

Effect of soil nitrogen stress on the relative growth rate of annual and perennial grasses in the Intermountain West

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Abstract A high relative growth rate (RGR) is thought to be an important trait allowing invasive annual grasses to exploit brief increases in nitrogen (N) supply following disturbance in the Intermountain West. Managing soils for low N availability has been suggested as a strategy that may reduce this growth advantage of annual grasses and facilitate establishment of desirable perennial grasses. The objective of this study was to examine the degree to which soil N availability affects RGR and RGR components of invasive annual and desirable perennial grasses. It was hypothesized that (1) invasive annual grasses would demonstrate a proportionately greater reduction in RGR than perennial grasses as soil N stress increased, and (2) the mechanism by which low N availability decreases RGR of annual and perennial grasses would depend on the severity of N stress, with moderate N stress primarily affecting leaf mass ratio (LMR) and severe N stress primarily affecting net assimilation rate (NAR). Three annual and three perennial grasses were exposed to three levels of N availability. RGR and components of RGR were quantified over four harvests. Moderate N stress reduced RGR by decreasing LMR and severe N

stress lowered RGR further by decreasing NAR. However, reduction in RGR components was similar between invasive and natives, and as a consequence, annual grasses did not demonstrate a proportionately greater reduction in RGR than perennials under low N conditions. These results suggest managing soil N will do little to reduce the initial growth advantage of annual grasses. Once perennials establish, traits not captured in this short-term study, such as high tissue longevity and efficient nutrient recycling, may allow them to compete effectively with annuals under low N availability. Nevertheless, if soil N management does not facilitate the initial establishment of perennials in annual grass infested communities, then there is little likelihood that such techniques will provide a long-term benefit to restoration projects in these systems.

Keywords Annual grasses · *Bromus tectorum* · Great Basin · Nutrients · *Taeniatherum caput-medusae*

Introduction

In nitrogen (N) limited, semi-arid systems, increases in soil N availability following disturbance are expected to be a central factor influencing invasive plant establishment (Stohlgren et al. 1999; Davis et al. 2000). A high relative growth rate (RGR) is thought to be an important trait allowing invasives to exploit these brief increases in N supply (Baker 1974;

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Grotkopp et al. 2002; Burns 2004). Following disturbance, a high RGR allows seedlings of invasives to initially establish a more extensive root and shoot system than natives. This initial size advantage allows invasives to capture more resources than natives and minimizes their exposure to drought stress as upper surface soils dry during the growing season (Grotkopp and Rejmanek 2007).

Soil management techniques that lower N availability, such as cover cropping or carbon addition, have been suggested as a strategy to reduce the initial growth rate advantage of invasives species following disturbance (Blumenthal et al. 2003; Krueger-Mangold et al. 2006). Support for this idea comes from studies on native species showing that while fast-growing species tend to maintain higher absolute growth rates than slow-growing species on infertile soils, fast-growing species demonstrate the greatest reduction in RGR when nutrients are limiting (Robinson and Rorison 1988; Shipley and Keddy 1988; Fichtner and Schulze 1992; Meziane and Shipley 1999a). However, specific tests of the hypothesis that low N availability decreases RGR of invasives proportionately more than natives are limited. Such information may allow more accurate prediction of when soil N management may be most likely to shift weed-infested plant communities to a more desired state.

There may be a number of mechanisms by which soil N stress differentially impacts the RGR of native and invasives. RGR can be factored into two components, net assimilation rate (NAR, rate of dry matter production per unit leaf area) and leaf area ratio (LAR, leaf area per unit total plant mass) (Evans 1972; Causton and Venus 1981). NAR is primarily determined by the balance of carbon gained through photosynthesis and carbon lost through respiration. LAR reflects the amount of leaf area a plant develops per unit total plant mass and therefore depends on the proportion of biomass allocated to leaves relative to total plant mass (leaf mass ratio, LMR) and how much leaf area a plant develops per unit biomass allocated to leaves (specific leaf area, SLA). Specific leaf area, in turn, is a function of leaf tissue density and leaf thickness (Meziane and Shipley 1999b). Although SLA consistently has been identified as a central factor driving interspecific variation in RGR and as a trait associated with invasiveness (Poorter 1989; Leishman et al. 2007), and nutrient stress can decrease SLA and NAR, low nutrient availability appears to have the largest affect

on RGR by decreasing LMR (Poorter and Nagel 2000; Taub 2002). There are some theoretical grounds for predicting fast-growing species will demonstrate a proportionately greater reduction in LMR in infertile soil than slow-growing species (Chapin 1980; Grime et al. 1991). However, empirical support for these predictions has been mixed (Christie and Moorby 1975; Grime and Curtis 1976; Elberse and Berendse 1993; Reynolds and D'Antonio 1996; Meziane and Shipley 1999a), and it is not known if N stress causes a proportionately greater reduction in LMR of invasives compared to natives.

The mechanism by which low N availability decreases RGR may depend on the severity of N stress. For example, plants may respond to moderate N stress by increasing biomass allocation to roots, but under severe N stress, NAR may be the most important variable driving a reduction in RGR (de Groot et al. 2002). Research on native species has shown that while NAR is higher in fast-growing compared to slow-growing species under N-rich conditions, when N is limiting this difference diminishes (Fichtner and Schulze 1992; Meziane and Shipley 1999a; Taub 2002). If these findings hold for native and invasive species, severe N limitations may reduce RGR of invasives proportionately more than natives due to negative effects on NAR.

