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Contribution of relative growth rate to root foraging by annual and perennial grasses from California oak woodlands

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Abstract Plants forage for nutrients by increasing their root length density (RLD) in nutrient-rich soil microsites through root morphological changes resulting in increased root biomass density (RBD), specific root length (SRL), or branching frequency (BF). It is commonly accepted that fast-growing species will forage more than slow-growing species. However, foraging responses may be due solely to differences in relative growth rates (RGR). There is little evidence, after the effects of RGR are removed, that the fast versus slow foraging theory is correct. In a pot study, we evaluated foraging of four grass species that differed in RGR: one fast-growing annual species, *Bromus diandrus*, two intermediate-growing species, annual *Bromus hordeaceus* and perennial *Elymus glaucus*, and one slow-growing perennial species, *Nassella pulchra*. We harvested plants either at a common time (plants varied in size) or at a common leaf number (plants similar size, surrogate for common biomass). By evaluating species at a common time, RGR influenced foraging. Conversely, by evaluating species at a common leaf number, foraging could be evaluated independent of RGR. When RGR was allowed to contribute to foraging (common time harvest), foraging and RGR were positively correlated. *B. diandrus* (fast RGR) foraged to a greater extent than did *E. glaucus* (intermediate RGR) and *N. pulchra* (slow RGR). *E. glaucus* (intermediate RGR) foraged to a greater extent than *N. pulchra* (slow RGR). Root growth within nutrient-rich microsites was due to significant increases in RBD, not to modifications of SRL or BF. However, when RGR was not allowed to influence foraging (common leaf number harvest), none of the four species significantly enhanced RLD in nutrient-rich compared to control microsites. This suggests that RGR strongly influenced the ability of these grass species to forage and also supports the need to evaluate plastic root traits independent of RGR.

Keywords *Bromus diandrus* · *Bromus hordeaceus* · *Elymus glaucus* · *Nassella pulchra* · Root plasticity

Abbreviations *BF* Branching frequency—distance internal to internal branches—mm · *RBD* Root biomass density—Root biomass per soil volume—g m^{-3} · *RLD* Root length density—Root length per soil volume—km m^{-3} · *RWR* Root weight ratio—Root mass per total biomass—kg kg^{-1} · *SLA* Specific leaf area—Leaf area per leaf biomass—m^2 kg^{-1} · *SRL* Specific root length—Root length per root biomass—km kg^{-1} · *RGR* Relative growth rate—Δ biomass per total biomass per time—g g^{-1} day^{-1} · *RTD* Root tissue density—Root biomass per root volume—kg m^{-3}

Introduction

In soils, essential plant nutrients are heterogeneously distributed both spatially and temporally (Jackson and Caldwell 1993; Gross et al. 1995; Ryel et al. 1996). In response to heterogeneous nutrient distribution, plants can selectively alter root growth in nutrient-rich microsites, thereby enhancing nutrient acquisition (Drew 1975; Crick and Grime 1987; Campbell and Grime 1989). This root foraging is the result of increased root length density (RLD) (Gross et al. 1993; Fransen et al. 1998). Species may enhance RLD by (1) increasing root biomass allocation per volume of soil (root biomass density, RBD) or through morphological alterations including (2) producing finer roots (specific root length, SRL) or (3) decreasing the distance between internal root branches (branching frequency, BF) (Grime et al. 1991; Fitter 1994; Bilbrough and Caldwell 1995; Fransen et al. 1999a).

A generally accepted theory is that fast-growing species are evolutionarily specialized to exploit nutrient-rich soil microsites by generating relatively higher RLD

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in nutrient-rich microsites than are slow-growing species (Passioura and Wetselaar 1972; Crick and Grime 1987; Campbell and Grime 1989; Granato and Raper 1989; Hutchingson and de Kroon 1994; Fransen et al. 1998, 1999a; Einsmann et al. 1999). Recently, comparisons of foraging and root allocation involving species with different relative growth rates (RGR), but from the same family, have produced conflicting results (Van de Vijver 1993; Larigauderie and Richards 1994; Fransen et al. 1999a). To examine this theory, species-specific foraging traits must be evaluated without the confounding effects of RGR.

