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Does a tradeoff exist between morphological and physiological root plasticity? A comparison of grass growth forms

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Abstract — A series of experiments were conducted to evaluate the potential tradeoff between morphological and physiological root plasticity in caespitose and rhizomatous grass growth forms in semi-arid and mesic communities. Morphological and physiological root plasticity were evaluated with in-growth cores and excised root assays, respectively. The rhizomatous grass in the semi-arid community was the only species to display significant physiological root plasticity, but all species possessed the capacity to proportionally increase ^{15}N uptake with increasing concentrations of $(^{15}NH_4)_2SO_4$ solution. Neither the caespitose nor the rhizomatous grass displayed morphological root plasticity in response to nitrogen addition in the mesic community. In contrast, significant morphological root plasticity occurred in species of both growth forms in the semi-arid community. These data suggest that the compact architecture and the ability to accumulate nutrients in soils directly beneath caespitose grasses did not increase selection pressure for physiological root plasticity at the expense of morphological root plasticity and that the coarse grained foraging strategy and low density of large diameter roots did not increase morphological root plasticity at the expense of physiological root plasticity in rhizomatous grasses. These preliminary data suggest that 1) a high maximum uptake rate for nitrogen in these perennial grasses may minimize the expression of physiological root plasticity, 2) morphological and physiological root plasticity may represent complimentary, rather than alternative, foraging strategies, and 3) the expression of root plasticity may be strongly influenced by abiotic variables within specific habitats. USDA-ARS © 1999 Published by Éditions scientifiques et médicales Elsevier SAS

Clonal plants / plant foraging / plant-soil relations / resource heterogeneity

1. INTRODUCTION

Plant foraging represents the process by which roots and shoots are positioned within a habitat to exploit heterogeneously distributed resources [15]. Plant foraging for heterogeneously distributed soil resources has largely emphasized morphological root plasticity, which can be defined by increased root length or mass (i.e. root proliferation) in response to localized nutrient enrichment [33, 44]. Plants may also effectively exploit nutrients by physiological root plasticity which involves a disproportionate increase in the rate of nutrient absorption (i.e. absorption kinetics) per unit tissue mass or length when a zone of high nutrient concentration is encountered [10, 28, 31, 32]. This mechanism may be particularly important when soil resources are temporally and spatially too unpredictable to allow effective exploitation by morphological root plasticity [30] and when nutrient pulses are of insufficient magnitude or duration to offset foraging costs associated with morphological root plasticity [24].

The relative expression of physiological and morphological root plasticity is likely influenced by growth form [11], life history strategy [13], and habitat characteristics [9, 30] of individual species. In grassland communities, caespitose and rhizomatous growth forms possess different abilities for exploiting heterogeneously distributed soil resources based on unique architectural constraints [7, 17]. Ramets are compactly arranged with minimal inter-ramet distances in caespitose grasses, but they are more dispersed on spacers of various length and branch angles in rhizomatous grasses. Resource availability may also influence the relative expression of root plasticity between these two growth forms because caespitose species are most abundant in semi-arid environments while rhizoma-

tous species are most abundant in mesic environments in the North American Great Plains [41]. The relative importance of above- and belowground resource availability on plant-soil relationships varies along this environmental gradient [8] and may disproportionately affect the foraging strategies of these contrasting growth forms.

Plant-induced nutrient accumulation in soils beneath caespitose, but not rhizomatous, grasses may further influence the relative expression of root plasticity between these two growth forms [19, 26, 29, 45]. Greater concentrations and pools of soil organic carbon and total nitrogen have been documented to occur in shallow soils directly beneath the basal circumference of caespitose grasses compared to similar soils between clones, in both mesic and semi-arid grassland communities [19]. Plant-induced nutrient concentration in soils beneath caespitose grasses may have influenced the foraging strategy of species possessing this growth form by limiting the benefits of soil exploration relative to the associated costs of root construction and maintenance (e.g. [15]).