Annual grass invasion of the Intermountain West, a landscape historically dominated by slow-growing perennials, is considered one of the most serious invasions in North America (D'Antonio and Vitousek 1992). In these systems, N availability limits growth and only small increases in N supply following disturbance are needed promote invasion (Paschke et al. 2000; Brooks 2003). Once established, annual grasses maintain site dominance and suppress the establishment of desired perennial grasses, even when these species are sown (Laycock 1991; Humphrey and Schupp 2004). Although slow-growing species often possess a suite of traits that allow them to be better competitors than fast-growing species under nutrient-poor conditions (e.g., high herbivory tolerance, tissue longevity, high root allocation and tight nutrient recycling) (Wedin and Tilman 1993; Aerts 1999; Fraser and Grime 1999), they may need to survive several growing seasons before the full benefits of these traits are realized. If managing soil N reduces the initial growth advantage of annual grasses by reducing RGR, then this strategy might facilitate establishment of desirable perennials

and provide an opportunity for these species to realize the benefit of other traits associated with competitive ability in nutrient-poor systems.

The objective of this study is to examine the degree to which soil N availability affects RGR and RGR components of invasive annual and desirable perennial grasses. It was hypothesized that (1) invasive annual grasses would demonstrate a proportionately greater reduction in RGR than perennial grasses as soil N stress increased, and (2) the mechanism by which low N availability decreases RGR of annual and perennial grasses would depend on the severity of N stress, with moderate N stress primarily affecting LMR and severe N stress primarily affecting NAR.

Materials and methods

Study species, growth conditions and harvests

The study species selected for this experiment included three annual grasses that have extensively invaded the Intermountain West and three perennial grass species widely used in efforts to restore these systems (Table 1). Two perennial species, *Pseudoroegneria spicata* and *Elymus elymoides*, are native to the Intermountain West while *Agropyron desertorum* is an introduced perennial grass native to Siberia that has been bred for reclamation programs. *Agropyron desertorum* is better able to interfere with the growth of invasive annuals than the native bunchgrasses making this species a useful comparison to include (Harris and Wilson 1970). The annual grasses used in this study are native to Eurasia and the Mediterranean region. Of the annual grasses *B. tectorum* and *T. caput-medusae* appear to be the most serious invaders with *B. tectorum* most capable of invading the broadest

range of habitats. *Ventenata dubia* is less widespread than the other annual grasses, but introduction of *V. dubia* has been more recent. Consequently, the potential ecological impacts of this species are less well known (Northam and Callihan 1994).

The study was conducted in spring 2007 in a common garden at the Eastern Oregon Agricultural Research Center, Burns, OR, US. The experiment was a completely randomized design consisting of six species, three N levels (0.04, 0.4 and 4.0 mM), and four harvests with ten replicates per treatment per harvest. Individual seeds of each species were planted in small paper pots and germinated under ambient environmental conditions. Seeds of perennial species were obtained from a commercial supplier while annual grass seed was collected from local populations. Planting times were staggered so that all species emerged within the same week. One week after emergence seedlings were transplanted into pots filled with a 1:2 mixture of sandy loam field soil and coarse sand. All transplanted seedlings were at the one leaf stage. Within a species, similar-sized plants were selected for the experiment to reduce variation in RGR estimates due to initial size differences. Pot sizes for the first and second harvest were 12 cm diameter×30 cm deep. Larger pots (20 cm diameter×50 cm deep) were used for the third and fourth harvest. The first harvest was conducted 1 week after transplanting. The second, third and fourth harvests were conducted at 10 day intervals after the first harvest. A preliminary study demonstrated that smaller pot sizes did not alter seedling growth compared to larger pots during the first 3 weeks of growth. Average minimum and maximum air temperature during the experiment was 5.05°C and 26.1°C, respectively. During the course of the experiment photosynthetically active radiation at solar noon averaged 1,790 $\mu\text{mol m}^{-2} \text{s}^{-1}$. From 0700 to 1900 PAR

Table 1 List of the six species used in this study

Functional group	Common name	Species	Species abbreviation
Annual	Cheatgrass	<i>Bromus tectorum</i> L.	BRTE
	Medusahead	<i>Taeniatherum caput-medusae</i> (L.) Nevski	TACA
	Ventenata	<i>Ventenata dubia</i> (Leers) Coss.	VEDU
Perennial	Crested wheatgrass	<i>Agropyron desertorum</i> (Fisch. ex Link) J.A. Schultes	AGDE
	Bluebunch wheatgrass	<i>Pseudoroegneria spicata</i> (Pursh) A. Löve	PSSP
	Bottlebrush squirreltail	<i>Elymus elymoides</i> (Raf.) Swezey	ELEL

Species are arranged by functional group (annual grass or perennial grass). Nomenclature follows the USDA PLANTS database (<http://plants.usda.gov/>)

averaged $797 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the course of the experiment.