Effects of RGR are intermingled with species-specific foraging traits (Grime et al. 1991; Fransen et al. 1999b). RGR generally increased when previously limiting nutrients became more available (Lambers and Poorter 1992; Elberse and Berendse 1993; Larigauderie and Richards 1994; Huante et al. 1998). Hence, when roots proliferated in nutrient-rich microsites, root and shoot growth rates were elevated due to increased uptake of limiting nutrients (Fransen et al. 1999b). Further, if roots of fast and slow-growing species, regardless of species-specific root foraging responses, are evaluated at a common time, fast-growing species may increase RLD more than slow-growing species solely due to their inherently higher RGR (Grime et al. 1991; Fransen et al. 1999b). Researchers have tried to compensate for this synergistic effect by harvesting species independently of one another based on a general root proximity to the edge of the pot or growth rates (Einsmann et al. 1999; Fransen et al. 1998). However, foraging has not been evaluated without the confounding effects of RGR; there is little or no evidence that after the effects of RGR are removed, fast-growing species will differ from slow-growing species in their ability to forage for nutrients.

To explore the contributions of RGR to foraging, we evaluated foraging of four Mediterranean-climate grass species that differed in RGR: fast-growing annual *Bromus diandrus* Roth, intermediate-growing annual *Bromus hordeaceus* L., intermediate-growing perennial *Elymus glaucus* Buckley, and slow-growing perennial *Nassella pulchra* A. Hitchc. We harvested plants at a common time (plants varied in size) and at a common leaf number (plants similar in size, a surrogate for common biomass). We expected that when RGR was allowed to influence foraging (constant time harvest) results would support the theory. We predicted that fast-growing *B. diandrus* would forage in nutrient-rich microsites more than intermediate- and slow-growing grass species. Similarly, we predicted that intermediate-growing grass species would forage in nutrient-rich microsites more than slow-growing *N. pulchra*. Conversely, by evaluating these four species at a common leaf number, responses of plastic plant traits such as foraging can be evaluated independent of RGR (Van de Vijver 1993; Coleman et al. 1994; Fransen et al. 1999b). When effects of RGR were removed (common leaf number harvest) we expected that there would be little or no difference in foraging between fast- and slow-growing species.

Materials and methods

Species, RGR, soil, and site characteristics

Grass species were selected that occurred in Californian oak woodlands (Bartolome and Gemmill 1981; Jackson 1985; Jackson et al. 1990). We chose two exotic annual grass species originating from the Mediterranean Basin, *B. diandrus* and *B. hordeaceus*, and two California native perennial species, *E. glaucus* and *N. pulchra*. RGR were calculated from leaf biomass measurements of non-fertilized plants and fertilized plants using the formula: $RGR=[\ln(M_2)-\ln(M_1)]/(t_2-t_1)$. Seeds of all four species were collected from University of California, Davis experimental research plots in Yolo County, California (38°N, 121°48′W, elevation 20 m a.s.l.).

Soil was collected from the Sierra Foothill Research and Extension Center, located approximately 32 km NE of Marysville, Calif. (39°15′N, 121°17′W, elevation 67–161 m a.s.l.). Soil was removed from an AB horizon (10–30 cm) of an Argonaut silt loam Mollic Hapoxeralf (Dahlgren et al. 1997; Jackson et al. 1988) and sieved through a 4 cm sieve. Soil characteristics were: 1.4% C, 0.12% total N, pH=6.1, and CEC=37 mEq/100 g. Total C and N were measured on a C/N analyzer (Fisons Instruments, Beverly, Mass.). For further soil characterization, see Dahlgren et al. (1997) and Jackson et al. (1988).

