Nitrogen Uptake by Perennial and Invasive Annual Grass Seedlings: Nitrogen Form Effects

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Invasive annual cheatgrass (Bromus tectorum L.) and medusahead wildrye (Taeniatherum caput-medusae (L.) Nevski sp. asperum (Simonk.) Melderis) have decreased livestock productivity and biological diversity and increased the frequency of wildfire on rangelands in the western United States. On disturbed sites, squirreltail (Elymus sp.), a short-lived North American perennial, appears to compete against invasive exotic annuals when available soil N and nitrification are reduced. We tested the hypothesis that differences in N uptake activity could account for this phenomenon. North American seedlings of perennial bluebunch wheatgrass [Pseudoroegneria spicata (Pursh) Á. Löve], four populations of squirreltail, and two invasive exotic annuals were cultured in the laboratory on NH₄⁺, NO₃⁻, or NH₄NO₃ nutrient solutions, and N uptake activity (mol kg⁻¹ root dry wt. h⁻¹) was measured. The overall biomass means of 4-wk-old seedlings cultured with NO₃−, NH₄NO₃, and NH₄+ were 72, 67, and 42 mg seedling⁻¹, respectively. Regardless of N form, cheatgrass biomass was as much as 4.2-fold greater than any of the other grasses including medusahead, which exceeded the biomass of all perennials except one. Cheatgrass had 1.5- to 2.2-fold greater NO₃− uptake activity than the perennials, but the NO₃− uptake activity of medusahead exceeded only two of the squirreltail populations. Ammonium uptake activities of perennials were not consistently more favorable than those of the annuals. The vigorous seedling growth of the invasive annuals coupled with the greater NO₃− uptake activity of cheatgrass appear to be primary traits of the invasive annuals, driving their superior N capture and competition compared with these North American perennial grasses.

Abbreviations: DAP, days after planting.

Landscape disturbances in the Intermountain West have resulted in serious invasions of previously perennial-dominated plant communities by exotic annual grasses (D’Antonio and Vitousek, 1992; Davies and Johnson, 2008). The exotic annual grasses medusahead wildrye (medusahead) and cheatgrass have extensively invaded these rangelands (Young and Evans, 1970; Pellant and Hall, 1994; Miller et al., 1999), resulting in decreased biological diversity and reduced abundance of desirable forages for wildlife and livestock (Vail, 1994). Inestations by exotic annual grasses increase the frequency and severity of wildfires (D’Antonio and Vitousek, 1992; Peters and Bunting, 1994), destabilize watershed hydrologic cycles (Holt and Rice, 1996), and intensify weed dominance in these rangeland ecosystems. In addition, these invasive annual grasses disrupt the conservative nutrient and organic matter cycles associated with the functional diversity of rangeland ecosystems (Smith et al., 1994) to one with more rapid mineralization, increased nutrient availability, and degraded C storage capacity (Ehrenfeld, 2003; Prater et al., 2006; Sperry et al., 2006; Davies et al., 2007).