Nitrogen was supplied as both NO_3^- and NH_4^+ in a one-quarter strength modified Hoagland's solution (Epstein 1972). Supplemental salts (KH_2PO_4 , K_2SO_4 and CaCl_2) were added in the 0.04 and 0.4 mM N treatments to maintain similar levels of other macronutrients. Pots were saturated with nutrient solution three times a week and heavily watered with distilled water once a week to minimize nutrient accumulation. The watering solution drained quickly from this very coarse mixture of sand and sandy field soil. Volumetric water content following watering was less than 14% suggesting these water inputs did not induce anaerobic stress. Eight pots within each N level treatment were randomly selected and watered to field capacity with their respective nutrient solution 4 h before the final harvest. A composite soil sample from the 0–5, 15–20 and 25–30 soil layers was collected from these pots during the final harvest and analyzed for total inorganic N (NO_3^- and NH_4^+) colorimetrically following Forster (1995) for NH_4^+ and Miranda et al. (2001) for NO_3^- . Shortly after being watered to field capacity, the 0.04, 0.4 and 4.0 mM N treatments resulted in total soil inorganic N levels of 0.3 ± 0.1 , 1.4 ± 0.2 and $16.2 \pm 0.6 \text{ mg kg}^{-1}$, respectively ($n=8$, $\pm\text{SE}$) which is within the range that soil inorganic N concentration can vary in these systems (Cui and Caldwell 1997; Peek and Forseth 2003; James et al. 2006).

Growth analysis and statistics

For each harvest aboveground biomass was clipped and separated into leaves and stems. Roots were recovered by washing over a fine mesh screen. Leaf fresh weight and area and root length (WinRHIZO, Regent Instruments Inc., Saint-Foy, Canada) were recorded. All material was then dried at 65°C and weighed. Leaf material was finely ground and analyzed for N concentration by micro-Dumas combustion using a CN analyzer (Carlo Erba, Milan, Italy). Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), leaf mass ratio (LMR), leaf dry matter (DM) content and leaf thickness were calculated over all harvest intervals. Calculations of means and SE followed Causton and Venus (1981) for ungraded and unpaired harvest. The Excel file published in Hunt

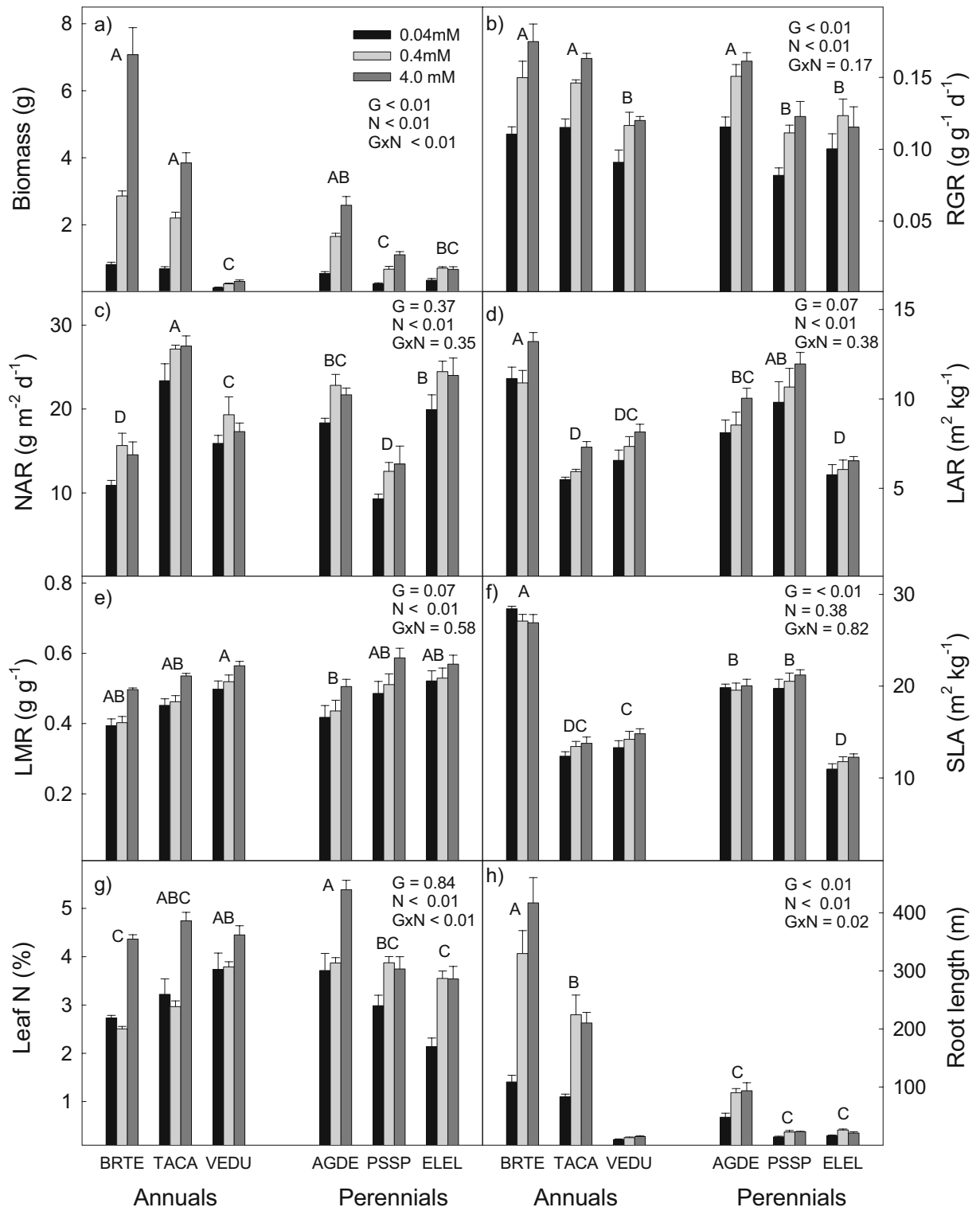
et al. (2002) (http://www.ex.ac.uk/~rh203/growth_analysis.html) was used to perform the calculations. Leaf DM was used as an estimate of leaf tissue density (Ryser and Lambers 1995). Leaf thickness was estimated following Atkin et al. (1996). Analysis of variance was used to analyze how soil N availability influences RGR and RGR components of annual and perennial grasses (SAS 2001). ANOVA assumptions were evaluated using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. When homogeneity of variance was violated data were weighted by the inverse of the variance (Neter et al. 1990). Annuals tend to have a higher inherent RGR than perennial grasses (Garnier 1992) and fast-growing species are expected to maintain a higher absolute growth rate than slow-growing species in infertile soils (Lambers and Poorter 1992). Thus, while a main effect of functional group on RGR is expected, an interaction between functional group and N stress would indicate that N stress had a greater relative effect on one functional group's RGR compared to another.

