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# Root plasticity of native and invasive Great Basin species in response to soil nitrogen heterogeneity

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**Abstract** Soil nutrients are heterogeneously distributed in natural systems. While many species respond to this heterogeneity through root system plasticity, little is known about how the magnitude of these responses may vary between native and invasive species. We quantified root morphological and physiological plasticity of co-occurring native and invasive Great Basin species in response to soil nitrogen heterogeneity and determined if trade-offs exist between these foraging responses and species relative growth rate or root system biomass. The nine study species included three perennial bunchgrasses, three perennial forbs, and three invasive perennial forbs. The plants were grown in large pots outdoors. Once a week for 4 weeks equal amounts of $^{15}NH_4{}^{15}NO_3$ were distributed in the soil either evenly through the soil profile, in four patches, or in two patches. All species acquired more N in patches compared to when N was applied evenly through the soil profile. None of the species increased root length density in enriched patches compared to control patches but all species increased root N uptake rate in enriched patches. There was a positive relationship between N uptake rate, relative growth rate, and root system biomass. Path analysis indicated that these positive interrelationships among traits could provide one explanation of how invasive forbs were able to capture 2 and 15-fold more N from enriched patches compared to the native grasses and forbs, respectively. Results from this pot study suggest that plant traits related to nutrient capture in heterogeneous soil environments may be positively correlated which could potentially promote size-asymmetric competition belowground and facilitate the spread of invasive species. However, field experiments with plants in different neighbor environments ultimately are needed to determine if these positive relationships among traits influence competitive ability and invader success.

**Keywords** Bunchgrasses · Forbs · Nutrients · Rangeland · Root foraging · Weeds

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## Introduction

Spatial and temporal variation in nutrient availability is a common feature of soils in natural systems (Stark 1994; Gross et al. 1995; Farley and Fitter 1999a). While a number of studies have shown that plants can increase resource capture in heterogeneous soil environments by making morphological and physiological adjustments to the root system (Hodge 2004) the magnitude of these foraging responses varies substantially among species (Robinson 1994). Several hypotheses have been proposed to explain this

variation in plasticity among species. For example, it has been hypothesized that species with high relative growth rates (RGR) will demonstrate a greater degree of morphological plasticity in response to soil nutrient heterogeneity than species with low RGR, that demonstrate a greater degree of physiological plasticity compared to species with high RGR (Grime 1979; Campbell and Grime 1989). Likewise, a trade-off between root system size and the ability of a species to selectively place roots in nutrient rich patches (root foraging precision) has been proposed, with species of small root systems predicted to forage more precisely for nutrients than species with larger root systems (Campbell et al. 1991).

Whether or not trade-offs exist between root traits has decidedly different ecological implications. If there are trade-offs among traits, then different species may be favored in different soil environments and heterogeneity in soil nutrient availability could potentially facilitate species coexistence. Alternatively, if there are positive relationships between traits, then heterogeneity in soil nutrient availability could promote size—asymmetric competition belowground, potentially inhibiting coexistence (Schwinning and Weiner 1998; Fransen et al. 2001; Rajaniemi and Reynolds 2004).

Given the impact nutrient heterogeneity may have on plant growth and species interactions it is not surprising that much research has focused on understanding the mechanisms of plant response to this variation. However, the majority of this research has been centered on crop species or compared species from different habitats or successional stages (e.g., Drew and Saker 1975; Campbell et al. 1991; Robinson 1994). Less is known about how root response to nutrient heterogeneity varies among species within a community and in particular, how nutrient heterogeneity may influence interactions between native and invasive species (Einsmann et al. 1999; Rajaniemi and Reynolds 2004; Stevens and Jones 2006; Padilla et al. 2007).

