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Nitrogen acquisition by annual and perennial grass seedlings: testing the roles of performance and plasticity to explain plant invasion

A. J. Leffler · T. A. Monaco · J. J. James

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Abstract Differences in resource acquisition between native and exotic plants is one hypothesis to explain invasive plant success. Mechanisms include greater resource acquisition rates and greater plasticity in resource acquisition by invasive exotic species compared to non-invasive natives. We assess the support for these mechanisms by comparing nitrate acquisition and growth of invasive annual and perennial grass seedlings in western North America. Two invasive exotic grasses (*Bromus tectorum* and *Taeniatherum caput-medusae*) and three perennial native and exotic grasses (*Pseudoroegneria spicata*, *Elymus elymoides*, and *Agropyron cristatum*) were grown at various temperatures typical of autumn and springtime when resource are abundant and dominance is determined by rapid growth and acquisition of resources. *Bromus tectorum* and perennial grasses had similar rates of nitrate acquisition at low temperature, but acquisition by *B. tectorum* significantly exceeded perennial grasses at higher temperature. Consequently, *B. tectorum* had the highest acquisition plasticity, showcasing its ability to take advantage of transient warm periods in autumn and

spring. Nitrate acquisition by perennial grasses was limited either by root production or rate of acquisition per unit root mass, suggesting a trade-off between nutrient acquisition and allocation of growth to structural tissues. Our results indicate the importance of plasticity in resource acquisition when temperatures are warm such as following autumn emergence by *B. tectorum*. Highly flexible and opportunistic nitrate acquisition appears to be a mechanism whereby invasive annual grasses exploit soil nitrogen that perennials cannot use.

Keywords Cheatgrass · *Bromus tectorum* · Exotic plant species · Intermountain West · Medusahead · Nitrate uptake · Phenotypic plasticity · *Taeniatherum caput-medusae*

Introduction

Invasion is necessarily a process by which a species that is rare or absent in a community increases in abundance (Tilman 2004). A successful invader must be capable of dispersing to the new community if it is absent, establishing, and increasing despite the presence of other species or harsh abiotic conditions. Invasion often follows a disturbance that makes a resource, such as physical space, light, or nutrients (Davis et al. 2000; Davis and Pelsor 2001), available

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to be exploited by members of the regional species pool (Hierro et al. 2006). Successful invasive plants may be those that arrive first (i.e., have priority access), tolerate the stressful or disturbed condition, or grow more rapidly than native species (Baker 1974; Grime 1974; Seabloom et al. 2003; Hierro et al. 2006; Pyšek and Richardson 2007). In each case, the invasive species gains an advantage by acquiring limited resources to a greater extent than native species. For invasive annual plants, performance during seedling establishment may be critical, because mortality is high and annuals begin from seed each year, whereas perennial plants rely on stored resources and access to large soil volumes (James et al. 2011). If performance differences between invasive annual species and native perennial species are substantial as seedlings, species interactions could be largely determined by growth shortly after emergence.

Various mechanisms may explain the ability of invasive annual species to displace native perennial species. First, invasive annual species may be functionally superior to native species, exploiting a resource earlier, more rapidly, or to a greater extent, such that native species become resource stressed (Daehler 2003). Second, invasive annual species may have greater plasticity in resource acquisition, which would effectively increase their niche breadth and allow greater resource capture in variable environments (Baker 1974; Richards et al. 2006; Daehler 2003; Droste et al. 2010). These mechanisms involve fundamental trade-offs in plant performance closely linked to a tissue economic hypothesis (Westoby et al. 2002; Wright et al. 2004; Díaz et al. 2004). This broad-scale hypothesis describes the trade-off between functional traits conferring high rates of resource acquisition, such as high specific leaf area or stomatal conductance, and traits conferring resource conservation, such as long tissue lifespan or investment in defense. Although invasive annual plant species are expected to employ an “acquisitive” life history simply because they are short lived (Grime 1974), it is unclear if resource acquisition as seedlings plays a role in invasion.