The natural log response ratio (lnRR) was used to examine the effect of N stress on RGR and RGR components (Hedges et al. 1999) where $\text{lnRR} = \ln(\text{Value}_{\text{lowN}}/\text{Value}_{\text{highN}})$. More negative values indicate a greater reduction in the growth parameter with decreasing soil N availability. Response ratios were calculated for the initial decrease in N availability from 4.0 to 0.4 mM and for the further decrease in N availability from 0.4 to 0.04 mM.

Results

Low N availability reduced biomass, leaf N and root length in both annual and perennial grasses (Fig. 1a,

Fig. 1 **a** Biomass, **b** relative growth rate (RGR), **c** net assimilation rate (NAR), **d** leaf area ratio (LAR), **e** leaf mass ratio (LMR), **f** specific leaf area (SLA), **g** leaf N and **h** root length of annual and perennial grasses growing under three levels of N availability (mean \pm SE). Biomass, leaf N and root length are values from the final harvest. All other parameters are averaged over the four harvests ($n=10$ per harvest). Calculations of mean follow Causton and Venus (1981) and Hunt et al. (2002) for ungraded and unpaired harvests. Species abbreviations follow Table 1. The effect of functional group (*G*, annual or perennial) and nitrogen availability (*N*, 0.04, 0.4, 4.0 mM) and their interaction are shown for each parameter. Uppercase letters over bars indicate significant differences among species averaged over the three levels of N availability as determined with Tukey pairwise comparisons ($P<0.05$)



g, h). Invasive annual grasses tended to produce more biomass and root length than perennials at all levels of N supply with the exception being the annual grass *V. dubia*, which produced significantly less biomass than the other invasive annual grasses. This suggests the overall differences between annual and perennial grasses in biomass and root length production was driven by the two annual grasses *B. tectorum* and *T. caput-medusae*. Low N availability also reduced tiller production in both species groups but annuals produced more tillers than perennials at both low (34 ± 5 versus 8 ± 1 plant⁻¹) and high N supply (143 ± 16 versus 14 ± 2 plant⁻¹) (mean \pm SE, $P < 0.001$).

While low N availability decreased RGR of all species (Fig. 1b) the magnitude of decline did not differ between annuals and perennials. At the lowest N level the invasive annual grasses maintained a higher RGR than native perennials ($P = 0.041$). Low soil N availability decreased NAR and LAR in all species (Fig. 1c–d). There was large variation in NAR and LAR among species within these functional groups and no evidence suggesting consistent differences in NAR and LAR among these annual and perennial grasses. Low soil N availability decreased LMR of annual and perennial grasses to a similar degree. Low soil N availability did not influence SLA of annual or perennial grasses (Fig. 1f). Similarly, factors influencing SLA such as leaf DM, thickness and ash content were not affected by soil N availability ($P > 0.2$, Table 2). Decreasing soil N from 4.0 to 0.4 mM reduced RGR mainly through a reduction in

Table 2 Leaf dry matter (DM) content, thickness and ash content of the six study species

Group	Species	DM (%)	Thickness (g FW m ⁻²)	Ash (%)
Annual	BRTE	18.1E	207C	17.2A
	TACA	29.3B	269B	18.1A
	VEDU	27.9CB	290A	ND
Perennial	AGDE	25.5D	216C	13.6C
	PSSP	27.1CD	200C	12.3C
	ELEL	31.5A	288A	15.4B

There was no significant effect of N availability on these leaf parameters ($P > 0.2$). Values are averaged across the three N levels. Ash on *V. dubia* was not determined (ND) because of insufficient leaf mass at the lower N levels. Different letters indicate significant differences among species as determined with Tukey pairwise comparisons ($P < 0.05$)

Table 3 Response ratio of RGR and RGR components for plants when N was reduced from 4.0 to 0.4 mM and when N was reduced further from 0.4 to 0.04 mM

Group	Species	Parameter	lnRR (4.0–0.4 mM)	lnRR (0.4–0.04 mM)
Annual	BRTE	RGR	-0.15	-0.30
		NAR	0.07	-0.36
		LMR	-0.21	-0.02
		SLA	0.01	0.05
	TACA	RGR	-0.11	-0.24
		NAR	-0.01	-0.15
		LMR	-0.15	-0.02
		SLA	-0.03	-0.08
	VEDU	RGR	-0.03	-0.25
		NAR	0.11	-0.19
		LMR	-0.08	-0.04
		SLA	-0.04	-0.07
Perennial	AGDE	RGR	-0.07	-0.27
		NAR	0.05	-0.22
		LMR	-0.15	-0.04
		SLA	-0.02	0.01
	PSSP	RGR	-0.10	-0.31
		NAR	-0.07	-0.30
		LMR	-0.14	-0.05
		SLA	-0.03	-0.04
	ELEL	RGR	0.07	-0.21
		NAR	0.02	-0.21
		LMR	-0.07	-0.02
		SLA	-0.04	-0.07

Response ratios were calculated using the natural log response ratio (lnRR) where $\lnRR = \ln(\text{Value}_{\text{lowN}} / \text{Value}_{\text{highN}})$ (Hedges et al. 1999). More negative values indicate a greater reduction in the growth parameter with decreasing soil N availability

LMR (Table 3). Reducing soil N from 0.4 to 0.04 mM N decreased RGR in most species mainly through a reduction in NAR.