The experiment was conducted outdoors on the campus of the University of California, Davis in Yolo County, California where the climate is Mediterranean (cool wet winters and hot dry summers) with an average annual precipitation of 440 mm. Total precipitation during the experimental period was 51 mm (UCD/NOAA Climate Station, http://atm.ucdavis.edu/weather/index.html). Plants were grown in 11.3 l pots (25×30 cm) containing 14 kg of soil media: 60% field soil, 30% coarse-grained sand, and 10% fritted clay. The sand and fritted clay improved drainage and facilitated root recovery. After seeding on 16 March 2000, pots were placed in holes in the ground in an area of full sun. Seedlings emerged 7–9 days later; plants were harvested over the next 2 months. Plants were watered daily with distilled water.

Experimental design and microsites

Four grass species and two fertilizer treatments (-/+) were distributed in a randomized, complete block design (4 species×2 fertilizer treatments×12 blocks=96 pots). Half of the 12 blocks (1×4 m) were randomly assigned to be harvested at a common time (6 replicates), the other half at a common leaf number (6 replicates). All plants were harvested during vegetative growth. For the common time harvest, grasses were harvested 50 days after seedling emergence. For the common leaf number harvest, grasses were harvested when they had 50 leaves, ranging from 34 to 61 days after seedling emergence. Only leaves >2 cm long were counted.

Twelve days after seedling emergence, fertilizer was added. Fertilizer was mixed with soil, placed in a small 1.5 mm plastic mesh cylinder (6×10 cm, volume =283 cm^3), and placed in half the pots. These cylinders contained 355 g of soil and 2.5 g of slow-release fertilizer (N:P:K:12-12-12, 4-month formulation, "Osmocote"). This fertilizer addition increased available soil N about 5-fold. Available soil N was calculated assuming 2% of the total soil N was available to plants. Pots contained either this fertilized cylinder (hereafter referred to as fertilized microsite, M_f) or a non-fertilized control mesh cylinder (hereafter referred to as control microsite, M_c) of the same dimensions containing only 355 g of soil. M_c and M_f were placed in pots by removing a soil core and inserting microsites 12 cm from the seedling and 5 cm below the soil surface, a location where RLD was expected to be high (Welker et al. 1991). Microsites represented 2.5% of total pot volume and their dimensions were similar to patches used by Jackson and Caldwell (1992).

Harvests

Aboveground grass biomass was clipped and total leaf area was measured (WinRHIZO 4.1C scanning system, Regent Instrument, Quebec, Canada). Aboveground tissue was dried (60°C) and weighed. Microsites (M_c, M_f) were excised with a soil knife. Additionally, a soil core (6×10 cm) was removed from the fertilized microsite pots (M_l) to validate localized root morphological responses in M_f. Soil cores were stored at 3°C until roots were separated from the soil (hydropneumatic root elutriator system, Gillison's Variety Fabrication, Benzonia, Mich.). Roots were stored in distilled water at 3°C until roots were scanned (WinRHIZO) and length, volume, and BF were determined (Bauhus and Messier 1999; Bouma et al. 2000). Roots were then dried and weighed.

In each pot, total root biomass was estimated by analyzing three soil cores (2×30 cm) and scaling to total pot volume. Soil cores were removed at 6, 12, and 18 cm from the pot edge. These three root samples from each pot were combined, dried, and weighed.

Nutrient and statistical analyses

Leaf %C and %N were measured on a C/N analyzer (Fisons Instruments, Beverly, Mass.). After dry-ashing leaf material, leaf %P and %K were measured using an ICP-AES (Thermo Jarrell Ash, Franklin, Mass.). Shapiro-Wilkes and Kolomogrov-Smirnov tests were performed on all data and transformations were made to meet assumptions of homoscedasticity prior to ANOVA (SAS/STAT 1995). RGR data were analyzed using a one-way analysis of variance. All pairwise comparisons were of interest and means were separated using Tukey's studentized range test. Foraging data were analyzed using a two-way analysis of variance. Means were separated using Fisher's least-significant-difference tests. All data in tables and figures are back-transformed values. Linear regressions (Sigma Plot 2000) of leaf number against total biomass were conducted on data from both harvest types.