Rapid resource acquisition requires a high uptake rate and production of the tissue necessary to acquire the resource. Invasive species often produce leaves and roots more rapidly than native species (Arredondo et al. 1998; Pyšek and Richardson 2007), have

higher rates of photosynthesis and water use (Feng et al. 2007; Zou et al. 2007, Cavaleri and Sack 2010), and may use water or nutrients more efficiently (Funk and Vitousek 2007; James 2008b). The importance of tissue production and tissue-specific rate of resource acquisition in determining whole-plant resource uptake is complex because environmental factors influencing tissue production are integrated over days to weeks, although uptake of nutrients is nearly instantaneous and rates can vary considerably with transient factors, such as temperature and sunlight. Consequently, relative differences in performance between native and invasive annual species can be dependent on environmental conditions (Daehler 2003; Heger and Trepl 2003).

The semiarid Intermountain West has experienced some of the most extensive plant invasions documented in North America (Chambers et al. 2007). This system is unique: Historically valley bottoms were a mix of shrubs and perennial grasses and forbs with a depauperate annual flora (West and Young 2000). Invasion has primarily been by *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead), which are annual grasses that establish following disturbance and now form dense stands over millions of hectares (Young 1992; Knapp 1996; Chambers et al. 2007; Humphrey and Schupp 2004). Similarly, exotic annual species have displaced native perennial vegetation throughout the world (Baker 1974; Lonsdale 1999).

The two primary invasive annual grasses in western North America possess traits consistent with the short-lived annual syndrome. Seeds of both species germinate in the autumn and complete their life cycle before summer water deficits are severe (Young 1992), seedlings have high rates of root and shoot growth (Arredondo et al. 1998; Monaco et al. 2003a, b) and rapidly dry near-surface soils (Clausnitzer et al. 1999; Leffler et al. 2005; Ryel et al. 2010), and both species respond to high soil N with more rapid growth than native grasses (James 2008a). Previous work suggests these invasive annual species produce extensive root systems with high specific root length, whereas native perennial grasses produce less root length, but thicker roots (Arredondo et al. 1998). Although these comparisons indicate rapid nutrient acquisition by invasive annual grasses, nutrient uptake is typically measured indirectly (James 2008b) and not in recently emerged seedlings.

Moreover, the role that growth environment plays in performance differences between invasive annual and native perennial grasses is critical in determining factors that drive invasion.

Our study examines how variable temperatures that are typical of the growing season influence differences in nitrogen uptake ability between young seedlings of two invasive annual grasses and three perennial grasses of the Intermountain West. We compare species for (1) tissue production, (2) uptake of nitrogen, and (3) plasticity in tissue production and uptake. We anticipate that these comparisons reveal the relative importance of tissue production and uptake rate in conferring an advantage to annual grasses in the Intermountain West.

Materials and methods

Study species

Five common grasses of the Intermountain West were selected to examine nitrogen uptake by seedlings as a driver of invasion. Three of the grasses were cultivars of perennial species found throughout the region and available from local seed producers. Two native perennial grasses included “Rattlesnake” bottlebrush squirreltail germplasm (*Elymus elymoides* [Raf.] Swezey ssp. *elymoides*), and “Anatone” bluebunch wheatgrass germplasm (*Pseudoroegneria spicata* [Pursh] A. Löve ssp. *spicata*). *Elymus elymoides* was selected because it is a short-lived perennial that can establish in annual-dominated ecosystems in the western USA (Hironaka and Tisdale 1963; Hironaka and Sindelar 1973), whereas *P. spicata* is a long-lived perennial grass. The third perennial grass was “Hycrest II” crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), a widely planted non-native grass developed from several populations in central Asia. Hycrest II was chosen for its vigorous growth and evidence that various cultivars of *A. cristatum* are largely resistant to invasion by annual grasses (Davies 2010).

We selected two non-native annual grasses that compete with the chosen native perennials in many areas of the Intermountain West: cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski). Seeds of these species were collected from populations in northern Utah, USA.

Growth conditions, experimental treatments, and measurements

Individuals of all species were grown in germination boxes for the duration of the experiment. Germination boxes were filled with ca. 2 cm of fine sand collected in Cache County, UT, and 100 seeds of a species were added to each of ten boxes yielding 50 boxes for each temperature experiment. Seeds and soil were wetted and boxes kept closed to maintain high humidity. Seeds were germinated in a dark growth chamber at 25°C (day 0). After 24 h, lights (ca. 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) in the growth chamber were turned on for a 14/10 h day/night cycle. After 72 h, chamber temperature was adjusted to experimental temperature and maintained regardless of day/night cycle. Germination fraction was high regardless of experiment; greater than 90% of the annual grass and greater than 75% of the perennial grass seed germinated and survived.

