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Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply

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ABSTRACT

Invasion of the historically perennial-dominated landscapes in the Great Basin by exotic winter annual grasses is one of the most serious plant invasions in North America. Evidence suggests invasive annuals outperform native perennials under N-poor and N-rich conditions. The objective of this study was to identify key traits contributing to the success of invasive annual grasses in these environments. Three invasive annual grasses, two native perennial grasses and one introduced perennial grass were exposed to three levels of N supply. Root biomass, root length, root N uptake rate, root and leaf morphology, leaf nitrogen productivity (leaf NP) as well as biomass and N allocation were quantified over four harvests. Path analysis indicated that leaf NP was the key trait contributing to variation in N capture among the species. Species with a higher leaf NP produced more root length and consequently captured more N under a range of soil N availability. This suggests variation in leaf NP may be one critical trait determining the ability of the resident plant community to resist establishment of these invaders. Restoration programs may be able to increase weed resistance by specifically selecting for this trait in revegetation efforts.

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1. Introduction

Invasion of the historically perennial-dominated landscapes in the Great Basin by exotic winter annual grasses is one of the most serious plant invasions in North America (D'Antonio and Vitousek, 1992). An increase in nitrogen (N) availability as a result of disturbance or reduced uptake by the native vegetation has been widely identified as a key mechanism facilitating the establishment of annual grasses in these otherwise nutrient-poor systems (Beckstead and Augspurger, 2004; Norton et al., 2007; Paschke et al., 2000). Invasive annuals possess a suite of traits such as high relative growth rate, short generation time and abundant seed production that are expected to be important adaptations to N-rich environments, while native perennials possess a suite of traits such as low relative growth rate, high nutrient conservation and storage that are expected to be important adaptations to N-poor environments (Chapin, 1980; Rejmanek and Richardson, 1996). Based on these expectations, invasive plant management and restoration programs commonly assume that managing soils for low N availability will favor the performance of native perennials over invasive annuals (Krueger-Mangold et al., 2006). While there is much research indicating that high N availability favors invasive annual grasses more than native perennial grasses, evidence continues to accumulate, suggesting invasive annuals also outperform native perennials under N-poor conditions (Monaco et al., 2003, 2004; Young and Mangold, 2008). Improved management of

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these invasive annuals requires a mechanistic understanding of how these invaders are able to maintain greater growth and competitive ability than natives under a range of soil N availability.

Growth and competitive ability of species in the Great Basin have been directly linked to the ability of a species to capture N (Bilbrough and Caldwell, 1997; James and Richards, 2007). This suggests that evaluating mechanisms influencing plant N capture may provide insight into how invasives are able to outperform natives under both low and high soil N supply. On the most basic level, simulation models predict that plant N capture will be related to the amount of root length present and N uptake rate per unit root length (Silberbush, 1996). The amount of root length produced depends on the amount of root biomass created and the amount of root length a plant can manufacture per unit biomass invested in roots (specific root length, SRL). The amount of root biomass produced, in turn, should depend on the proportion of biomass allocated to roots (root weight ratio, RWR) and on plant growth rate. While several factors contribute to plant growth rate, specific leaf area (SLA) has been identified as a central trait driving growth rate differences among species (Poorter, 1989). Species with a higher SLA produce thinner and less-dense leaves than species with a lower SLA. This allows species with a high SLA to construct more leaf area per unit biomass invested in leaves, resulting in a more rapid return on biomass and nutrients invested in leaves and, consequently, faster growth (Westoby et al., 2002).

In N-limited systems, it also can be useful to examine plant growth in terms of plant N productivity (increase in plant dry mass per unit plant N per unit time). Plant N productivity in grasses and herbaceous dicots is primarily driven by the proportion of total plant N allocated to leaves (leaf N ratio) as well as leaf N productivity (rate of dry matter gain per unit leaf N per unit time, leaf NP) (Garnier et al., 1995). Annual grasses in general have a higher SLA and SRL than perennials (Roumet et al., 2006). In addition, fast-growing species tend to have greater whole-plant N productivity than slow-growing species, and there is some evidence to suggest that as seedlings, fast-growing species exposed to low N supply can allocate more biomass to roots than slow-growing species, allowing fast-growing species to maintain greater N capture under low N supply (Poorter et al., 1990; van der Werf et al., 1993). Therefore, multiple traits may allow invasive annuals to outperform native perennials under high and low N availability.

