

# Nitrogen Enhances the Competitive Ability of Cheatgrass (*Bromus tectorum*) Relative to Native Grasses

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Invasion by cheatgrass and the associated high fire frequency can displace native plant communities from a perennial to an annual grass driven system. Our overall objective of this study was to determine the potential to favor desired native perennial bunchgrasses over annual grasses by altering plant available mineral nitrogen (N). In the first study, we grew cheatgrass and three native bunch grasses (native grasses were combined in equal proportions) in an addition series experimental design and applied one of three N treatments (0, 137, and 280 mg N/kg soil). Regression models were used to derive the effects of intra- and interspecific competition on individual plant yield of cheatgrass and the native bunch grasses (combined). In our second study, we compared the absolute growth rate of the four plant species grown in isolation in a randomized complete block design for 109 days under the same soil N treatments as the competition study. Predicted mean average weight of isolated individuals increased with increasing soil N concentrations for both cheatgrass and the three native perennials ( $P < 0.05$ ). Biomass of cheatgrass and its competitive ability increased with increasing soil N concentrations ( $P < 0.0001$ ) compared to the combined native bunchgrasses. However, the greatest resource partitioning occurred at the 137 mg N/kg soil N treatment compared to the 0 (control) and 280 mg N/kg soil treatments, suggesting there may be a level of N that minimizes competition. In the second study, the absolute growth of cheatgrass grown in isolation also increased with increasing N levels ( $P = 0.0297$ ). Results and ecological implications of this study suggest that increasing soil N leads to greater competitive ability of cheatgrass, and that it may be possible to favor desired plant communities by modifying soil nutrient levels.

**Nomenclature:** Bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) A. Love PSSP6; Idaho fescue, *Festuca idahoensis* Elmer FEID; needle and thread, *Hesperostipa comata* (Trin. and Rupr.) Barkworth HECO26; cheatgrass, *Bromus tectorum* L BRTE.

**Key words:** Invasive plants, plant available nitrogen, competition, interference, cheatgrass.

Each year billions of dollars are spent in the United States to control invasive plant species (Westbrooks 1998; Pimentel et al. 2005). One of the most expansive invasions is the establishment and dominance of cheatgrass (*Bromus tectorum* L.) into arid and semiarid rangelands of the western U.S. sagebrush (*Artemisia* L.) steppe (Bradley and Mustard 2006; D'Antonio and Vitousek 1992; Mack 1981; Young and Allen 1997). Cheatgrass is a cool season  $C_3$  annual grass that has infested over 22 million ha (54 million ac) in the western United States (Belnap et al. 2005; Duncan et al. 2004). The introduction of cheatgrass

has increased fire frequencies in this system from 30 to 110 years to 3 to 5 years (Chambers et al. 2007), with an estimated cost of controlling cheatgrass-fueled fires at about \$20 million/yr (Knapp 1996). The increase in fire frequency has not only reduced rangeland productivity, but has also caused major changes in species richness, vegetation composition, structure, wildlife habitat, and ecosystem processes (Harrison et al. 2003; Knapp 1996; Pyke et al. 2003).

Although the invasion success of cheatgrass may be dependent upon temperature at higher elevations and soil moisture availability at lower elevations (Chambers et al. 2007), previous studies suggest invasive annuals, such as cheatgrass, tend to dominate where disturbance creates high nutrient environments, particularly with respect to soil nitrogen (N) (Bidwell et al. 2006; Blumenthal 2006; Daehler 2003). The relative ability of individual plants to

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## Interpretive Summary

In native plant communities, nutrient availability to plants tends to decrease as succession proceeds in arid and semiarid systems. Invasion by exotic plant species often follows changes in soil processes, particularly nitrogen (N) and carbon (C) cycling. We conducted two studies simultaneously that evaluated the effects of nitrogen on competition between cheatgrass and three native bunchgrasses (combined in equal proportions) and compared the absolute growth of the four species grown in isolation. Cheatgrass and the combined native grasses were grown in growth tubes (competition study) in various combinations of density, and one of three nitrogen treatments was applied to each growth tube. Our study did not support the hypothesis that native late-seral species will produce more biomass and be more competitive than annual grasses at low N levels. Cheatgrass appears to outperform native bunchgrasses by growing faster and therefore preempting resources. Our results suggest that native bunchgrasses cannot effectively compete with cheatgrass, especially under high soil nutrient concentrations. However, there may be a level of soil N concentration whereby competition between native bunchgrasses and cheatgrass is minimized. Management of soil resources appears to be essential during restoration of invaded rangelands by invasive annual grasses. Prevention, early detection, and eradication programs are critical for conserving rangelands that are free of invasive annual grasses.

preempt nutrients for growth often determines the success of those individuals (Radosевич et al. 2007). This implies that managing soil N may be one important aspect of managing invasive annual grasses, particularly after a disturbance. However, the underlying mechanisms of competition between cheatgrass and native perennial grasses such as bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Love, Idaho fescue (*Festuca idahoensis* Elmer), and needle and thread (*Hesperostipa comata* (Trin. and Rupr.) Barkworth)] with respect to mineral-N are poorly understood.

