrass was at the two- or four-leaf stage when downy brome was planted. N treatments were low (ambient) or high (N added to maintain 10 mg kg^{-1} [$0.1286 \text{ oz lb}^{-1}$]). Larger bluebunch wheatgrass avoided suppression by downy brome regardless of N. Under concurrent sowing, doubling downy brome density decreased bluebunch wheatgrass biomass by $22.6\% \pm 2.38 \text{ SE}$. In contrast, when bluebunch wheatgrass had a four-leaf size advantage, the same increase in downy brome density decreased bluebunch wheatgrass biomass by $4.14\% \pm 2.31$. Larger bluebunch wheatgrass also suppressed downy brome more effectively, but N enrichment decreased the suppressive ability of bluebunch wheatgrass.

Nomenclature: Bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) Á. Löve; downy brome, *Bromus tectorum* L.

Key words: Addition series design, exotic annual grass, priority effects, revegetation.

Downy brome (*Bromus tectorum* L.) invasion across arid and semiarid rangelands of the western United States has been associated with loss of sagebrush–steppe habitat, altered fire regimes, species shifts, and widespread biotic impoverishment (D’Antonio and Vitousek 1992; Knapp 1996; Mack 2011). This species can become dominant on rangelands following a disturbance, sometimes forming near monocultures that may be an alternate stable state for the plant community, preventing recolonization by native species (Chambers et al. 2007; Humphrey and Schupp 2004; Mack 2011). The importance of revegetating rangelands dominated by downy brome with perennial species as an approach to restoring desired plant communities has long been recognized (Allen 1995; Davies et al. 2010; Hull and Stewart 1948; Whitson and Koch 1998), although these efforts are often unsuccessful (Mack 2011). Competition between established downy brome plants and perennial species seedlings could be one factor in revegetation failures (Harris 1967; Hull and Stewart 1948; James et al. 2011; but see James and Svejcar 2010).

Size differences between seedlings cause reduced growth rates for the smaller competitor and may allow the larger

individuals to remove a disproportionate amount of resources, with implications for plant community assembly (Connolly and Wayne 1996; Firbank and Watkinson 1990; Freckleton and Watkinson 2001). Life history differences between downy brome and perennial grasses could cause the size disparities that may hinder the success of revegetation programs, with downy brome seedlings gaining a size advantage over perennial seedlings through their earlier emergence and higher growth rates (Harris 1967; Harris and Wilson 1970; Humphrey and Schupp 2004). Perennial grasses are usually sown in the fall, may germinate in either fall or spring, and generally emerge the spring following planting (James et al. 2012). In contrast, most downy brome plants follow a winter annual life history, (Harris 1967; Mack and Pyke 1983) and have an established root system by spring that allows them to initiate growth earlier than do perennial grass seedlings (Aguirre and Johnson 1991; Harris and Wilson 1970). This initial advantage is further compounded by the higher relative growth rate of downy brome in comparison with that of perennial grasses (Arredondo et al. 1998; Mangla et al. 2010).

Competitive ability of a species also varies with resource availability and could affect plant community composition after revegetation activities (Berendse and Elberse 1990; Firn et al. 2010). Nutrient-acquisition patterns associated with annual vs. perennial life histories have been described as acquisitive for the former and conservative for the latter,

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* Research Assistant, Assistant Professor, and Associate Professor, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59715. Corresponding author’s E-mail: noelleorloff@gmail.com

Management Implications

This study demonstrated the importance of both order of emergence and nitrogen (N) availability in the competitive relationship between bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Á. Löve] and downy brome (*Bromus tectorum* L.). First, we found that larger bluebunch wheatgrass seedlings avoided suppression by downy brome more effectively and that they did so regardless of N availability. However, although larger bluebunch wheatgrass also suppressed downy brome more effectively, N enrichment decreased the ability of bluebunch wheatgrass to suppress downy brome. Our results suggest that order of emergence for desired perennial vs. exotic annual grasses may be an important aspect of revegetation planning and that avoiding conditions that lead to N increases, such as soil disturbance, could allow perennial grasses to better suppress downy brome. To establish an initial size difference that favors seeded species, managers could modify the standard timing of revegetation practices to ensure that perennial species receive a sufficient head start. Another way to promote an initial size difference would be to use transplants or plugs to restore critical sites.

and traits associated with these patterns may help explain relative competitive ability (Grime 1977; Roumet et al. 2006). For example, high leaf N productivity contributed to faster uptake and growth of exotic annual grasses downy brome and medusahead [*Taeniatherum caput-medusae* (L.) Nevski] compared with native, perennial grasses bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] and squirreltail [*Elymus elymoides* (Rafin) Swezey] (James 2008b). Further, annual species, such as downy brome, respond to increases in soil N by increasing uptake, resulting in higher growth rates and seed production, whereas slower-growing, perennial seedlings have less plasticity in nutrient uptake (Chapin 1980; Crawley 1997; Leffler et al. 2011). Therefore, downy brome may be more effective at quickly using available nutrients than are native, perennial grasses, making downy brome competitive in both high- and low-N environments (James et al. 2011; Monaco et al. 2003; Vasquez et al. 2008; Wilson et al. 1966).

Although the importance of relative emergence time in the competitive relationship between downy brome and perennial seedlings has been identified (Aguirre and Johnson 1991; Harris and Wilson 1970), the utility of giving desired plants an initial size advantage has not been fully explored. For example, little is known about the importance of time of emergence, stand density, and resource availability in influencing the competitive relationship between downy brome and perennial grass seedlings. To fill this knowledge gap, we conducted a greenhouse study to investigate the effect of relative size, soil N availability, and plant density on the competitive interactions between downy brome and bluebunch wheatgrass, with the intent of improving rangeland revegetation practices. Bluebunch wheatgrass was chosen for this study

because it is one of the most widely distributed native bunchgrasses on rangelands in the northern Rocky Mountain region, and it is a valuable forage for livestock and wildlife (Zlatnik 1999). We predicted that giving bluebunch wheatgrass an initial size advantage over downy brome would increase its relative competitive ability (i.e., its ability to suppress downy brome and to avoid suppression by downy brome). We further predicted that N enrichment would reduce the ability of bluebunch wheatgrass to suppress downy brome.

Materials and Methods

Experimental Design. The study was conducted in a light- and temperature-controlled greenhouse (average 28/17 C [82/63 F] day/night temperatures) at the Plant Growth Center, Montana State University (MSU), Bozeman, MT. Supplemental light was applied as needed to achieve 16-h days. The study was conducted twice with trial one completed between August and November 2009 and trial two conducted from March to June 2010. Each trial followed an addition-series factorial design with four density treatments for each species, three bluebunch wheatgrass size-cohort treatments, and two N-level treatments. Each of the resulting 96 treatment combinations were replicated four times in a randomized complete-block arrangement for a total of 384 pots (experimental units) per trial.