Plants were grown at four target temperatures: 5, 10, 15, and 25°C, each using a different set of 50 germination boxes containing newly emerged seedlings. A single growth chamber was used for each temperature condition so sample units experienced the same chamber effects. Germination boxes were rotated within the chamber every one to two days. Temperature in the growth chamber was recorded every 15 min with a data logger (model Watchdog B101, Spectrum Technologies, Plainfield, IL). Although the target temperatures were as above, recorded mean temperatures during the experiments were 6.3, 10.6, 15.7, and 25.2°C, respectively.

Measurements included shoot length, N (as NO_3^-) acquisition, final root (R_M) and shoot (S_M) dry mass, and root-to-shoot dry mass ratio (RS). Shoot length (H) was measured on days 5, 8, and 10 (H_5 , H_8 , H_{10} , respectively) on five individuals in each germination box. Nitrate acquisition assays were performed when shoots reached ca. 10 cm in length.

Nitrate acquisition was determined with a short-term incubation in a ^{15}N solution (BassiriRad et al. 1993). On the assay day, 25 ml of 60 at.% K^{15}NO_3 was added to eight of the ten germination boxes for each species. The remaining two boxes were treated as controls, receiving 25 ml of K^{14}NO_3 (natural abundance of ^{15}N is ca. 0.36 at.%). Controls were necessary to account for any background variation in ^{15}N . After a 2-h incubation, soils in each

germination box were saturated with a chilled 50-mM KCl solution to stop nitrate acquisition. Shoots and roots were then harvested separately from each box, washed once in 50-mM KCl, then five times in distilled water. The resulting root and shoot tissue was dried at 75°C for at least 48 h, weighed, and ground to a fine powder using a shaker mill (model 2000, SPEX CertiPrep, Metuchen, NJ). Tissue samples were analyzed for ^{15}N at.% by the stable isotope facility at the University of California, Davis. Standard deviation among repeated measurements of a standard was less than 0.005 at.%. Nitrate acquisition was calculated by determining the difference in tissue ^{15}N content between labeled plants and control plants. Excess ^{15}N in root and shoot tissue was combined, and acquisition is expressed as mass-specific absorption rate (SAR_M , $\mu\text{g N g}^{-1}$ dry root tissue h^{-1}) or whole-plant N uptake rate (PNU, $\mu\text{g N h}^{-1}$).

Statistical analysis

Significant differences among treatments were determined with ANOVA models using the GLM procedure in SAS (version 9.2, SAS Institute Inc., Cary, NC). Shoot length was examined with a partially nested repeated-measures design (Quinn and Keough 2002) that included temperature, species, and day of measurement as fixed effects, and germination box and measurement within box as random effects. R_M , S_M , RS, SAR_M , and PNU were analyzed with two-way ANOVA using species and temperature as fixed effects. Variables were log-transformed as necessary to satisfy assumptions of linear models. Four contrasts within GLM were conducted for biomass and uptake variables: The first and second evaluated whether both invasive annuals and both native perennials had similar traits, respectively; contrast three examined differences between *B. tectorum* (the species with the highest SAR_M) and all other species; contrast four compared *B. tectorum* to *A. cristatum* (the perennial with the highest SAR_M). Contrasts were performed using only the main effect of species, which was significant for all variables. Plasticity for each species and trait was quantified as the difference between the maximum trait value and the minimum trait value normalized by maximum trait value among the four temperature conditions (Valladares et al. 2000). Confidence intervals about the mean plasticity index among study species were constructed to

determine if each species was more or less plastic than expected for each trait. All differences are considered significant at $P \leq 0.05$.

Results

Temperature and species were significant predictors of all response variables (Tables 1 and 2). In each case, we found significant interactions between species and temperature, or in the case of shoot length, species, temperature, and day of measurement, indicating differences in plasticity existed among species. Furthermore, differences for all variables between the two invasive annual grass species were common, as were differences between the native perennial species. Despite considerable variation among species for numerous traits, *B. tectorum* was clearly superior in N acquisition at the seedling stage.