A complex array of environmental factors and plant attributes interact throughout the introduction, colonization, and eventual naturalization stages of the invasion process on landscapes suffering long-term chronic disturbances (Tilman, 1997; Daehler, 2003; Radosevich et al., 2003). Disturbances can enhance resource supply that provides invaders with a performance advantage (Daehler, 2003) and can enhance the invasiveness of annual weedy species (Huenene et al., 1990; Burke and Grime, 1996; Davis et al., 2000; Norton et al., 2007). Additions of mineral N to a mid-seral old-field favored productivity of cheatgrass more than perennial species (Paschke et al., 2000). Available N in the form of NO₃− but not NH₄+ enhanced the establishment of medusahead, while soil treatments to immobilize available N decreased the establishment of medusahead (Young et al., 1995, 1998) and reduced the dominance of cheatgrass in a mid-seral old field (Paschke et al., 2000). When seedlings of cheatgrass, medusahead, and two desirable North American perennial grasses were grown individually in pots with a wide range of mineral N supply (0.04, 0.4, and 4.0 mmol L⁻¹ as a mixture of NH₄+ and NO₃− sources), total biomass, root biomass, and root length of the invasive annuals were greater than those of the perennials at each level of N supply, while the overall average N uptake rate per unit root length for the perennials was greater than or equal to that of the annuals during the first 49 d after coleoptile emergence.
(James, 2008). Similarly, medusahead seedling productivity was considerably greater than that of a North American perennial grass in individual (accumulated biomass, leaf area, and root length traits) and mixed (interference and growth rate traits) plantings at both low (0 mmol L$^{-1}$ NO$_3^-$ and PO$_4^{3-}$) and high (8.4 mmol L$^{-1}$ NO$_3^-$ and 0.6 mmol L$^{-1}$ PO$_4^{3-}$) levels of nutrient availability (Young and Mangold, 2008). These field and pot experiments indicate that N form and resource availability can affect the productivity of invasive annuals and that the competitiveness of the invasive annuals persists across a wide range of N supply. Possible physiological differences in N acquisition between invasive exotic annual and desirable perennial grasses, however, are uncertain. Differences in N acquisition might be particularly important for reestablishment of desirable perennial grasses in nutrient-rich disturbed rangelands.

Acquisition of soil N by plants depends on root architecture, expression of ion transporters, and growth-driven demand for N (Lea and Azevedo, 2006). Comparisons between pot-grown invasive annual and desirable perennial grass seedlings revealed that variation in N acquisition among the species provided with a mixed mineral N source was primarily a function of root length (strongly correlated with root biomass) rather than uptake per unit length of root (James, 2008). In our study, we tested the hypothesis that desirable perennial grasses have more favorable NH$_4^+$ and less favorable NO$_3^-$ uptake activities (mol N kg$^{-1}$ dry wt. root h$^{-1}$) than invasive annual grasses at near-optimal growth temperature. Because nutrient mobility of NH$_4^+$ and NO$_3^-$ are greatly different in soil, we used hydroponic seeding culture to assess root physiological capacities for acquisition of different mineral N sources.

**MATERIALS AND METHODS**

**Annual and Perennial Grass Species**

Caryopses of the annual grass species were collected in 1997 from populations growing at about 1450 m on southwest-facing slopes in Cache County, Utah. The site of the cheatgrass population was 41°46′7″N, 111°47′11″W and that of the medusahead population was 41°32′18″N, 111°48′0″W. Caryopses of five perennial grasses were obtained from the USDA-ARS Forage and Range Research Laboratory in Logan, UT. Perennial species included ‘Golder’ (Gibbs et al., 1991) bluebunch wheatgrass, ‘Sand Hollow’ (Jones et al., 1998) and ‘Seaman’s Gulch’ (T-1219) big squirreltail [Elymus multisetus (J.G. Sm.) Burtt Davy], and ‘Little Camas’ (T-1206) and ‘Little Wood’ (T-1171) bottlebrush squirreltail [E. elymoides (Raf.) Swezey ssp. brevifolius (J.G. Sm.) Barkworth and E. elymoides ssp. elymoides, respectively].

Seeds were removed by hand from caryopses of the cheatgrass and squirreltail entries. The North American squirreltail grasses included in our characterization of mineral N uptake were selected because they are recognized as favorable candidates for the restoration of rangeland invaded by cheatgrass and medusahead (Jones, 1998). The North American bluebunch wheatgrass was chosen because it is often dominant in many of the plant communities of the Intermountain West (Zlatnik, 1999).