Densities of bluebunch wheatgrass were 0, 2, 6, 12 plants pot^{-1} (0, 111, 333, and 667 plants m^{-2} [0, 10, 31, and 62 plants ft^{-2}]) and densities of downy brome were 0, 5, 10, 20 plants pot^{-1} (0, 278, 556, and 1112 plants m^{-2}). Downy brome densities used in the experiment were based on observed densities at Buffalo Jump State Park, approximately 37 km (23 mi) west of Bozeman. Bluebunch wheatgrass densities were based on recommendations for rangeland drill-seeding rates (Sheley et al. 2008). Cohort treatments were applied by introducing downy brome seeds into the pots with three different cohorts of bluebunch wheatgrass; both species were planted together as seeds (0L cohort), or downy brome seeds were planted when most plants in bluebunch wheatgrass cohorts had two leaves (2L cohort) or four leaves (4L cohort). Nitrogen treatment levels were low (1 mg $\text{NO}_3^- \text{kg}^{-1}$ [0.01286 oz $\text{NO}_3^- \text{lb}^{-1}$], no N added) or high (N added to maintain 10 mg $\text{NO}_3^- \text{kg}^{-1}$). To complement the addition-series experiment, individual plants of both species (trial 1, $n = 24$; trial 2, $n = 48$) were grown to determine response of both species to N treatments (trials 1 and 2) and bluebunch wheatgrass cohort response to N treatments (trial 2) in the absence of competition.

A steam-sterilized soil mixture (50% washed concrete sand, 25% mineral soil, 25% sphagnum peat moss) was placed in 7.9-L (2-gal) pots (15.2-cm diam by 43.2-cm

depth [6-in diam by 17-in depth]). Nitrate was leached from the soil by adding 28.5 L of water to each pot. After leaching, soil samples were analyzed for nitrate (composite from 10 pots, one sample per replicate; AgVise Laboratories, Northwood, ND), and average nitrate was 1 mg kg^{-1} . The N treatment was applied 7 d after planting the 0L bluebunch wheatgrass cohort and downy brome. Ammonium sulfate prills (21–0–0, N–P–K; 0.3 g) were dissolved in 1.5 L of water and applied to each high-N pot. At the same time, 1.5 L of water was applied to each low-N pot to control for the effect of additional water. No supplemental nutrients were added to low-N pots. The N treatment ($10 \text{ mg NO}_3^- \text{ kg}^{-1}$) was applied three times at 21-d intervals, for a total N application rate of 31.5 mg kg^{-1} during the course of the study. This value falls within the range of average annual net N mineralization in the Great Plains (Burke et al. 1997) and is also comparable to rates used in other competition experiments (e.g., Abraham et al. 2009; Lowe et al. 2002; Monaco et al. 2003; Paschke et al. 2000).

Bluebunch wheatgrass ‘Goldar’ variety seeds were obtained from the USDA Natural Resources Conservation Service, Aberdeen Plant Materials Center (Aberdeen, ID), and downy brome seeds were hand collected in 2008 at the MSU Red Bluff Research Ranch near Norris, MT. Bluebunch wheatgrass 2L and 4L cohort treatments were planted at 2 and 4 wk, respectively, before planting the 0L cohort treatment. Seeds of both species were sprinkled evenly on the soil surface and covered with 0.5 cm of soil. Seedlings of both species were thinned or transplanted at the one-leaf stage as needed to approximate target densities. Water was applied with an automated drip-irrigation system. To allow each cohort to establish, pots were watered at 0.5 L pot^{-1} daily for 35 d to keep the soil near field capacity. For the remainder of the experiment, plants were watered twice a week at a rate of 0.5 L pot^{-1} . The plants grew for 74 d after downy brome and 0L bluebunch wheatgrass were planted. At that time, aboveground biomass of each species was harvested from each pot to 5 mm (0.2 in) above the soil surface. Final density for both species was recorded at the time of harvest. Additionally, belowground biomass of single-plant pots was obtained by washing roots. All biomass was dried to constant mass and weighed.

Statistical Analysis. Analyses were conducted using R software (R Foundation for Statistical Computing, Vienna, Austria) including the nlme and gmodels packages (Pinheiro et al. 2011; R Development Core Team 2008; Warnes et al. 2007). To determine differences in how downy brome and bluebunch wheatgrass responded to N enrichment in the absence of competition (single-plant pots), we calculated the proportional change in single plant shoot and root biomass in response to N using natural log-

transformed response ratios ($\ln RR = \ln(\text{biomass}_{\text{highN}} / \text{biomass}_{\text{lowN}})$) (Hedges et al. 1999; James 2008a). Higher positive $\ln RR$ values indicate more growth in the high-N compared with low-N treatments. Pots were randomly paired by N (bluebunch wheatgrass and downy brome) and cohort (bluebunch wheatgrass only), and the $\ln RR$ for shoot and root biomass was calculated for each pair. To determine whether bluebunch wheatgrass cohorts differed in their response to N, we performed an ANOVA with $\ln RR$ of bluebunch wheatgrass shoot and root mass as the response variables and cohort as the predictor variable (23 pairs). When differences occurred, we performed Tukey’s Honestly Significant Difference (HSD) post hoc tests to compare treatment means. To investigate whether downy brome was more responsive to N than bluebunch wheatgrass, we performed Welch’s two-sample t tests with shoot and root $\ln RR$ as the response variables and species as the predictor (20 pairs).

To assess the effect of relative size, intraspecific and interspecific competition, and N availability on bluebunch wheatgrass and downy brome growth, per capita biomass of each species was modeled using a mixed-model analysis of covariance, following Milliken and Johnson (2002) and Crawley (2007). Fixed categorical variables were bluebunch wheatgrass cohort and N availability, fixed continuous variables were bluebunch wheatgrass and downy brome final densities, and the trial was included as a random variable. We performed natural log transformations of per capita biomass to normalize the distributions and natural log transformations of bluebunch wheatgrass and downy brome densities to linearize the relationships. We fitted full models with all three-way interactions included and simplified them by removing individual parameters based on P values ($\alpha = 0.05$). We then refit them, based on restricted maximum-likelihood estimation (Zuur et al. 2009). We used heteroskedastic models to account for nonconstant variance between N levels (Pinheiro and Bates 2000).

In our analysis, the effect of intraspecific competition was estimated by the regression coefficient associated with the density of one species on itself, whereas the effect of interspecific competition was estimated by the regression coefficient associated with the density of one species on the other (Goldberg and Landa 1991). Regression surface equations for each treatment combination are of the following form:

$$\log(\text{mass}) = \beta_0 + \beta_{DB} \log(DBn) + \beta_{BB} \log(BBn) \quad [1]$$

where mass is the average biomass of the target species, DBn is downy brome density, and BBn is bluebunch density. Competition coefficients (β_{DB} and β_{BB}) can be used to calculate the multiplicative change in biomass in response to increasing density of each species. For example, a doubling of downy brome density would be associated

with a multiplicative change in target biomass of $2^{\beta_{DB}}$ or a decrease of $(1 - 2^{\beta_{DB}}) \times 100\%$.