As seedling development progressed, the ranking of species changed with respect to height. Early height growth of *T. caput-medusae* was more rapid than other species, regardless of growth temperature, but perennial grasses were similar in height after 1 week (Fig. 1). Differences among species were most pronounced on day 5 depending on growth temperature. *Bromus tectorum* was the shortest species by the 10th day of the experiment. The following contrasts of shoot length were significant: *Taeniatherum caput-medusae* was taller than *B. tectorum*; *E. elymoides* was taller than *P. spicata* (Table 3); *B. tectorum* was shorter than the other species grouped, yet was shorter

Table 1 Partially nested, repeated-measures ANOVA examining shoot length following measurement on days 5, 8, and 10 of the invasive annual grasses *B. tectorum* and *T. caput-medusae*, the native perennial grasses *P. spicata* and *E. elymoides*, and the non-native perennial grass *A. cristatum* in four experimental temperature conditions

Source	df	SS	F	P
Species	4	635.5	85.6	<0.001
Temperature	3	3783	679	<0.001
Temperature \times species	12	74.74	3.35	<0.001
Day	2	2291	3460	<0.001
Temperature \times day	6	134.8	67.9	<0.001
Species \times day	8	110.9	41.9	<0.001
Temperature \times day \times species	24	17.85	2.25	<0.001

Table 2 Two-way ANOVA examining biomass of roots (R_M) and shoots (S_M), root-to-shoot ratio (RS), mass-specific N absorption rate (SAR_M), and whole-plant N uptake (PNU) of the invasive annual grasses *B. tectorum* and *T. caput-medusae*,

the native perennial grasses *P. spicata* and *E. elymoides*, and the non-native perennial grass *A. cristatum* in four experimental temperature conditions

Response	Source	df	SS	F	P
R_M	Species	4	0.488	258	<0.001
	Temperature	3	0.077	53.8	<0.001
	Temperature × species	12	0.047	8.32	<0.001
S_M	Species	4	0.060	79.2	<0.001
	Temperature	3	0.025	43.5	<0.001
	Temperature × species	12	0.010	4.22	<0.001
RS	Species	4	20.9	33.2	<0.001
	Temperature	3	28.4	60.1	<0.001
	Temperature × species	12	9.09	4.80	<0.001
SAR_M	Species	4	15.5	33.9	<0.001
	Temperature	3	50.6	147	<0.001
	Temperature × species	12	14.8	10.8	<0.001
PNU	Species	4	14.6	24.5	<0.001
	Temperature	3	34.2	76.8	<0.001
	Temperature × species	12	14.2	7.98	<0.001

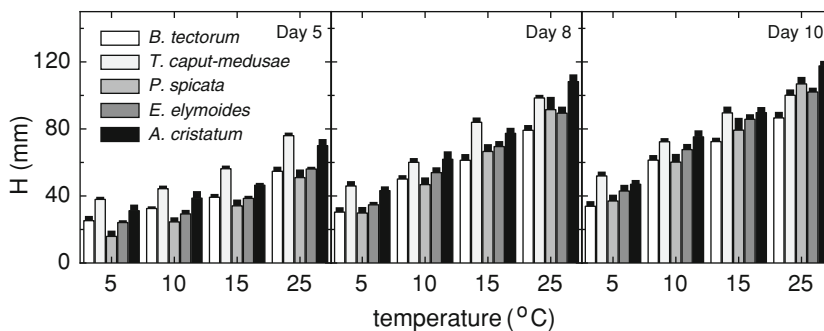


Fig. 1 Shoot length (H) of the invasive annual grasses *B. tectorum* and *T. caput-medusae*, the native perennial grasses *P. spicata* and *E. elymoides*, and the non-native perennial grass

A. cristatum on days 5, 8, and 10 in four experimental temperature conditions. Values are means ($\pm 95\%$ CI) of five measurements in each of ten germination boxes per species

than *A. cristatum* alone (Table 3); and *P. spicata* was more plastic over the temperature range than other species in shoot growth (Table 4).

Species varied considerably for root mass (R_M), with the lowest value for the perennial grass *E. elymoides*, and the highest value for the annual grass *T. caput-medusae* (Fig. 2). With the exception of moderately lower R_M at 25°C, the influence of temperature on R_M was minimal. The following contrasts of R_M were significant (Table 3): *Taeniatherum caput-medusae* had greater R_M than *B. tectorum*; *P. spicata* had greater R_M than *E. elymoides*; *B. tectorum* had lower R_M than the

average of all other species; *B. tectorum* had lower R_M than *A. cristatum*; and *B. tectorum* and *T. caput-medusae* were plastic in R_M (Table 4).