A compact architecture, high density of fine roots [47] and capacity to concentrate nutrients in soils beneath caespitose grasses may have increased selection pressure for physiological root plasticity at the expense of morphological root plasticity. In contrast, the coarse grained foraging strategy of rhizomatous grasses, characterized by placement of juvenile ramets at various locations and densities from parental ramets and a low density of more coarse roots [47], may have increased selection pressure for morphological root plasticity at the expense of physiological root plasticity (but see [43]). Contrasting root architectures between species of the two growth forms may also contribute to potential tradeoffs in foraging strategies because root diameter and total root length are recognized as the most important variables influencing nutrient uptake ([20, 40], but see [5]). While morphological root plasticity has been evaluated in both caespitose [27, 33] and rhizomatous grasses [13, 16, 27], investigations of physiological root plasticity have been confined to only caespitose grasses [11, 12, 31]. In addition, the relative expressions of physiological and morphological root plasticity have not been simultaneously investigated in the same species.

A series of experiments were conducted to evaluate the potential tradeoff between morphological and physiological root plasticity in these contrasting grass growth forms in semi-arid and mesic communities. Two specific hypotheses were tested: 1) caespitose grasses would exhibit greater physiological than morphological root plasticity; and 2) rhizomatous grasses would exhibit greater morphological than physiological root plasticity. Morphological and physiological root plasticity of a dominant caespitose and rhizomatous grass species in each community were investigated by evaluating root proliferation with in-growth cores and uptake kinetics of a stable isotope of nitrogen with excised root assays, respectively.

2. MATERIALS AND METHODS

2.1. Site descriptions

The semi-arid shortgrass community is located at the Central Plains Experimental Range (CPER) in north-central Colorado, approximately 60 km northeast of Fort Collins (40°49' N, 107°46' W) and the mesic tallgrass community is located at the Konza Prairie Research Natural Area (KPRNA) in eastern Kansas near Manhattan (39°05' N, 96°35' W). These two sites are located on the western and eastern edge of the North American Great Plains, respectively, and are characterized by substantial differences in mean annual precipitation (2.7-fold), and organic carbon (2.9-fold) and total nitrogen (2.3-fold) in the surface soil (0–10 cm) [49]. The semi-arid site is located on a swale topographical position, has a mean annual precipitation of 321 mm, a mean annual temperature of 8.6 °C [34], and the vegetation is predominately (90 % of basal area) *Bouteloua gracilis* [35]. The mesic site is located on a level summit topographical position, has a mean annual precipitation of 835 mm, a mean annual temperature of 12.8 °C [1], and the dominant species are *Sorghastrum nutans*, *Andropogon gerardii* and *Schizachyrium scoparium*. Long-term (> 25 years) moderately grazed sites were sampled within each community.

S. scoparium (C_4, caespitose) and *A. gerardii* (C_4, rhizomatous), and *B. gracilis* (C_4, caespitose) and *Pascopyrum smithii* (C_3, rhizomatous) clones were investigated in a mesic and semi-arid grassland community, respectively, to determine how environmental characteristics may influence these two forms of root plasticity. Precipitation during the investigation was 52 % of the long-term average at the mesic community (123 mm from mid-May to mid-July), but relatively high (161 % of average) at the semi-arid community (182 mm).

2.2. Physiological root plasticity

Soils were removed to a depth of 10 cm from beneath caespitose grasses ($n = 6$ for each species) with basal areas of approximately 150 cm^2 and from 30×30 cm areas ($n = 6$ for each species) of

rhizomatous-dominated vegetation from long-duration grazed sites in each community and transported back to a field laboratory. Roots were washed manually from the soil and retained if they were < 1 mm in diameter with a light yellow color and firm consistency. Roots from each soil sample were separated into four random samples of 2.42 ± 0.06 (mean ± 1 SE) g dry weight. Root subsamples were placed in cheesecloth bags and immersed in a 0.5-mM solution of $CaCl_2$ at 25 °C for 15 min. One of the four subsamples was removed from the $CaCl_2$ solution and used to determine background ^{15}N atom %. The three remaining subsamples were immersed in one of three $(^{15}NH_4)_2SO_4$ solutions containing 1, 10, or 25 mM $^{15}NH_4$ for roots from the semi-arid community or 10, 50, or 100 mM $^{15}NH_4$ for roots from the mesic community. Greater nitrogen concentration in surface soil in the mesic compared to the semi-arid community [49] prompted us to use different $^{15}NH_4$ concentrations for evaluating species of these two communities. Uptake kinetics were determined on NH_4^+ rather than NO_3^- as this is the prevailing inorganic form in similar grasslands [18, 39]. All solutions were adjusted to pH 7.5, well-mixed and aerated, and contained 0.01 M sucrose as an energy source and 0.5 mM $CaCl_2$ to maintain membrane integrity [31, 46]. After immersing subsamples for 10 min in the respective ^{15}N solutions, roots were subjected to three successive rinses of 2 min each in unlabelled $(NH_4)_2SO_4$ solutions of identical concentrations. Rinse solutions were maintained near 5 °C and used to replace any ^{15}N adsorbed to root surfaces. Roots were blotted dry before being oven dried at 60 °C for 5 d. Precautions were taken to complete ^{15}N uptake experiments within 2 h after soil sample collection in the field to minimize detrimental effects of root excision on ammonium uptake [4]. Dried root subsamples were weighed and ground to pass a 40-mesh screen. Approximately 7.5 mg root mass was loaded in tin capsules and analyzed for ^{15}N atom % using a Carlo-Erba NA-1500 elemental analyzer interfaced with a VG-Isomass mass spectrometer (Isotope Services Inc., Los Alamos NM, USA). Mean ($n = 6$) background ^{15}N atom % values (*S. scoparium*: 0.41268, *A. gerardii*: 0.39586, *B. gracilis*: 0.38595, *P. smithii*: 0.38244) were subtracted from the ^{15}N atom % values of respective samples to determine ^{15}N atom % excess values for each root subsample [6].