The broad objectives of this study were to examine the interrelationship among traits expected to be major drivers of plant N capture in N-limited systems and to identify key trait differences that may contribute to the success of annual invasive grasses under both low and high N availability (Fig. 1). The species selected for this experiment include three annual grasses that are native to Eurasia and the Mediterranean region but have extensively invaded the Great Basin and three perennial grasses that are widely used in efforts to restore these systems (Table 1). Two of the perennial species, *Pseudoroegneria spicata* and *Elymus elymoides*, are native to the Great Basin, while *Agropyron desertorum* is an introduced perennial grass native to Siberia that has been bred for reclamation programs. *Agropyron desertorum* has a better ability to
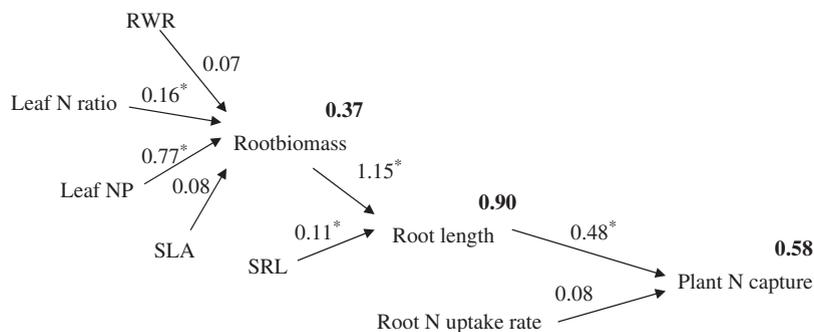

Fig. 1. Path model describing how variation in root length, root N uptake rate, root biomass, specific root length (SRL), specific leaf area (SLA), leaf N productivity (leaf NP) root weight ratio (RWR) and leaf N ratio correlates with N capture among the six study species. Data are pooled across the three N levels. Running the path model separately for each of the three N levels did not significantly improve model fit or alter path coefficients. For each path effect, the standardized partial regression coefficient is given and the significance of the path is indicated as *($p < 0.05$). Numbers in bold are the total variance explained (R^2) for each dependent variable. Measurements were quantified across four harvests spaced in 10-day intervals.

Table 1
List of the six species used in this study

Functional group	Common name	Species	Variety	Species abbreviation
Annual	Cheatgrass	*Bromus tectorum* L.		BRTE
	Medusahead	*Taeniatherum caput-medusae* (L.) Nevski		TACA
	Ventenata	*Ventenata dubia* (Leers) Coss.		VEDU
Perennial	Crested wheatgrass	*Agropyron desertorum* (Fisch. ex Link) J.A. Schultes	Hycrest II	AGDE
	Bluebunch wheatgrass	*Pseudoroegenaria spicata* (Pursh) A. Löve	Anatone	PSSP
	Bottlebrush squirreltail	*Elymus elymoides* (Raf.) Swezey	Toe Jam Creek	ELEL

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

interfere with the growth of invasive annuals than the native grasses, making this species a useful comparison to include (Harris and Wilson, 1970). It was hypothesized that a combination of trait differences related to root biomass production, root physiology and root and leaf morphology allow invasive annual grasses to capture more N than native perennials under both low and high N availability.

2. Materials and methods

2.1. Study species, growth conditions, harvests and measurements

The invasive annual and desirable perennial grasses used for the experiment are listed in Table 1.Of the annual grasses, *Bromus tectorum* and *Taeniatherum 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 grasses, but has been introduced more recently; thus, 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 10 replicates per treatment per harvest. Seeds of *B. tectorum* and *T. caput-medusae* were collected in the field east of Burns (43°22′N, 118°22′W) and seeds of *V. dubia* were collected west of Burns (44°18′N, 120°52′W). Seeds of bunchgrasses were obtained from commercial growers. Bunchgrass varieties are listed in Table 1. 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 coleoptile 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. Pot sizes for the first and second harvest were 12 cm dia × 30 cm deep. Larger pots (20 cm dia × 50 cm deep) were used for the third and fourth harvest. The first harvest was conducted one 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 seedling growth.

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 minimized nutrient accumulation. Eights 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 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 ± 0.6 mg kg^{-1}, respectively ($n = 8, \pm$ SE), which is within the range that soil inorganic N concentration can vary in these systems (Cui and Caldwell, 1997; James et al., 2006; Peek and Forseth, 2003).