Typically, in native arid and semiarid ecosystems, mineral-N in soils is often low (increased immobilization) and competition between plants is a key process controlling dynamics (Fowler 1986; Redente et al. 1992). Furthermore, slow nutrient cycling relative to plant and microbial demand for N is also critical in these systems. The capacity of native plant species to capture and retain resources in infertile soils or fertile soils with high plant densities (Grime 2007) is an important characteristic of plant species performance and, ultimately, succession (Krueger-Mangold et al. 2006). Native perennial grasses have been shown to dominate and prevail over invasive annual grasses when mineral-N is reduced (McLendon and Redente 1992). Most native perennial species have relatively slow growth rates, but are able to efficiently utilize nutrients in limited supply relative to plants with high growth rates (Arredondo et al. 1998; Daehler 2003; Harpole 2006). Results from studies by Redente et al. (1992) and Herron et al. (2001) suggest that native perennial species have a greater ability to

acquire N at low levels of availability than invasive species. Low mineral-N may increase the intensity and importance of competition as plants vie more intensely for essential nutrients (Welden and Slauson 1986).

In contrast, many invasive annual species such as cheatgrass have high intrinsic growth rates as individual plants (Ehrenfeld 2003) and may dominate because they can germinate in the fall, establish roots during the winter, and grow rapidly in the spring, preempting soil resources (Berendse and Elberse 1990; Radosевич et al. 1997). Furthermore, recent studies conducted by Monaco et al. (2003), and Young and Mangold (2008), demonstrate that invasive annual grasses are also capable of dominating in low nutrient environments. Attributes such as these enable cheatgrass to invade and dominate native plant communities, particularly after a disturbance has occurred. Cheatgrass may create a positive feedback mechanism between plant size and resource uptake, resulting in the exponential growth of individual plants (see Radosевич et al. (2007) for additional information). Thus, once a plant community is dominated by cheatgrass, the successional trajectory can easily move toward an annual driven system, especially if disturbance (e.g., fire) occurs repeatedly.

There is a substantial need for management strategies that address the underlying ecosystem processes that facilitate invasion and drive succession. The concept of managing soil N to manage invasive plants has been understudied. Our underlying hypotheses are that (1) high soil mineral-N concentrations may be one of the drivers of invasion by invasive annual grasses during the native perennial grass seed germination and seedling establishment phase following a disturbance, and (2) low mineral-N gives native perennial grasses the competitive advantage during this phase. Restoration of ecosystems that have previously been invaded may be more successful if mineral-N is also addressed during restoration efforts, thereby giving desired native perennial plant species a competitive advantage. The term competition is used in the sense of negative interference (i.e., any direct or indirect negative impact) of one plant over another (Casper and Jackson 1997; Fowler 1986) or the ability to avoid or tolerate suppression (Goldberg and Barton 1992). The ability of native perennial grasses to compete more effectively for mineral-N at low levels may increase the intensity and importance of competition.

The overall objective of this study was to determine the potential to favor slower growth-rate, longer-lived species over invasive annual grasses by altering plant available mineral-N. The specific objectives were to (1) determine the relative biomass production of a group of three native perennial species (combined in equal proportions) with that of cheatgrass along a soil nitrogen gradient, and (2) compare the competitive relationship and growth rate of cheatgrass and three native perennial grasses (combined) as

soil nitrogen is altered. In order to evaluate the effect of competition between cheatgrass and several native perennial bunchgrasses in general, rather than between cheatgrass and one particular native perennial species, we combined the native bunchgrasses together and evaluated them as a group. We employed an addition series study and methods of analysis proposed by Spitters (1983) to test the hypotheses that (1) native perennial species will produce more biomass and be more competitive than cheatgrass at low mineral-N levels, and (2) cheatgrass will produce more biomass and be more competitive than native perennial species at high mineral-N levels. Addition series experiments are a form of additive design where total densities and proportions are varied among species. This approach is valuable because the effects of intra- and interspecific competition can be separated through systematic variation of total density and species proportions (Radosevich 1987), and because it has been used effectively in previous competition studies (Herron et al. 2001; Sheley and Larson 1995; Young and Mangold 2008).