The broad objective of this study was to quantify variation in root morphological and physiological plasticity of co-occurring native and invasive species in response to soil nitrogen (N) heterogeneity and determine if trade-offs exist between these foraging responses and species RGR or root system size. The species selected for this study are widely distributed in the sagebrush steppe of the Great Basin. Nutrients in these resource-poor systems are typically supplied in short-lived patches (Jackson and Caldwell 1993; Ryel et al. 1996). The ephemeral nature of nutrient supply in the sagebrush steppe suggests that the ability of a species to respond rapidly to nutrient patches through root plasticity may be an important trait influencing competitive ability and survival in this system. The nine species chosen for this study represent three important functional groups in this system, native perennial bunchgrasses, native perennial forbs, and invasive perennial forbs introduced from Eurasia and the Mediterranean region (Table 1). We hypothesize that: (1) all species will acquire more N when N is applied in patches compared to when N is applied evenly through the soil profile, (2) native grasses and forbs, which generally have a lower RGR than invasive forbs, will respond to N heterogeneity through physiological plasticity whereas invasive forbs will respond to N heterogeneity primarily

**Table 1** List of the nine species used in this study

| Functional group | Common name | Species | Species abbreviation |
|---|---|---|---|
| Bunchgrass | Bluebunch wheatgrass | *Pseudoroegenaria spicata* (Pursh) A. Löve | PSSP |
| | Thurber's needlegrass | *Achnatherum thurberianum* (Piper) Barkworth | ACTH |
| | Idaho fescue | *Festuca idahoensis* Elmer | FEID |
| Native forb | Arrowleaf balsamroot | *Balsamorhiza sagittata* (Pursh) Nutt. | BASA |
| | Grey hawksbeard | *Crepis intermedia* Gray | CRIN |
| | Long-leaf phlox | *Phlox longifolia* Nutt. | PHLO |
| Invasive forb | Diffuse knapweed | *Centaurea diffusa* Lam. | CEDI |
| | Rush skeletonweed | *Chondrilla juncea* L. | CHJU |
| | Dalmatian toadflax | *Linaria dalmatica* (L.) P. Mill. | LIDA |

Nomenclature follows the USDA PLANTS database (http://plants.usda.gov/)

through morphological plasticity, and (3) a trade-off will exist between root system size and foraging precision.

## Methods

### Study system and materials

In spring 2005, small plants of the native and invasive forbs (canopy dimensions *c*. 6 × 6 × 8 cm) or tillers of the native bunchgrasses (canopy dimensions *c*. 5 × 5 × 10 cm) were planted individually into large pots (25 cm dia × 30 cm deep). All plants were collected from local populations except *Balsamorhiza sagittata* which was purchased as seedlings from a commercial grower. Pots were filled with a 1:1 mixture of field soil and coarse sand to provide a low N soil media. Field soil was collected from the top 20 cm at the Northern Great Basin Experimental Range (43 29′ N, 119 43′ W; *c*. 1400 m elev.), about 56 km west of Burns, Oregon, USA. The soils at the site are sandy loam to loamy sand, Typic Durixerolls (Lentz and Simonson 1986) with total N averaging around 0.08%. Pots were placed in an outdoor garden at the Eastern Oregon Agricultural Research Center, Burns, OR, USA. Plants were allowed to grow for a month before treatments were applied. During this period plants were kept well-watered and received a 200 ml application of one-eighth strength of Hoagland's solution to promote establishment (Epstein 1972). Plants that died within a week of the planting were replaced.

### Experimental design and N patch treatments

Within each of eight blocks, three plants of each species were randomly assigned to receive one of three spatial patterns of N supply for a total of 216 pots (9 species × 3 spatial N patterns × 8 blocks = 216). Each plant received 0.208 mmol of 20 atom% $^{15}NH_4{}^{15}NO_3$ each week for 4 weeks either homogenously, in four patches, or in two patches. In the homogenous treatment 1 l of 0.208 mM $^{15}NH_4{}^{15}NO_3$ was applied evenly over the soil surface every week. A needle and syringe were used to create patches in the two- and four-patch treatments. Each patch was centered 7 cm from the base of the plant. Each patch was created by evenly distributing 25 ml of the labeled solution in five injection points over a 5 cm area. The $^{15}N$ solution was injected through the 5–15 cm soil layer. Injections were made in the same locations each week creating ephemeral nutrient patches with diffuse borders, as they occur likely in the field. Treatments assigned to two patches received 25 ml of 4.16 mM $^{15}NH_4{}^{15}NO_3$ in each patch and treatments with four patches received the same volume of solution in each patch at half the concentration. Plants assigned to patch treatments received approximately 1 l of water the day before each label application to make the soil water content comparable to the homogenous treatment. Based on soil bulk density and the initial inorganic N concentration of the potting media, the N additions in the two- and four-patch treatments were expected to increase soil N to around 10 and 5 mg $kg^{-1}$, respectively, which was within the range that inorganic N can vary in sagebrush steppe systems (Cui and Caldwell 1997; Peek and Forseth 2003).