**Seeding Establishment and Culture**

Caryopses were germinated and seedlings grown at room temperature (~20–22°C) using plastic culture assemblies placed in a lid of a 15-L tank containing various solutions. In the field, germination and seedling growth would normally be substantially lower and would require environmental chambers that were unavailable for our study. The room temperatures used for germination and growth, however, approach those considered optimal for annual and perennial cool-season grasses (Hill et al., 1985; Hardegree and Van Vactor, 1999; Yan and Hunt, 1999), and consequently a maximum level of nutrient demand. Germination was achieved by placing caryopses on the surface of agar (0.75% w/v, 2.0 mL) in 20-L disposable beakers with a 16-mm hole in the bottom that was covered by a 2-mm (no. 10) mesh plastic screen and the agar. Eight to 10 caryopses of a single grass entry were placed crease side down with the embryo toward the center of the culture assembly and with the base of the assembly positioned just above the surface of a gently aerated solution of 0.5 mmol L$^{-1}$ CaSO$_4$. Tanks were covered with a clear plastic food film and placed on a cart receiving indirect illumination from a light bench set for a 16-h light/8-h dark cycle. Within 3 d after planting (DAP), cheatgrass and medusahead roots had extended into the solution and the shoots had elongated 25 mm, enough to contact the clear plastic film. The clear plastic film covering these entries was removed and from all other entries 1 d later when they had reached similar growth. Any caryopsis failing to germinate was removed before small black plastic beads were added to ~20-mm depth in each culture assembly to prevent light penetration into the solution. The culture tanks were then placed on the light bench (150 by 60 cm), which received about 350 μmol m$^{-2}$ s$^{-1}$ photosynthetically active radiation from a single combination lamp enclosure with one 400-W metal halide lamp and one 600-W high-pressure sodium lamp (Sunlight Supply Inc., Vancouver, WA). The lamp moved slowly lengthwise back and forth 60 cm on a motorized track enhancing uniformity of light distribution across the bench.

At 8 DAP, the 0.5 mmol L$^{-1}$ CaSO$_4$ solution was replaced with aerated 10% N-free Hoagland basal nutrients (Hoagland and Arnon, 1950), full-strength trace element concentration, 1.0 mg Fe L$^{-1}$ supplied as Fe-nitrilotriacetate chelate (Wallace and Wallace, 1983) and one of three N sources (only NH$_4^+$ as NH$_4$Cl, only NO$_3^-$ as KNO$_3$, or NH$_4$NO$_3$; Fig. 1). All solutions were completely replaced as needed to maintain N concentrations within 20% of the initial level until 25 to 26 DAP. Nutrient solution inorganic N concentrations were measured using an automated flow injection analyzer. Nutrient solutions with only NO$_3^-$ or NH$_4$NO$_3$ were monitored using a pH meter and manually adjusted with dilute HCl as needed to maintain pH 6.1. For the nutrient solution with only NH$_4^+$ as the N source, the solution was buffered at pH 6.1 with 2.0 mmol L$^{-1}$ 2-(N-morpholino)ethanesulfonic acid (MES) to avoid rapid decreases in the pH of solutions containing only NH$_4^+$ as the N source.