We compared response surfaces associated with the effects of interspecific and intraspecific competition between N and cohort treatment combinations (Milliken and Johnson 2002). To determine whether bluebunch wheatgrass cohort changed intraspecific and interspecific competitive interactions, we tested for interactions between the cohort treatment and the density of each species in models describing each target species. Similarly, to determine whether N enrichment modified intraspecific and interspecific competition, we tested for interactions between N treatment and density of each species. We also tested for three-way interactions among N, cohort, and density of each species to determine whether N modified the effect of cohort on intraspecific and interspecific competition. When interactions occurred, we performed Wald tests to determine whether the differences between competition coefficients were equal to zero ($\alpha = 0.05$) among relevant levels of factors N and cohort (Warnes et al. 2007).

Results

Effects of Resource Availability and Cohort on Individual Plant Biomass. The response of bluebunch wheatgrass shoot biomass to N, as estimated by $\ln RR$ values, differed by cohort (ANOVA, $F = 3.598$, with $df = 2$ and 20 ; $P = 0.046$; Figure 1a). Specifically, bluebunch wheatgrass shoot growth in the 2L cohort was about five times more responsive to N enrichment than was the 4L cohort ($P = 0.050$ from Tukey's HSD test). No differences were detected between the 0L and 2L or 4L cohorts according to post hoc tests (Figure 1a). We failed to detect a difference in $\ln RR$ values for root biomass between the three bluebunch wheatgrass cohorts (ANOVA, $F = 1.651$, with $df = 2$ and 20 ; $P = 0.217$; Figure 1b).

Because bluebunch wheatgrass cohorts differed in their responses to N, we compared only the $\ln RR$ of the 0L bluebunch wheatgrass cohort with downy brome because they were planted concurrently. We did not detect differences in changes in shoot or root biomass production between these two species in response to N (two-sample t tests, $P = 0.700$ and 0.987 , respectively; Figures 1c and 1d). Bluebunch wheatgrass and downy brome shoot mass in the high-N treatment were 1.5 ± 0.52 and 1.2 ± 0.42 times larger than in the low-N treatment, respectively.

Effect of Resource Availability, Cohort, and Competition on Bluebunch Wheatgrass Biomass. As predicted, when bluebunch wheatgrass cohort size increased, it was better able to avoid suppression by downy brome, as reflected by the less-pronounced effect of increasing downy brome density observed in later cohorts compared with

concurrent sowing (Figure 2). Further, N enrichment increased the effect of intraspecific competition for any given cohort, shown qualitatively in Figure 2 as increases in biomass are driven more by bluebunch wheatgrass than by downy brome density (lines are more vertical) in the high-N compared with low-N treatment. However, contrary to the prediction that N enrichment would modify the effect of interspecific competition on bluebunch wheatgrass, our failure to detect a downy brome density by N interaction indicated that N availability did not modify interspecific competition ($P = 0.264$; data not presented).

The relative time of bluebunch wheatgrass and downy brome emergence modified interspecific competition as shown by a downy brome density by cohort interaction ($P < 0.001$; Table 1), with the effect of interspecific competition decreasing when bluebunch wheatgrass had an initial size advantage (Table 2). Further analysis of the effect of interspecific competition among cohort treatments indicated that when both species were planted concurrently (0L cohort), each doubling of downy brome density decreased bluebunch wheatgrass per capita biomass by $22.6\% \pm 2.38$ ($P < 0.001$; Table 2) regardless of N availability. In the 2L and 4L cohort treatments, doubling downy brome density decreased bluebunch wheatgrass per capita biomass by $8.62\% \pm 2.31$ ($P < 0.001$) and $4.14\% \pm 2.31$ ($P = 0.007$), respectively (Table 2), regardless of N availability. We failed to detect a difference between interspecific competition coefficients for the 2L and 4L cohorts (Wald test, $t = 1.55$, $P = 0.121$), suggesting that bluebunch wheatgrass with a two- or four-leaf initial size advantage equally avoided suppression by downy brome.

Bluebunch wheatgrass initial size and N availability also modified the effect of intraspecific competition as shown by a bluebunch wheatgrass density by cohort interaction ($P < 0.001$; Table 1) and a bluebunch wheatgrass density by N interaction ($P < 0.001$; Table 1). Larger bluebunch wheatgrass consistently had the greatest effect on per capita bluebunch wheatgrass biomass. For example, doubling 4L bluebunch wheatgrass density had a $30.7\% \pm 6.31$ larger effect on per capita biomass than it did in the 0L cohort (Wald test, $t = 5.61$; $P = 0.007$) and a $15.9\% \pm 6.58$ larger effect compared with the 2L cohort (Wald test, $t = 2.67$; $P = 0.004$). Further, the effect that bluebunch wheatgrass had on its own biomass increased with N availability; the effect of doubling bluebunch wheatgrass density was $20.4\% \pm 5.20$ larger in the high-N treatment compared with the low-N treatment (Wald test, $t = 4.37$; $P < 0.001$).

Effect of Resource Availability, Cohort, and Competition on Downy Brome Biomass. As predicted, when bluebunch wheatgrass had an initial size advantage, the influence of downy brome density decreased. Following