Similar to R_M , shoot mass (S_M) differed among species (Table 2) and was minimally influenced by temperature except at 25°C where S_M was higher. The perennial grass *E. elymoides* had the lowest S_M . Contrasts indicated greater S_M in *T. caput-medusae* compared to *B. tectorum* and greater S_M in *P. spicata* compared to *E. elymoides* (Table 3). *Bromus tectorum*, however, had similar S_M to all species combined but *A. cristatum* alone had higher S_M than *B. tectorum* (Table 3). Compared to the other species, plasticity in

Table 3 ANOVA contrasts based on the main effect of “species.” Values are F/P with $DF = 1$. Responses include height average during days 5, 8, and 10 (H), biomass of roots (R_M) and shoots (S_M), root-to-shoot ratio (RS), mass-specific N absorption rate (SAR_M) N-uptake, and whole-plant N uptake (PNU)

Response	Contrast			
	1	2	3	4
H	192 <0.001	19.1 <0.001	96.4 <0.001	149 <0.001
R_M	338 <0.001	509 <0.001	45.2 <0.001	8.36 0.004
S_M	12.7 <0.001	183 <0.001	1.71 0.193	5.16 0.024
RS	58.8 <0.001	57.3 <0.001	16.3 <0.001	0.15 0.702
SAR_M	112 <0.001	17.9 <0.001	64.6 <0.001	12.6 <0.001
PNU	12.7 <0.001	38.9 <0.001	32.8 <0.001	4.30 0.040

Contrast 1 = *B. tectorum* versus *T. caput-medusae*; Contrast 2 = *P. spicata* versus *E. elymoides*; Contrast 3 = *B. tectorum* versus all other species; Contrast 4 = *A. cristatum* versus *B. tectorum*

Table 4 Plasticity index values for measured traits of each species in four experimental temperature conditions. Responses include height on days 5, 8, and 10 (H_5 , H_8 , H_{10}),biomass of roots (R_M) and shoots (S_M), root-to-shoot ratio (RS), mass-specific N absorption rate (SAR_M) N-uptake, and whole-plant N uptake (PNU)

Trait	Invasive annuals		Perennials		
	<i>B. tectorum</i>	<i>T. caput-medusae</i>	<i>P. spicata</i>	<i>E. elymoides</i>	<i>A. cristatum</i>
H_5	0.54	0.50†	0.69*	0.57	0.55
H_8	0.62	0.53†	0.67*	0.61	0.60
H_{10}	0.61	0.48†	0.65*	0.58	0.60
R_M	0.40*	0.40*	0.32†	0.35	0.33
S_M	0.44*	0.22	0.29	0.11†	0.32
RS	0.65*	0.47	0.45	0.40†	0.51
SAR_M	0.94*	0.60†	0.69	0.67	0.87
PNU	0.90*	0.51†	0.52†	0.73	0.82

Asterisk and † denotes values above and below the 95% confidence interval about the mean described by the five species, respectively

S_M for *B. tectorum* was significantly higher, and *E. elymoides* was significantly lower (Table 4).

Variation in root-to-shoot ratio (RS) was considerable among species, and differences were strongly influenced by temperature (Fig. 2). At the lowest two temperatures, RS of *P. spicata*, *B. tectorum*, and *T. caput-medusae* were similar. Values of RS for *B. tectorum* and *P. spicata* declined with increasing temperature, whereas they increased for *T. caput-medusae* up to 15°C. All species exhibited

their lowest RS at 25°C. At the highest temperature, values of RS for *T. caput-medusae* and *P. spicata* were greater than *B. tectorum*, *E. elymoides*, and *A. cristatum*. Contrasts indicated higher RS in *T. caput-medusae* than *B. tectorum*, higher RS in *P. spicata* than *E. elymoides*, lower RS in *B. tectorum* compared with other species, and *B. tectorum* and *A. cristatum* had similar RS (Table 3). These comparisons are, however, highly influenced by temperature. RS was more plastic in *B. tectorum* and less