For each harvest, aboveground biomass was clipped and immediately separated into leaves and stems. Roots were recovered by gently washing over a fine mesh screen. Root length was measured (WinRHIZO, Regent Instruments Inc., Saint-Foy, Canada), afterwards all materials were dried at 65 °C and weighed. Leaf and root material was finely ground and analyzed for N concentration by micro-Dumas combustion using a CN analyzer (Carlo Erba, Milan, Italy). SLA, leaf NP, LNR, RWR, root biomass, root length, SRL, root N uptake rate and total plant N capture were calculated over all harvest intervals. Calculations of means and SE followed Causton and Venus (1981) for ungraded and unpaired harvest. The Excel file in Hunt et al. (2002) (http://www.ex.ac.uk/~rh203/growth_analysis.html) was used for the calculations.

2.2. Path model development and statistics

Path analysis and structural equation modeling were used to evaluate the degree to which different parameters contributed to interspecific variation in plant N capture. Total N capture was expected to be a direct function of total root length produced and the N uptake rate per unit root length (Silberbush, 1996). Total root length, in turn, was expected to be influenced primarily by the amount of root biomass produced and SRL (the amount of root length produced per unit biomass invested in roots). Previous research on grasses and herbaceous dicots has demonstrated that differences in leaf thickness or density, N allocation and nitrogen utilization efficiency can be important drivers of growth rate differences among species (Garnier et al., 1995; Poorter, 1989). Therefore, in this experiment, the amount of root biomass produced during a given harvest interval was expected to be a function of SLA, leaf N ratio and leaf NP as well as a function of the amount of biomass allocated to roots (RWR). Path coefficients, their significance level and the fit of the structural model to the data were evaluated with the CALIS procedure in SAS (SAS, 2001). Total effects of an independent variable on a dependent variable consist of direct and indirect effects. Direct effects are indicated by single-headed arrows in the path diagram. Indirect effects occurred when a variable was linked to a dependent variable through one or more intermediary variables. Model fit was evaluated with the Goodness of Fit Index (GFI) and Normed Fit Index (NFI). Values of these indices

greater than 0.9 are generally considered as an indication of good model fit (Hatcher, 1994; Schumacker and Lomax, 2004). ANOVA was used to examine how parameters included in the path model differ among the study species (SAS, 2001). Shapiro–Wilk test and Levene's test were used to evaluate normality and homogeneity of variance, respectively. Variance for most variables was not homogeneous, so data were weighted by the inverse of the variance (Neter et al., 1990).

3. Results

3.1. Variation in N capture among the study species

Averaged across the three levels of N supply the model fit indices, GFI and NNI were 0.88 and 0.92. Running separate models for the three levels of N availability did not significantly improve the model fit or alter path coefficients (data not shown), indicating that the components driving variation in N capture among the species remained relatively consistent across different levels of N availability. The variables included in the model explained 58% of the variation in N capture among the study species (Fig. 1). The amount of root length produced was the main path driving variation in N capture with the uptake rate per unit root explaining little of the variation in N capture among the study species. Variation in root length was primarily correlated with differences in root biomass produced rather than differences in SRL among the study species. Variation in the amount of root biomass produced was correlated with leaf nitrogen productivity (leaf NP) and the proportion of N allocated to leaves (leaf N ratio) but not due to differences in SLA or RWR among the study species. Combined, these variables explained 37% of the variation in root biomass produced by the study species. The indirect effects of leaf NP and leaf N ratio on plant N capture were 0.41 and 0.19, respectively.

3.2. Influence of N availability on root biomass, resource allocation, morphology and physiology of annual and perennial grasses

Low N availability reduced tiller number in all species except *E. elymoides* (Fig. 2A). Low N availability decreased root length and biomass in all species (Fig. 2B and C). However, invasive annual grasses on average produced more tillers, root length and biomass than the native perennials, *P. spicata* and *E. elymoides*, at both low and high N supply ($p < 0.05$). Tiller number, total biomass and root length were lower in *V. dubia* than the other invasive annuals, indicating that differences in growth between invasive annuals and native perennials were primarily driven by *B. tectorum* and *T. caput-medusae*. Biomass production by the introduced perennial *A. desertorum* was comparable to *T. caput-medusae* but lower than *B. tectorum* at the different levels of N supply. The annual grasses *T. caput-medusae* and *B. tectorum* produced more root length than *A. desertorum* at all levels of N supply ($p < 0.05$). Rankings of root biomass production by the study species at the final harvest remained similar across the three levels of N supply (Fig. 3). The annual grasses *B. tectorum* and *T. caput-medusae* produced more root biomass than the native perennials at all levels of N supply but produced similar amounts of root biomass as *A. desertorum*.