### Materials and Methods

Two studies were conducted concurrently in a greenhouse at the Eastern Oregon Agricultural Research Center in Burns, OR. The greenhouse is only covered with 4% shade cloth (light averaged  $1,333.0 \mu\text{mol}/\text{m}^2/\text{s}$  between 10:00 A.M. and 4:00 P.M.) so the temperature was not environmentally controlled. The first study was a competition study comparing the growth and competitive relationship of bluebunch wheatgrass, Idaho fescue, and needle and thread (native grasses combined in equal proportions) with that of cheatgrass along a soil nitrogen gradient. The second study was an absolute growth rate analysis of each of the four species over the same nitrogen gradient as the competition study. Polyvinyl chloride (PVC) pipes (15-cm-diam [6 in]) with a depth of 0.6 m (2 ft) were used as growth tubes for the competition study and 5-cm-diam PVC pipes (0.6 m depth) for the growth analysis study. Each growth tube was cut in half lengthwise and then taped back together with duct tape. This allowed for easy access to root biomass at the end of the study. The bottom of each growth tube was covered with weed cloth to allow for leaching and reduce the potential for anaerobic soil conditions.

**Ion Exchange Probes.** Nitrogen treatments were also applied to the same size growth tubes and soil mixture and replicated six times in a randomized complete block design in order to evaluate what N would be available without any plant related influences under our different N treatments. Cation and anion Plant Root Simulator<sup>1</sup> (PRS-probes) were used to monitor the total monthly accumulated  $\text{NO}_3^-$  and  $\text{NH}_4^+$ . The PRS-probes were inserted vertically

and flush with the soil surface, thereby allowing the ion exchange membrane (IEM) to effectively measure mineral-N. Initially, the PRS-probes were buried for 1 week and then exchanged with fresh PRS-probes to determine saturation levels. Because the PRS-probes were far below saturation levels after 1 week, the probes were exchanged every 30 days throughout the study, thereby avoiding saturation. After removal, PRS-probes were washed free of soil in the lab with deionized water and then scrubbed with a coarse brush to ensure complete removal of residual soil. The PRS-probes were then sent back to Western Ag Innovations for analyses of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$ . The burial IEM can be used to provide a nutrient supply rate to an ion sink, which is expressed as the amount of nutrient adsorbed per surface area of IEM during the duration of the burial (Casals et al. 1995; Hangs et al. 2004). The soil N supply rate for the PRS-probes within each treatment, therefore, is expressed as  $\mu\text{g-N}/10 \text{ cm}^2/60 \text{ days}$ .

**Competition Study.** On March 23, 2007, cheatgrass and the three native bunch grasses (native grasses combined in equal proportions) were planted into the prepared growth tubes in randomized blocks of four addition-series matrices (Radosevich 1987; Spitters 1983). Four density levels of cheatgrass (3, 9, 18, or 54 pure live seeds per growth tube) were planted with the same 4 density levels of native bunchgrasses for a total of 16 density combinations. The three native bunchgrasses were combined together into equal proportions to achieve the desired density levels then fully mixed with the cheatgrass seeds before planting. Two treatments that alter mineral-N availability and a control (no N addition) were applied to each addition-series matrix and replicated three times. Thus, there were four densities of cheatgrass times four densities of the combined bunchgrasses times three treatment levels times three reps for a total of 144 experimental units. The bluebunch wheatgrass seed was the 'Anatone' variety collected in Washington and was purchased from L & H Seed Company, Connell, WA. Idaho fescue seed ('Joseph' variety) was collected in Idaho and was purchased from Clearwater Seed Company, Clarkston, WA. The needle and thread seed was collected in Utah and was purchased from Granite seed Company, Lehi, UT. Cheatgrass seed was collected locally in Harney County, OR.

The soil used in the study was collected from the Oregon Northern Great Basin Experimental Range and is mapped as the Gradon series (sandy loam; fine-loamy, mixed, frigid, Argiduridic Durixerolls). This soil was sieved through a 6-mm [0.24 in] mesh screen and mixed with river washed sand (1 : 1 by weight). River washed sand was used to stimulate a nutrient-poor soil and allow for leaching. Each growth tube was initially irrigated with 8 L of water to leach N and equilibrate to field capacity. The

soil was sampled from five randomly selected growth tubes and analyzed prior to seeding to determine concentrations of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ . Soil analysis prior to sowing seeds indicated that the soil contained about  $4.53 \mu\text{g NH}_4^+\text{-N/g}$  soil and  $0.08 \mu\text{g NO}_3^-\text{-N/g}$  soil.