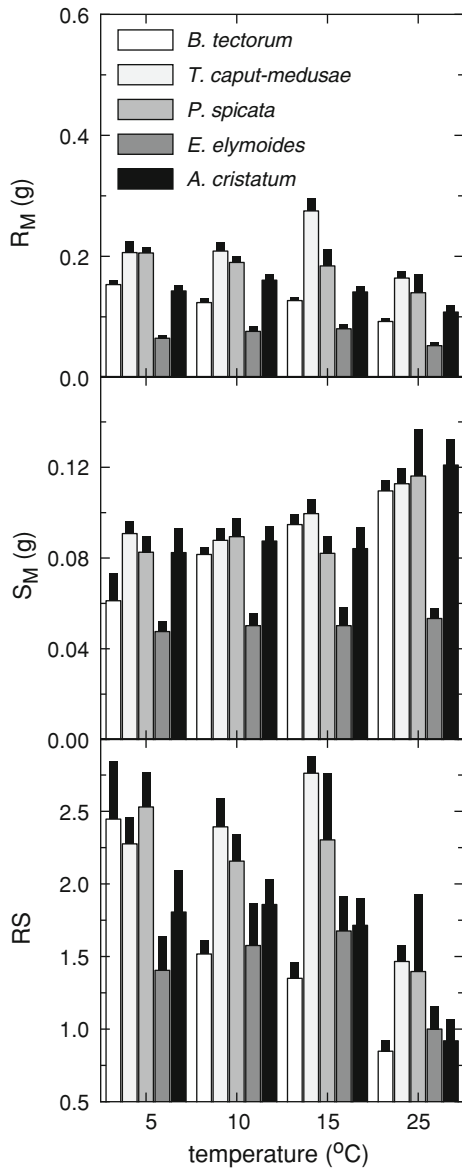


Fig. 2 Root mass (R_M), shoot mass (S_M), and root-to-shoot ratio (RS) of the invasive annual grasses *B. tectorum* and *T. caput-medusae*, the native perennial grasses *P. spicata* and *E. elymoides*, and the non-native perennial grass *A. cristatum* in four experimental temperature conditions. Values are means ($\pm 95\%$ CI) of all individuals in ten germination boxes per species

plastic in *E. elymoides* than mean plasticity of species combined (Table 4).

Temperature dramatically influenced mass-specific absorption rate (SAR_M) and whole-plant N uptake rate (PNU, Fig. 3) and species responded differently to variation in temperature. In nearly all cases, the highest rates were observed at 25°C. Most interestingly, SAR_M

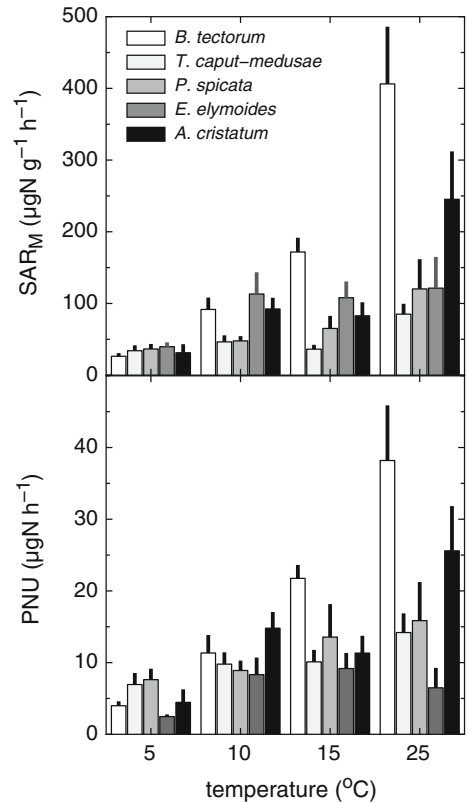


Fig. 3 Mass-specific absorption rate of nitrogen (SAR_M) and whole-plant nitrogen uptake rate (PNU) of the invasive annual grasses *B. tectorum* and *T. caput-medusae*, the native perennial grasses *P. spicata* and *E. elymoides*, and the non-native perennial grass *A. cristatum* in four experimental temperature conditions when N is supplied as NO_3^- . Values are means ($\pm 95\%$ CI) of eight uptake measurements per species

and PNU differed significantly between the two invasive annual grasses and between the two native perennial grasses (Table 3). Averaged across all temperatures, the invasive annual grass *B. tectorum* had clearly the highest SAR_M and PNU of all species, and the perennial grass *A. cristatum* had higher SAR_M and PNU than the other perennial grasses. Plasticity in SAR_M and PNU was significantly higher for *B. tectorum*, yet lower for *T. caput-medusae* than other species (Table 4). PNU in *P. spicata* was less plastic than in other species (Table 4).