2.3. Morphological root plasticity

Morphological root plasticity was assessed in the long-term grazed sites in each community using twenty root in-growth cores (5 cm diameter × 10 cm deep) located between individual rhizomatous and caespitose clones. Soil cores were initially removed from each community in mid-May, sieved through a 1-mm screen in the field and placed back into the cored hole after lining it with a mesh screen (0.5 × 1.0 cm openings). Dry, slow-release nitrogen fertilizer was added to one-half of the in-growth cores at rates of 112 and 224 $kg \cdot ha^{-1}$ in the semi-arid and mesic community, respectively. The fertilizer rate at the semi-arid community has previously resulted in increased forage production [23] and was doubled for the mesic community to reflect soil nitrogen differences between the two communities [49]. The identical locations were re-cored in mid-July to extract the soil and roots within the mesh screen. Soils were placed in Ziploc bags and transported to a laboratory at Texas A&M University. Roots were hand sorted from soil samples, washed, oven dried at 60 °C for 5 d and weighed.

2.4. Statistical analysis

Data for the physiological plasticity experiment were standardized by unit root mass [31]. We tested this data for significant effects of growth form (caespitose vs. rhizomatous) and ^{15}N solution concentrations on ^{15}N uptake using a two-way ANOVA [38] with mean separation by Duncan's multiple range test at the 0.05 level of probability. Individual regression equations were generated for species of both growth forms between two successive ^{15}N solution concentrations. Slopes between the ^{15}N solution concentrations and growth forms were then compared within and between species in each community to determine the presence of a significant difference between the two independent regressions (see p. 258 in [42]). Morphological plasticity data was tested for significant effects of growth form (caespitose vs. rhizomatous) and nitrogen addition on root mass in the in-growth cores using a two-way ANOVA with mean separation by Duncan's multiple range test at the 0.05 level.

3. RESULTS

3.1. ^{15}N root uptake

All four species absorbed greater amounts of ^{15}N with increasing solution concentrations at each community (*figure 1A, B*). The caespitose grass absorbed significantly more ^{15}N than the rhizomatous grass at all ^{15}N solution concentrations in the mesic community (*figure 1A*). The magnitude of ^{15}N uptake was 118, 74 and 38 % greater for the caespitose than the rhizomatous grass at the 10, 50 and 100 mM ^{15}N solution concentrations, respectively. In contrast, the rhizomatous grass had greater ^{15}N uptake (40–60 %) than the caespitose grass in the semi-arid community, although the difference was only significant at the