Seeds were broadcast on the soil and manually arranged uniformly and covered with approximately 2 mm of soil. The soil surface was periodically moistened with a fog mister and covered with plastic until seedlings emerged. Seedlings of species other than what was seeded were removed throughout the experiment as needed. At the start of the experiment the greenhouse temperatures were still below freezing during the night and part of the day, which delayed seed germination. Therefore, nitrogen treatments were initiated 47 days (when 50% of seeds were germinated) after sowing seeds. The total N applied to each treatment over the course of the study was (1) 0.0 mg N/kg soil (control; no N added), (2) 137 mg N/kg soil, and (3) 280 N/kg soil applied as  $\text{NH}_4\text{NO}_3$ . Ammonium nitrate was applied in solution in five increments every 14 days during irrigation. Macro- and micronutrients (K, Ca, Mg, S, Fe, Cl, Mn, Zn, Cu, B, and Mo) were applied as a 10% modified Hoagland's solution along with N treatments to ensure that plant growth was not limited by nutrients other than N. Each growth tube was watered every 3 days with 500 ml of tap water, which was run through a filter to remove mineral-N.

Vegetation was harvested 109 days following seeding when the cheatgrass was beginning to drop seed. The final densities by species and above- and belowground biomass for each species were collected by opening the growth tube lengthwise and washing the soil mix from the roots. Densities for each species were determined and the roots and shoots for each species were carefully separated using a water bath. Above- and belowground biomass material was dried at 60 C for 48 hours.

Data were grouped by treatment and incorporated into multiple linear regression models separately for each treatment (Spitters 1983; Young and Mangold 2008). Cheatgrass and native bunchgrass (combined) individual total biomass (above- and belowground) per plant was predicted using cheatgrass and combined native bunchgrass final densities per growth tube at the end of the study as independent variables. Final densities ranged between 1 and 57 individuals for both cheatgrass and the combined native bunchgrasses, which span the continual densities along the plane of the x-axis. The regressions were of the form:

$$y_c = \beta_{0c} + \beta_{cc}N_c + \beta_{cn}N_n \quad (\text{cheatgrass})$$

$$y_n = \beta_{0n} + \beta_{nn}N_n + \beta_{nc}N_c \quad (\text{combined natives})$$

where  $y_c$  and  $y_n$  represent the response or average total biomass per individual plant for cheatgrass and combined native grasses, respectively. The regression coefficients  $\beta_{0c}$

and  $\beta_{0n}$  represent the y-intercept, or the maximum total biomass for individual plants of cheatgrass and the combined native grasses (group) grown in isolation.  $\beta_{cc}N_c$  and  $\beta_{nn}N_n$  is the product of the coefficient of intraspecific competition of species c and n and its density ( $N_c$  and  $N_n$ ). Intraspecific competition can be interpreted as the effect of density ( $N_c$  or  $N_n$ ) of the same species upon its own mean biomass ( $\beta_{cc}$  or  $\beta_{nn}$ ).  $\beta_{cn}N_n$  and  $\beta_{nc}N_c$  is the product of the coefficient of interspecific competition of species b and n with its density. Interspecific competition can be interpreted as the effect of neighboring density ( $N_c$  or  $N_n$ ) upon the mean biomass of the response species ( $\beta_{cn}$  or  $\beta_{nc}$ ).

The relative competitive ability of each species is calculated as:

$$\text{RC}_c = \beta_{cc}/\beta_c \quad (\text{cheatgrass})$$

$$\text{RC}_n = \beta_{nn}/\beta_n \quad (\text{combined natives})$$

where  $\text{RC}_c$  and  $\text{RC}_n$  are the relative competitive abilities of species c and n. For example, if the relative competitive ability for cheatgrass is 7.0, we may say that cheatgrass senses the presence of one cheatgrass as strongly as the presence of 7.0 combined native grasses. Relative competitive abilities of each species are used to calculate niche differentiation (ND) or resource partitioning (Spitters 1983):

$$\text{ND}_{c \text{ vs. } n} = [\beta_{cc}N_c/\beta_{cn}N_n]/[\beta_{nc}N_c/\beta_{nn}N_n]$$

Niche differentiation increases as ND departs from unity (1.0). In other words, cheatgrass and the three combined native bunchgrasses are decreasingly limited by the same resources as ND departs from zero. Non-significant competition coefficients indicate the competitive effect is essentially zero.

Slopes from the regression models for each nutrient treatment were compared by calculating variance ratios using the equation:

$$\text{VR}_i = [(RSS_i - \text{RSS}_1)/(df_i - df_1)]/(\text{RSS}_1/df_1)$$

where  $\text{VR}_i$  is the Variance Ratio<sub>i</sub>,  $\text{RSS}_i$  is the pooled residual sum of squares,  $\text{RSS}_1$  is the combined residual sums of squares of the treatments being compared,  $df_i$  is the pooled error degrees of freedom, and  $df_1$  is the combined error degrees of freedom of the treatments being compared. A variance ratio larger than the critical F ( $\alpha$ , df-numerator, df-denominator) value ( $\alpha = 0.05$ ) rejects the null hypothesis that the slopes of the regression lines are equal (Snedecor and Cochran 1980). SAS 9.1 Proc reg was used for analysis of regression models.