### Harvest and measurements

At the beginning of the experiment, 15 additional plants of each species were harvested to develop regression equations to estimate initial biomass of each plant. These initial biomass estimates and the final plant biomass harvested at the end of the study were used to calculate RGR for each species during the experiment using the formula: $RGR = [\ln(M_f) - \ln(M_i)]/t_2 - t_1]$ where $M_f$ and $M_i$ are final and initial plant biomass.

About 5 weeks after the spatial N supply treatments were initiated, pots were harvested by block. Above ground biomass was clipped and separated into leaves and stems. Leaves and stems were then triple rinsed with distilled water, dried at 65°C, weighed and ground to a fine powder. Tissue N concentration and $^{15}N$ enrichment were measured on an isotope ratio mass spectrometer (Fisons Instruments, Beverly, MA) at the University of California Davis Stable Isotope Facility. Calculations of $^{15}N$ content followed Nadelhoffer and Fry (1994) where $^{15}N$ content (mg $plant^{-1}$) = $m_f \times [(N_f - N_i)/(N_{lab} - N_i)]$, where $m_f$ is the mass of the N pool (mg), $N_f$ and $N_i$ are the final and initial atom% $^{15}N$ of the sample, and $N_{lab}$ is the atom% $^{15}N$ of the labeled solution.

Soil cores (5 cm dia from the 5 to 15 cm soil layer) were collected from the enriched patches to quantify

root length density (RLD). Two control cores were collected from these pots at a similar depth and distance from the plant base. Soil cores were collected in the homogenous treatment in a similar fashion. Roots were gently washed from the soil in the cores over a fine meshed screen to recover very fine lateral roots. Roots were then stored at 4°C until they were scanned for length with WinRHIZO (Regent Instruments Inc., Saint-Foy, Canada) to determine RLD (Bouma et al. 2000). The ability of a species to selectively allocate root length to nutrient rich patches (i.e., root foraging precision) was calculated using a log response ratio where lnRR = $\ln(RLD_{enriched}/RLD_{control})$ (Hedges et al. 1999; Rajaniemi and Reynolds 2004) and $RLD_{enriched}$ and $RLD_{control}$ are RLD in the nutrient and control patches, respectively. Increasing positive values of lnRR indicated increasing precision in root placement. A one sample *t*-test was conducted to determine if lnRR was significantly greater than zero.

Root $NO_3^-$ and $NH_4^+$ uptake rates were measured in the two-patch treatment. Two subsamples of fine roots (<1 mm dia, approximately 15 mg dry weight) were removed from both the enriched and non-enriched patches in the two-patch treatment. These subsamples were immediately placed in teabags and equilibrated in 0.5 mM $CaCl_2$ at 20°C. Within 30 min of sampling, the subsamples were submerged in solutions containing either 500 μM $^{15}NH_4Cl$ or $K^{15}NO_3$ for 30 min. The uptake solutions were well-mixed, aerated and contained 1% sucrose and 0.5 mM $CaCl_2$ (Jackson et al. 1990). After the incubation period, all samples were washed in a series of 2 mM KCl solutions and a final rinse in distilled water to remove any $^{15}N$ adsorbed to the root surface. The N uptake assays were completed within an hour after harvesting to minimize the effect of root excision on N uptake capacity (Bloom and Caldwell 1988). Roots were dried at 65°C, ground to a fine powder and analyzed for N concentration and $^{15}N$ enrichment following the same procedure used to quantify leaf and stem $^{15}N$. Root $NO_3^-$ and $NH_4^+$ uptake rates were expressed on a root dry mass basis (μmol $g^{-1}$ $h^{-1}$).