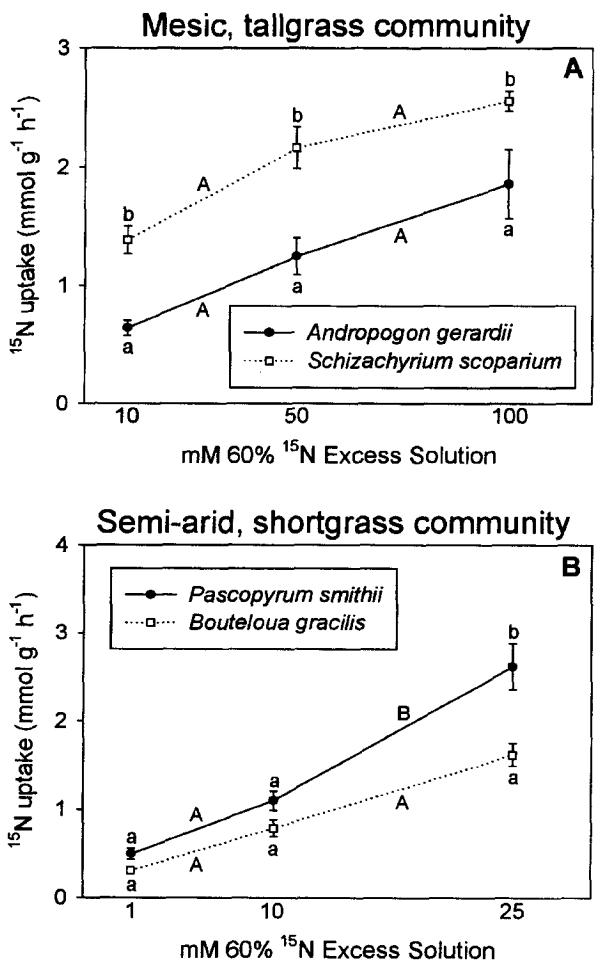

Figure 1. Mean (± 1 SE, $n = 6$) rates of ^{15}N uptake per unit root mass for excised roots assayed in three concentrations of $(^{15}NH_4)_2SO_4$ solutions for A) a rhizomatous (*Andropogon gerardii*) and a caespitose (*Schizachyrium scoparium*) grass in a mesic, tallgrass community, and B) a rhizomatous (*Pascopyrum smithii*) and a caespitose grass (*Bouteloua gracilis*) in a semi-arid, shortgrass community. Uptake rates within each ^{15}N solution concentration followed by the same lowercase letter are not significantly different for grass growth form ($P > 0.05$). Slopes for uptake rates between pairs of ^{15}N solution concentrations are not significantly different for grass growth form if uppercase letters are the same ($P > 0.05$). See *table I* for individual regression line variables.

highest ^{15}N solution concentration (*figure 1B*). The magnitude of ^{15}N uptake was similar for three of the four species at the one identical ^{15}N solution concentration (10 mM) used in both communities. However, *S. scoparium* absorbed approximately twice the amount of ^{15}N compared to the other three species.

3.2. Physiological root plasticity

Neither the caespitose nor the rhizomatous grass exhibited physiological root plasticity in the mesic community (*figure 1A*). The rhizomatous grass displayed a slight, but not significant, increase in the rate of ^{15}N uptake with increasing ^{15}N solution concentrations. In contrast, uptake rates declined for the caespitose grass at higher ^{15}N concentrations (*table I*). The rhizomatous, but not the caespitose, grass displayed physiological root plasticity in the semi-arid community (*figure 1B*). The rhizomatous grass had significantly greater uptake rates with increasing ^{15}N solution concentrations, while the caespitose grass exhibited only a slight increase (*table I*).

3.3. Morphological root plasticity

While roots of both grass growth forms were present within all in-growth cores in the mesic community, neither the caespitose nor the rhizomatous grass displayed morphological root plasticity in response to nitrogen addition (*figure 2A*). The rhizomatous grass had 57 and 124 % greater root mass than the caespitose grass in control and fertilized in-growth cores, respectively. At the semi-arid community, caespitose grass roots were found within all in-growth cores, but rhizomatous grass roots occurred in only 50 and 80 % of the control and nitrogen fertilized in-growth cores, respectively. Both growth forms displayed significant morphological root plasticity in response to nitrogen fertilizer (*figure 2B*). Consistent plastic responses were found in both growth forms with increases of 71 and 72 % greater root mass with nitrogen addition for the caespitose and rhizomatous grass, respectively. The caespitose grass produced 180 % greater root mass in the in-growth cores than the rhizomatous grass for both the control and nitrogen addition treatments. Caespitose grasses produced comparable amounts of root mass within the control in-growth cores in both communities. However, the rhizomatous grass in the mesic community produced 327 % more root mass within control in-growth cores than did the rhizomatous grass in the semi-arid community.