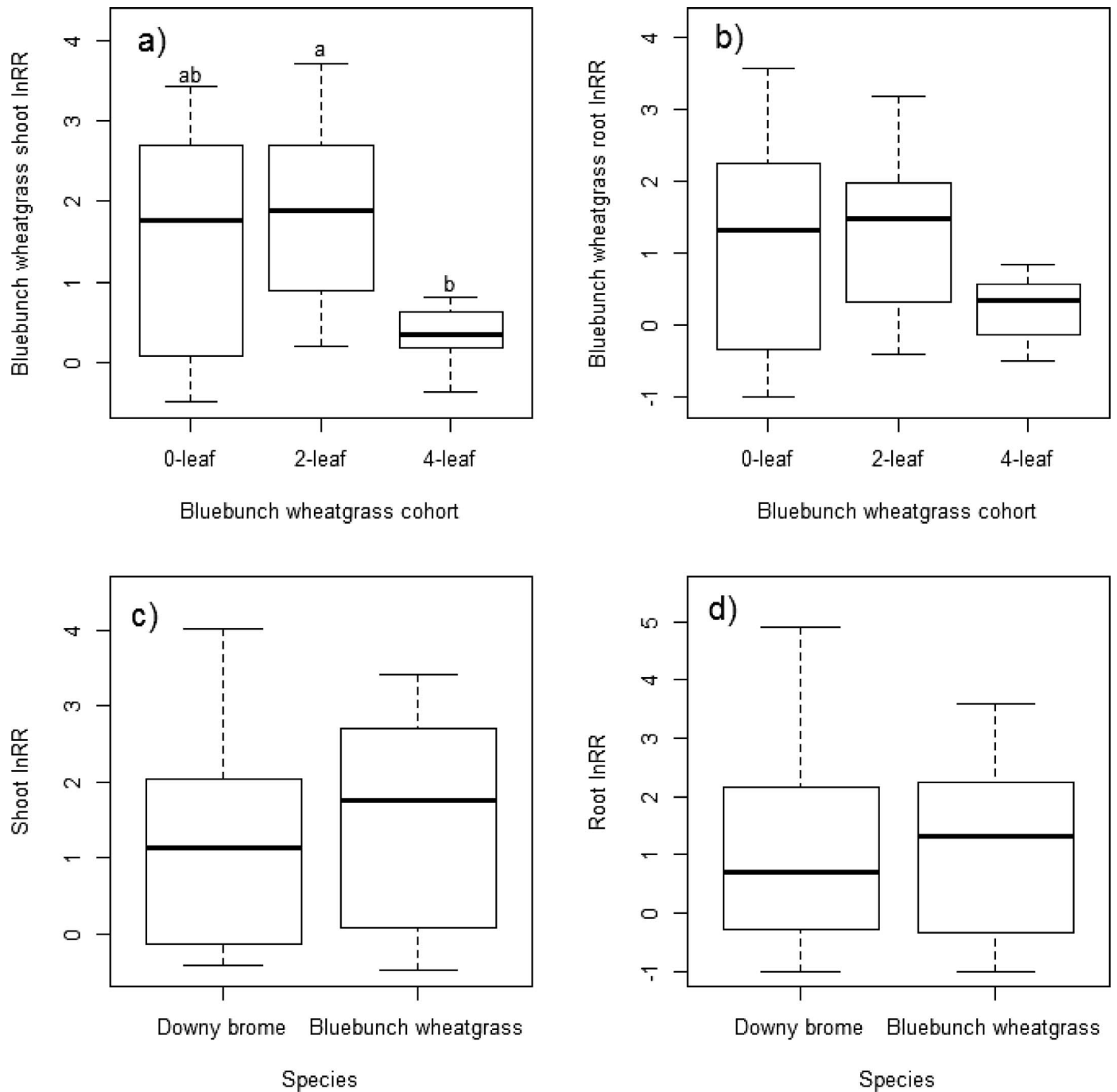


Figure 1. Response ratios were calculated using the natural log-response ratio ($\ln RR$), where $\ln RR = \ln(\text{biomass}_{\text{highN}} / \text{biomass}_{\text{lowN}})$. Higher $\ln RR$ values indicate a greater shoot or root biomass response to nitrate addition. *Cohort* refers to bluebunch wheatgrass cohort treatment; *0-leaf* is concurrent sowing of bluebunch wheatgrass and downy brome, *2-leaf* is downy brome planted into bluebunch wheatgrass cohort at the two-leaf stage, and *4-leaf* is downy brome planted into bluebunch wheatgrass cohort at the four-leaf stage. (a) Letters separate treatment means that are significantly different according to Tukey's Honestly Significant Difference post hoc tests ($\alpha = 0.05$). (b–d) Treatment means did not differ for Figures 1b, 1c, or 1d.

our prediction that downy brome would be more competitive with increased N, the effect of interspecific competition decreased with N enrichment. When downy brome was grown with established bluebunch wheatgrass

plants, the interspecific competition coefficient increased, as shown by a larger effect of increasing bluebunch wheatgrass density in larger cohorts. The effect of interspecific competition was less pronounced in the

