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# Competition from *Bromus tectorum* removes differences between perennial grasses in N capture and conservation strategies

Jeffrey T. Walker · Jeremy J. James ·  
Rebecca E. Drenovsky

## Abstract

**Background and aims** Competition from the annual grass *Bromus tectorum* threatens aridland perennial bunchgrass communities. Unlike annuals, perennials must allocate part of their first year nitrogen (N) budget to storage rather than growth, potentially placing them at a competitive disadvantage.

**Methods** We evaluated N acquisition and conservation for two perennial bunchgrasses, *Agropyron desertorum* and *Pseudoroegneria spicata*, at the seedling stage to investigate potential trade-offs between storage and growth when grown with and without *B. tectorum* under two levels of soil N.

**Results** *Agropyron desertorum* had higher growth rates, N uptake, and N productivity than *P. spicata* when grown without *B. tectorum*, but trait values were similarly low for both species under competition. Without

competition, N resorption was poor under high soil N, but it was equally proficient among species under competition.

**Conclusions** *A. desertorum* had higher growth rates and N productivity than *P. spicata* without competition, suggesting these traits may in part promote its greater success in restoration programs. However, *B. tectorum* neighbors reduced its trait advantage. As plant traits become more integral to restoration ecology, understanding how N capture and conservation traits vary across candidate species and under competition may improve our ability to select species with the highest likelihood of establishing in arid, nutrient-limited systems.

**Keywords** Drylands · Low nutrient adapted species · Nitrogen productivity · Resorption

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## Introduction

Non-native invasive annual grasses represent one of the largest threats to nutrient-poor systems across the globe (D'Antonio and Vitousek 1992). Invasion of these systems, historically dominated by slow-growing perennial species, largely has been attributed to increased nutrient availability due to altered disturbance regimes and anthropogenic nutrient inputs (Kolb et al. 2002; Brooks 2003). While much rigorous research has described how patterns of invasion and invasion resistance relate to changes in resource availability in nutrient-poor systems, we know substantially less about the mechanisms underlying these patterns. Of particular importance is

understanding how drivers of whole-plant nutrient budgets, including nutrient capture, use and conservation, are influenced by competition and how these traits vary among coexisting species (Aerts 1999; Yuan et al. 2007). Such mechanistic insight is critical to developing effective management and restoration strategies for nutrient-poor systems following disturbance (James et al. 2044a; Chambers et al. 2044).

The Intermountain West of the United States is one model system where understanding the relationship between competition and nutrient conservation is particularly important. These nutrient-poor systems were historically dominated by native perennial grasses but over the last century these species have been continuously displaced by the invasive annual grass, *Bromus tectorum* (L.), which now dominates over 6 million hectares in the Intermountain West (Knapp 1996). In these communities, uptake and use patterns of limiting nutrients, such as nitrogen, may influence competitive outcomes between *B. tectorum* and perennial grasses, such as *Pseudoroegneria spicata* (Pursh) A. Löve and *Agropyron desertorum* (Fisch. ex Link) J.A. Schultes, two perennial grass species commonly integrated into invasive plant management and restoration programs. *P. spicata* is a slow-growing, native perennial grass, whereas *A. desertorum* is a faster-growing, non-native forage species. Although efficient nutrient conservation and storage should favor these perennial species in nutrient poor soils in the long-term, at the seedling stage they may be at a disadvantage (James et al. 2011a). At this life stage, perennial seedlings must forage for all nutrients directly from the soil, as they have not yet developed nutrient reserves. As a result, perennial and annual grass seedlings experience similar reductions in growth rates when nitrogen is limiting (James 2008a). However, at the end of the growing season, perennial plants must allocate a portion of their nutrient budget to storage or towards developing long-lived tissues, whereas annual grasses are able to invest all available nutrients into reproduction (James et al. 2011a). Thus, growth and survival of perennial plants will depend on soil nutrient availability, plant nutrient uptake, efficient nutrient use and recycling, and competition for soil resources.

Trait differences between *P. spicata* and *A. desertorum* influence plant nutrient demand and biomass allocation patterns, and thus, with soil nutrient availability, drive differences in nutrient uptake capacity (Chapin 1980). Nutrient demand increases with growth rate, aboveground

allocation, and plant size (Lambers and Poorter 1992; James and Richards 2005); thus, nutrient uptake should be higher in faster growing species with lower root allocation such as *A. desertorum* compared to slower growing species such as *P. spicata*. If nutrient uptake exceeds demand, excess nutrients can be stored (Jeoffroy et al. 2002), to support future growth and reproduction when demand exceeds uptake (Bloom et al. 1985; Chapin et al. 1990). However, differences in root allocation may offset these nutrient budget gains. In low nutrient soils, high constitutive root allocation in slow-growing perennial species, like *P. spicata*, may promote long-term nutrient uptake, due to low ion diffusion rates (Chapin 1980; Aerts 1999), but under increased nutrient availability, high root allocation may decrease nutrient productivity, growth rates, and long-term fecundity (Rodgers and Barneix 1988; Lambers and Poorter 1992; Lambers et al. 2008). In contrast, highly plastic annual species may alter biomass allocation patterns depending on soil nutrient availability (Funk 2008), thus increasing nutrient productivity, a key trait distinguishing growth rate differences between native and invasive grass species in low nitrogen environments (Garnier et al. 1995; James 2008b).