4. DISCUSSION

Caespitose grasses did not possess greater physiological than morphological root plasticity, nor did rhizomatous grasses possess greater morphological than physiological root plasticity, in either the mesic or semi-arid community. Consequently, both of the initial hypotheses were rejected. This indicates that the compact architecture and the ability to accumulate nutrients in soils directly beneath caespitose grasses did not

Table I. Linear regression equation values between ^{15}N solution concentrations (1, 10 and 25, and 10, 50 and 100 mM ^{15}N at the semi-arid and mesic community, respectively) and ^{15}N uptake per unit root mass for contrasting grass growth forms (caespitose vs. rhizomatous) in a mesic (Konza Prairie Research Natural Area, Manhattan, Kansas) and semi-arid (Central Plains Experimental Range, Nunn, Colorado) grassland. Asterisks indicate significant ($P < 0.05$) increases in slopes of regression lines between ^{15}N solution concentration pairs within a growth form in each community. See *figure 1* for regression lines.

			^{15}N solution concentration pair					
			Low-middle			Middle-high		
Community	Species	Growth form	Slope	R^2	P-value	Slope	R^2	P-value
Mesic	*Schizachyrium scoparium*	Caespitose	0.77	0.57	0.0043	0.40	0.29	0.0687
	Andropogon gerardii	Rhizomatous	0.61	0.56	0.0051	0.61	0.26	0.0923
Semi-arid	*Bouteloua gracilis*	Caespitose	0.48	0.68	0.0010	0.84	0.73	0.0004
	Pascopyrum smithii	Rhizomatous	0.60	0.70	0.0007	1.52*	0.74	0.0003

increase selection pressure for physiological root plasticity at the expense of morphological root plasticity and that the coarse grained foraging strategy and low density of large diameter roots did not increase morphological root plasticity at the expense of physiological root plasticity in rhizomatous grasses.

Two alternative hypotheses can be inferred from these data regarding the relative expression of morphological and physiological root plasticity. First, proportional increases in the magnitude of ^{15}N uptake over a relatively wide range of increasing solution concentrations indicate that efficient absorption kinetics are an important component of nutrient acquisition in these grasses. Fine roots of these species appear to possess a maximum uptake rate that enables them to effectively exploit nitrogen over the range of concentrations found in these grassland soils without a disproportionate increase in the rate of nitrogen uptake at greater nitrogen concentrations (i.e. physiological root plasticity). Simulation models indicate that increases in uptake kinetics can compensate for the reduction in whole-plant nutrient uptake in soils with heterogeneously distributed nutrients [30, 37]. The expression of physiological root plasticity by *P. smithii* in the semi-arid community may have been associated with an increase in the maximum uptake rate for nitrogen at higher concentrations because of an increased number of absorption sites [21]. The greater magnitude of ^{15}N uptake displayed by *S. scoparium* compared to *A. gerardii* was very likely a function of greater fine root density per unit mass in the caespitose species [47]. A high density of fine roots, in addition to effective absorption kinetics, very likely contributes to the ability of *S. scoparium* to exploit nutrients to very low concentrations (e.g. [48]).

The second alternative hypothesis for the limited expression of morphological and physiological root plasticity in these grasses is that these two mechanisms may represent complimentary, rather than alternative, foraging strategies to enhance plant nutrient acquisition. Both foraging strategies were expressed by only one of the four species, the rhizomatous grass *P. smithii* in the semi-arid environment. However, current knowledge of the costs and benefits of physiological and morphological plasticity in various environments is insufficient to provide a mechanistic interpretation of the potential tradeoff between these two foraging strategies [28].

Contrasting responses in root plasticity between growth forms in semi-arid and mesic communities suggest that prevailing abiotic variables may greatly influence the expression of physiological and morphological root plasticity in addition to species-specific responses (e.g. [2, 25]). A 2.7-fold difference in mean annual precipitation between the mesic and semi-arid grassland communities establishes water as an important abiotic variable influencing the expression of root plasticity [49]. The availability of soil water influences nutrient movement by diffusion and mass flow and affects the development of nutrient depletion zones near root surfaces [12, 36]. The occurrence of 30 % less precipitation at the mesic than the semi-arid community during this investigation may have greatly constrained root responses to nitrogen fertilization. Relatively high levels of fertilizer application with below average precipitation at the mesic site may have contributed to lower root production in fertilized compared to unfertilized in-growth cores. However, contrasting patterns of root plasticity were not solely a function of precipitation because plants in the unfertilized in-growth cores in the mesic community produced as much or more root mass than did plants in the semi-arid community.