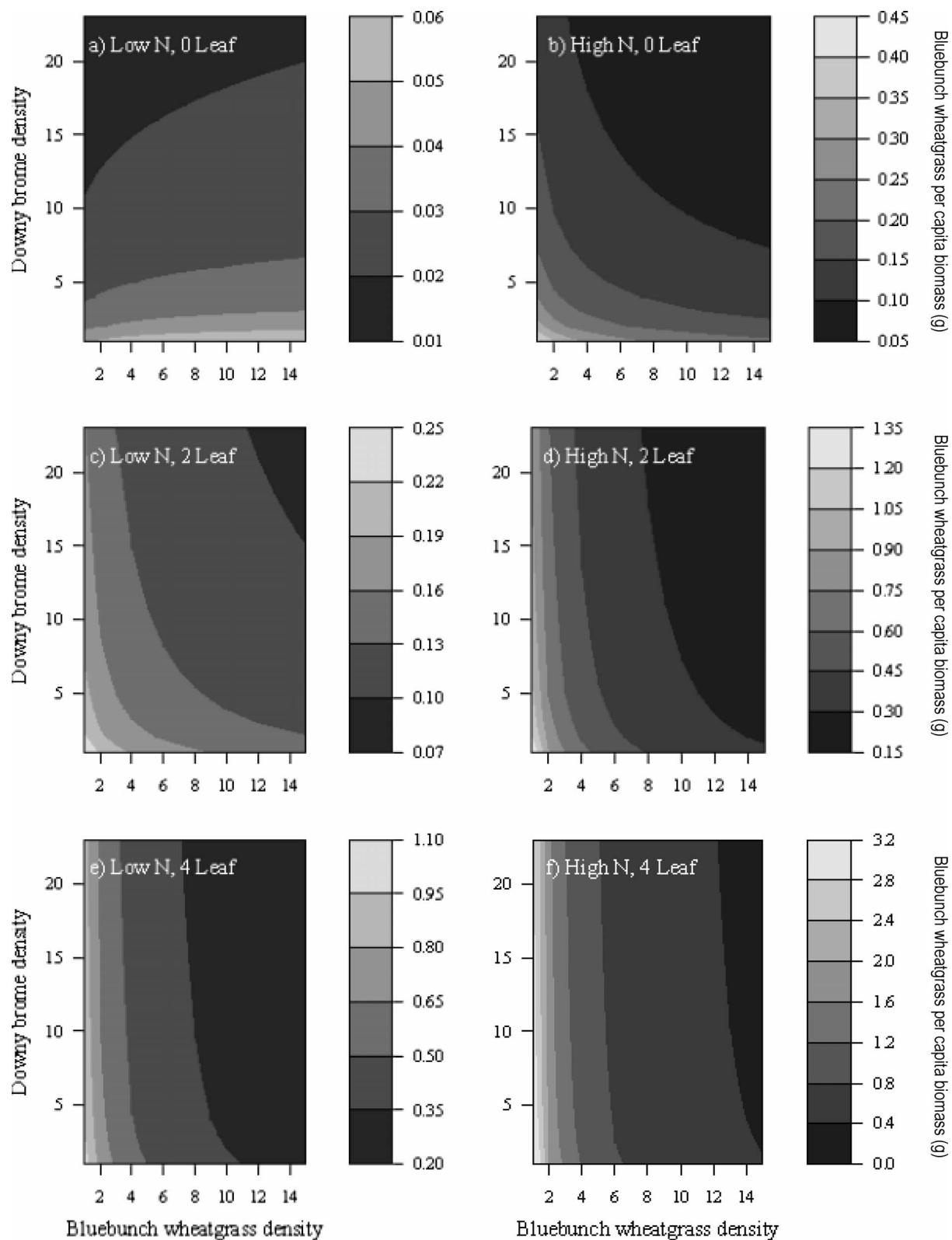


Figure 2. Predicted response of per capita bluebunch wheatgrass biomass (g) to bluebunch wheatgrass and downy brome density under nitrogen (N) by cohort treatment combinations. Low N is $1 \text{ mg kg}^{-1} \text{ N}$; high N is $31.5 \text{ mg kg}^{-1} \text{ N}$. Abbreviations: 0L, concurrent sowing of bluebunch wheatgrass and downy brome; 2L, downy brome planted into bluebunch wheatgrass cohort at the two-leaf stage; 4L, downy brome planted into bluebunch wheatgrass cohort at the four-leaf stage. Grayscale represents per capita biomass (g) of bluebunch wheatgrass. Scale varies among treatment combinations.

Table 1. Results from ANOVA conducted to assess the effect of plant density, N availability, and cohort (fixed effects) on bluebunch wheatgrass per capita biomass (natural log transformed).

Parameter ^a	Numerator df	Denominator df	F value	P value
Intercept	1	630	1284	< 0.001
Bluebunch wheatgrass density	1	630	86.05	< 0.001
Downy brome density	1	630	111	< 0.001
N	1	630	498	< 0.001
Cohort	2	630	667.4	< 0.001
Bluebunch wheatgrass density × N	1	630	17.79	< 0.001
Bluebunch wheatgrass density × cohort	2	630	17.75	< 0.001
Downy brome density × cohort	2	630	22.53	< 0.001
N × cohort	2	630	36.55	< 0.001

^a N refers to nitrogen availability treatment (1 mg kg⁻¹ or 31.5 mg kg⁻¹). *Cohort* refers to bluebunch wheatgrass cohort treatment, where the two species were seeded concurrently, or downy brome seeds were planted into pots with two- or four-leaf cohorts of bluebunch wheatgrass.

high-N treatment (Figure 3). The relative importance of intraspecific and interspecific competition can be qualitatively observed in Figure 3, where more-vertical lines indicate an increase in the relative effect of bluebunch wheatgrass density on downy brome biomass.

Relative time of emergence and N enrichment modified the interspecific competition coefficient as reflected by the bluebunch wheatgrass density by N by cohort interaction (P = 0.003; Table 3). The effect of interspecific competition increased as the bluebunch wheatgrass cohort increased from 0L to 4L. However, with the exception of the 0L cohort, interspecific competition coefficients were smaller in the high-N compared with low-N treatment, indicating less effect of bluebunch wheatgrass on downy

brome in the high-N treatment (Table 4). In the low-N treatment, doubling bluebunch wheatgrass density in the 2L and 4L cohorts decreased downy brome per capita biomass by 30.3% ± 6.51 and 43.0% ± 6.51 (P < 0.001; Table 4), respectively, whereas there was no discernible effect of interspecific competition in the low-N, 0L cohort (P = 0.699; Table 4). In the high-N treatment, doubling bluebunch wheatgrass density in the 0L, 2L, and 4L cohort decreased downy brome biomass by 9.25% ± 2.81, 18.2% ± 2.81, and 28.8% ± 2.81, respectively (P < 0.001; Table 4).

Intraspecific competition was not modified by cohort or N treatments, as indicated by the failure to detect a downy brome density by N or downy brome density by cohort

Table 2. Regression surface-equation coefficients from ANOVA conducted to assess the effect of intraspecific and interspecific competition over different levels of N availability and bluebunch wheatgrass cohort on bluebunch wheatgrass per capita biomass.^a

N × cohort treatment combination ^b	Competition coefficients ^c		
	β ₀ (intercept)	β _{BB} (intraspecific competition)	β _{DB} (interspecific competition)
Low N × zero-leaf	-3.0 (0.18)***	0.083 (0.081)	-0.37 (0.034)***
Low N × two-leaf	-1.4 (0.18)***	-0.20 (0.080)**	-0.13 (0.033)***
Low N × four-leaf	-0.012 (0.17)	-0.44 (0.077)***	-0.061 (0.033)*
High N × zero-leaf	-0.89 (0.18)***	-0.25 (0.077)**	-0.37 (0.034)***
High N × two-leaf	0.29 (0.18)	-0.53 (0.075)***	-0.13 (0.033)***
High N × four-leaf	1.2 (0.17)***	-0.78 (0.073)***	-0.061 (0.033)**

^a df = 630 for all estimates.

^b Low N is 1 mg kg⁻¹ N; high N is 31.5 mg kg⁻¹ N. *Zero-leaf* is concurrent sowing of bluebunch wheatgrass and downy brome, and *two-leaf* and *four-leaf* are downy brome planted into pots with two-leaf and four-leaf bluebunch wheatgrass cohorts, respectively.

^c Intraspecific and interspecific competition refer to the regression coefficients associated with increasing bluebunch wheatgrass and downy brome density, respectively. Competition coefficients can be used to calculate the multiplicative change in biomass in response to increasing density of each species. For example, a doubling of downy brome density would be associated with a multiplicative change in target biomass of 2^{β_{DB}}, or a decrease of (1 - 2^{β_{DB}}) × 100%.

* P < 0.10; ** P < 0.05; *** P < 0.001. P values are for the null hypothesis that the estimate equals zero.