Leaf NP of most species peaked at intermediate levels of N supply (Fig. 4A). Averaged across N levels, *B. tectorum* and *T. caput-medusae* had a higher leaf NP than the native perennials *P. spicata* and *E. elymoides* but rates comparable to the introduced *A. desertorum*. While *B. tectorum* had a higher SLA than the other species, there was no trend for annuals to have a higher SLA than perennials and N supply had no effect on SLA of any of the study species (Fig. 4B). Leaf N ratio tended to decrease as soil N availability declined with the exception being *V. dubia*, which maintained a comparable leaf N ratio across the different N levels (Fig. 4C). There were differences in leaf N ratio among species but the bulk of N captured by seedlings of all species appeared to be allocated to leaves regardless of soil N availability.

All species increased RWR as soil N availability decreased but annuals did not consistently have a lower RWR at high N availability than perennials (Fig. 4D, $p > 0.05$). The observed interaction appeared to be a result of differences in the magnitude of response among species with some species like *B. tectorum*, *T. caput-medusae* and *A. desertorum* showing large changes in RWR across the different levels of N supply while *V. dubia* and *E. elymoides* demonstrated smaller changes. Annual grasses had a consistently higher SRL than perennials across the different levels of N supply (Fig. 4E). Nitrogen uptake per unit root length declined in all species as soil N availability decreased (Fig. 4F). Averaged across the three levels of N supply, the perennials *A. desertorum* and *P. spicata* had the highest rates of N uptake per unit root while the perennial *E. elymoides* had root N uptake rates comparable to the invasive annuals *B. tectorum* and *T. caput-medusae*. Similar to RWR, the significant species by N-level interaction appeared to be a result of differences in the magnitude of response among species, with *V. dubia* demonstrating a much smaller increase in root N uptake at high N supply compared to the other species. Rankings of total N capture by the study species remained similar across the three levels of N supply with the annuals *B. tectorum* and *T. caput-medusae* capturing more N than the native perennials *P. spicata* and *E. elymoides* but similar amounts of N compared to introduced *A. desertorum* (Fig. 5A–C). *V. dubia* allocated the most N to leaves compared to roots but had a total N pool comparable to the native perennials *P. spicata* and *E. elymoides*.

4. Discussion and conclusions

Variation in leaf NP was the key trait driving differences in N capture among the study species. The path analysis illustrates that leaf NP was the primary factor that correlated with variation in root biomass (Fig. 1). Consequently, species
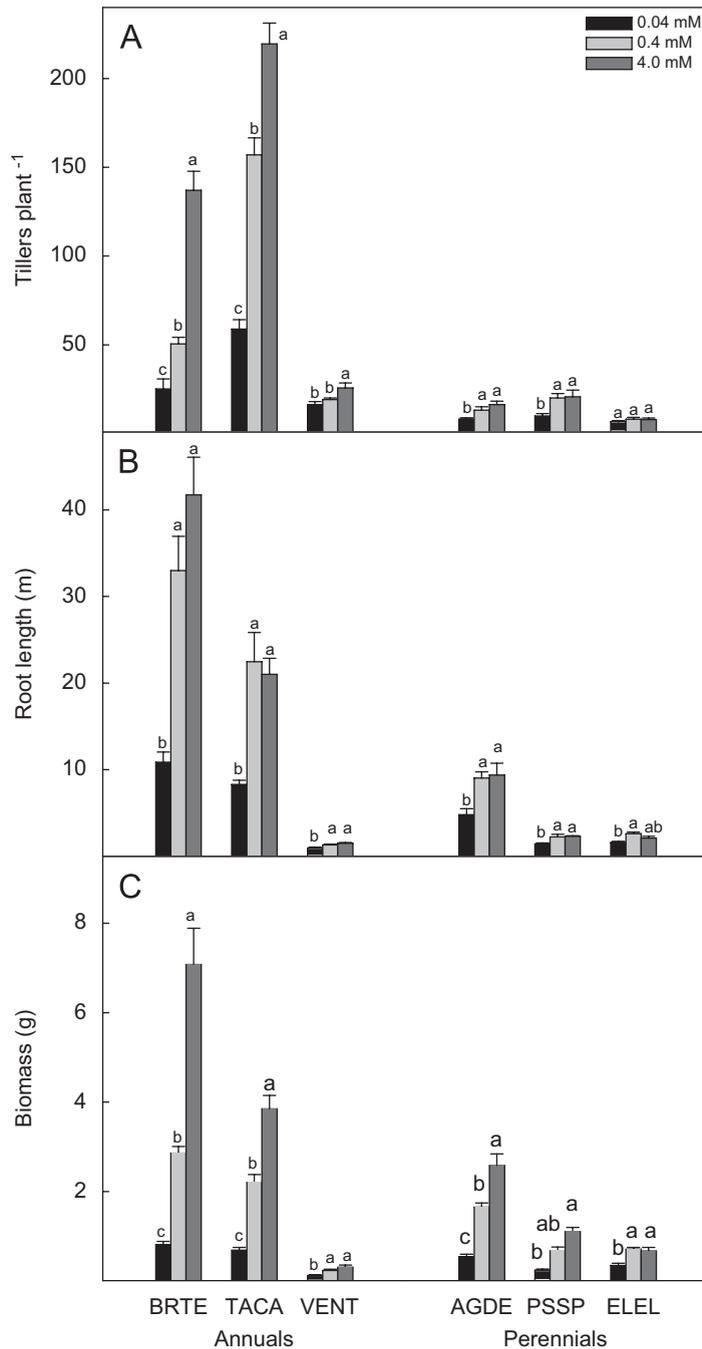
Fig. 2. (A) Tiller number, (B) root length and (C) total biomass of annual and perennial grasses exposed to three levels of N availability (mean+SE). Species abbreviations follow Table 1. Lowercase letters over bars indicate significant differences among N levels within a species as determined with Tukey pairwise comparisons ($p < 0.05$).