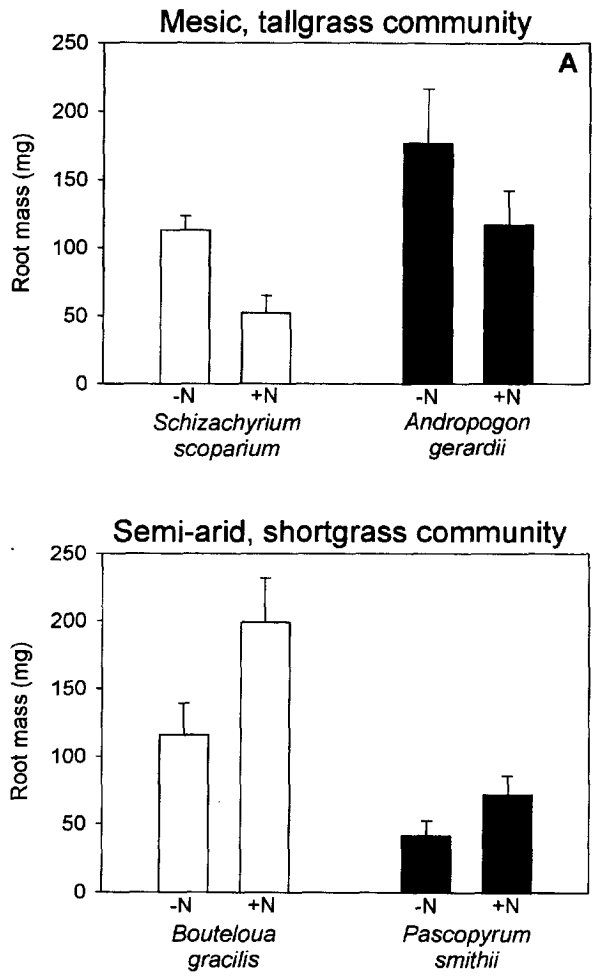

Figure 2. Mean (± 1 SE, $n = 10$) root mass in in-growth cores (5 × 10 cm) located between grass growth forms for A) a caespitose (*Schizachyrium scoparium*) and rhizomatous (*Andropogon gerardii*) grass in a mesic, tallgrass community and B) a caespitose (*Bouteloua gracilis*) and rhizomatous (*Pascopyrum smithii*) grass in semi-arid, shortgrass community. Dry nitrogen fertilizer was added to one-half ($n = 10$) of the in-growth cores in mid-May at rates of 112 and 224 kg·ha^{-1} (+N) in the semi-arid and mesic community, respectively, while the remaining in-growth cores were not fertilized (–N). In-growth cores were removed in mid-July. *P*-values are 0.0744 and 0.1003 for growth form and fertilizer, respectively, in the mesic community, and 0.0429 and 0.0160 for growth form and fertilizer, respectively in the semi-arid community.

The absence of morphological or physiological root plasticity by either growth form in the mesic community is consistent with the conceptual model of plant-soil interactions along a precipitation gradient suggesting that the importance of belowground constraints decreases with increasing precipitation [8]. It can be inferred from this model that the absence of root plasticity in both grass growth forms in the mesic community may be associated with increasing constraints of aboveground resource availability (e.g. light). Shading has been documented to reduce both nitrogen and phosphorus exploitation in the perennial grass *Agropyron desertorum* by compromising morphological plasticity to a greater extent than physiological plasticity [3, 14]. The absence of morphological root plasticity in the mesic community is also consistent with the results of Fransen and colleagues [22] indicating that this foraging strategy is ecologically insignificant for the acquisition of heterogeneously distributed nutrients in grasses adapted to various locations along a gradient of nutrient availability. This implies that root absorption kinetics is an important process for exploiting heterogeneously distributed nutrients between perennial grasses (e.g. [12, 31, 37]). However, morphological root plasticity has been documented in both perennial rhizomatous [16, 27] and caespitose grasses [27, 33].

These results are necessarily preliminary because they are based on a comparison of two species representing each of two growth forms located in distinct environments. However, these data provide an initial test of potential tradeoffs between morphological and physiological root plasticity and suggest that 1) high maximum uptake rates for nitrogen in these perennial grasses may minimize the expression of physiological root plasticity, 2) these mechanisms may be complimentary rather than alternative, and 3) the expression of root plasticity may be strongly influenced by abiotic variables within specific habitats. Further investigation of foraging strategies in field settings will increase our understanding of the contribution of these processes to plant function and distribution at regional scales.

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