In low nutrient environments, nutrient retention can be as important as nutrient capture in driving whole-plant nutrient budgets (Chapin 1980; Killingbeck 1996) and may be of particular importance when plants are experiencing competitive stress (Yuan et al. 2007). The ability of stress-tolerant species to reduce nutrient losses through longer-lived tissues and greater nutrient resorption from senescing tissues is essential in nutrient-poor habitats, as an increased capacity for resorption reduces plant dependence on soil nutrient uptake (Chapin 1980; Aerts 1996). Thus understanding the mechanisms in which coexisting perennial species may differentially respond to competitors in low nutrient systems will require a detailed understanding of nutrient uptake and biomass allocation, as well as an understanding of the degree to which co-existing species may differ in ability to conserve nutrients overtime.

The broad goal of our study was to examine how key drivers of plant nitrogen budgets, including nitrogen capture, allocation and conservation, vary across *A. desertorum* and *P. spicata* and to quantify how these nitrogen budget drivers are influenced by *B. tectorum* competition. Although field densities of perennial grass seedlings are often less than 5 plants per m<sup>-2</sup> (James and Svejcar 2010), they can exceed 500–1000 plants per m<sup>-2</sup> for *B. tectorum* seedlings (Concilio et al. 2013;

Johnston 2015), suggesting potential for strong competitive pressure from *B. tectorum* even at the seedling stage. Additionally, previous greenhouse experiments exploring competitive outcomes among *B. tectorum* and *P. spicata* suggest that interspecific competition from *B. tectorum* decreases biomass production more than intraspecific competition for *P. spicata* (Blank 2010). Long recognized as a serious competitor to *P. spicata*, *B. tectorum* roots can grow approximately 50 % faster than *P. spicata* (Harris 1967). In contrast, under greenhouse conditions, seedling root and shoot growth were similar between *A. desertorum* and *B. tectorum* (Monaco et al. 2003), and *A. desertorum* is considered a stronger resource competitor than *P. spicata* when grown with *B. tectorum*, largely based on its faster growth rate (Harris and Wilson 1970). Based on these observations, we expected that the faster growth rate of *A. desertorum* compared to *P. spicata* would be associated with higher N uptake rates due to higher N demand and greater competitive ability, but that the more slowly growing *P. spicata* would be associated with more proficient N resorption and storage. As a result of this suite of traits, we expected *A. desertorum* would be a stronger competitor than *P. spicata* against the invasive annual grass, *B. tectorum*.

## Materials and methods

### Study location and study species

The experiment was conducted at the Eastern Oregon Agricultural Research Center (EOARC, Burns, Oregon, U.S.A.; 43° 31' N, 119° 01' W). Our focal plants included two perennial bunchgrass species: *Pseudoroegneria spicata* (Pursh) A. Löve (Bluebunch Wheatgrass) and *Agropyron desertorum* (Fisch. ex Link) J.A. Schultes (Crested Wheatgrass). These two bunchgrasses are widely distributed in the Great Basin and Intermountain West of the United States and are key species in large-scale restoration programs there. A major threat to the success of these restoration programs is competitive pressure from the non-native annual grass, *Bromus tectorum* L. (Cheatgrass). Thus, our experiment tested how competitive pressure from *B. tectorum* influences performance of the two focal bunchgrass species.

*Pseudoroegneria spicata* is a native, late-successional, perennial bunchgrass species found throughout the Intermountain West (Mack 1981; Miller et al. 1986).

*Pseudoroegneria spicata* seeds typically germinate in the fall under adequate soil moisture conditions, and seedlings spend the winter dormant, resuming active growth in late spring (Miller et al. 1986). *Agropyron desertorum* is a non-native, non-invasive perennial grass species originating from Eurasia that was introduced into the Intermountain West in the twentieth century as a rangeland forage species. Despite its non-native status, it is a highly favored forage species and remains widely planted in the Intermountain West. *Agropyron desertorum* is phenologically very similar to *P. spicata* (Caldwell et al. 1981; Nowak and Caldwell 1986). Both species have similar germination times, but *A. desertorum* has a greater ability to respond to nutrient pulses (Cui and Caldwell 1997), as *A. desertorum* may allocate more carbon to roots than *P. spicata*. *Agropyron desertorum* has a faster overall growth rate (James 2008b) and a lower N use efficiency (NUE, measured as biomass production / N concentration) than *P. spicata* under similar growing conditions (Cui and Caldwell 1997). *Bromus tectorum* is a fast-growing, non-native annual grass known to be a serious invader in the region. Populations of this species were established in the late nineteenth century and spread rapidly through the early twentieth century, most prominently in overgrazed regions that were once dominated by *P. spicata* (Mack 1981). Throughout much of the region, it has formed monocultures, and the combination of its prolific biomass production and early season senescence has caused a shift in fire regimes (D'Antonio and Vitousek 1992).

### Experimental design and measurements

The experiment was carried out in individual pots set within a gravel garden plot using a randomized complete block design. Each block contained 2 focal species X 2 levels of N X 2 levels of competition; additionally, three harvests occurring during the experiment (early, middle, and late) were incorporated into the block design for a total of 24 bunchgrasses per block at the beginning of the experiment. Each block was replicated eight times for a total of 192 bunchgrasses. Additionally, 8 pots per species were seeded for an initial, pre-treatment harvest.

Seeds of bunchgrass species were planted on April 20, 2011 in Cone-Tainers (2.56 cm diameter X 18 cm deep; Stuewe and Sons, Inc.) containing a 2:1 mixture of coarse sand and sandy loam field soil collected from the

Northern Great Basin Experimental Range (43°22'N, 122°18'22'W; 1300 m elevation; as per James 2008a); three seeds were planted in each Cone-Tainer. *Pseudoroegneria spicata* seeds were acquired from the Washington State Department of Agriculture; *A. desertorum* seeds were purchased from Bruce Seed Farm, Inc. (Townsend, MT). Seedlings received 1/4 strength modified Hoagland's solution (Epstein 1972) on May 5, 11 and 20 to stimulate growth. During this time, seedlings were moved outside in the daytime (excluding windy or rainy days) but kept inside during the night to cold-harden the seedlings. On May 16, 2011 seedlings were randomly thinned to one plant per Cone-Tainer. Germination and early growth occurred in the greenhouse at the EOARC.