**Nitrogen-15 Uptake Activity Assay**

The $^{15}$N uptake assays were conducted on seedlings 26 to 27 DAP. At 22 h before the measurement of $^{15}$N uptake, the nutrient solution was replaced twice, once for 18 h followed by another 4-h preconditioning period. The preconditioning nutrient solution contained N and other nutrients at the same concentration as the $^{15}$N-enriched (>99 atom%) uptake assay solutions. Before measuring $^{15}$N uptake during the middle of the daily 16-h light period, seedlings were removed from the preconditioning
tanks at 2-min intervals and the roots allowed to freely drain for 30 s before rinsing the roots in 1.0 mmol L\(^{-1}\) CaSO\(_4\) (three 2-L containers, three dips in each) and transferring them to 15-L tanks of 1.0 mmol L\(^{-1}\) CaSO\(_4\) for 30 min. Following the same sequence, seedlings were removed at 2-min intervals from the 1.0 mmol L\(^{-1}\) CaSO\(_4\) tank and the roots were allowed to freely drain for 30 s before being transferred to tanks containing 15 L of aerated nutrient solution (pH 6.1, NH\(_4^+\) solution buffered with 2.0 mmol L\(^{-1}\) MES) composed of 10% N-free Hoagland basal nutrients plus full-strength trace elements, 1.0 mg Fe L\(^{-1}\), and one of four sources of \(^{15}\)N as 0.5 mmol L\(^{-1}\) \(^{15}\)NH\(_4\)Cl, K\(\text{\(^{15}\)NO}_3\), \(\text{\(^{15}\)NH}_4\text{\(^{15}\)NO}_3\) or \(\text{\(^{15}\)NH}_4\text{\(^{15}\)NO}_3\). After 2 h, the seedlings were removed (again at 2-min intervals) from the \(^{15}\)N uptake solution and the roots were allowed to freely drain for 30 s before rinsing them in 1.0 mmol L\(^{-1}\) M CaSO\(_4\) (three 2-L containers, three dips in each, regularly replaced) and transferring them to 15-L tanks of 1.0 mmol L\(^{-1}\) CaSO\(_4\) for 4 min followed by seedling harvest and separation into shoot and root tissues. The plant tissues were oven dried to constant weight at 60°C, ground to a fine powder with a ball mill, and analyzed for total N and \(^{15}\)N enrichment using an automated flash combustion instrument connected to an isotope ratio mass spectrometer (RoboPrep and TracerMass, Europa Scientific, Crewe, UK). The normal \(^{15}\)N abundance of tissues were measured in plants included with those cultured for the \(^{15}\)N uptake assays and was used to calculate the atom% excess \(^{15}\)N of plants from the \(^{15}\)N uptake assays. Plant accumulation of N from the \(^{15}\)N uptake solutions was calculated as the sum of the products of tissue total N and atom% excess \(^{15}\)N. Measurements of \(^{15}\)N uptake activity are expressed as hourly rates per kilogram root dry weight.

**Data Analyses**

The experimental unit was a seedling culture assembly that normally contained about eight seedlings of a single grass entry. Separate experiments were conducted for each of the three N sources (NH\(_4^+\), NO\(_3^-\), or \(\text{NH}_4\text{NO}_3\)). Depending on the experiment, there were four to eight replicates of each seeding entry. Entries were arranged in a completely randomized design within the culture tanks. For the NH\(_3\)NO\(_3\) experiment, two separate nutrient tanks with either \(\text{\(^{15}\)NH}_4\text{\(^{15}\)NO}_3\) or \(\text{\(^{15}\)NH}_4\text{\(^{15}\)NO}_3\) contained four replicates of each entry, which were pooled to give eight replicates for seedling dry weight and N concentration means. Because each experiment was independent, a one-way ANOVA was conducted by N source using the Fit Model platform of JMP 6.0.3 software (SAS Institute, 2006). The F test of the entry effect in the one-way ANOVA model was considered significant at \(P \leq 0.05\). Comparison of least-squares means of grass entries in the separate models for each N source used the Tukey honestly significant difference test \((\alpha = 0.05)\) in JMP 6.0.3 software.

![Germination/Emergence and 15N Uptake Assay Sequence](image)

**Fig. 1.** Hydroponic culture and pretreatment sequence used to measure seedling accumulation of \(^{15}\)N during a 2-h N-uptake assay period. Starting at 8 d after planting (DAP) seedlings were grown with nutrient solutions containing one of three different N sources. During seedling growth, nutrient solutions were replaced before depleting more than 20% of the N. Photographs from a preliminary culture trial similar to those used for the \(^{15}\)N uptake assay experiments depict nonrandomized culture assemblies of seedlings at 7 and 28 DAP following growth for 21 d in complete 10% Hoagland no. 2 solution (NH\(_4^+\) + NO\(_3^-\) N sources) with 100% full-strength trace elements.
RESULTS AND DISCUSSION