**Growth Analysis Study.** Growth analysis of the four species was conducted at the same time and under the same environmental conditions as the competition study. Absolute growth rate was used to compare inherent growth

differences of each of the four species. Each species was grown in isolation in a randomized complete block design for 109 days under the same soil N treatments as the competition study. The soil used in the growth analysis experiment was the same soil mixture described in the competition study. Pots were filled with soil and saturated to field capacity. Each of the four species was seeded in individual growth tubes. Five seeds of each individual species were broadcast evenly on the soil surface. Seeds were then covered with approximately 2 mm of dry soil. The soil surface was kept moist with a fog mister and covered with plastic until seedlings emerged. Upon emergence, plants were thinned to a single individual plant per growth tube. Growth tubes were watered with 250 ml every 3 days. Each plant was harvested for above- and belowground dry weight biomass after 109 days of growth and dried (60 C) for 48 hours. We used SAS 9.1 Proc glm to perform ANOVA. Means were separated using Tukey HSD ( $\alpha = 0.05$ ).

## Results and Discussion

**Soil Nitrogen Availability.** Results from the PRS-probes strongly suggest that we were able to establish a N gradient across our treatments. Accumulated total mineral-N for the control (no N added), 137, and 280 mg/kg treatments were 69.3, 120.7, and 266.4  $\mu\text{g N}/10 \text{ cm}^2/60 \text{ days}$ , respectively (Figure 1). Interestingly, total  $\text{NH}_4^+$  accumulation was not significantly different across all treatments ( $P = 0.3163$ ). In contrast,  $\text{NO}_3^-$  accumulation was not only significantly greater than  $\text{NH}_4^+$  accumulation ( $P < 0.0001$ ), but was also significantly different ( $P < 0.0001$ ) across all treatments. This suggests that there was a considerable amount of microbial activity or nitrification. Johnson et al. (1995) also found high rates of N mineralization after soil disturbance during potting. This is an important point to consider when doing pot studies. Although binding of  $\text{NH}_4^+$  to the PRS-probes may have been a problem and cannot be ruled out, previous studies that have used this particular brand of probes have not encountered this problem (Drohan et al. 2005). In addition, the PRS-probes for both cation and anion were far below saturation levels (data not shown). Some immobilized N may have been mineralized as a result of soil disturbance during potting. In our study, however, our objective was not to determine the preference of mineral-N form between plant species. Our objective was to determine the potential to favor native perennial grasses by reducing plant available mineral-N.

**Competition Study.** The predicted biomass ( $\beta_{oc}$ ) of cheatgrass and the combined natives ( $\beta_{on}$ ) in isolation increased with increasing N concentration (Table 1). However, in all treatment levels of N, the predicted total

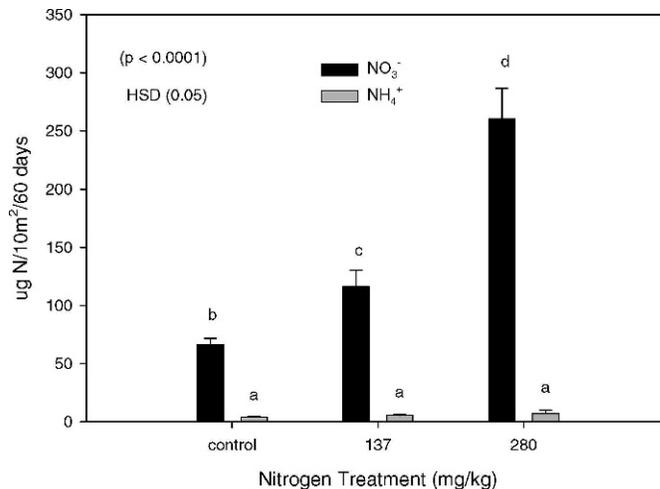


Figure 1. Cumulative total nitrogen (N) absorbed on PRS-probes after 60 days as a function of N applications. Error bars are  $\pm$  standard error of the mean.