Root system biomass was used as an index of root system size (Einsmann et al. 1999; Rajaniemi and Reynolds 2004). To quantify root system biomass and amount of $^{15}N$ retained in roots, pots were sliced open and the rest of the root system was washed from the soil. After drying, the bulk roots were weighed and a subsample was ground to a fine powder for $^{15}N$ analysis. Total plant $^{15}N$ capture was calculated by summing the $^{15}N$ content of shoots and roots.

## Statistical analysis and path model development

Measurements that did not involve repeated sampling of the same plant were analyzed with ANOVA (SAS 2001). Assumptions of ANOVA were evaluated using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. When these assumptions were not met, data were weighted by the inverse of the variance (Neter et al. 1990). Repeated measures ANOVA was used when comparing root responses of the same individual plant in control and enriched patches. The between-subject effects were block and species. Because the root system of the same plant was sampled in the control and patch treatment, within-subject effects were patch type and the interaction between patch type and the between-subject effects. Following ANOVA, linear contrasts were used to test a priori hypotheses about differences in N capture and root responses between functional groups. When these comparisons were not orthogonal, sequential Bonferroni corrections were made to maintain an experiment-wise error rate of $\alpha = 0.05$ (Rice 1989). Because we had no a priori basis for predicting individual species responses we compared species responses within functional groups using Tukey's studentized range test.

Path analysis and structural equation modeling were used to determine how RGR, root system scale, and root system plasticity influence N capture in spatially heterogeneous environments. This model was based on previous mathematical models and empirical results of nutrient flow to roots and plant nutrient capture in relation to root length, growth rate and physiology (Campbell et al. 1991; Barber 1995). Path coefficients, their significance level and the fit of the structural model to the data were evaluated with the CALIS procedure in SAS. The total correlations between independent and dependent variables were decomposed into direct and indirect effects with direct effects 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 by comparing the predicted covariance matrix based on the specified model with the observed covariance structure from our data. We used the Goodness of Fit Index (GFI) and Normed Fit Index (NFI) as indices of model fit. Values of GFI and NFI > 0.9 are generally considered indicative of good agreement between the matrices (Hatcher 1994; Schumacker and Lomax 2004).

## Results

### Functional group and species attributes

The three functional groups (bunchgrass, native forb, and invasive forb) differed in RGR during the experiment and there was also significant variation in RGR within functional groups (Fig. 1a). Invasive forbs had a greater RGR than bunchgrasses and native forbs ($P < 0.01$) and bunchgrasses had a greater RGR than native forbs ($P = 0.01$). An effect of spatial pattern of N supply on RGR was not observed ($P > 0.05$). While species within functional groups differed in root biomass, there were also significant differences in root biomass between functional groups (Fig. 1b). Invasive forbs had greater root biomass than bunchgrasses ($P = 0.04$) and native forbs ($P < 0.01$) and bunchgrasses had greater root biomass than native forbs ($P < 0.01$). These differences were not affected by the spatial pattern of N supply ($P > 0.05$). The amount of biomass allocated to roots relative to total plant biomass (RMR) tended to be similar among species within functional groups (Fig. 1c) but bunchgrasses and native forbs had greater RMR than invasive forbs ($P < 0.01$).

### Plant N capture

All species captured more N when N was supplied in patches compared to when N was supplied homogenously ($P < 0.01$; Fig. 2). Likewise, bunchgrasses, native forbs, and invasive forbs captured more N when N was supplied in two patches compared to when the same amount of N was distributed among four patches ($P < 0.01$, $P = 0.03$, and $P < 0.01$, respectively). Invasive forbs captured more N from patches compared to bunchgrasses and native forbs ($P < 0.01$).