Discussion

We observed considerable difference within two species of invasive annual grass and within two

species of native perennial grass in tissue production and nitrogen uptake. In fact, these differences are so pronounced we cannot conclude that annual seedlings performed differently than perennial seedlings. The invasive annual grass *B. tectorum* was a clear exception with the highest mass-specific absorption rate (SAR_M) and whole-plant N uptake rate (PNU) of all species examined (Fig. 3). Nitrogen uptake of *B. tectorum* was similar to several species at lower temperatures, yet considerably higher under warmer conditions. Consequently, plasticity in SAR_M may play a role in the success of *B. tectorum* as a seedling.

Seedlings of invasive annual grasses were not uniformly more productive than native perennial grasses (Fig. 1). In fact, whole seedling biomass of *P. spicata* was similar to *T. caput-medusae*, the invasive annual with the highest biomass; but *E. elymoides*, another native perennial, had the lowest biomass of all species examined (Fig. 2). The similarity in biomass of *P. spicata* compared with invasive annuals was also maintained across temperature treatments. The two invasive annual grasses had among the highest (*T. caput-medusae*) and lowest (*B. tectorum*) root-to-shoot ratio (RS) of all species examined (Fig. 2). Consequently, tissue production alone by recently emerged seedlings is unlikely an important factor responsible for invasive annual grass dominance, except when contrasting their performance with *E. elymoides*. Studies suggest faster growth by these invasive annual grasses compared with native perennials (Arredondo et al. 1998; Monaco et al. 2003b) but examine growth over longer time periods; our conclusions are limited to recently emerged seedlings and are consistent with other short-term studies (Arredondo et al. 1998; Monaco et al. 2003a).

Invasive annual grasses were also not uniformly superior in nitrogen uptake, although SAR_M and PNU for *B. tectorum* were clearly superior to others (Fig. 3). Native perennial grasses maintained similar or greater SAR_M compared with *T. caput-medusae*, and PNU by *P. spicata* seedlings exceeded PNU of *T. caput-medusae*. The low SAR_M of *T. caput-medusae* is somewhat striking given its rapid shoot growth and high tissue mass. Low SAR_M may be caused by low-light conditions in the growth chamber not providing enough energy, limitation by nutrients other than nitrogen, or failure of the inducible high-affinity transport system (iHATS) to receive the

necessary soil [N] to be triggered (Glass et al. 2002). It is also possible that individuals of *T. caput-medusae* were using seed provisions that had not been fully exhausted and high SAR_M would be expressed later. High rates of N uptake, similar to those reported for *B. tectorum*, have been shown in *T. caput-medusae* (James 2008b).

Low temperature suppressed SAR_M in all species (Fig. 3). At 5°C, all species are likely limited by low respiration rate, a consequence of low temperature. At warmer temperatures, however, differences among species in SAR_M become evident. Previous studies suggest that species vary in temperature sensitivity (Chapin et al. 1986; Warren 2009). Processes external to plants, such as the temperature influence on ion diffusivity (Nye and Tinker 1977) or microbial competition (Warren 2009), may limit nitrogen acquisition. Alternatively, processes internal to plants, such as transpiration rate controls on mass flow of ions (Warren 2009) or coordination of nitrogen acquisition and relative growth rate (Rodgers and Barneix 1988; Tian et al. 2006), may allow for adaptation to specific temperature regimes. Cold-adapted species appear less sensitive to temperature variation than species from warmer locations (Chapin et al. 1986), and NO_3^- acquisition is more sensitive to temperature variation than uptake of other N forms (Chapin et al. 1986; Gessler et al. 1998).

Perennial grass seedlings, especially *A. cristatum*, were able to exploit soil nitrogen equally as well as *B. tectorum* under cooler conditions (i.e., 10°C). However, at temperatures greater than 15 °C, *B. tectorum* clearly acquires nitrogen at higher rates than the native perennial grass seedlings (Fig. 3). Thus, performance differences between these invasive annual and native perennial grasses are dependent on environmental conditions. Although superior performance of invasive species has been documented (Daehler 2003; Pyšek and Richardson 2007), studies often take place under controlled conditions that represent only a portion of the environmental variation they experience naturally. Exploring performance over a broader range of environmental conditions may yield a more robust understanding of functional differences among plant species.