biomass for an isolated individual was greater for cheatgrass than the combined native grasses similar to Lowe et al. (2003). The predicted biomass for an isolated cheatgrass ( $\beta_{oc}$ ) ranged from 0.58 g (control) to 1.49 g at the high N treatment level. The predicted maximum weight of an isolated individual of cheatgrass by Sheley and Larson (1995) when grown with yellow starthistle was 1.8 g (96 days after planting), which is similar to our results even though they used two different growth forms. The absolute value of negative competition coefficients is considered when interpreting the strength of competition. Intraspecific competition ( $\beta_{cc}N_c$ ) for cheatgrass was significant ( $P < 0.05$ ) for all three treatments and was more intense (larger absolute value of competition coefficients) than interspecific competition ( $\beta_{cn}N_n$ ). The interspecific competition of native grasses on cheatgrass ( $\beta_{cn}N_n$ ) was significant for the control (no N added) and the high N treatments ( $P < 0.05$ ), but not for the low N treatment. This suggests the density of the combined native grasses at this particular N level had no effect on cheatgrass biomass. Intra- ( $\beta_{cc}N_c$ ) and interspecific ( $\beta_{cn}N_n$ ) coefficients were about the same for cheatgrass at the highest treatment level. Cheatgrass interspecific competition coefficients for the control model were  $-0.0056$  compared to  $-0.0007$  for the native grasses. In other words, with the addition of one more native or cheatgrass plant, the predicted biomass of cheatgrass was depressed (as indicated by the negative coefficient) by  $0.0056 \text{ g}$  and  $0.0007 \text{ g}$  for the native perennials.

Conversely, the predicted biomass for isolated native grasses ( $\beta_{on}$ ) ranged from 0.06 g (control) to about 0.12 g at the high treatment level (Table 1). We expected that the predicted combined native grasses in isolation would have a greater biomass at the lowest (control) N level compared to cheatgrass. However, our results do not support our first

Table 1. Multiple linear regression models for cheatgrass and native grasses growth tube density predicting the individual plant biomass (g/plant).

N Treatment (mg/kg)	$Y = \beta_{0c}^a$	$\beta_{cc}N_c$	$\beta_{cn}N_n$	$R^{2b}$	Slope <sup>b</sup> comparison
Cheatgrass biomass					
Control	0.5797 ( $\pm 0.049$ ) P < 0.0001	-0.0084 ( $\pm 0.001$ ) P < 0.0001	-0.0056 ( $\pm 0.002$ ) P < 0.05	0.483	a
137	0.8884 ( $\pm 0.133$ ) P < 0.0001	-0.015 ( $\pm 0.004$ ) P = 0.0003	-0.002 ( $\pm 0.005$ ) P = 0.674	0.261	b
280	1.491 ( $\pm 0.13$ ) P < 0.0001	-0.0199 ( $\pm 0.004$ ) P < 0.0001	-0.0139 ( $\pm 0.006$ ) P < 0.05	0.439	c
Native bunchgrasses biomass					
Control	0.0553 ( $\pm 0.005$ ) P < 0.0001	-0.0004 ( $\pm 0.0002$ ) P < 0.05	-0.0007 ( $\pm 0.0002$ ) P < 0.0001	0.422	a
137	0.0739 ( $\pm 0.007$ ) P < 0.0001	-0.0007 ( $\pm 0.0003$ ) P < 0.05	-0.001 ( $\pm 0.0002$ ) P < 0.0001	0.389	a
280	0.117 ( $\pm 0.023$ ) P < 0.0001	-0.0013 ( $\pm 0.0009$ ) P = 0.209	-0.0015 ( $\pm 0.0006$ ) P < 0.05	0.149	b

<sup>a</sup> Abbreviations:  $\beta_{0c}$ , the predicted mean biomass of an individual cheatgrass plant grown in isolation;  $\beta_{cc}N_c$ , effect of cheatgrass density on cheatgrass biomass per plant;  $\beta_{cn}N_n$ , effect of the native grasses on cheatgrass biomass per plant;  $\beta_{0n}$ , the predicted mean biomass of an individual native grass plant grown in isolation;  $\beta_{nn}N_n$ , effect of native grass density on native grass biomass per plant;  $\beta_{nc}N_c$ , effect of a cheatgrass on native grass biomass per plant.

<sup>b</sup> The coefficient of determination ( $R^2$ ) is included for each model. Slope comparisons with different letters indicate significant difference of slope for the prediction of each species biomass model.

hypothesis that native perennial species will produce more biomass and be more competitive than annual grasses at low N levels, which is consistent with results from previous studies (Young and Mangold 2008). The effect of native grass density on native grass biomass ( $\beta_{nn}N_n$ ) per plant was significant for the control and the low N treatment, but not for the high N treatment (P = 0.209). However, the native grass interspecific competition ( $\beta_{nc}N_c$ ) coefficients were significant (P < 0.05) for all three treatment levels ranging from -0.0007 (control) to -0.0015 for the high N treatment. This suggests that interspecific competition is more important than intraspecific competition for the native perennial grasses.