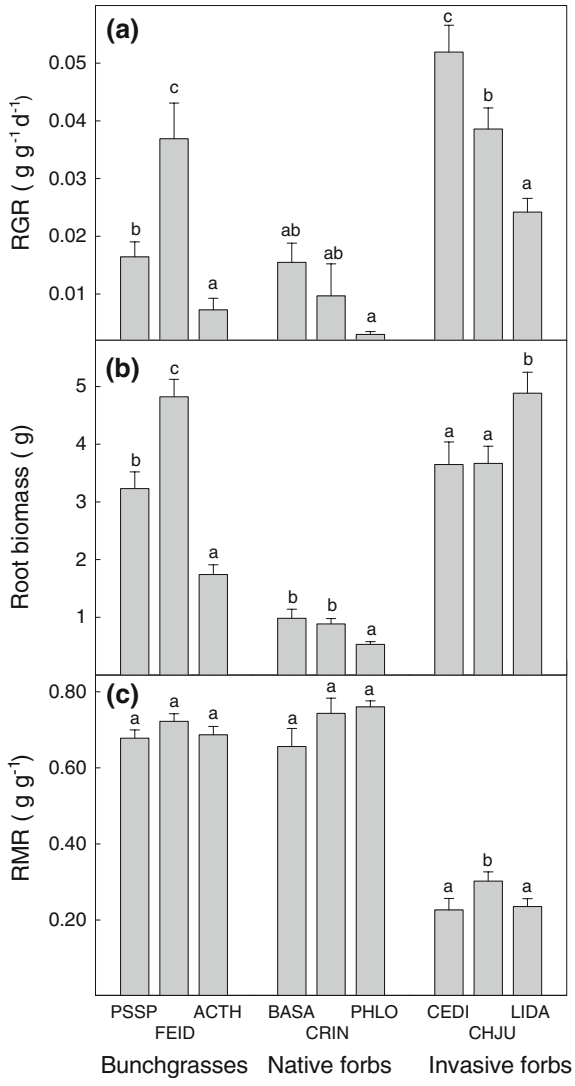


**Fig. 1** (**a–c**) Relative growth rate (RGR), root biomass and root mass ratio (RMR) for each study species within the three functional groups (mean ± SE, $n$ = 18–24). Values are averaged over the different N supply treatments. Bars with different letters indicate significant differences *within* functional groups ($P < 0.05$, Tukey's studentized range test)

### Root responses

While RLD was not significantly different between bunchgrasses and invasive forbs ($P = 0.23$), native forbs had lower RLD than bunchgrasses and invasive forbs ($P < 0.01$; Fig. 3). Root length density did not differ between the four-patch and two-patch treatment for any species ($P > 0.05$) and RLD was not greater in enriched patches compared to control

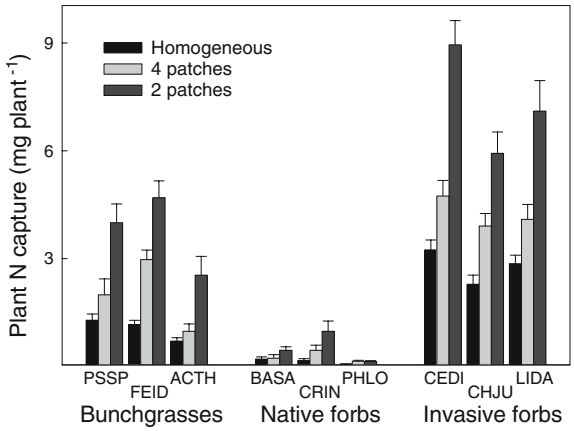


**Fig. 2** Effect of the spatial pattern of N supply on N capture by the nine study species (mean ± SE, $n = 6–8$). The same total amount of N was applied in all treatments

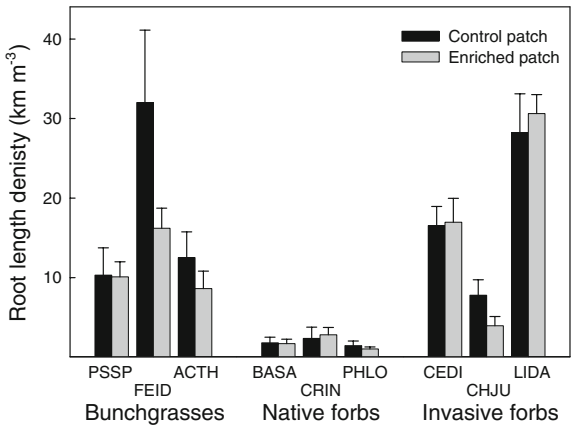


**Fig. 3** Root length density (RLD) of the study species in control and enriched patches. Species responses are averaged across both patch treatments (mean ± SE, $n = 12–16$)