Although tissue production alone is unlikely to explain performance differences between the seedlings studied here, it clearly interacts with SAR_M to separate species based on PNU. Low root mass (R_M)

in *E. elymoides* suppressed its expression of PNU relative to other species, whereas high root mass in *T. caput-medusae* had the opposite effect (Figs. 2 and 3). Consequently, species can employ two different strategies to obtain an advantage in N capture following emergence; deploy much tissue with moderate ability to obtain N or little tissue with considerable uptake capacity. Furthermore, these strategies are not likely mutually exclusive, and may result from temporal variation in N availability. Because root growth is a delayed response to resource pulses and high-uptake capacity can be rapidly expressed (Cui and Caldwell 1997; Ivans et al. 2003), high SAR_M should enable rapid N acquisition when nitrogen availability is transient.

High phenotypic plasticity is suggested as an important factor contributing to invasion success (Baker 1974; Richards et al. 2006), and many invasive species are highly plastic for biomass allocation (Daehler 2003). In support of this proposition, we observed tenfold greater SAR_M in *B. tectorum* at 25°C than at 5°C (Fig. 3), which suggests that plasticity for this trait, and associated R_M , shoot mass (S_M), and PNU, likely plays a role in the ability of *B. tectorum* to displace native perennial species. Much higher RS plasticity in *B. tectorum* in response to temperature also indicates that *B. tectorum* has greater capacity to allocate biomass to the tissue that will most increase growth. The other invasive annual grass, *T. caput-medusae*, also exhibited high plasticity in root mass, but low plasticity in SAR_M and PNU. In comparison, plasticity in SAR_M for perennial grasses was either not different or significantly lower than the mean of all species. While plasticity of *B. tectorum* for flowering time in response to plant density (Rice and Mack 1991) and seed germination among populations (Meyer and Allen 1999) is low, plasticity for dry mass and seed production in response to plant density is high (Rice and Mack 1991). Additionally, plasticity in growth following nitrogen addition is also high (James 2008a, 2008b). These observations, combined with recent molecular evidence suggesting *B. tectorum* in the western USA is dominated by several highly plastic genotypes (Ramakrishnan et al. 2006), support the idea that trait plasticity plays a strong role in invasion of this grass.

High SAR_M and plasticity for RS of young *B. tectorum* seedlings may be particularly advantageous in the Intermountain West when emerging in

the autumn, when soil N resources are plentiful following transient rains and accessed by few other species (Booth et al. 2003; Hooker et al. 2008). By using this resource in the autumn when soil temperatures are high, *B. tectorum* may gain a size advantage over perennial grasses (Wedin and Tilman 1993) that primarily emerge in the springtime, when soil temperatures are low. We cannot, however, overlook the importance of the historic flora and recent disturbances in the Intermountain West. The native flora largely lacks annual species (West and Young 2000), and soil N remains low year round in undisturbed perennial communities (Booth et al. 2003; Hooker et al. 2008). Consequently, winter annuals, such as *B. tectorum*, do not have an N resource to exploit during the autumn in intact perennial communities. Similarly, our observation of higher SAR_M in *A. cristatum* than the other perennial grasses suggests that this trait may play a role in excluding *B. tectorum* from disturbed areas revegetated with *A. cristatum* (Davies 2010).

Rapid growth is a strong predictor of invasion (Grotkopp et al. 2002; Pyšek and Richardson 2007; Dawson et al. 2010), and invasion by rapidly growing annuals is not a problem unique to the Intermountain West. Invasive annual species rely on the altered resource availability caused by increased disturbance frequency and positive feedbacks to maintain their dominance (Simberloff and Von Holle 1999; Davis et al. 2000; Brooks et al. 2004). Rapid acquisition of N shortly after emergence is one mechanism that can apply broadly to semiarid lands now dominated by annuals. It is not, however, the only mechanism, because we observed low SAR_M in *T. caput-medusae*.

Our data support the hypothesis that plant invasion is a dynamic process (Davis et al. 2000; Davis and Pelsor 2001) that requires matching of species and their traits to environmental conditions (e.g., a lock-and-key model, Heger and Trepl 2003). Invasion is difficult to predict and species that are not currently invasive may become so should appropriate conditions occur. In the case of invasive annual species, however, opportunities exist every year to suppress their population when practitioners can take advantage of conditions favorable for the establishment of native species.

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