While there were few consistent differences in how soil N stress affected the RGR of annual and perennials, there was significant variation in RGR components among species within a functional group (Fig. 1c–f). For example, the annual grass *T. caput-medusae* had a higher NAR than perennial species at all N levels, while the annual grass *B. tectorum* demonstrated a NAR lower than or comparable to the perennial grasses. *Bromus tectorum*, on the other hand, demonstrated a higher LAR and SLA than the perennial grasses, while *T. caput-medusae* had a LAR and SLA comparable to or lower than the perennial grasses.

Discussion

While the potential for invasives to achieve a higher RGR than their native or non-invasive counterparts is well-documented (Grotkopp et al. 2002; Grotkopp and Rejmanek 2007; James and Drenovsky 2007), only a handful of studies have examined the degree to which nutrient stress impacts RGR of these species groups. To date this literature has largely supported the idea that nutrient stress constrains RGR of invasive species to rates comparable to native or non-invasive species (Burns 2004; Garcia-Serrano et al. 2005). Contrary to these studies, and the first hypothesis, invasives in this study did not demonstrate a proportionately greater reduction in RGR than natives when grown under low N conditions.

Contrasting results between the current study and previous work could be due, in part, to the confounding influence of life history differences between invasive and non-invasive species in this study. Annuals tend to produce less dense root tissue than perennials, thus creating more root surface area per unit biomass invested in roots (Roumet et al. 2006). While a consistent biomass allocation difference between annuals and perennials was not observed, annuals may have been able to more fully exploit the soil N pool under N-limiting conditions by creating more root surface area per unit root biomass, and thus, experience a less severe reduction in RGR (Ryser and Lambers 1995). However, *B. tectorum* also maintained a higher SLA than perennials, while *T. caput-medusae* also maintained a higher NAR than perennials. These differences were not observed between the less serious invader *V. dubia* and the perennial grasses, indicating SLA and NAR are important traits of invaders that are not exclusively unique to annuals in this system.

Although previous research has suggested SLA as the main driver of RGR variation among species from different habitats (Poorter 1989), in this study, species achieving comparable RGR did so in different ways. For example, *E. elymoides* maintained a higher NAR than *P. spicata* while *P. spicata* maintained higher SLA than *E. elymoides*, ultimately resulting in a comparable RGR among the native perennials. A similar trade-off was observed between the annual grasses *B. tectorum* and *T. caput-medusae*. In general, NAR and SLA are negatively correlated, as a high NAR requires a large investment in photo-

synthetic machinery and thus lowers SLA (Konings 1989).

In support of the second hypothesis, the mechanism by which low N decreases RGR of annual grasses and perennials depended on the severity of N stress. Following an initial reduction in N availability, all plants decreased LMR but maintained a comparable NAR. Severe N stress decreased NAR but had no further effect on LMR. A meta-analysis by Poorter and Nagel (2000) suggested low N availability reduces RGR mainly by decreasing LMR, although effects of nutrient stress on SLA and NAR also were observed. Under moderate N stress, increased root biomass allocation, which lowers LMR, may allow plants to capture sufficient N to avoid a reduction in photosynthetic rates, buffering negative effects of low soil N availability on NAR (Meziane and Shipley 1999a). Few studies have examined how severity of N stress influences the degree to which LMR and NAR influence RGR. While N stress did not change the relative influence of LMR and NAR on RGR of barley (Elberse et al. 2003), NAR was the most important factor explaining the effect of severe N and P limitations on RGR of tomato (de Groot et al. 2001; de Groot et al. 2002). Above a certain root weight ratio, further root biomass allocation may not be advantageous (van der Werf et al. 1993). Without additional increases in root biomass it may not be possible for a plant to maintain adequate nutrient capture, and as a result, NAR may decline.

There was no evidence to suggest that severe N stress reduced NAR of invasives more than natives. This observation contrasts with previous work suggesting slow-growing species have a smaller NAR reduction than fast-growing species under infertile conditions (Fichtner and Schulze 1992; Meziane and Shipley 1999a; Taub 2002). While the reduction in NAR was comparable among species, there was some evidence suggesting this decrease in NAR may have occurred in different ways. NAR is positively correlated with photosynthesis but negatively correlated with whole-plant respiration rate (Konings 1989). Reduced NAR of the native species, *P. spicata* and *E. elymoides*, was associated with decreased leaf N concentration, suggesting N stress may have reduced NAR by lowering leaf photosynthetic capacity (Hirose and Werger 1987). In contrast, reduced NAR of the introduced perennial, *A. desertorum*, and the invasive

annuals was not associated with decreased leaf N or an appreciable change in biomass allocation, suggesting changes in whole-plant respiration rates may determine NAR of these species at low N.