with a higher leaf NP tended to produce more root length and capture more N (Figs. 2 and 5). The large influence of leaf NP on root biomass observed in this experiment is in agreement with research showing a positive relationship between leaf NP and plant relative growth rate (Poorter et al., 1990; Wright and Westoby, 2000). When similar-sized seedlings of species differing in leaf NP first establish, the species with a higher leaf NP can produce more biomass per unit time than species with lower leaf NP. RWR and SLA did not correlate with variation in root biomass among the species (Fig. 1). This indicates that differences in root biomass among species are not due to differences in how species allocate biomass or to differences in the rate of return on biomass invested in leaves, but instead due to the fact that species with a higher leaf NP generate greater total biomass and thus produce larger root systems that can explore more of the soil volume. The proportion
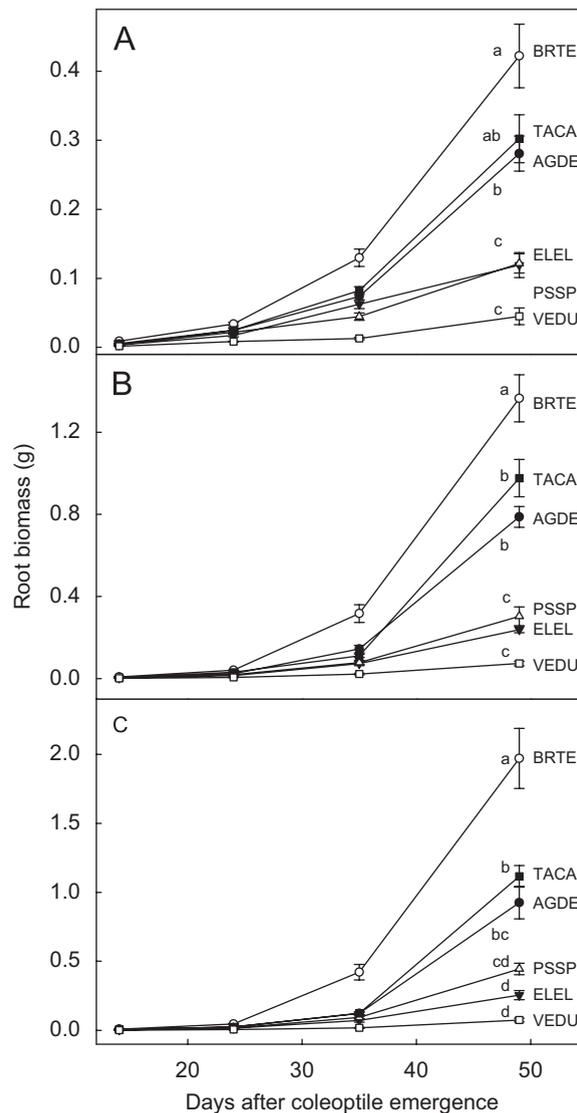
Fig. 3. Root biomass of the six study species at each of the four harvests for plants exposed to (A) 0.04, (B) 0.4 or (C) 4.0 mM N (mean+SE). Species abbreviations follow Table 1. Lowercase letters indicate significant differences in root biomass among species within each N level at the final harvest as determined with Tukey pairwise comparisons ($p<0.05$).

of N allocated to leaves (leaf N ratio) correlated little with variation in root biomass among species (Fig. 1). While whole-plant nitrogen productivity and growth is driven, in part, by the amount of N allocated to leaves, the few studies examining the relationship between N allocation and growth rate have been inconsistent (Garnier and Vancaeyzeele, 1994; Poorter et al., 1990). Modeling studies, however, have indicated that increases in leaf N ratio may only lead to a small increase in plant growth rate (van der Werf et al., 1993) and it may be that differences in leaf N ratio due to phylogeny obscure a potentially small positive relationship between leaf N ratio and relative growth rate (Garnier et al., 1995).