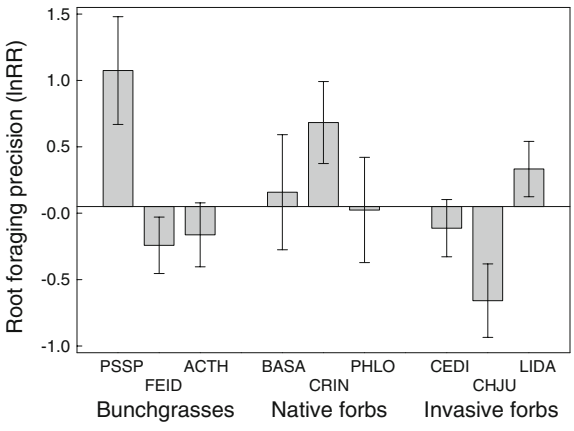


**Fig. 4** Root foraging precision of the study species calculated using a log response ratio where lnRR = ln ($RLD_{enriched}$/$RLD_{control}$). Species responses are averaged across both patch treatments (mean ± SE, $n = 12–16$). Positive values indicate greater precision in root placement while values not significantly different from zero indicate that root placement was similar in enriched and non-enriched soil patches

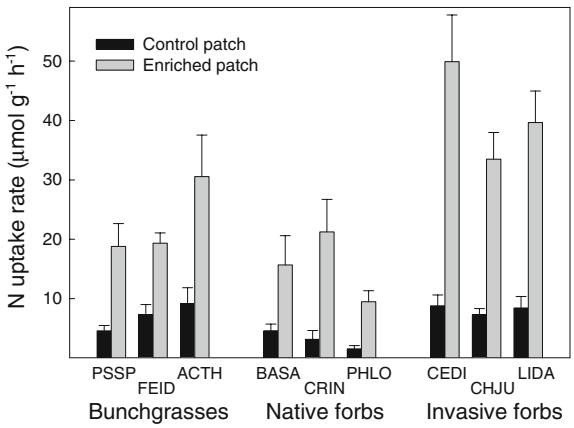


**Fig. 5** Nitrogen uptake rate ($NO_3^- + NH_4^+$) of roots growing in a control or enriched patch (mean ± SE, $n = 6–8$). Uptake rates were measured on the two-patch treatment only

patches ($P = 0.53$). As a result, root foraging precision did not differ significantly from zero for any functional group or study species within a functional group ($P > 0.05$, one sample $t$-test for mean; Fig. 4).

Root uptake rates for $NH_4^+$ and $NO_3^-$ in the two-patch treatment did not differ significantly for any species so values for root uptake rates for all species were averaged over both N forms. Native forbs had lower uptake rates in control patches compared to bunchgrasses and invasive forbs ($P < 0.01$) but root N uptake rate in control patches did not differ between bunchgrasses and invasive forbs (Fig. 5; $P = 0.32$). While all species had greater root uptake rates in enriched patches compared to control patches ($P < 0.01$) this varied by species (patch type × species; $P = 0.02$). Invasive forbs had greater root uptake rates in enriched patches compared to bunchgrasses and native forbs ($P < 0.01$). There was a trend for bunchgrasses to have higher uptake rates than native forbs in enriched patches ($P = 0.08$). There was also a trend for root system mass to be positively correlated with uptake rate ($r = 0.56$, $P = 0.11$).

Path analysis

The model fit indices, GFI and NFI, were 0.93 and 0.93, respectively, indicating that the path model fit the data to a reasonable level. The variables included in the model explained 73% of the variations in plant N capture (Fig. 6). Root system mass and root N uptake rate had strong and significant paths to plant N capture ($P < 0.01$) while the path from root foraging precision to plant N capture was not significant ($P = 0.15$). Relative growth rate had a significant path to root N uptake rate and root system mass and explained 32% and 19% of the variation in these variables, respectively.