Slope comparisons (variance ratios) for cheatgrass models were significantly different from each other across all treatments (Table 1). In contrast, only the high N treatment variance ratio differed significantly for the combined native grasses. Cheatgrass and the combined native grasses both increased their total biomass with increasing N and became more competitive. However, cheatgrass was able to accumulate biomass at a greater proportion and became even more competitive compared to the combined native grasses. Thus, cheatgrass appears to establish a positive feedback mechanism between size and resource uptake. As plant available N increases, cheatgrass takes advantage of the increased N because of its high

growth rate relative to the native perennials, and increases root and shoot biomass over that of native perennials. In other words, with a greater root biomass (root length and surface area, etc.) relative to perennials, cheatgrass is able to take advantage of areas of low N concentrations relative to perennials. Thus, its competitive ability is enhanced, thereby creating a positive feedback. Lowe et al. (2003) also found that cheatgrass gained more biomass and outcompeted blue grama grass (*Bouteloua gracilis* (Willd ex Kunth) Lag. ex Griffiths) as N availability increased. This attribute may be one reason that cheatgrass has the ability to occupy space and preempt soil resources (Casper and Jackson 1997).

The root : shoot ratios for cheatgrass were significantly higher (P < 0.0001) than the combined native grasses for all N treatment levels (Figure 2). However, only the high N treatment was significantly higher than the control for cheatgrass root : shoot ratio. Conversely, Monaco et al. (2003) show values for root : shoot ratios of cheatgrass that are consistently lower than the native perennial grasses. However, the density in their study was five plants per pot while ours varied across densities and proportions.

The relative competitive ratios ( $\beta_{cc}/\beta_{cn}$ ) for cheatgrass were greater than one for all treatment levels (Table 2). Interestingly, the highest ratio for cheatgrass at 7.5 was in the low N treatment. Cheatgrass was affected by the

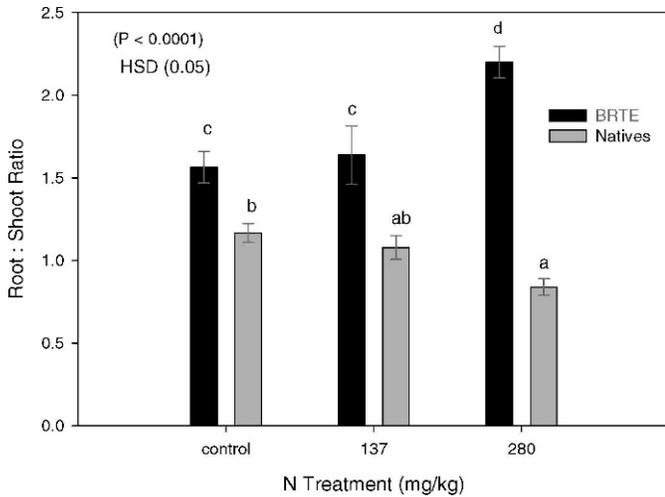


Figure 2. Root and Shoot ratio for cheatgrass and combined native grasses as a function of N treatment averaged across all density treatments (taken from competition study). Error bars are  $\pm$  standard error of the mean.

presence of one cheatgrass plant as strongly as the presence of 7.5 combined native grasses at this N level. This suggests that intraspecific competition is more important for cheatgrass than competition by the native grasses. Sheley and Larson (1995) show that cheatgrass and yellow starthistle are influenced by intraspecific interference more than interspecific interference when rooting depth was unrestricted. Lowe et al. (2003) found that intraspecific competition was more important relative to interspecific competition for cheatgrass as N availability increased, while the reverse occurred for blue grama. In contrast, the relative competitive ratios for the combined native grasses were less than one for all treatment levels. This suggests that the combined native grasses were influenced more by interspecific competition than by intraspecific competition.

The control and high N treatment resulted in the greatest niche overlap ( $ND_{c \text{ vs. } n}$ ), at 0.86 and 1.24, respectively. We would expect greater niche overlap at the lowest N level because competition for a limiting resource is intense. However, even though the combined native grasses became more competitive with increasing N

Table 2. The relative competitiveness (RC) and niche differentiation (ND) for cheatgrass and native bunchgrasses.

N Treatment (mg/kg)	$RC_c^a$ : cheatgrass	$RC_n^a$ : Native bunchgrasses	$ND_{c \text{ vs. } n}^a$ ratio
Control	1.5	0.57	0.86
137	7.5	0.7	5.24
280	1.43	0.87	1.24

<sup>a</sup> Non-significant competition coefficients were used instead of zero to calculate RC and ND because they were the best estimate of those values.