Seedling Growth

At 7 DAP, before replacement of the aerated 0.5 mmol L\(^{-1}\) \(\text{CaSO}_4\) solution with aerated complete nutrient solutions, root lengths of annual cheatgrass and medusahead were visibly longer than those of the perennial grass species, while visible differences in shoot lengths among the grass species were less pronounced (Fig. 1). Seedling root biomass values of annual medusahead and cheatgrass were consistently greater than those of the perennial grass species after about 3 wk of growth with nutrient solutions containing \(\text{NH}_4^+\), \(\text{NO}_3^-\), or \(\text{NH}_4\text{NO}_3\) sources of N (Fig. 2). The root biomass of Goldar was among the least of the perennial grass species when grown with only \(\text{NH}_4^+\) or only \(\text{NO}_3^-\) and was not different from the other perennials when grown with \(\text{NH}_4\text{NO}_3\). Compared with the relatively small nonsignificant numerical differences in root biomass between the two annual species and often nonsignificant differences among the five perennial grasses, the differences in root biomass between the invasive annuals and North American perennial grasses were substantial. The average root biomass of the invasive annuals compared with the native perennial grasses was 1.6- to 2.7-fold greater with \(\text{NH}_4^+\), 1.6- to 2.9-fold greater with \(\text{NO}_3^-\), and 2.3- to 4.0-fold greater with \(\text{NH}_4\text{NO}_3\) as the N source. These results are consistent with greater root growth of cheatgrass and medusahead than bluebunch wheatgrass (‘Anatone’ germplasm) and bottlebrush squirreltail (‘Toe Jam Creek’ germplasm) grown for 49 d after coleoptile emergence in a sand–soil mix and watered with nutrient solution (James, 2008). They differ from those of Monaco et al. (2003a), however, who found no differences in root biomass among the same seven annual and perennial grasses used in the present study after 17 wk of greenhouse growth in soil well fertilized with \(\text{NO}_3^-\) and \(\text{NH}_4^+\) (with and without nitrification inhibitor) sources of N. Perhaps the additional 13 wk of root growth in the greenhouse overcame the differences in root growth observed during the first 4 wk of hydroponic culture. The initial root growth advantage of the hydroponically cultured invasive annuals compared with the native perennials could lead to enhanced capture of soil resources during the early stages of seedling establishment.

Shoot biomass followed trends similar to those of the root biomass for our hydroponically grown seedlings. Regardless of the N source, the shoot biomass of the two invasive annual species was substantially greater than or equal to that of the perennial grasses, and annual cheatgrass accumulated more shoot biomass than annual medusahead with \(\text{NH}_4^+\) (67%), \(\text{NO}_3^-\) (88%), or \(\text{NH}_4\text{NO}_3\) (42%) as the N source (Fig. 2). There were differences in shoot biomass among the perennial species grown with only \(\text{NH}_4^+\), with the two big squirreltail entries (Sand Hollow and Seaman’s Gulch) greater than or equal to the two bottlebrush squirreltail entries (Little Camas and Little Wood), which were greater than or equal to Goldar bluebunch wheatgrass. The accumulation of shoot biomass among the perennial grasses, however, was not different for the \(\text{NO}_3^-\) and \(\text{NH}_4\text{NO}_3\) nutrient solutions (Fig. 2). The large differences in shoot productivity were generally consistent with other reports comparing the performance of invasive annuals and perennials of the Intermountain West at both high and low supplies of N (Monaco et al., 2003a,b; James, 2008; Young and Mangold, 2008).

Seedling overall total (shoot + root) biomass accumulation by entries grown with only \(\text{NO}_3^-\), \(\text{NH}_4\text{NO}_3\), and only \(\text{NH}_4^+\) sources of N were 71.7, 66.9, and 42.0 mg seedling\(^{-1}\), respectively. This numerical trend observed with the grasses used in our study was consistent with reports that only a few species [e.g., \(\text{Oryza sativa}\) L., \(\text{Vaccinium}\) spp., \(\text{Picea glauca}\) (Moench) Voss] grow well with \(\text{NH}_4^+\) as the primary or only source of N (Kronzucker et al., 1997). Increased root respiration coupled with toxicity avoidance through efflux of \(\text{NH}_4^+\) across the plasmalemma of the root cells of plants well supplied with only \(\text{NH}_4^+\) (Britto et al., 2001) may...
be one contributor to reduced biomass accumulation by some plants depending on only \( \text{NH}_4^+ \) for N nutrition.