## Discussion

All species acquired more N when N was supplied in patches compared to when N was supplied uniformly, supporting our first hypothesis. These observations are consistent with previous work on perennial bunchgrasses from nutrient-poor and -rich habitats (Fransen et al. 1999) and are likely due to an effect of soil N concentration on N capture and greater N uptake rates of roots growing in patches. Namely, N uptake rate is expected to increase linearly as soil N concentration increases. Therefore, in this experiment, concentrating the same amount of N in patches could result in greater N capture than the uniform supply treatment even without physiological adjustments to the root system (Barber and Silberbush 1984). In addition, for all species, roots growing in patches had a greater N uptake rate than roots growing outside of the patches. With this physiological adjustment, higher N concentrations are needed to saturate N uptake capacity (Barber 1995), likely allowing these species to capture more N in the patch treatments compared to when N was supplied uniformly.

Our hypothesis that native species with low RGR would respond to nutrient patches primarily through physiological plasticity while invasive species with high RGR would respond to nutrient heterogeneity through morphological plasticity was not supported. While all species had greater root N uptake rates in enriched patches compared to control patches, none of the species had greater root length density in enriched patches relative to control patches. In addition, invasive forbs, which had a higher RGR than natives, also had higher root N uptake rates than the natives in enriched patches. These observations largely contrast with previous theoretical and empirical work. For example, the C–S–R model of plant strategies developed by Grime (1979) predicts that species with low RGR maintain a slow-growing, long-lived root system and should therefore exhibit greater root physiological plasticity than species with high RGR. In a review of 27 species with different RGR, Robinson and Van Vuuren (1998) found that the increase in root nutrient uptake rates in enriched patches compared to controls averaged around 2.4-fold for slow-growing species but only about 1.3-fold for fast-growing species, supporting the initial predictions of Grime (1979).

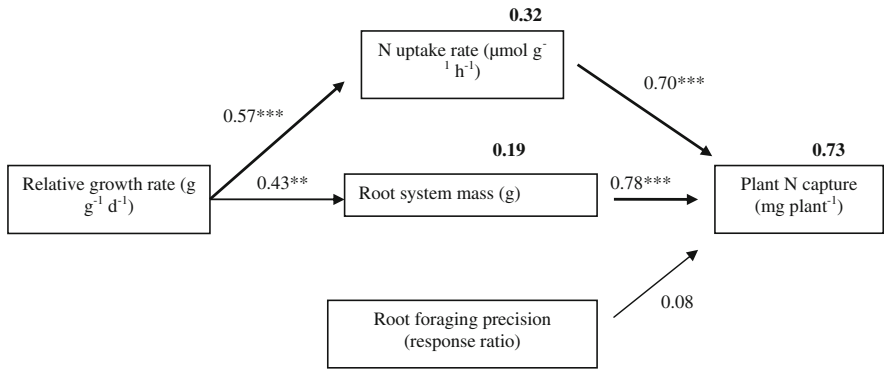


**Fig. 6** Path model to determine how variation in RGR, root system mass, and root foraging precision and root N uptake rate contributes to variation in N capture in spatially heterogeneous environments. For each path effect the standardized partial regression coefficient is given and the significance of the path is indicated as *** $P < 0.0001$, ** $P < 0.001$. Numbers in bold are the total variance explained ($r^2$) for each dependent variable

The relationship between RGR and physiological plasticity in root nutrient uptake capacity has been largely unexplored in the context of invasive species and the results from this current study suggest alternative hypotheses about the relationship between RGR and root physiological plasticity need to be considered. For example, research in cropping systems has demonstrated that during periods of rapid biomass production root N uptake rates are often elevated due to greater plant N demand (Siddiqi et al. 1990; Mattsson et al. 1992; Schenk 1996). Therefore, instead of a trade-off between RGR and physiological plasticity, invasive species with high RGR may be able to increase root N uptake rate to a greater degree than native species with low RGR due to greater plant N demand.

Because of the lack of foraging precision demonstrated by our study species under these experimental conditions, our hypothesis about a trade-off between root system sizes and foraging precision could not be evaluated. In contrast to our study, the majority of experiments investigating plant responses to nutrient patches have demonstrated various degrees of foraging precision in a range of species (Robinson 1994; Robinson and Van Vuuren 1998). One of the species used in this study, *P. spicata*, has demonstrated substantial foraging precision in some previous studies (Eissenstat and Caldwell 1988; Black et al. 1994; Larigauderie and Richards 1994) but not others (Jackson and Caldwell 1989; Ivans et al. 2003). One factor that may contribute to these observed discrepancies in foraging responses, even when the same species is considered, may be the level of mycorrhizal colonization. While we did not quantify mycorrhizal association in this study, mycorrhizae can greatly increase the ability of plants to capture nutrients and may dampen the degree to which plants forage for nutrients (Koide and Elliot 1989). Most evidence, however, indicates that while mycorrhizae may be important for phosphorous capture they contribute substantially less to the ability of a plant to capture N from patches (Hodge 2004). Therefore, differences in mycorrhizal colonization between experiments appear to be a less likely explanation for the lack of root proliferation observed in this experiment.