The comparable effects of soil N stress on LMR of native and invasive species does not support the prediction that fast-growing species will demonstrate greater plasticity in biomass allocation than slow-growing species. One potential reason for this lack of difference may be because biomass allocation does not adequately represent allocation to physiological functions (Korner and Renhardt 1987). Another reason may be that environmental conditions constrain biomass allocation in this system. Grotkopp and Rejmanek (2007) have shown that in seasonally dry systems the most successful invaders balanced fast seedling growth and biomass allocation to roots. In the current experiment, averaged across N treatments, invasive annuals and native perennials had comparable LMR, and root weight ratio of all species in the high N treatment exceeded 0.4 (data not shown). These observations suggest seasonal drought may limit the plasticity of invasive and native biomass allocation to a similar degree.

While the SLA of these species did not change with N stress, this does not mean that inherent differences in SLA among native and invasive species are not important in determining competitive outcomes in nutrient poor-systems. Although a high SLA has been correlated with invasiveness, a high SLA may not be advantageous when nutrients are limiting (Hamilton et al. 2005; Leishman et al. 2007). In nutrient-limited systems, conservation of previously captured resources is expected to be at least as important to plant performance as rapid growth and resource capture (Berendse and Aerts 1987). Constructing long-lived leaves that are well-defended from herbivores decreases SLA, and consequently, RGR, but increases nutrient conservation (Coley 1988; Reich et al. 1997). Even though RGR of fast and slow-growing species were not differentially affected by N stress in this experiment, if slow-growing native species demonstrate greater herbivory tolerance because of a low SLA, then these species may be competitively superior on infertile sites (Fraser and Grime 1999). There are three lines of evidence, though, that suggest herbivory may do little to alter competitive interactions among invasive and native species in this system. First, two of the

invasives (*V. dubia* and *T. caput-medusae*) had a SLA lower than or comparable to the natives. Based on the above theory, we would not expect these invasives to be more susceptible to herbivory than natives. Second, there is evidence that SLA differences among species in this system are related to drought tolerance, and it is possible that seasonal drought exerts a stronger selective pressure on SLA than herbivory (Harris and Wilson 1970). Third, recent research suggests invasives in their new range may be more resistant to generalist herbivores than natives (Joshi and Vrieling 2005; Leger and Forister 2005). While herbivory was not examined in this experiment, these factors suggest the impact of herbivory in this system could range from having no effect on interactions between natives and invasives to potentially favoring the growth of invasives over natives.

Conclusion

In the Intermountain West there has been much interest in using soil N management to reduce the initial growth rate and competitive ability of annual grasses in order to provide an opportunity for perennial grasses to establish (Krueger-Mangold et al. 2006). In this study, however, invasives and natives demonstrated a proportionately similar reduction in RGR with increasing N stress. While the small number of species used in this experiment and the comparatively small differences in RGR among species mean that these results need to be interpreted with caution, the patterns of response observed in this experiment suggest managing soil N will do little to reduce the initial growth advantage of these annual grasses. Given the short-term nature of this study, it was not possible to assess how these relationships may change over multiple growing seasons. It is possible that once perennials establish, traits such as high tissue longevity and efficient nutrient recycling may allow them to compete effectively with annuals under low N availability. Field studies on populations that specifically include trophic interactions over multiple generations ultimately are needed to quantify the effects of soil N stress on the demography of invasive annual and native perennial grasses. Nevertheless, if soil N management does not directly facilitate the establishment of perennials in annual grass infested communities by reducing

differences in RGR, then there is little likelihood that such techniques will provide a long-term benefit to restoration projects in these systems.