The ratios of shoot to root biomass appear to differ depending on N source. Overall, ratios were 3.03 ± 0.11 for seedlings grown with only \( \text{NH}_4^+ \), 3.57 ± 0.13 for those grown with only \( \text{NO}_3^- \), and 4.57 ± 0.17 for those grown with \( \text{NH}_4\text{NO}_3 \). With \( \text{NH}_4^+ \) as the N source, the shoot/root biomass of medusahead (2.43) was significantly less than that of cheatgrass (4.03). Among seedlings grown with \( \text{NO}_3^- \) as the only N source, the ratio of medusahead (2.67) was less than that of cheatgrass (5.41). With \( \text{NH}_4\text{NO}_3 \), the ratio of shoot to root biomass for seedlings of medusahead (3.11) was less than that of Sand Hollow (5.81), which was not greater than that of Seaman’s Gulch (5.71) and cheatgrass (5.09). Regardless of the N source, the ratio of shoot to root biomass was greater for cheatgrass than medusahead. Thus a consistent difference in biomass partitioning between the invasive annuals and the perennial grasses was not observed in our study. These results for hydroponically grown seedlings are consistent with our previous work (Monaco et al., 2003b), but they differ markedly from those observed for these species supplied mineral N and grown in a sand–soil mix (James, 2008) and soil (Monaco et al., 2003a). The overall proportion of root weight in the total biomass (mean ± SE, \( n = 20 \)) of hydroponically grown cheatgrass (0.172 ± 0.007) and medusahead (0.265 ± 0.006) were about 1.5- to 2.9-fold less than pot-grown cheatgrass and medusahead (James, 2008; Monaco et al., 2003a). These differences are not unexpected given that the mobility of soil nutrients that interact strongly with charged soil colloids is markedly different than the mobility of these nutrients in hydroponic culture.

**Nitrogen Concentration and Nitrogen-15 Uptake Activity**

Overall shoot and root N concentrations of grass seedlings grown with only \( \text{NH}_4^+ \) nutrient solution were 47.0 and 52.7 g kg\(^{-1}\), respectively, those grown with only \( \text{NO}_3^- \) nutrient solution were 42.8 and 40.8 g kg\(^{-1}\), respectively, and those grown with \( \text{NH}_4\text{NO}_3 \) nutrient solution were 37.3 and 35.3 g kg\(^{-1}\), respectively. Within each N source, there were significant differences in shoot N concentrations among the entries, but significant differences in root N concentration among the entries were observed just for those seedlings cultured with only \( \text{NH}_4^+ \) (Table 1). Concentrations of shoot N for medusahead were among the greatest for all entries regardless of the N source, but medusahead had among the lowest root N concentrations of entries grown with only \( \text{NH}_4^+ \) as the N source.

Nutrient supplies for the hydroponically grown seedlings in our study were held nearly constant by periodic replacement, which prevented the N sources from being depleted more than 20%. Consequently, the level of nutrition supply of the seedlings was essentially at steady state and would not have limited the growth of the seedlings. With respect to mineral N uptake, the solution N concentrations were well in excess of the concentrations that are known to limit transport rates of the high- and low-affinity systems of vascular plants (Glass et al., 2002). The uptake rates we measured represent net uptake rates (the difference between influx and efflux transport).