One likely reason that root proliferation was not observed in this study but has been commonly observed in other studies may be due to how the nutrient patches were created. In our study, we injected N at weekly intervals that likely resulted in fairly ephemeral N patches. Cui and Caldwell (1997) and Ivans et al. (2003) showed that plants in the Great Basin respond to brief pulses of N availability mainly through changes in root N uptake rate with new root growth either greatly lagging the nutrient flush or not occurring at all if the pulse is too brief. Most experiments on plant response to nutrient heterogeneity have generally utilized a more constant form of nutrient enrichment (e.g., slow-release fertilizer or frequent injections of nutrient solution) resulting in relatively long-lived nutrient patches (e.g., Campbell et al. 1991; Black et al. 1994; Rajaniemi and Reynolds 2004). The ephemeral nature of nutrient patches has been recognized (Lamb et al. 2004), particularly in arid and semi-arid systems (Cui and Caldwell 1997; James and Richards 2006). Results from this pot study, as well as previous field studies in the Great Basin, suggest root proliferation may be minimal when N is restricted to brief pulses.

Results from our path analysis identified combinations of traits that may contribute to the success of invasive forbs in the heterogeneous, nutrient poor soils of the sagebrush steppe as well as other ecosystems. For example, in our study there was a positive correlation between root system mass and root N uptake rate with invasive forbs having higher RGR, greater root biomass and higher N uptake rates per unit root biomass than the native species.

Variation in both root biomass and N uptake rate per unit root biomass were important in contributing the variation in ability of a species to capture N from ephemeral patches. Variation in both variables, in turn, was influenced by variation in RGR. The interrelationship among traits described in this working model provides one possible explanation of how invasive forbs were able to capture 2 and 15-fold more N from enriched patches compared to the native grasses and forbs, respectively. Although identifying traits of invading species has been an area of intense research interest, often these traits are considered in relation to the individual effects they may have on invasion. Our results suggest that it may be useful to place some emphasis on understanding how the interrelationship between suites of traits may influence the success of invasive plants.

In this study, we observed a positive relationship between RGR, root system size and plasticity in root N uptake rate. Instead of a trade-off between traits, these

results suggest that within a plant community, traits related to nutrient capture may be positively correlated, potentially promoting size-asymmetric competition belowground (Einsmann et al. 1999; Farley and Fitter 1999b; Rajaniemi and Reynolds 2004). This may be one mechanism facilitating the spread of invasive species in nutrient-poor systems. Importantly, however, we also observed substantial variation in some of these traits among species within a functional group (i.e., native and invasive forbs). The limitations of using conventional functional classification schemes (e.g., forb, grass, or shrub) to predict ecosystem properties such as invasion resistance has been demonstrated (Wright et al. 2006). In support of this idea, our results suggest that root traits related to N capture may be more similar between invasive forbs and native bunchgrasses than between invasive forbs and native forbs. This suggests native bunchgrasses might be more important in interfering with invasive forb establishment and growth than would otherwise be predicted based on conventional functional classification schemes. It is important to note, however, that this study only evaluated plastic root responses of individual plants in pots. While the pots used in this study were relatively large, this approach can induce a number of experimental artifacts (e.g. Brown et al. 1991) suggesting that these results should be interpreted with some caution. In addition, our experiment did not determine how these responses vary in the presence of neighbors. The benefits of these various traits may change depending on interactions with neighboring plants and composition of the nutrient patch (Cahill and Casper 1999; Robinson et al. 1999). Ultimately, field experiments with plants in different neighbor environments will provide an important next step in determining how these positive relationships among traits influence competitive ability and invader success.

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