References

- Aerts R (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant–soil feedbacks. *J Exp Bot* 50:29–37 DOI [10.1093/jexbot/50.330.29](https://doi.org/10.1093/jexbot/50.330.29)
- Atkin OK, Botman B, Lambers H (1996) The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland *Poa* species. *Funct Ecol* 10:698–707 DOI [10.2307/2390504](https://doi.org/10.2307/2390504)
- Baker HG (1974) The evolution of weeds. *Ann Rev Ecol Syst* 5:1–24 DOI [10.1146/annurev.es.05.110174.000245](https://doi.org/10.1146/annurev.es.05.110174.000245)
- Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? *Funct Ecol* 1:293–296
- Blumenthal DM, Jordan NR, Russelle MP (2003) Soil carbon addition controls weeds and facilitates prairie restoration. *Ecol Appl* 13:605–615 DOI [10.1890/1051-0761\(2003\)013\[0605:SCACWA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0605:SCACWA]2.0.CO;2)
- Brooks ML (2003) Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *J Appl Ecol* 40:344–353
- Burns JH (2004) A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. *Divers Distrib* 10:387–397 DOI [10.1111/j.1366-9516.2004.00105.x](https://doi.org/10.1111/j.1366-9516.2004.00105.x)
- Causton DR, Venus JC (1981) The biometry of plant growth. Edward Arnold, London
- Chapin FS (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233–260 DOI [10.1146/annurev.es.11.110180.001313](https://doi.org/10.1146/annurev.es.11.110180.001313)
- Christie EK, Moorby J (1975) Physiological responses of semiarid grasses. I. The influence of phosphorus supply on growth and phosphorus absorption. *Aust J Agric Res* 26(3):423–436 DOI [10.1071/AR9750423](https://doi.org/10.1071/AR9750423)
- Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74:531–536 DOI [10.1007/BF00380050](https://doi.org/10.1007/BF00380050)
- Cui MY, Caldwell MM (1997) A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant Soil* 191:291–299 DOI [10.1023/A:1004290705961](https://doi.org/10.1023/A:1004290705961)
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Ann Rev Ecol Syst* 23:63–87
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534 DOI [10.1046/j.1365-2745.2000.00473.x](https://doi.org/10.1046/j.1365-2745.2000.00473.x)
- de Groot CC, Marcelis LFM, Boogaard Rvd, Lambers H (2001) Growth and dry-mass partitioning in tomato as affected by phosphorus nutrition and light. *Plant Cell Environ* 24:1309–1317 DOI [10.1046/j.0016-8025.2001.00788.x](https://doi.org/10.1046/j.0016-8025.2001.00788.x)
- de Groot CC, Marcelis LFM, van den Boogaard R, Lambers H (2002) Interactive effects of nitrogen and irradiance on growth and partitioning of dry mass and nitrogen in young tomato plants. *Functional Plant Biology* 29:1319–1328 DOI [10.1071/FP02087](https://doi.org/10.1071/FP02087)
- Elberse IAM, Van Damme JMM, Van Tienderen PH (2003) Plasticity of growth characteristics in wild barley (*Hordeum spontaneum*) in response to nutrient limitation. *J Ecol* 91:371–382 DOI [10.1046/j.1365-2745.2003.00776.x](https://doi.org/10.1046/j.1365-2745.2003.00776.x)
- Elberse WT, Berendse F (1993) A comparative study of the growth and morphology of eight grass species from habitats with different nutrient availabilities. *Funct Ecol* 7:223–229 DOI [10.2307/2389891](https://doi.org/10.2307/2389891)
- Epstein E (1972) Mineral nutrition of plants: principles and perspectives. Wiley, New York
- Evans GC (1972) The quantitative analysis of plant growth. University of California Press, Berkeley
- Fichtner K, Schulze ED (1992) The effect of nitrogen nutrition on growth and biomass partitioning of annual plants originating from habitats of different nitrogen availability. *Oecologia* 92:236–241 DOI [10.1007/BF00317370](https://doi.org/10.1007/BF00317370)
- Forster JC (1995) Soil nitrogen. In: Alef K, Nannipieri P (eds) Methods in applied soil microbiology and biochemistry. Academic, San Diego, pp 79–87
- Fraser LH, Grime JP (1999) Interacting effects of herbivory and fertility on a synthesized plant community. *J Ecol* 87:514–525 DOI [10.1046/j.1365-2745.1999.00373.x](https://doi.org/10.1046/j.1365-2745.1999.00373.x)
- Garcia-Serrano H, Escarre J, Garnier E, Sans XF (2005) A comparative growth analysis between alien invader and native *Senecio* species with distinct distribution ranges. *Ecoscience* 12:35–43 DOI [10.2980/i1195-6860-12-1-35.1](https://doi.org/10.2980/i1195-6860-12-1-35.1)
- Garnier E (1992) Growth analysis of congeneric annual and perennial grass species. *J Ecol* 80:665–675 DOI [10.2307/2260858](https://doi.org/10.2307/2260858)
- Grime JP, Curtis AV (1976) The interaction of drought and mineral nutrient stress in calcareous grassland. *J Ecol* 64:975–988 DOI [10.2307/2258819](https://doi.org/10.2307/2258819)
- Grime JP, Campbell BD, Mackey JML, Crick JC (1991) Root plasticity, nitrogen capture and competitive ability. In: Atkinson D (ed) Plant root growth: an ecological perspective. Blackwell, Oxford, pp 381–397
- Grotkopp E, Rejmanek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *Am J Bot* 94:526–532 DOI [10.3732/ajb.94.4.526](https://doi.org/10.3732/ajb.94.4.526)
- Grotkopp E, Rejmanek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *Am Nat* 159:396–419 DOI [10.1086/338995](https://doi.org/10.1086/338995)
- Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecol Lett* 8:1066–1074 DOI [10.1111/j.1461-0248.2005.00809.x](https://doi.org/10.1111/j.1461-0248.2005.00809.x)
- Harris GA, Wilson AM (1970) Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperatures. *Ecology* 51:529–534 DOI [10.2307/1935392](https://doi.org/10.2307/1935392)
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156
- Hirose T, Werger MJA (1987) Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. *Physiol Plant* 70:215–222 DOI [10.1111/j.1399-3054.1987.tb06134.x](https://doi.org/10.1111/j.1399-3054.1987.tb06134.x)