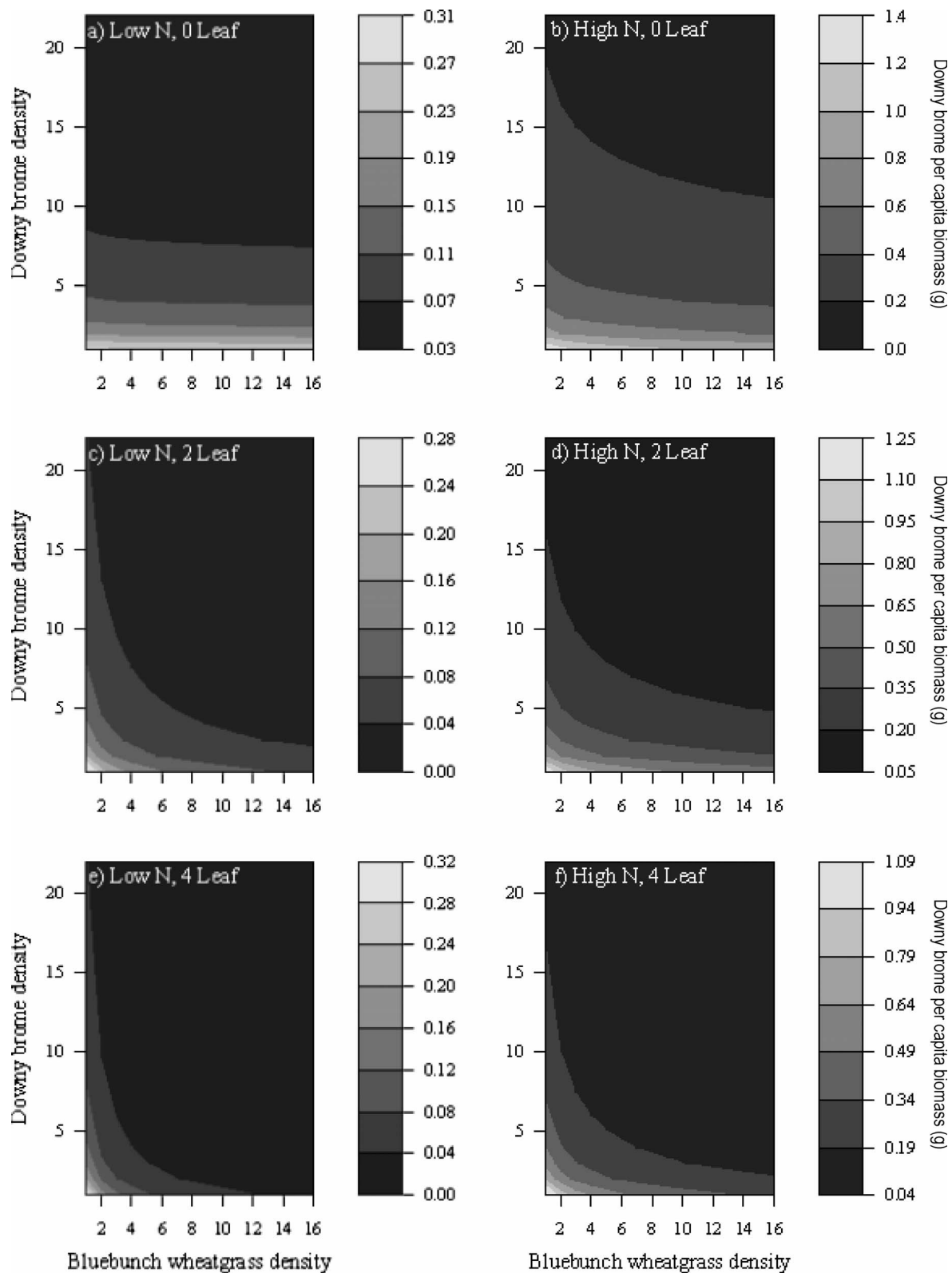


Figure 3. Predicted response of per capita downy brome biomass (g) to bluebunch wheatgrass and downy brome density under nitrogen (N) by cohort treatment combinations. Low N is $1 \text{ mg kg}^{-1} \text{ N}$; high N is $31.5 \text{ mg kg}^{-1} \text{ N}$. Abbreviations: 0L, concurrent sowing of bluebunch wheatgrass and downy brome; 2L, downy brome planted into bluebunch wheatgrass cohort at the two-leaf stage; 4L, downy brome planted into bluebunch wheatgrass cohort at the four-leaf stage. Grayscale represents per capita biomass (g) of bluebunch wheatgrass. Scale varies among treatment combinations.

Table 3. Results from ANOVA conducted to assess the significance of plant density, N availability, and cohort (fixed effects) on downy brome per capita biomass (natural log-transformed).

Parameter ^a	Numerator df	Denominator df	F value	P value
Intercept	1	605	222.4	< 0.001
Bluebunch wheatgrass density	1	605	251.6	< 0.001
Downy brome density	1	605	127.0	< 0.001
N	1	605	891.1	< 0.001
Cohort	2	605	90.22	< 0.001
Bluebunch wheatgrass density × N	1	605	5.836	0.016
Bluebunch wheatgrass density × cohort	2	605	32.99	< 0.001
N × cohort	2	605	3.727	0.025
Bluebunch wheatgrass density × N × cohort	2	605	5.899	0.003

^a N refers to nitrogen availability treatment (1 mg kg⁻¹ or 31.5 mg kg⁻¹). *Cohort* refers to bluebunch wheatgrass cohort treatment, where the two species were seeded concurrently, or downy brome seeds were planted into pots with two- or four-leaf cohorts of bluebunch wheatgrass.

interaction (Table 3). For all treatments, doubling downy brome density decreased per capita biomass by 36.3% ± 2.88 (P < 0.001; Table 4). Additionally, the effect of interspecific competition on downy brome biomass never exceeded that of intraspecific competition, even in the 4L cohort treatment. According to post hoc Wald tests, downy brome density had a larger effect on its own biomass than bluebunch wheatgrass did in all treatments except low-N 2L and 4L, where there was no statistical difference between the intraspecific and interspecific competition coefficients ($t = 1.32$ and -1.59 ; P = 0.186 and 0.113, respectively).

Discussion

Priority effects arising from life history differences between desired and exotic grasses may affect seedling establishment of desired species, and N availability may modify that effect (Abraham et al. 2009; Corbin and D'Antonio 2004; Firn et al. 2010; James et al. 2011; Stevens and Fehmi 2011). In this study, relative initial size played a considerable role in the competitive relationship between bluebunch wheatgrass and downy brome. N availability was also important in early stages of growth, but not in the way we predicted. In accordance with our first

Table 4. Regression surface equation coefficients from ANOVA conducted to assess the effect of intraspecific and interspecific competition, N availability, and cohort on downy brome per capita biomass (natural log transformed).^a

N × cohort treatment combination ^b	β_0 (Intercept)	Competition coefficients ^c	
		β_{DB} (intraspecific competition)	β_{BB} (interspecific competition)
Low N × zero-leaf	-1.3 ± 0.20***	-0.65 ± 0.041***	-0.032 ± 0.082
Low N × two-leaf	-1.2 ± 0.23***	-0.65 ± 0.041***	-0.52 ± 0.091***
Low N × four-leaf	-1.2 ± 0.23***	-0.65 ± 0.041***	-0.81 ± 0.091***
High N × zero-leaf	-0.31 ± 0.18*	-0.65 ± 0.041***	-0.14 ± 0.040***
High N × two-leaf	-0.20 ± 0.19	-0.65 ± 0.041***	-0.29 ± 0.040***
High N × four-leaf	-0.18 ± 0.19	-0.65 ± 0.041***	-0.49 ± 0.040***

^a df = 608 for all estimates.

^b Low N is 1 mg kg⁻¹ N; high N is 31.5 mg kg⁻¹ N. *Zero-leaf* is concurrent sowing of bluebunch wheatgrass and downy brome, and *two-leaf* and *four-leaf* are downy brome planted into pots with two-leaf and four-leaf bluebunch wheatgrass cohorts, respectively.