Both the initial harvest (representing pre-treatment growth) and transplant events (for experimental plants) took place on June 8, 2011. Eight seedlings of each species were harvested before treatments were initiated for initial biomass and root, shoot, and leaf tissue N concentrations (methods later). Concurrently, 96 seedlings of each species were transplanted into individual experimental pots (25 cm diameter X 19 cm deep) filled with the same sand-field soil mixture and promptly watered. Transplanted seedlings were randomly assigned to one of three harvests: early (July 7–8, 2011), middle (August 8–9, 2011), or late (January 7–8, 2012), as well as one of the competition treatments (with or without *B. tectorum* neighbors) and one of the N treatments (low or high). The three resulting inter-harvest periods captured the fast-growth acquisition phase (between the initial and early harvest), a period of steady growth (between the early and middle harvest), and a final period, during which plants were gradually water-stressed to simulate seasonal drought and promote leaf senescence (between the middle and late harvest). Targeting these specific time periods allowed us to assess nutrient uptake, use, recycling and storage throughout the first growing season for both species.

For the competition treatments, the two bunchgrass species were grown either with or without *B. tectorum* neighbors. One caveat of this design is that differences between intraspecific and interspecific competition cannot be determined. Intraspecific competition was not assessed in this experiment, as density of perennial bunchgrass species, even at the seedling stage, is low and not a major driver of community interactions. Average field densities for *B. tectorum* seedlings in

invaded rangeland can exceed 500–1000 plants  $\text{m}^{-2}$  (Concilio et al. 2013; Johnston 2015). In contrast, even in grasslands dominated by adult *A. desertorum* plants, *A. desertorum* seedling densities range from 0 to 24 plants  $\text{m}^{-2}$  (Hulet et al. 2010), and restoration targets for seedling densities of *P. spicata* are  $\approx 5$  plants  $\text{m}^{-2}$  (Boyd and James 2013). For plants experiencing competition, perennial grass seedlings were transplanted into pots that had been seeded previously with *B. tectorum* seeds (May 26, 2011; one perennial grass seedling per pot, 50 *B. tectorum* seeds per pot); this seeding rate resulted in *B. tectorum* average seedling densities of 633 plants  $\text{m}^{-2}$ . *Bromus tectorum* seedlings were <3 cm in height when perennial seedlings were transplanted. Nitrogen treatments were applied as five, 1 L nutrient pulses throughout the growing season as modified Hoagland's solution; two pulses occurred before the early and middle harvests and one occurred before the late harvest period. The low N treatment was 0.16 mM N ( $\approx 0.009$  g N  $\text{m}^{-2}$ ) for the first pulse and 0 mM N for later pulses, whereas the high N treatment was 1.6 mM N ( $\approx 0.09$  g N  $\text{m}^{-2}$ ) for the first two pulses (prior to the early harvest period) and 4 mM N ( $\approx 0.22$  g N  $\text{m}^{-2}$ ) for later pulses (prior to the middle and late harvest periods). In similar rangeland field soils, total exchangeable inorganic N ranged from 0.025–0.075 g N  $\text{m}^{-2}$  (Svejcar and Sheley 2001); thus our N additions represent approximately 3 % of field values in the low N treatment up to 290 % of field values in the high N treatment. Nitrogen concentrations were increased prior to middle and late harvests in an attempt to strengthen soil N pools for high N treatments and to account for greater N demand of larger plants. All other nutrients were maintained at 1/10 strength for the early harvest period and 1/4 strength for the middle and late harvest periods. Between pulses, plants were maintained at field capacity with tap water.

Soil inorganic N was measured seven times across the course of the experiment. To account for repeated sampling, soils were harvested from additional pots representing the full factorial combination of species, competition, and N treatments ( $n = 4$  pots per combination). Soils were analyzed for  $\text{NO}_3^-$  following Miranda et al. (2001) and for  $\text{NH}_4^+$  following Forster (1995). Averaged across seven sampling periods, mean inorganic N was  $2.5 \pm 0.7$ ,  $3.3 \pm 0.3$ ,  $0.8 \pm 0.4$ , and  $1.5 \pm 0.4$  mg  $\text{kg}^{-1}$  in the no competition, low N treatment; no competition, high N treatment; competition, low N treatment; and competition, high N treatment, respectively (data are



means  $\pm$  S.E.). These values are within ranges typically observed in this system (Cui and Caldwell 1997; Peek and Forseth 2003; James et al. 2006).

During each harvest, above- and belowground biomass of target plants was collected and separated into leaves, stems, and roots. Throughout the experiment, senescing leaves were collected and composited for each replicate. Samples were rinsed with deionized water, oven-dried at 55 °C for 48 h, and weighed. Allocation to roots was assessed as root mass ratio

(root mass divided by total plant biomass; RMR). After weighing, samples were finely ground and analyzed for total N concentration (all bunchgrass replicates) with a CN analyzer (Costech Analytical Technologies, Valencia CA).