A greater leaf NP appears to be a central factor allowing the most serious invaders, *B. tectorum* and *T. caput-medusae*, to outperform natives under low and high N supply. Even at the lowest N supply, these invasive annuals had on average over a 1.5-fold greater leaf NP than the native bunchgrasses *P. spicata* and *E. elymoides* (Fig. 4A). The greater leaf NP of these annuals compared to native perennials could be due to differences in how N is allocated within the leaf, respiration or photosynthetic N use efficiency. While more detailed measurements are needed to understand what combinations of factors are contributing to these differences in leaf NP, in grasses and herbaceous dicots leaf NP is driven mainly by photosynthetic N use efficiency (Garnier et al., 1995), suggesting the ability of these annual grasses to fix more carbon per unit leaf N than native perennials may be one important trait contributing to their success in N-poor systems. Research in other systems has demonstrated a tendency for annuals to have a higher leaf NP than perennials (Garnier and
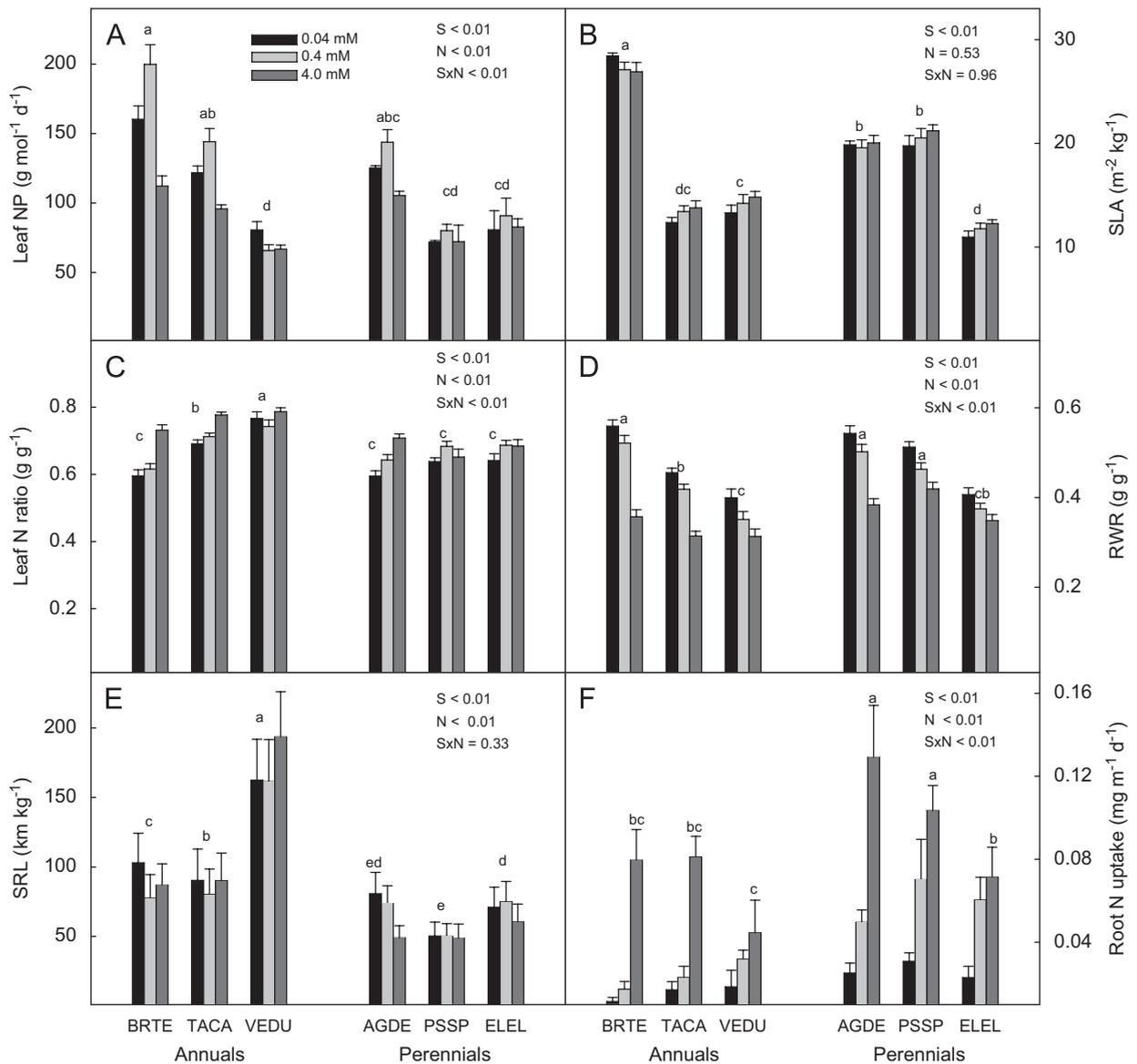
Fig. 4. (A) Leaf N productivity (leaf NP), (B) specific leaf area (SLA), (C) leaf N ratio, (D) root weight ratio (RWR), (E) specific root length (SRL) and (F) root N uptake rate. Parameters are averaged over the four harvests ($n = 10$ per harvest). Calculations of means and SE follow Causton and Venus (1981) and Hunt et al. (2002) for ungraded and unpaired harvests. Species abbreviations follow Table 1. The effect of species (S) and N availability (N, 0.04, 0.4, 4.0 mM) and their interaction are shown for each parameter. Lowercase letters over bars indicate significant differences among species averaged over the three levels of N availability as determined with Tukey pairwise comparisons ($p < 0.05$).