^c Intraspecific and interspecific competition refer to the regression coefficients associated with increasing bluebunch wheatgrass and downy brome density, respectively. Competition coefficients can be used to calculate the multiplicative change in biomass in response to increasing density of each species. For example, a doubling of downy brome density would be associated with a multiplicative change in target biomass of $2^{\beta_{DB}}$, or a decrease of $(1 - 2^{\beta_{DB}}) \times 100\%$.

* P < 0.10; ** P < 0.05; *** P < 0.001. P values are for the null hypothesis that the estimate equals zero.

prediction, we found that giving bluebunch wheatgrass an initial size advantage over downy brome increased its ability to both suppress downy brome and to avoid being suppressed by downy brome. However, we found mixed evidence to support our second prediction that N enrichment would reduce the ability of bluebunch wheatgrass to compete with downy brome. N enrichment generally decreased the ability of bluebunch wheatgrass to suppress downy brome. However, in contrast with our predictions, N enrichment did not modify the effect of downy brome on bluebunch wheatgrass.

As predicted, bluebunch wheatgrass that established before downy brome emergence suppressed downy brome more effectively, with the competitive effect of bluebunch wheatgrass increasing with cohort age. We observed this pattern over both N treatments. In accordance, Firn et al. (2010) determined that the native Australian perennial grasses pitted bluegrass [*Bothriochloa decipiens* (Hack.) C.E. Hubb.] and kangaroo grass (*Themeda triandra* Forsk.) more-effectively suppressed weeping lovegrass [*Eragrostis curvula* (Schrader) Nees], an exotic, perennial grass, when the native grasses were sown 21 d before the exotic one. We also observed that increasing bluebunch wheatgrass initial size allowed it to avoid suppression by downy brome more effectively. This result is consistent with Abraham et al. (2009), where productivity of the perennial grasses purple needlegrass [*Nassella pulchra* (Hitc.) Barkworth] and red fescue (*Festuca rubra* L.) strongly increased if they emerged 14 d before ripgut brome (*Bromus diandrus* Roth), an exotic, winter annual grass. Further, Stevens and Fehmi (2011) observed that when the native, perennial grass Arizona cottontop [*Digitaria californica* (Benth.) Henr.] had a 21-d advantage in emergence time over the exotic, perennial buffelgrass [*Pennisetum ciliare* (L.) Link], the biomass of the native greatly increased compared with concurrent sowing. Our results, along with results of similar studies, suggest that allowing perennial grasses to attain a certain size before annual grasses emerge allows them to avoid suppression and may increase desired species establishment in the field.

There is strong evidence that first principles about relative time of emergence gained from our study and recent greenhouse studies (Abraham et al. 2009; Firn et al. 2010; Stevens and Fehmi 2011) could be extended to a field setting with the aim of improving seeded species establishment. In a field experiment conducted in California, the long-term importance of initial size was demonstrated, with 3-mo-old transplants of Oregon bentgrass (*Agrostis oregonensis* Vasey), red fescue, and purple needlegrass surviving their first season and effectively suppressing the exotic, annual grasses ripgut brome, rattail fescue [*Vulpia myuros* (L.) K.C. Gmel.], and slender oat (*Avena barbata* Pott ex Link.) during the next 3 yr (Corbin and D'Antonio 2004).

The ability of downy brome to suppress bluebunch wheatgrass growth did not change with N availability. This was surprising because we expected N enrichment to increase the competitive ability of downy brome compared with that of bluebunch wheatgrass. However, this result corresponds with our single-plant analysis, where N enrichment increased productivity of both species by a similar magnitude. Our findings were also consistent with James (2008a) where nutrient stress did not result in a reduction in downy brome growth compared with bluebunch wheatgrass and the native perennial bunchgrass squirreltail. Further, in a meta-analysis of addition-series plant-competition experiments between perennial seedlings and annual grasses, James et al. (2011) found that the competitive effects of annual grasses on perennials did not change with N enrichment, in part, because annual grasses maintained higher growth rates than did perennial grasses, regardless of N availability. The authors concluded that if perennial seedlings can germinate and establish successfully, then N enrichment may increase desired seedling performance, even with annual grasses present. Our study provides further evidence for this conclusion.

Although N enrichment did not change the effect of downy brome on bluebunch wheatgrass, we did observe an interactive effect of bluebunch wheatgrass cohort and N availability on downy brome. When the two species were sown concurrently, high N allowed bluebunch wheatgrass to suppress downy brome more effectively. However, when bluebunch wheatgrass had an initial size advantage, it suppressed downy brome less effectively with N enrichment. Similar to conclusions drawn by James et al. (2011), our results suggest that although N enrichment may not decrease desired species establishment in the presence of downy brome, it could lead to increased fitness of downy brome and larger populations in subsequent growing seasons. In accordance, Wilson (1966) showed that heavy fertilization of mixed downy brome and bluebunch wheatgrass communities increased downy brome yields by 400 to 600%, while decreasing bluebunch wheatgrass yields by 50%. Further, Paschke (2000) determined that adding N to an old-field system increased the relative abundance of annual weedy plants, while experimentally decreasing N increased the abundance of perennial species.

Site preparation techniques designed to decrease available soil resources in rangeland systems, such as sucrose application or nurse-crop plantings, have been proposed to decrease competitive ability of invasive species and increase perennial species establishment (Firn et al. 2010; Mangold and Sheley 2008; Perry et al. 2010). Similar to James (2008a), Abraham (2009), and James et al. (2011), our results suggest that in early stages of growth, reducing soil N may not decrease exotic, annual grass effect on seeded, perennial grasses. However, our results also suggest that reducing soil N may allow seeded, perennial grasses to

better suppress exotic annual grass. Further, based on research conducted in higher-N environments (Wilson et al. 1966), revegetation of Conservation Reserve Program or former agricultural land dominated by downy brome may benefit from practices designed to decrease N availability.

Our results complement growing evidence that developing management practices that allow perennial species to emerge first and attain a size advantage over exotic, annual grasses may improve seedling establishment in rangeland revegetation projects (Abraham et al. 2009; Corbin and D'Antonio 2004; Firn et al. 2010; Stevens and Fehmi 2011). Relative initial size of competing plants can have long-lasting effects in a plant community, with larger individuals extracting a disproportionate amount of resources and suppressing smaller neighbors (Connolly and Wayne 1996; Freckleton and Watkinson 2001; Ross and Harper 1972). If competition for resources is a driving factor in revegetation failures, the long-term consequences of these size asymmetries could inhibit perennial species establishment on sites dominated by downy brome. Management actions that negate effects arising from order of emergence may improve establishment of perennial species.