#### Statistical analysis

Rates of N uptake per plant were calculated as:

$$\text{N uptake per plant} = (\Delta \text{ total N pool}/t) * ((\ln(\text{Root mass}_{\text{final}}) - \ln(\text{Root mass}_{\text{initial}})) / \Delta \text{ root mass})$$

Where the total N pool is equivalent to total plant mass times N concentration per replicate,  $t$  is the number of days between harvest periods,  $\text{root mass}_{\text{initial}}$  is the mean root mass per plant at the beginning of the harvest period, and  $\text{root mass}_{\text{final}}$  is the root mass per replicate plant at the end of the harvest period. N uptake ( $\text{mg g}^{-1} \text{ d}^{-1}$ ) was calculated for the periods of initial to early harvest, early to mid-harvest, and mid to late-harvest. Relative growth rate (RGR,  $\text{g g}^{-1} \text{ d}^{-1}$ ) was calculated for the same time periods:

$$\text{RGR} = (\ln(\text{biomass}_{\text{final}}) - \ln(\text{biomass}_{\text{initial}})) / t$$

These calculations followed the recommendations of Causton and Venus (1981) for unpaired and ungraded harvests and were modeled after the equations proposed by Hunt et al. (2002). Univariate ANOVAs were run for N uptake and RGR for both time periods; effects in the model included species, N treatment, competition treatment, and block, as well as the interactions between treatment factors. Nitrogen productivity (NP,  $\text{g mol}^{-1} \text{ d}^{-1}$ ) was calculated as:

$$\text{NP} = \text{RGR} / \text{Whole plant N concentration}$$

Mid-harvest RGR and nutrient concentrations were used for this calculation, as RGR was maximal at this time point. N resorption proficiency was determined after the late season harvest and reported as the concentration of nutrients in senesced leaves (Killingbeck 1996). Individual univariate ANOVAs were run for analysis of NP, mid-harvest leaf N concentrations, early, mid, and late-harvest root mass ratio, and senesced leaf N concentrations, using the same model design as for N uptake and RGR. Linear contrasts were

used to determine relationships between individual treatments when there was a significant three-way interaction among species, N treatment, and competition treatment. N pools for roots, stems, and leaves at each harvest period were related to total N pools for all plants via linear regression followed by ANCOVA to test for differences in slope between harvests, indicating a change in the relationship between N pools among harvests. Assumptions of normality and equal variance were tested using the Shapiro Wilks test and Levene's test, respectively. Models were weighted by the inverse of the variance in cases in which variances were unequal among treatment groups. All statistical tests were run on SAS Institute software (v9.2). Given the potential for significant interactions among model effects, only the highest order, significant interaction terms are presented in the results, as appropriate.

## Results

### Relative growth rate & biomass allocation

RGR between the initial and early harvest was significantly different between N treatments for both species (N effect:  $P = 0.02$ , Table 1). High N plants grew at an average rate of  $0.052 \text{ g g}^{-1} \text{ d}^{-1}$  compared with low N plants at  $0.046 \text{ g g}^{-1} \text{ d}^{-1}$ . The effect of competition on growth rate was significantly different between species (Species\*Competition:  $P = 0.02$ ), with a greater decline in RGR for *A. desertorum* than *P. spicata* when grown with than without *B. tectorum* neighbors. From the early to mid-harvest, RGRs were significantly different between species (Species effect:  $P = 0.008$ ) and

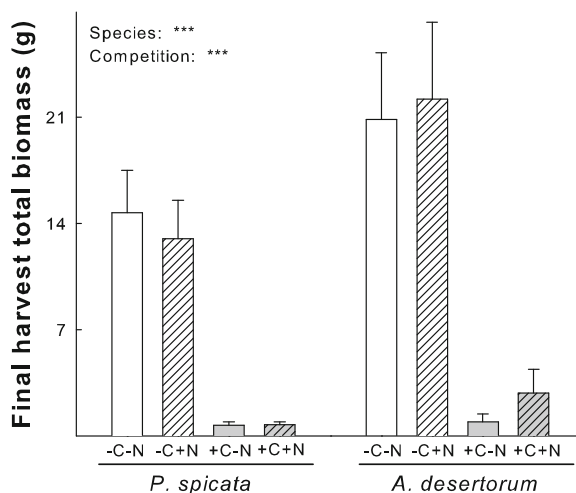
**Table 1** RGR ( $\text{g g}^{-1} \text{d}^{-1}$ ), RMR and N Uptake rates ( $\text{mg g}^{-1} \text{d}^{-1}$ ) for both perennial grass species across the three harvest periods. Data are averages  $\pm$  SD ( $N = 7-8$ ). Negative values for uptake indicate a net loss of nitrogen