Within each N source, there were significant differences in the \( ^{15}\text{N} \) uptake activities among the entries (Fig. 3). For seedlings grown with only \( \text{NH}_4^+ \) nutrient solution, the rate of net accumulation of \( ^{15}\text{NH}_4^+ \) by Seaman’s Gulch big squirreltail was greater than or equal to that of the two invasive annual species. Also, the rates of net accumulation of \( ^{15}\text{NH}_4^+ \) by annual medusahead and the North American perennials Goldar bluebunch wheatgrass and Little Wood and Little Camas bottlebrush squirreltail were not different, but they were about 25 to 41% less than Sand Hollow and Seaman’s Gulch, the two big squirreltail entries. For seedlings grown with only \( \text{NO}_3^- \) nutrient solution, the rate of net accumulation of \( ^{15}\text{NO}_3^- \) by cheatgrass...
was greater than all other entries, and that of Little Camas was less than medusahead and among the least of the perennial grass entries. Except for the invasive annual cheatgrass, the other entries had rates of net accumulation of $^{15}$NH$_4^+$ that numerically exceeded the rates of $^{15}$NO$_3^-$ accumulation from labeled solutions of NH$_4$NO$_3$ by 17 (Little Wood) to 129% (Goldar). Among the entries grown with NH$_4$NO$_3$, the net uptake rate of $^{15}$NH$_4^+$ from NH$_4$NO$_3$ by Seaman's Gulch and medusahead was not different from that of Sand Hollow bighorn wheat and Goldar bluebunch wheatgrass, and exceeded all other entries by 46 to 74%. The net rate of $^{15}$NO$_3^-$ uptake from NH$_4$NO$_3$ by annual cheatgrass exceeded (39–140%) that of all other entries except Sand Hollow bighorn wheat when grown with NH$_4$NO$_3$.

Because the net rates of $^{15}$NH$_4^+$ uptake of the hydroponically cultured North American perennial grasses were not consistently more favorable than that of the exotic invasive annuals (Fig. 3), there is no compelling reason to expect that these perennial grasses would capture more N in an NH$_4^+$-dominated soil environment, an unlikely occurrence in the North American rangelands where these species grow. Given the superior root growth of the annual invasive species, this could enhance their accumulation of NH$_4^+$-N if an NH$_4^+$-dominated soil environment occurred, as well as other immobile soil nutrients. Even though cheatgrass had a net rate of NO$_3^-$ uptake that was 1.5- to 2.2-fold greater than all nearly the perennial grasses (Fig. 3), that of medusahead, the other invasive annual grass, exceeded only that of Little Camas bottlebrush squirreltail (only NO$_3^-$) and Goldar bluebunch wheatgrass (NH$_4$NO$_3$). Consequently, the net NO$_3^-$ uptake activities of invasive annual grass root tissue did not exhibit a unified advantage compared with that of the perennial grasses. A number of possibilities could account for the superior net NO$_3^-$ uptake activity of cheatgrass. These include a greater number of NO$_3^-$ influx transporters, reduced efflux channel activities, and less sensitivity to post-transcriptional downregulation of NO$_3^-$ influx transporters (Glass et al., 2002; Lea and Azevedo, 2006). Because of the greater root biomass of the invasive annuals, however, N capture by these annual seedlings in a NO$_3^-$-dominated soil environment would be expected to exceed that of the perennial grasses, which is consistent with N capture across a wide range (0.04–4.0 mmol L$^{-1}$ N) supplied to the same species grown in a sand–soil mix (James, 2008). Except for cheatgrass, the net uptake activity for NH$_4^+$ was 17 to 129% numerically greater than that of NO$_3^-$ when both N sources were present in the nutrient solution at equal concentration.

Compared with the desirable North American perennial grasses, the competitive advantage of invasive annuals appears to be determined by the greater seedling vigor of the annuals (Aguirre and Johnson, 1991; Arredondo et al., 1998; Young and Mangold, 2008) and by more favorable net NO$_3^-$ uptake activity of cheatgrass (Fig. 3). Enhanced N mineralization on rangelands invaded by annual exotic grasses (Ehrenfeld, 2003; Sperry et al., 2006) and increases up to 12-fold in soil mineral N levels following fire (Blank et al., 1994, 1996; Stubbs and Pyke, 2005) present serious and possibly insurmountable challenges to the re-establishment of desirable perennials. Perhaps drastically changing soil available N by altering microbial communities, grazing, mowing, and the selection of bridge species may offer opportunities to restore invaded sites (Vasquez et al., 2008). Alternatively, rangeland managers may choose to reassess the role of cheatgrass as one forage component of grazing systems in the Intermountain West (Young and Clements, 2007) on sites that would not be amendable by other management practices. To prevent further invasive species negative impacts, efforts may be better spent to limit the spread and replacement of medusahead into cheatgrass-invaded rangelands (Davies and Johnson, 2008) before medusahead reduces the value of these rangelands even further.

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