Vancaeyzeele, 1994). However, in this study a difference in leaf NP was not observed between the less-serious annual invader *V. dubia* and the native perennial grasses. This provides support for the notion that a high leaf NP is an important trait of the most widespread invaders that is not necessarily unique to annuals in this system.

Annual grasses had a higher SRL than perennial grasses, consistent with previous observations of annual and perennials in many other systems (Fig. 2E) (Roumet et al., 2006; Ryser and Lambers, 1995). However, variation in SRL did not correlate with variation in root length among species, suggesting that the higher SRL of annuals is a less-important trait contributing to the successes of invaders compared to factors influencing root biomass production. Differences in SRL among annuals and perennials are expected to represent a fundamental trade-off between rapid resource acquisition and resource conservation (Chapin, 1980; Grime, 1977; Roumet et al., 2006). A high SRL is expected to allow annuals to explore more soil volume per unit biomass invested in root and also result in a short root life span, suggesting this trait may be beneficial in nutrient-rich environments. In contrast, a low SRL is expected to allow perennials to maintain long-lived roots tolerant to environmental stress but reduce the amount of soil volume explored per unit biomass invested in roots, suggesting this trait may be beneficial in nutrient-poor environments. However, in this study, the most serious invasive annuals *B. tectorum*
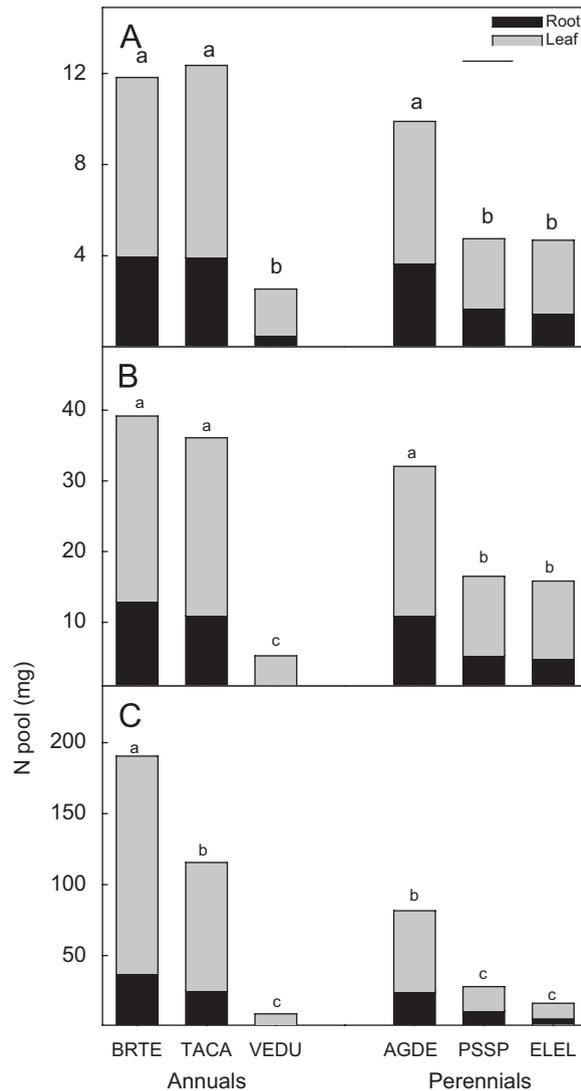
Fig. 5. Total, leaf and root N pools of the six study species exposed to (A) 0.04, (B) 0.4 or (C) 4.0 mM N (mean+SE). Species abbreviations follow Table 1. Lowercase letters indicate significant differences in total N pools among species within each N level at the final harvest as determined with Tukey pairwise comparisons ($p < 0.05$).

and *T. caput-medusae* maintained a high SRL and greater N capture under N-poor conditions compared to native annuals providing little support for such a trade-off.