		RGR ( $\text{g g}^{-1} \text{d}^{-1}$ )			RMR (%)			N uptake ( $\text{mg g}^{-1} \text{d}^{-1}$ )		
		Early harvest	Mid harvest	Late harvest	Early harvest	Mid harvest	Late harvest	Early harvest	Mid harvest	Late harvest
Monoculture	<i>P. spicata</i>									
	Low N	0.05 $\pm$ 0.01	0.08 $\pm$ 0.01	0.006 $\pm$ 0.002	0.35 $\pm$ 0.05	0.32 $\pm$ 0.07	0.46 $\pm$ 0.13	3.92 $\pm$ 1.72	4.14 $\pm$ 1.53	0.23 $\pm$ 0.10
	High N	0.06 $\pm$ 0.01	0.08 $\pm$ 0.02	0.003 $\pm$ 0.001	0.33 $\pm$ 0.05	0.30 $\pm$ 0.10	0.39 $\pm$ 0.07	4.80 $\pm$ 0.84	4.69 $\pm$ 1.50	0.36 $\pm$ 0.23
<i>A. desertorum</i>	Low N	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01	0.005 $\pm$ 0.002	0.27 $\pm$ 0.05	0.24 $\pm$ 0.03	0.39 $\pm$ 0.08	7.06 $\pm$ 1.44	4.28 $\pm$ 2.10	0.25 $\pm$ 0.08
	High N	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01	0.003 $\pm$ 0.002	0.24 $\pm$ 0.03	0.22 $\pm$ 0.06	0.39 $\pm$ 0.05	8.83 $\pm$ 1.03	6.94 $\pm$ 1.84	0.38 $\pm$ 0.10
Competition	<i>P. spicata</i>									
	Low N	0.03 $\pm$ 0.01	0.01 $\pm$ 0.01	0.003 $\pm$ 0.003	0.53 $\pm$ 0.06	0.48 $\pm$ 0.09	0.90 $\pm$ 0.04	0.55 $\pm$ 0.32	-0.09 $\pm$ 0.12	0.13 $\pm$ 0.03
	High N	0.04 $\pm$ 0.01	0.01 $\pm$ 0.01	0.003 $\pm$ 0.003	0.54 $\pm$ 0.07	0.33 $\pm$ 0.14	0.90 $\pm$ 0.04	0.79 $\pm$ 0.29	-0.08 $\pm$ 0.50	0.20 $\pm$ 0.09
<i>A. desertorum</i>	Low N	0.04 $\pm$ 0.01	0.01 $\pm$ 0.01	0.003 $\pm$ 0.002	0.42 $\pm$ 0.03	0.34 $\pm$ 0.07	0.70 $\pm$ 0.17	0.94 $\pm$ 0.30	-0.20 $\pm$ 0.23	0.16 $\pm$ 0.06
	High N	0.04 $\pm$ 0.01	0.02 $\pm$ 0.01	0.006 $\pm$ 0.006	0.39 $\pm$ 0.04	0.31 $\pm$ 0.06	0.70 $\pm$ 0.14	8.83 $\pm$ 1.03	6.94 $\pm$ 1.84	0.12 $\pm$ 0.07

competition treatments (Competition effect:  $P < 0.0001$ ). *A. desertorum* had higher growth rates than *P. spicata*, although competition significantly decreased RGR in both species. Although not significant, there was a trend for N addition to partially ameliorate RGR suppression in *A. desertorum*; in this treatment, its RGR was over 3-fold greater than the average of any other treatment combination including the presence of *B. tectorum*. By the final harvest, RGR had slowed across all treatments, but there was a significant competition\*N interaction ( $P = 0.02$ ). When grown without *B. tectorum* neighbors, RGR tended to be higher in the low N treatment, but when grown with *B. tectorum* neighbors, RGR tended to be higher in the high N treatment, due predominantly to the greater RGR of *A. desertorum* in response to high N.

Based on these differences in growth rates among species and treatments, *A. desertorum* produced significantly more biomass than *P. spicata* (species effect:  $P < 0.001$ ; Fig. 1), and both species grown without *B. tectorum* neighbors grew significantly larger than plants under competition by the end of the experiment (competition effect:  $P < 0.001$ ; Fig. 1). Only *A. desertorum* plants grown without *B. tectorum* neighbors produced seed heads (data not shown).

At the early harvest, root mass ratio (RMR) differed between species ( $P < 0.0001$ ) and competition treatments ( $P < 0.0001$ ), with *P. spicata* investing more biomass in roots than *A. desertorum*, and with plants experiencing competition allocating more biomass belowground than plants grown without *B. tectorum*



**Fig. 1** Total biomass production per plant at the final harvest. Abbreviations include: N, nitrogen; C, competition. Data are means  $\pm$  SD ( $N = 8$ )

neighbors (Table 1). Similar trends were observed at the mid-harvest for differences among species ( $P = 0.0002$ ) and competition treatments ( $P < 0.0001$ ). Additionally, soil N availability influenced RMR at the mid-harvest ( $P = 0.01$ ), with low N plants investing more biomass belowground than high N plants. At the final harvest, there was a significant species\*competition interaction ( $P = 0.0025$ ), with *P. spicata* allocating more biomass belowground than *A. desertorum*, particularly when experiencing competition. Overall, biomass allocation to roots tended to increase throughout the growing season.

### N uptake

By the early harvest (Table 1), plants growing without *B. tectorum* neighbors acquired nutrients at significantly higher rates than plants with competitors. The magnitude of this effect differed significantly between species ( $P < 0.0001$ ) and between N treatments ( $P = 0.0027$ ). Early-season uptake rates for *A. desertorum* plants grown alone were approximately 2-fold greater than the rates of *P. spicata* grown alone. For plants experiencing competition, uptake rates for *A. desertorum* were 1.5-fold greater than *P. spicata*. Among plants growing without *B. tectorum* neighbors and receiving high N, uptake rates were approximately 1.25-fold greater than those receiving low N. For plants experiencing competition, uptake rates were 1.8-fold greater in plants receiving high N than those receiving low N.

Over the time period from early- to mid-harvest, competition continued to have a significant impact on uptake rates ( $P < 0.0001$ ). Of the plants grown with *B. tectorum* neighbors, only *A. desertorum* in the high N treatment showed positive rates of uptake. During this time period, the two species differed in their response to N treatments ( $P = 0.02$ ). Low N resulted in a greater reduction to uptake rates in *A. desertorum* than in *P. spicata*. For plants grown without *B. tectorum* neighbors, uptake rates for *P. spicata* remained relatively consistent over the first two harvest periods, whereas uptake rates for *A. desertorum* decreased between the early and mid-harvest periods.