Results

Species RGR

When species were ranked by RGR, *B. diandrus* had the highest rate (M_c=0.130 day^{-1}, M_f=0.144 day^{-1}), followed by *B. hordeaceus* (M_c=0.124 day^{-1}, M_f=0.136 day^{-1}) and *E. glaucus* (M_c=0.119 day^{-1}, M_f=0.130 day^{-1}) (n=5–6). *Nassella pulchra* had the lowest rate of all four species (M_c=0.107 day^{-1}, M_c=0.114 day^{-1}). Significant differences (P<0.05) in RGR between the species, regardless of being exposed to M_c or M_f, were as follows: *B. diandrus* =A, *B. hordeaceus* =AB, *E. glaucus* =B, and *N. pulchra* =C. Based on these results, we separated species into three RGR categories: fast-growing (*B. diandrus*), intermediate-growing (*B. hordeaceus* and *E. glaucus*), and slow-growing (*N. pulchra*).

Foraging influenced by RGR (common time harvest)—plant characteristics

In response to M_f, shoot biomass and total biomass increased for all species, although not significantly for slow-growing *N. pulchra* (Table 1). Only fast-growing *B. diandrus* increased root biomass significantly in response to M_f. Specific leaf area (SLA) differed among species, but was not altered by M_f; average SLA (m^2 kg^{-1}) were: *B. diandrus* =48, *B. hordeaceus* =44, *E. glaucus* =40 and *N. pulchra* =17.

Leaf %N increased significantly in response to M_f for all species except fast-growing *B. diandrus* (Fig. 1). However, for all four species there were no significant

Table 1 Foraging influenced by RGR (common time harvest). Characteristics of four Mediterranean-climate grass species: fast-growing *Bromus diandrus* (*Brdi*), intermediate-growing *Bromus hordeaceus* (*Brho*) and*Elymus glaucus* (*Elgl*), and slow-growing *Nassella pulchra* (*Napu*). Roots were characterized from either fertilized (M_f) or unfertilized microsites (M_c). For each characteristic, back-transformed means (n=5–6) followed by different letters are significantly different (P<0.05). For abbreviations see list at the beginning of the paper

Characteristic	Microsite	Relative growth rates			
		Fast *Brdi*	Intermediate		Slow *Napu*
			Brho	*Elgl*	
Leaf no./plant	M_c	92.2 b	112.4 b	45.2 c	46.2 c
	M_f	170.6 a	155.6 a	66.2 c	48.4 c
Biomass/plant					
Shoot (g)	M_c	2.34 c	1.76 cd	1.15 de	0.57 e
	M_f	5.28 a	3.34 b	2.18 c	0.80 e
Root (g)	M_c	0.61 bc	0.53 bc	0.36 cde	0.13 e
	M_f	0.94 a	0.74 ab	0.41 cd	0.25 de
Total (g)	M_c	2.95 c	2.29 c	1.52 d	0.69 e
	M_f	6.21 a	4.07 b	2.59 c	1.06 de
RWR	M_c	0.21 a	0.24 a	0.24 a	0.19 a
	M_f	0.15 a	0.19 a	0.17 a	0.23 a
Roots from microsite					
RLD (km m^{-3})	M_c	25.2 b	27.1 b	5.9 c	2.0 d
	M_f	86.0 a	50.4 ab	32.5 b	5.1 c
BF (mm)	Mc	9.0 ab	9.4 ab	9.5 ab	10.6 a
	M_f	7.8 b	8.3 b	7.7 b	9.8 ab
RBD (g m^{-3})	M_c	105.6 b	96.0 bc	40.9 c	8.2 d
	M_f	530.0 a	204.4 b	126.4 b	13.3 d
SRL (km kg^{-1})	M_c	238.8 abc	283.4 ab	145.0 c	245.5 abc
	M_f	162.0 bc	246.7 abc	256.6 abc	384.9 a