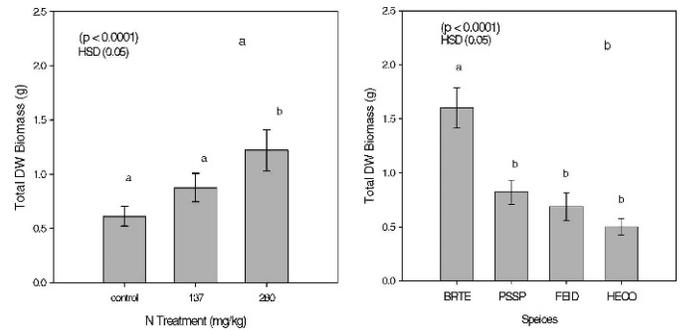


Figure 3. Absolute growth of the four plant species grown in isolation for 109 days across a N gradient, showing (a) total biomass of all four species combined as a function of N treatment and (b) total biomass of cheatgrass BRTE, bluebunch wheatgrass PSSP, Idaho fescue FEID, and needle and thread HECO across all treatment levels. The interaction of species  $\times$  treatment was not significant ( $P = 0.125$ ). Error bars are  $\pm$  standard error of the mean.

levels, cheatgrass became even more competitive because of its faster growth rate and increased biomass, which allowed it to preempt soil resources relative to the perennials. As a result, niche overlap became more intense because of the requirement for resources with increasing biomass. The greatest deviation from unity (niche differentiation) or resource partitioning occurred at the low N treatment with a value of 5.24, suggesting there may be a level of N that minimizes competition. However, these types of niches can change as nutrients change spatially, chemically, and temporally relative to the plant species uptake patterns (Kahmen et al. 2006, James and Richards 2007). Furthermore, this implies that during the seedling establishment phase of restoration, there may be an optimal level of plant available N for which to manage in order to minimize niche overlap.

**Absolute Growth Study.** Only the main effects of species and treatment were significant ( $P < 0.0001$ ), but not their interaction ( $P = 0.125$ ), which supports our results of the competition study whereby low N levels did not shift the competitive balance toward the combined native grasses. The absolute growth of cheatgrass grown in isolation increased with increasing N levels ( $P = 0.0297$ ) supporting the regression models for cheatgrass in the competition study. When the total dry weight of all four species was combined, only the high N treatment was significantly different ( $P < 0.0001$ ) than the control (Figure 3a). Inconsistent with our first hypothesis, cheatgrass had a greater absolute growth rate at all treatment levels compared to the combined grasses.

Based on the PRS-probe results, some mineralized N in our control treatment was present. The N level in the control may have been sufficient to allow for the high growth rate of

cheatgrass, allowing it to preempt N over that of the native grasses. The combined total dry weight across all treatments for cheatgrass was 1.6 g compared to 0.82, 0.68, and 0.5 g for bluebunch wheatgrass, Idaho fescue, and needle and thread, respectively (Figure 3b). The average biomass across all treatments for cheatgrass was somewhat higher when grown in isolation than the average predicted biomass across all treatments in the competition study, which was 0.99 g. Unlike the competition study, the root : shoot ratios in the growth study were not significantly different ( $P > 0.05$ ) from each other. This suggests that the allocation of nutrients by individuals in the absence of competition may differ from allocation of nutrients made by individuals in the presence of competition (Crain 2006).

Our results are inconsistent with Herron et al. (2001) who were able to change the competitive balance in favor of bluebunch wheatgrass interacting with knapweed, by using annual rye as a cover crop to lower mineral-N. Cheatgrass was able to compete effectively even at our lowest N level (control) in our study. Because our control treatments still had some mineralized N, this may have been sufficient for cheatgrass to maintain its growth rate characteristics and preempt soil resources, and thus, not allow us to adequately test our first hypothesis. In a similar study to ours, however, Young and Mangold (2008) also found that medusahead outperformed squirreltail across all nutrient treatments, suggesting that medusahead seedlings will likely dominate over squirreltail seedlings even at low N levels (J. Mangold, personal communication). Monaco et al. (2003 p. 287) states that “caution should be taken when assuming that low nutrient demand of perennial grasses translates into greater competitive ability under low N conditions.” Our study, and those of others (Monaco et al. 2003; Young and Mangold 2008) suggests that invasive annual grasses are able to compete effectively in both high and low N levels, and that N may not be the sole driver of invasion. Natural selection may have operated on other traits that indirectly influence relative growth rates or competitive ability (James and Drenovsky 2007) such as nutrient retention or tolerance to herbivory, which may or may not contribute to the success of natives in nutrient poor environments. In this case, any differences in soil N pools may not change the outcome of competition between slow and fast growing plant species unless all other underlying factors are considered in combination.

However, because our results suggest that there may be a level of mineral-N whereby niche overlap is minimized; this has interesting implications in terms of management and restoration of invaded ecosystems. For example, mineral-N could be managed by altering soil microbial communities or using cover crops/bridge species and soil amendments during restoration to increase resource partitioning during the seedling establishment phase. Initially, the niche axes on which species can be expected

to segregate in plant communities needs to be identified (Silvertown 2004). In this way, restoration efforts may be more successful and sustainable since the underlying cause of invasion and succession is modified in the management or restoration process.

## Sources of Materials

<sup>1</sup> Plant Root Simulator Probe, Western Ag Innovations, Saskatoon, SK, Canada.

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