From the mid- to late-harvest, N uptake was low across all treatments and was influenced by a significant competition\*nitrogen effect ( $P = 0.04$ ). Plants grown without *B. tectorum* neighbors tended to have greater N uptake in the high N treatments, whereas plants grown

with *B. tectorum* neighbors tended to have greater N uptake in the low N treatments.

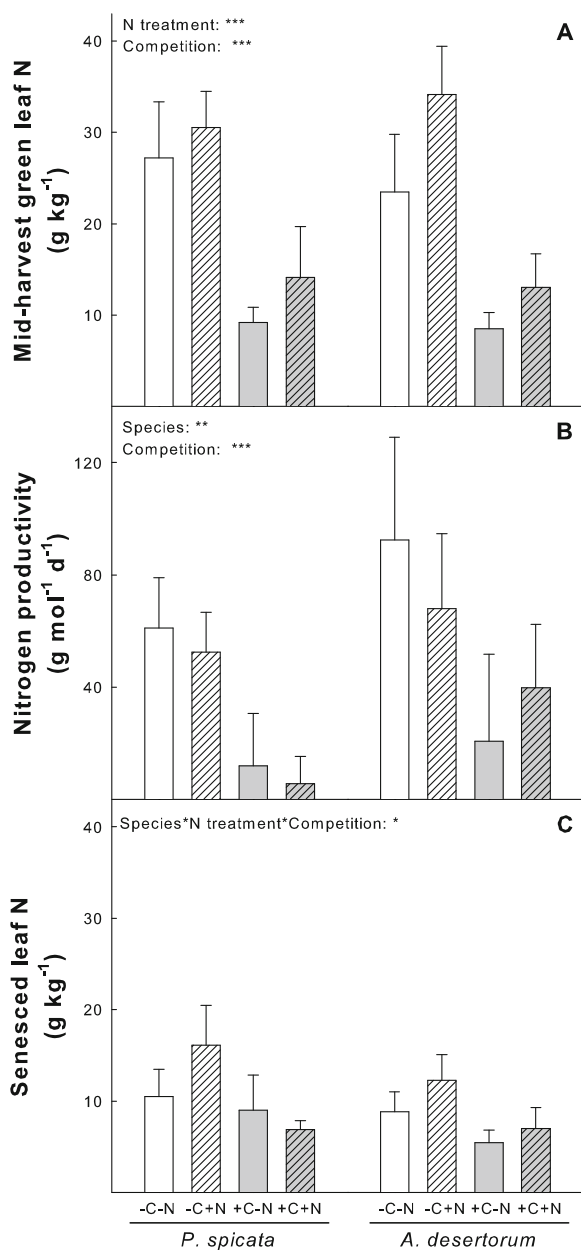
### Plant N status, use, allocation, and conservation

Mid-season green leaf N concentrations differed significantly between N treatments ( $P < 0.0001$ ) and competition treatments ( $P < 0.0001$ ; Fig. 2a). High N treatments had 1.3-fold higher leaf N concentration than low N treatments. Plants grown without *B. tectorum* neighbors had 2.6-fold greater N concentrations than those experiencing competition. Green leaf N did not differ significantly between species, nor were interactions between treatments significant ( $P > 0.05$ ). Nitrogen (N) productivity differed significantly between species ( $P = 0.0002$ ) and competition treatments ( $P < 0.0001$ ). In general, N productivity was higher in *A. desertorum* than *P. spicata* and was greater in plants grown alone than those with *B. tectorum* neighbors (Fig. 2b).

For senesced leaf N concentration, there was a significant three-way interaction between species\*soil N availability\*competition ( $P = 0.028$ ; Fig. 2c). Linear contrasts indicated that when plants were grown without *B. tectorum* neighbors, senesced leaf N concentration was greater in plants with higher soil N availability ( $P < 0.0001$ ). However, senesced leaf N concentration was similar among N treatments in plants experiencing competition ( $P > 0.05$ ). This same trend was observed when the species were examined individually. Both *A. desertorum* and *P. spicata* grown without *B. tectorum* neighbors had higher senesced leaf N when grown at higher soil N availability (*P. spicata*,  $P = 0.0002$ ; *A. desertorum*,  $P = 0.017$ ). Despite the significant three-way interaction, however, no significant differences were observed among N treatments within species for plants grown with *B. tectorum* neighbors using linear contrasts ( $P > 0.05$ ). Thus, although under competition there was a trend for poorer resorption with greater N availability in *P. spicata* and more proficient resorption with greater N availability in *A. desertorum*, it was not significant.

Relative to the total N pool, the leaf N pool decreased ( $P < 0.0001$ ), the stem N pool remained constant ( $P > 0.05$ ), and the root N pool increased ( $P < 0.0001$ ) from early and mid-harvests to the late harvest across all species and treatments (Fig. 3a-i), as determined by differences in slopes between harvests for these traits. These patterns indicate decreased N allocation to leaves and increased N allocation to roots through the growing season. Across species and treatments, allocation to the





**Fig. 2** Green leaf N concentration (g kg<sup>-1</sup>) for the mid-harvest period, indicating plant nutrient status when plants were at their maximal growth rate (a); N productivity (g mol<sup>-1</sup> d<sup>-1</sup>), indicating how efficiently N is being used to produce new biomass (b); And senesced leaf N concentration (g kg<sup>-1</sup>) for the final-harvest period, indicating N resorption proficiency (c). Abbreviations as in Fig. 1. Data are means  $\pm$  SD ( $N = 8$ )