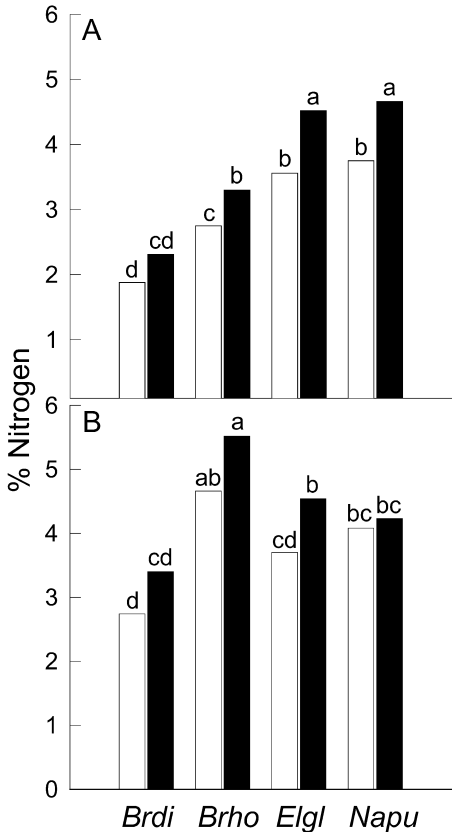

Fig. 1A, B Effects of RGR on foraging for nitrogen. **A** Common time harvest, effects of RGR on foraging included; **B** Common leaf number harvest, effects of RGR on foraging eliminated. Leaf percent nitrogen of four Mediterranean-climate grass species: fast-growing *Bromus diandrus* (*Brdi*), intermediate-growing *Bromus hordeaceus* (*Brho*) and *Elymus glaucus* (*Elgl*), and slow-growing *Nassella pulchra* (*Napu*). Treatments: unfertilized microsites (M_c) (*white bars*), fertilized microsites (M_f) (*black bars*). For each harvest, back-transformed means (common time n=5–6; common leaf number n=3–6) indicated by different letters are significantly different ($P \leq 0.05$)

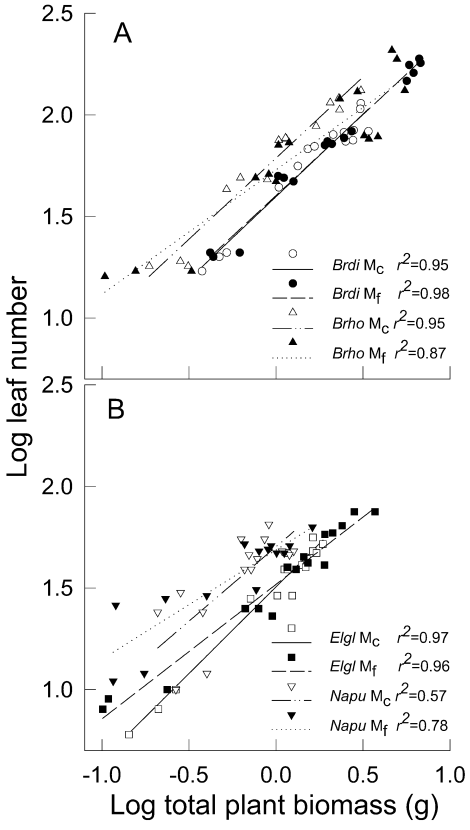

Fig. 2A, B Effect of fertilization [unfertilized (M_c) or fertilized (M_f) microsites] on correlations between total plant biomass and leaf number. **A** Annual grasses: *Bromus diandrus* (*Brdi*) and *Bromus hordeaceus* (*Brho*), **B** perennial grasses: *Elymus glaucus* (*Elgl*) and *Nassella pulchra* (*Napu*)

differences in leaf %C or %P in response to M_f (data not shown). Leaf %C ranged from 43% (*E. glaucus*) to 34% (*B. hordeaceus*). Leaf %P ranged from 0.28% (*N. pulchra*) to 0.53% (*B. hordeaceus*).