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Literature Cited

- Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecol.* 201:445–456.
- Aguirre, L. and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *J. Range Manag.* 44:347–354.
- Allen, E. B. 1995. Restoration ecology: limits and possibilities in arid and semiarid lands. Pages 7–15 in *Proceedings of the Wildland shrub and arid land restoration symposium*. Las Vegas, NV: Intermountain Research Station.
- Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *J. Range Manag.* 51:584–589.
- Berendse, F. and W. T. Elberse. 1990. Competition and nutrient availability in heathland and grassland ecosystems. Pages 93–116 in J. Grace and D. Tilman, eds. *Perspectives on Plant Competition*. San Diego, CA: Academic.
- Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology* 78:1330–1340.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes great basin sagebrush ecosystems invulnerable by *Bromus tectorum*? *Ecol. Monogr.* 77:117–145.
- Chapin, F. S. III. 1980. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11:233–260.
- Connolly, J. and P. Wayne. 1996. Asymmetric competition between plant species. *Oecologia* 108:311–320.
- Corbin, J. D. and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85:1273–1283.
- Crawley, M. J. 1997. Life history and environment. Pages 73–131 in M. J. Crawley, ed. *Plant Ecology*. Malden, MA: Blackwell.
- Crawley, M. J. 2007. *The R Book*. West Sussex, England: J. Wiley. 872 p.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23:63–87.
- Davies, K. W., A. M. Nafus, and R. L. Sheley. 2010. Non-native competitive perennial grass impedes the spread of an invasive annual grass. *Biol. Invasions* 12:3187–3194.
- Firbank, L. G. and A. R. Watkinson. 1990. On the effects of competition: from monocultures to mixtures. Pages 165–192 in J. Grace and D. Tilman, eds. *Perspectives on Plant Competition*. San Diego, CA: Academic.
- Firn, J., A. MacDougall, S. Schmidt, and Y. M. Buckley. 2010. Early emergence and resource availability can competitively favor natives over a functionally similar invader. *Oecologia* 163:775–784.
- Freckleton, R. P. and A. R. Watkinson. 2001. Asymmetric competition between plant species. *Funct. Ecol.* 15:615–623.
- Goldberg, D. E. and K. Landa. 1991. Competitive effect and response—hierarchies and correlated traits in the early stages of competition. *J. Ecol.* 79:1013–1030.
- Grime, J. P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111:1169–1194.
- Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecol. Monogr.* 37:89–111.
- Harris, G. A. and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* 51:530–534.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156.
- Hull, A. C. and G. Stewart. 1948. Replacing cheatgrass by reseeding with perennial grass on southern Idaho ranges. *J. Am. Soc. Agron.* 40:694–703.
- Humphrey, L. D. and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *J. Arid Environ.* 58:405–422.
- James, J. J. 2008a. Effect of soil nitrogen stress on the relative growth rate of annual and perennial grasses in the Intermountain West. *Plant Soil* 310:201–210.
- James, J. J. 2008b. Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. *J. Arid Environ.* 72:1775–1784.
- James, J. J., R. E. Drenovsky, T. A. Monaco, and M. J. Rinella. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecol. Appl.* 21:490–502.
- James, J. J., M. J. Rinella, and T. Svejcar. 2012. Grass seedling demography and sagebrush steppe restoration. *Rangeland Ecol. Manag.* 65:409–417.
- James, J. J. and T. Svejcar. 2010. Limitations to postfire seedling establishment: the role of seeding technology, water availability, and invasive plant abundance. *Rangeland Ecol. Manag.* 63:491–495.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert—History, persistence, and influences to human activities. *Global Environ. Chang.* 6:37–52.

- Leffler, A. J., T. A. Monaco, and J. J. James. 2011. Nitrogen acquisition by annual and perennial grass seedlings: testing the roles of performance and plasticity to explain plant invasion. *Plant Ecol.* 212:1601–1611.
- Lowe, P. N., W. K. Lauenroth, and I. C. Burke. 2002. Effects of nitrogen availability on the growth of native grasses and exotic weeds. *J. Range Manag.* 55:94–98.
- Mack, R. N. 2011. Fifty years of ‘waging war on cheatgrass’, research advances, while meaningful control languishes. Pages 253–265 in D. M. Richardson, ed. *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. Oxford, UK: Wiley-Blackwell.
- Mack, R. N. and D. A. Pyke. 1983. The demography of *Bromus tectorum*—variation in time and space. *J. Ecol.* 71:69–93.
- Mangla, S., R. L. Sheley, and J. J. James. 2010. Field growth comparisons of invasive alien annual and native perennial grasses in monocultures. *J. Arid Environ.* 75:206–210.
- Mangold, J. M. and R. L. Sheley. 2008. Controlling performance of bluebunch wheatgrass and spotted knapweed using nitrogen and sucrose amendments. *West. N. Am. Nat.* 68:129–137.
- Milliken, G. A. and D. E. Johnson. 2002. *Analysis of Messy Data. Volume 3: Analysis of Covariance*. Boca Raton, FL: Chapman and Hall. 605 p.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *J. Range Manag.* 56:282–290.
- Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144–158.
- Perry, L. G., D. M. Blumenthal, T. A. Monaco, M. W. Paschke, and E. F. Redente. 2010. Immobilizing nitrogen to control plant invasion. *Oecologia* 163:13–24.
- Pinheiro, J. C. and D. M. Bates. 2000. *Mixed effects models in S and S-Plus*. New York: Springer. 528 p.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, the R Development Core Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–101. Vienna, Austria: R Development Core Team.
- R Development Core Team. 2008. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Ross, M. A. and J. L. Harper. 1972. Occupation of biological space during seedling establishment. *J. Ecol.* 60:77–88.
- Roumet, C., C. Urcelay, and S. Diaz. 2006. Suites of root traits differ between annual and perennial species growing in the field. *New Phytol.* 170:357–368.
- Stevens, J. M. and J. S. Fehmi. 2011. Early establishment of a native grass reduces the competitive effect of a non-native grass. *Restor. Ecol.* 19:399–406.
- Sheley, R., J. Mangold, K. Goodwin, and J. Marks. 2008. *Revegetation guidelines for the Great Basin: considering invasive weeds*. Washington, DC: USDA, Agricultural Research Service. 52 p.
- Vasquez, E., R. Sheley, and T. Svejcar. 2008. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Sci. Manag.* 1:287–295.
- Warnes, G. R., B. Bolker, T. Lumley, and R. C. Johnson. 2007. gmodels: Various R programming tools for model fitting. R package version 2.14.1. Vienna, Austria: R Development Team.
- Whitson, T. D. and D. W. Koch. 1998. Control of downy brome (*Bromus tectorum*) with herbicides and perennial grass competition. *Weed Technol.* 12:391–396.
- Wilson, A. M., G. A. Harris, and D. H. Gates. 1966. Fertilization of mixed cheatgrass–bluebunch wheatgrass stands. *J. Range Manag.* 19: 134–137.
- Zlatnik, E. 1999. *Pseudoroegneria spicata*. <http://www.fs.fed.us/database/feis/>. Accessed May 12, 2011.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. New York: Springer. 574 p.

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