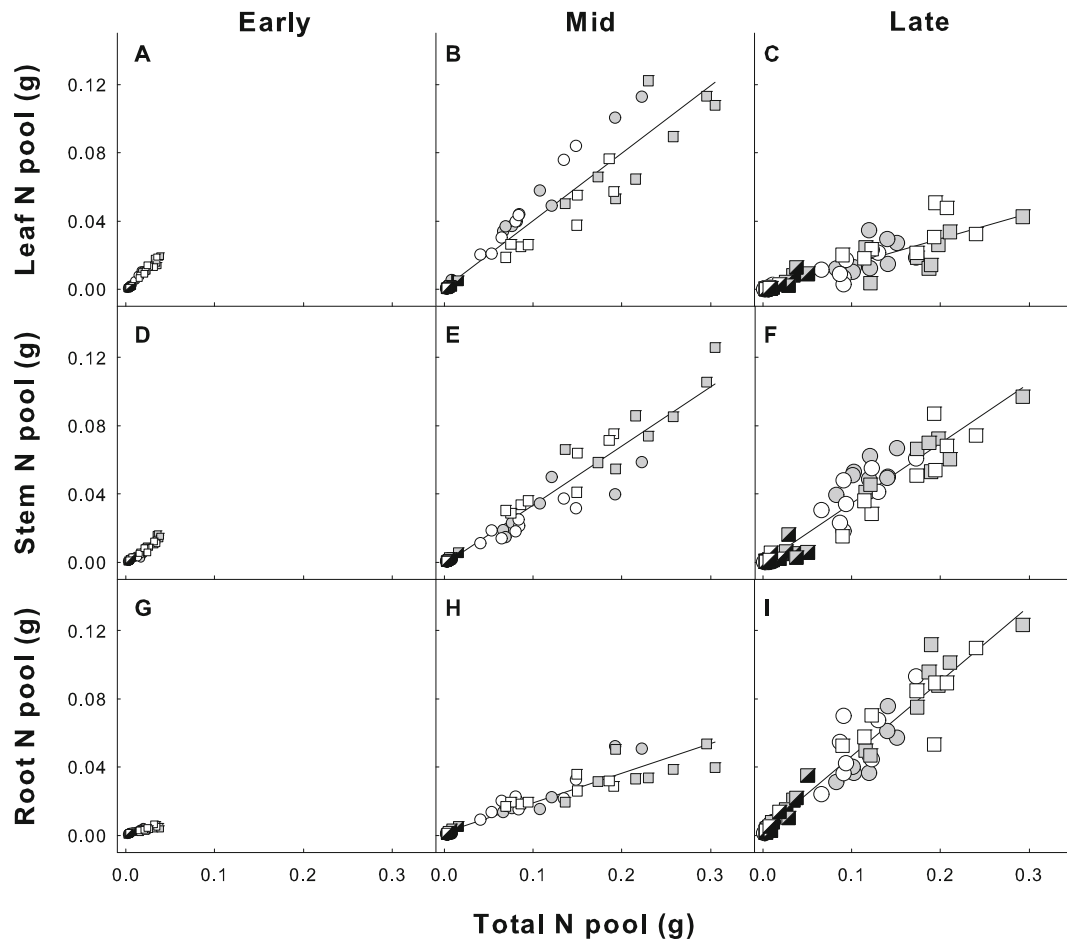
leaf N pool shifted from  $\approx 23$ –52 % of the total N pool at the mid harvest to  $\approx 15$ –35 % of the total N pool at the late harvest (data not shown). In general, across both the mid and late harvests, plants grown without *B. tectorum* neighbors had larger leaf, stem, root, and total N pools

than plants grown with *B. tectorum* neighbors. In fact, total N pools for both species were an order of magnitude greater without competitive pressure from *B. tectorum* (Fig. 3a-i).

## Discussion

In contrast to our hypotheses, *A. desertorum* was not a stronger competitor than *P. spicata* when grown with *B. tectorum* neighbors. In fact, significant trait differences between the perennial grass species when grown in monoculture disappeared when grown in competition with *B. tectorum* neighbors, and, importantly, greater soil N availability did not ameliorate the suppressive effects of competition on growth or other traits, in most cases. Thus, as more complexity and realism were incorporated into our treatments, trait-based predictions of competitive ability based on monoculture experiments were not supported. For example, although *A. desertorum* had greater RGR and soil N uptake rates than *P. spicata* when grown without *B. tectorum*, competition decreased RGR and N uptake in both species, with N uptake rates nearly an order of magnitude lower than for plants grown without *B. tectorum* neighbors between the initial and early harvest. Here, competitive stress reduced resources for growth, thus decreasing plant N demand and uptake across both species. These data are consistent with literature closely linking uptake with growth rate (Rodgers and Barneix 1988; Garnier et al. 1989; James and Richards 2005), based on N demand.

Competition also favored root allocation, with RMR increasing in plants grown with *B. tectorum* neighbors, particularly for *P. spicata*. However, high RMR did not promote N uptake, with mass-based rates exceedingly low in plants experiencing competition. In fact, three of the four treatment groups experiencing competition had negative average uptake rates from early to mid-harvest, indicating a net loss of N. In other studies, RMR increased allometrically as a function of plant size in high nutrient scenarios (Muller et al. 2000). This contradiction (greater root allocation at both low and high N availability) highlights that similar changes in RMR can indicate responses to different environmental cues and further emphasizes the necessity of obtaining a whole plant perspective to understand allocational shifts. In our study, the increase of RMR in response to competitive stress appears more as a survival strategy



**Fig. 3** Linear regression of leaf (a–c), stem (d–f), and root (g–i) N pools (g) of all plants relative to total N pools, indicating potential shifts in N allocation among seasonal harvests. Data points are individual plants from the three different harvest periods, which are represented by symbols of increasing size. Circles are

*P. spicata* and squares are *A. desertorum*. White symbols indicate low N plants, gray symbols indicate high N plants, and plants experiencing competition from *B. tectorum* additionally are half-filled with black

for plants that are adapted to enduring periods of low nutrient availability, and less like a competitive strategy (sensu Goldberg 1990) to deplete common resources.