- Humphrey LD, Schupp EW (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 DOI [10.1016/j.jaridenv.2003.11.008](https://doi.org/10.1016/j.jaridenv.2003.11.008)
- Hunt R, Causton DR, Shipley B, Askew AP (2002) A modern tool for classical plant growth analysis. *Ann Bot* 90:485–488 DOI [10.1093/aob/mcf214](https://doi.org/10.1093/aob/mcf214)
- James JJ, Drenovsky RE (2007) A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology & Management* 60:395–400 DOI [10.2111/1551-5028\(2007\)60\[395:ABFRGR\]2.0.CO;2](https://doi.org/10.2111/1551-5028(2007)60[395:ABFRGR]2.0.CO;2)
- James JJ, Aanderud ZT, Richards JH (2006) Seasonal timing of N pulses influences N capture in a saltbush scrub community. *J Arid Environ* 67:688–700 DOI [10.1016/j.jaridenv.2006.03.014](https://doi.org/10.1016/j.jaridenv.2006.03.014)
- Joshi J, Vrieling K (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecol Lett* 8:704–714. DOI [10.1111/j.1461-0248.2005.00769.x](https://doi.org/10.1111/j.1461-0248.2005.00769.x)
- Konings H (1989) Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. In: Lambers H (ed) Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic, The Hague, pp 101–123
- Korner C, Renhardt U (1987) Dry matter partitioning and root length/leaf area ratios in herbaceous perennial plants with diverse altitudinal distribution. *Oecologia* 74:411–418. DOI [10.1007/BF00378938](https://doi.org/10.1007/BF00378938)
- Krueger-Mangold J, Sheley RL, Svejcar TJ (2006) Toward ecologically-based invasive plant management on rangeland. *Weed Sci* 54:597–605 DOI [10.1614/WS-05-049R3.1](https://doi.org/10.1614/WS-05-049R3.1)
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv Ecol Res* 23:187–261
- Laycock WA (1991) Stable states and thresholds of range condition on North American rangelands: a viewpoint. *J Range Manag* 44:427–433 DOI [10.2307/4002738](https://doi.org/10.2307/4002738)
- Leger EA, Forister ML (2005) Increased resistance to generalist herbivores in invasive populations of the California poppy (*Eschscholzia californica*). *Divers Distrib* 11:311–317. DOI [10.1111/j.1366-9516.2005.00165.x](https://doi.org/10.1111/j.1366-9516.2005.00165.x)
- Leishman MR, Haslehurst T, Ares A, Baruch Z (2007) Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytol* 176:635–643 DOI [10.1111/j.1469-8137.2007.02189.x](https://doi.org/10.1111/j.1469-8137.2007.02189.x)
- Meziane D, Shipley B (1999a) Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. *Funct Ecol* 13:611–622 DOI [10.1046/j.1365-2435.1999.00359.x](https://doi.org/10.1046/j.1365-2435.1999.00359.x)
- Meziane D, Shipley B (1999b) Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. *Plant Cell Environ* 22:447–459. DOI [10.1046/j.1365-3040.1999.00423.x](https://doi.org/10.1046/j.1365-3040.1999.00423.x)
- Miranda KM, Espey MG, Wink DA (2001) A rapid, simple spectrophotometric method for simultaneous determination of nitrate and nitrite. *Nitric Oxide* 5:62–71 DOI [10.1006/niox.2000.0319](https://doi.org/10.1006/niox.2000.0319)
- Neter J, Wasserman W, Kutner MH (1990) Applied linear statistical models: regression, analysis of variance and experimental design. Irwin, Homewood
- Northam FE, Callihan RH (1994) New weedy grasses associated with downy brome. General Technical Report—Intermountain Research Station INT-313, 211–212. USDA Forest Service, Ogden
- Paschke MW, McLendon T, Redente EF (2000) Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144–158 DOI [10.1007/s100210000016](https://doi.org/10.1007/s100210000016)
- Peek MS, Forseth IN (2003) Microhabitat dependent responses to resource pulses in the aridland perennial, *Cryptantha flava*. *J Ecol* 91:457–466 DOI [10.1046/j.1365-2745.2003.00778.x](https://doi.org/10.1046/j.1365-2745.2003.00778.x)
- Poorter H (1989) Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In: Lambers H (ed) Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic, The Hague, pp 45–68
- Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Aust J Plant Physiol* 27:595–607
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci U S A* 94:13730–13734 DOI [10.1073/pnas.94.25.13730](https://doi.org/10.1073/pnas.94.25.13730)
- Reynolds HL, D'Antonio C (1996) The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. *Plant Soil* 185:75–97 DOI [10.1007/BF02257566](https://doi.org/10.1007/BF02257566)
- Robinson D, Rorison IH (1988) Plasticity in grass species in relation to nitrogen supply. *Funct Ecol* 2:249–257 DOI [10.2307/2389701](https://doi.org/10.2307/2389701)
- Roumet C, Urcelay C, Diaz S (2006) Suites of root traits differ between annual and perennial species growing in the field. *New Phytol* 170:357–368 DOI [10.1111/j.1469-8137.2006.01667.x](https://doi.org/10.1111/j.1469-8137.2006.01667.x)
- Ryser P, Lambers H (1995) Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant Soil* 170:251–265 DOI [10.1007/BF00010478](https://doi.org/10.1007/BF00010478)
- SAS (2001) SAS/STAT user's guide. Version 8. vol. 1–3. SAS Institute, Cary
- Shipley B, Keddy PA (1988) The relationship between relative growth rate and sensitivity to nutrient stress in twenty-eight species of emergent macrophytes. *J Ecol* 76:1101–1110 DOI [10.2307/2260637](https://doi.org/10.2307/2260637)
- Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Baskin M, Son Y (1999) Exotic species invade hot spots of native plant diversity. *Ecol Monogr* 69:25–46
- Taub DR (2002) Analysis of interspecific variation in plant growth response to nitrogen. *Can J Bot* 80:34–41 DOI [10.1139/b01-134](https://doi.org/10.1139/b01-134)
- van der Werf A, van Nuenen M, Visser AJ, Lambers H (1993) Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen supply. *Oecologia* 94:434–440 DOI [10.1007/BF00317120](https://doi.org/10.1007/BF00317120)
- Wedin D, Tilman D (1993) Competition among grasses along a nitrogen gradient—initial conditions and mechanisms of competition. *Ecol Monogr* 63:199–229 DOI [10.2307/2937180](https://doi.org/10.2307/2937180)