Foraging influenced by RGR (common time harvest)—root characteristics in microsites

When M_f was compared to M_c, RLD was higher for all species, although the increase was not significant for intermediate-growing *B. hordeaceus* (Table 1). Fast-growing *B. diandrus* produced the highest RLD in M_f and intermediate-growing *E. glaucus* produced higher RLD in M_f compared to slow-growing *N. pulchra*. Intermediate-growing *E. glaucus* had the greatest increase in RLD (M_c=5.9, M_f=32.5 km m^{-3}) in response to M_f compared to M_c.

Fast-growing *B. diandrus* and intermediate-growing *E. glaucus* had greater RBD in M_f versus M_c (Table 1). The magnitude of this response in RBD was greatest for *B. diandrus* (M_c=106, M_f=530 g m^{-3}). None of the four grass species significantly altered SRL or BF. RTD (data not shown) did not significantly differ between species or in response to M_f. Values ranged from 28 kg m^{-3} (*E. glaucus*, M_f) to 49 kg m^{-3} (*B. diandrus*, M_c).

Leaf number and total biomass correlations

Leaf number was used as a non-destructive proxy for plant biomass to determine when to harvest plants at a common mass. Leaf number and total biomass were linearly related and there was a robust correlation between leaf number and total plant biomass (ANCOVA, P<0.0001, Fig. 2). This correlation between leaf number and total biomass was higher for *B. diandrus* and *E. glaucus* with $r^2 \geq 30.95$ for M_c and M_f but lower for *B. hordeaceus* and *N. pulchra*.

Table 2 Foraging not influenced by RGR (common leaf number harvest). Characteristics of four Mediterranean-climate grass species: fast-growing *Bromus diandrus* (*Brdi*), intermediate-growing *Bromus hordeaceus* (*Brho*) and*Elymus glaucus* (*Elgl*), and slow-growing *Nassella pulchra* (*Napu*). Roots were characterized from either fertilized (M_f) or unfertilized microsites (M_c). For each characteristic, back transformed means (n=3–6) followed by different letters are significantly different (P<0.05). For abbreviations see list at the beginning of the paper

Characteristic	Microsite	Relative growth rates			
		Fast *Brdi*	Intermediate		Slow *Napu*
			Brho	*Elgl*	
Leaf no./plant	M_c	50.0 a	46.7 ab	42.2 bc	46.4 a
	M_f	48.7 a	49.0 a	41.2 c	49.3 a
Biomass/plant					
Shoot (g)	M_c	0.97 bc	0.56 d	1.11 ab	0.92 bc
	M_f	1.09 ab	0.69 cd	1.32 a	0.76 cd
Root (g)	M_c	0.22 ab	0.12 bcd	0.25 a	0.08 cd
	M_f	0.04 d	0.20 ab	0.10 cd	0.17 abc
Total (g)	M_c	1.19 ab	0.68 c	1.36 a	1.01 bc
	M_f	1.13 ab	0.89 bc	1.42 a	0.93 bc
RWR	M_c	0.18 ab	0.17 ab	0.18 ab	0.08 bc
	M_f	0.03 c	0.23 a	0.07 c	0.19 a
Roots from microsite					
RLD (km m^{-3})	M_c	2.21 c	4.13 abc	4.93 abc	2.45 c
	M_f	4.32 abc	9.66 ab	12.56 a	3.86 bc
BF (mm)	Mc	9.5 a	8.2 a	8.9 a	10.0 a
	Mf	7.4 a	8.0 a	8.3 a	9.6 a
RBD (g m^{-3})	M_c	11.1 ab	13.02 ab	21.87 ab	17.78 ab
	M_f	9.88 b	35.03 ab	37.88 a	12.76 ab
SRL (km kg^{-1})	M_c	199.2 bc	317.8 ab	249.6 bc	143.1 c
	M_f	455.2 a	279.8 abc	357.5 ab	315.1 ab