As a result of differences in growth rates but no differences in mid-season leaf N concentrations, *A. desertorum* had greater N productivity than *P. spicata*. In the Intermountain West, high N productivity has been identified as a key trait underlying the success of non-native, invasive grasses, including *B. tectorum* (James 2008b), and thus selecting for species with high N productivity has been suggested for more successful restoration efforts. Although competition from *B. tectorum* decreased N productivity in both species, *A. desertorum* maintained greater N productivity across all treatments relative to *P. spicata*, suggesting *A. desertorum* more efficiently used

N to produce biomass. This greater efficiency likely was linked to lower root allocation in *A. desertorum*, and although not measured, a lower photosynthetic N use efficiency in *P. spicata* (Lambers et al. 2008). In support, *P. spicata* plants tended to allocate proportionally more of their N pool to leaves mid-season than *A. desertorum*, but this greater allocation did not result in a higher RGR or greater final biomass production. Instead, these data indicate greater luxury consumption of N, suggesting that plant N uptake had exceeded N demand. At the final harvest, *P. spicata* allocated proportionally more N to root N pools and had higher senesced leaf N concentrations than *A. desertorum*, across all treatments. This trend of poorer resorption in *P. spicata*, particularly when grown without *B. tectorum* neighbors, is consistent with past

studies, which found that plants that have accumulated nutrients to luxury levels resorbed less nutrients (Shaver and Melillo 1984). In contrast, *A. desertorum* did not appear to have a strong luxury consumption response, displaying smaller root N pools at the end of the experiment, more efficient use of N towards growth, and a trend towards more proficient N resorption.

One observation that should temper our interpretation regarding the relative importance of measured traits on plant N budgets is that soil N availability did not limit growth in most treatments. Although N often is the nutrient plants need in highest quantities, the only treatment in which plants clearly were N-limited was when *A. desertorum* competed with *B. tectorum* neighbors. Lack of evidence for N-limited growth in this study could be due to multiple factors. It may be that when we disturbed the soil to fill the pots, we released sufficient N to meet seedling demand. Alternatively, it is possible that due to soil disturbance or other factors, other resources, such as phosphorous, may have been limiting, thus constraining plant response to N addition. These caveats confine our ability to evaluate plasticity in plant biomass production and the importance of this plasticity under potential field scenarios. However, nutrient addition studies indicate that N is one of the key nutrients limiting biomass production in this and related steppe systems (e.g., Drenovsky et al. 2016), suggesting that some of the species-specific responses we observed in our pot study may have some relevance to the field. Given the nature of our study, we only are able to consider a short window of plant development and species interactions. Additionally, we acknowledge that other processes and conditions, including trophic interactions, drought, and safe site limitations may be stronger drivers of differences in population growth rate among the species studied here or other similar species in this system.

Effect and response traits are increasingly being used as a framework to understand species distribution and community assembly as well as patterns of plant invasion and invasion resistance (Suding et al. 2008; Drenovsky et al. 2012a). While much progress has been made in this field, research largely has centered on traits related to plant tissue construction and carbon capture (Diaz et al. 2004; Leishman et al. 2007; van Kleunen et al. 2010; Sandel and Dangremond 2012), whereas understanding how traits influencing whole plant nutrient budgets, in response to competition and low nitrogen availability, has remained relatively

unexplored (Drenovsky et al. 2012b; Funk 2013). Our key results indicated that the introduced perennial bunchgrass *A. desertorum* growing without *B. tectorum* neighbors allocated less biomass to roots, had greater root N uptake rates, and used N more efficiently than the native perennial bunchgrass *P. spicata* under both high and low N supply. These trait differences between species are largely consistent with the literature, showing that *A. desertorum* has a greater ability to establish from seed than native perennials, particularly in disturbed areas free of competition (e.g. Dewey 1986; James et al. 2011b). Importantly, however, these trait differences largely disappeared under competition, and our results provided no evidence that these perennial species greatly differed in their ability to resist competitive suppression by *B. tectorum*.

It is also important to recognize that numerous plant traits determine how seedlings respond to the suite of abiotic and biotic stressors influencing plant recruitment and survival and that different traits may be important for determining survival across life stages (Larson et al. 2015). Although our study did not investigate the relative importance of traits influencing seedling recruitment or manipulate other abiotic stressors, such as drought, that ultimately may influence survival (Mangla et al. 2011), our results suggest nutrient budget-related traits may contribute to the higher establishment and persistence of *A. desertorum* seedlings in the field when competitive pressure is low. However, for the plant developmental stages examined in this study, these same traits do not appear to increase the ability of *A. desertorum* to resist or inhibit the growth of *B. tectorum*, even under augmented soil N availability.

While *A. desertorum* is still widely used for stabilizing sites following disturbance, there is a growing interest and demand to identify locally sourced populations of native plant species that have high probabilities of surviving following seeding (Plant Conservation Alliance 2015). Nutrient conservation traits have almost been entirely excluded from native population screening efforts, and our results suggest some relatively simple measurements could be used to identify subsets of local populations that may have greater survival following restoration efforts, particularly if abundance of competing neighbors is managed. From a global perspective, our results suggest there may be large value in expanding work on plant ecological strategies to include traits related to nutrient conservation and productivity as well as understanding

how these key response traits change under competition or other environmental stresses.

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