Root N uptake rate is an important driver of plant N capture particularly as soil N availability increases or is restricted to brief ephemeral pulses (Jackson and Caldwell, 1996). Root N uptake rate of all species increased as soil N supply increased (Fig. 4F). However, the magnitude of increase was similar among species; hence, root N uptake rate was less important in explaining variation in plant N capture among the study species compared to root length. Grime (1979) predicted that species that maintain a long-lived root system should exhibit greater root physiological plasticity than species that maintain a short-lived root system. In partial support of this idea, two of the perennials, *A. desertorum* and *P. spicata*, demonstrated a higher N uptake rate than the invasive annuals, particularly at high soil N availability. It is possible that as N becomes progressively restricted to brief pulses, the relative importance of root N uptake capacity for whole-plant N capture might increase compared to root length (James and Richards, 2006).

A high RWR is expected to be an important adaptation to nutrient-poor soils (Chapin, 1980). While some work suggests perennial grasses maintain a higher RWR than annuals, this trait is highly plastic and changes with nutrient availability and ontogeny (Garnier, 1992; Jackson and Roy, 1986; van der Werf et al., 1993). In this experiment, there were no consistent differences in RWR among invasive annuals or desirable perennials and there was no evidence that species with a higher RWR were able to create more root biomass under N-poor conditions compared to species with a lower RWR (Fig. 4D). For example, the annual *B. tectorum* and perennials *A. desertorum* and *P. spicata* had a comparable RWR yet *B. tectorum* had over

a two-fold greater root biomass than these perennials under low and high N supply. Differences in RWR between annual and perennials are likely to be found when comparing established mature plants (Garnier, 1992). However, as seedlings, both of these groups may have little root reserves and may need to rely primarily on newly produced root and shoot material to capture the energy and nutrients need to support growth. Therefore, the similar RWR observed between invasive annuals and desirable perennials in this experiment may be because during this initial stage of seedling growth these species groups experience similar constraints on biomass allocation.

The species and experimental approach used in this study identified leaf NP as a key factor driving differences in plant N capture among species in nutrient-poor systems. There was little evidence suggesting that variation in N capture was due to species differences in root or leaf morphology, N or biomass allocation or root N uptake rate. Instead, a higher leaf NP appears to be the central trait contributing to the greater N capture and growth of the most serious invasive annuals *B. tectorum* and *T. caput-medusae* compared to native perennials under a range of soil N availability. On the other hand, leaf NP of *A. desertorum* was comparable to these annual grasses, indicating a likely mechanism that may contribute to the greater ability of this species to interfere with the establishment of these invaders compared to native grasses. Importantly, however, the annual grass *V. dubia* did not achieve a higher leaf NP than the native perennials, indicating other traits not necessarily related to N supply or leaf NP, such as early germination and short generation time, also contribute to the success of annuals in this system.

While there has been much emphasis placed on managing soil N following fire or other disturbance (Krueger-Mangold et al., 2006), these results suggest reducing soil N levels alone likely will not favor perennial grasses over invasive annual grasses. Even in low N soils, strategies such as early detection and mapping of annual grass populations as well as managing propagule pools of invasive and desirable plants likely will be key in reducing the spread of annual grasses. Establishing and maintaining plant communities that will resist invaders is a central goal of restoration ecologist and land managers (Sheley and Krueger-Mangold, 2003). The ability to design weed-resistant plant communities, however, depends heavily on the degree to which traits allowing invaders to establish can be identified. While this study only focused on the initial seedling stage and there are limitations to extrapolating results on individually potted plants to the field, these results suggest leaf NP may be a critical trait influencing the ability of the resident vegetation to resist establishment of the most serious annual invaders in the Great Basin. Restoration programs may be able to increase weed-resistance by specifically targeting this trait in revegetation efforts. Field studies examining patterns and magnitude of leaf NP in both native and desirable introduced species are an important next step in determining whether this trait can be developed into a useful predictor of invasion resistance in these systems and a useful management tool for restoring these systems.

Acknowledgments

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