Foraging not influenced by RGR (common leaf number harvest)—plant characteristics

Each species was harvested when it had produced 50 leaves. Fertilization (M_f) did not affect leaf number, shoot biomass, nor total biomass (Table 2); SLA also did not differ as a result of fertilization (data not shown). However, fertilization decreased root biomass of fast-growing *B. diandrus* and intermediate-growing *E. glaucus*. Conversely, slow-growing *N. pulchra* had slightly higher root biomass and significantly higher RWR in M_f versus M_c. For all species except *E. glaucus*, %N did not differ significantly in response to M_f (Fig. 1). Percent C did not differ for any of the four species (data not shown).

Foraging not influenced by RGR (common leaf number harvest)—root microsite characteristics

There was a tendency for all species to selectively place more roots in M_f, but RLD increases were not significant (Table 2). Fast-growing *B. diandrus* and slow-growing *N. pulchra* produced higher SRL, but did not alter RBD in M_f compared to M_c (Table 2). BF and RTD did not differ between species or in response to M_f; RTD values ranged from 120 kg m^{-3} (*B. diandrus*, M_c) to 40 kg m^{-3} (*E. glaucus*, M_c).

Discussion

Foraging influenced by RGR (common time harvest)

In our experiment when RGR contributed to foraging (common time harvest), foraging responses generally supported the theory that fast-growing plant species forage more than slow-growing species (Table 1). Fast-growing *B. diandrus* foraged (i.e., increased RLD M_f compared to M_c) to a greater extent than did either intermediate-growing *E. glaucus* or slow-growing *N. pulchra*. *E. glaucus* foraged to a greater extent than did slow-growing *N. pulchra* (Table 1). However, intermediate-growing *B. hordeaceus* did not significantly forage. Although this species demonstrated a trend towards foraging, the inclusion of multiple genotypes may have resulted in heightened variability of root foraging responses. In this study, foraging results represent an average plasticity of all genotypes of each species present. Genotypes of intermediate-growing *B. hordeaceus* have demonstrated variability in the probability of plant survival, total plant weight, and seed weight (Lonn et al. 1998).

A common mechanism for foraging is through the generation of more RBD in nutrient-rich microsites (Grime et al. 1991; Caldwell 1994; Fransen et al. 1999a). Similarly, in our study the basis for species foraging was due to significant increases in RBD, not to morphological alterations in SRL or BF. Fast-growing *B. diandrus* and intermediate-growing *E. glaucus* foraged by increasing the number of main root axes entering the microsites and not by changes in the inter-branch distance. Similarly, Fransen et al. (1999a) reported

elevated total root biomass in nutrient-rich microsites without alterations in BF. Although intermediate-growing *E. glaucus* and slow-growing *N. pulchra* tended to increased SRL, this trend was not significant and also not localized, since the average SRL for *E. glaucus* and *N. pulchra* in M_l soil cores (330 and 360 km kg^{-1} respectively) was not significantly different from the SRL in M_f (260 and 390 km kg^{-1} respectively). Modifications in SRL are rare and when they do occur, SRL are higher in nutrient-poor than nutrient-rich microsites (Robinson and Rorison 1987, 1988; Elberse and Berendse 1993; Hutchingson and De Kroon 1994).

Foraging results did not consistently benefit the plant (total plant biomass, leaf %N). For example, slow-growing *N. pulchra* foraged but total plant biomass did not increase. Fast-growing *B. diandrus*, which foraged to the greatest extent, did not increase leaf %N. This example may be a result of the biomass dilution of N concentration due to the higher RGR of *B. diandrus* (Coleman et al. 1993).

Foraging not influenced by RGR (common leaf number harvest)

Common mass comparisons are rare. We found only four studies that compared species at similar leaf or total plant biomass to evaluate the plasticity of aboveground and belowground plant traits (Rice and Bazzaz 1989; Poorter and Pothmann 1992; Coleman et al. 1993; Van de Vijver et al. 1993). This rarity may stem from the difficulty of harvesting plants at a similar biomass. In our study, leaf number was an accurate surrogate for total plant biomass within-species but not between species (Table 2). Within a species, there were no significant differences in total plant biomass for M_f versus M_c at a common leaf number; therefore individual species could be evaluated without the confounding effects of RGR. However, root foraging comparisons between species should be conducted only on species that do not differ significantly in total plant biomass. In this study, inter-species root foraging comparisons are appropriate for the following species combinations: *B. diandrus* versus *E. glaucus*, *B. diandrus* versus *N. pulchra*, and *B. hordeaceus* versus *N. pulchra* (Table 2).

In our experiment, when RGR did not contribute to foraging (common leaf number harvest), foraging by these four grass species was not detectable with our experimental design. All species did elevate RLD in M_f compared to M_c, but none of the four species foraged significantly (Table 2). Our inability to detect significant foraging in *B. diandrus* and *B. hordeaceus* in this harvest type may have resulted from the loss of a few replicates to rabbit browsing. However, in *E. glaucus* and *N. pulchra*, where replication was the same as in the common time harvest, we still did not detect significant foraging. Intermediate-growing *E. glaucus* enhanced leaf %N in response to the nutrient-rich microsite. This species may have benefited from the nutrient-rich microsite without a large proliferation of roots (Fig. 1). Van Vuuren et al. (1996) reported this same phenomenon where *Tricticum aestivum* captured 71% of its total N without a massive proliferation of roots.

Since we could not make statistical comparisons, we are only able to comment on trends between the two methods. The lack of foraging when RGR was removed suggests that RGR does enhance species foraging ability. When RGR was removed, species tended to increase RLD in nutrient-rich versus control microsites, but the trend was non-significant. It seems that RGR, not species-specific foraging traits was responsible for foraging results in the common time harvest. To validate these findings and quantify the contributions of plastic foraging traits and RGR to species foraging ability, future research should be conducted at a common biomass and over several harvests, which would allow multiple opportunities to assess alterations in selective root placement over time.

In a modeling study, Fransen et al. (1999b) attempted to disentangle species-specific root foraging traits from RGR by predicting the synergistic effects of RGR and selective root placement on changes in RBD as a function of a common time and a common biomass. Our results confirm their findings that faster-growing species, more than slow-growing species, produced more RBD in nutrient-rich microsites at a common time and that there is a positive interaction between foraging and RGR. Fast-growing *B. diandrus* and intermediate-growing *E. glaucus* produced at least 9.5 times more RBD and at least 6.4 times more RLD in nutrient-rich microsites than did slow-growing *N. pulchra* (Table 1). However, unlike the results of Fransen et al. (1999b), where a higher RGR alone did not result in a higher biomass accumulation, intermediate-growing and non-foraging *B. hordeaceus* produced more total biomass in response to the nutrient-rich microsite. When RGR was removed from foraging, Fransen et al. (1999b) calculated that foraging did not differ among species. Likewise, in our data, slow-growing *N. pulchra* produced comparable RLD in nutrient-rich microsites as fast-growing *B. diandrus*. Lastly, Fransen et al. (1999b) expressed concern about the appropriate measure of foraging with or without RGR. We agree with Fransen et al. (1999b) that if research is attempting to quantify foraging traits independently of RGR, species comparisons must be conducted at a common biomass. Species-specific RGR are often significant ecologically (Grime and Hunt 1975; Lambers and Poorter 1992) and should be considered in root foraging studies.

In conclusion, the relationship of RGR and foraging responses depended on how root foraging was measured. When RGR contributed to root foraging, species foraging ability increased along an RGR continuum, where faster-growing species foraged within nutrient-rich microsites to a greater extent than slower-growing species. However, when RGR were factored out of the measurements, foraging responses disappeared. This lack of foraging response suggests that RGR strongly influenced the ability of these species to forage for nutrients belowground. These results support the need to evaluate plastic root traits independent of RGR.

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