

Structural and chemical differences between shoot- and root-derived roots of three perennial grasses in a typical steppe in Inner Mongolia China

Deliang Kong · Huifang Wu · Meng Wang ·
Matthew Simmons · Xiaotao Lü · Qiang Yu ·
Xingguo Han

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Abstract Determining the variation in roots traits within a grass root system is important for understanding the role of fine roots in carbon and nutrient cycling in grassland ecosystems, where the majority of biomass and litter accumulation occur below-ground. However, few studies have been conducted in this regard. In this study, the structural and chemical traits of shoot-derived and root-derived roots were examined in three perennial grasses—*Cleistogenes squarrosa*, *Achnatherum sibiricum* and *Stipa grandis*—aiming to explore structural differ-

ences, responses to nitrogen and water addition in different types of roots and their correlations with aboveground plant nitrogen. Our results showed significant differences between these two root types, with root-derived roots having higher N concentration, tissue density, and specific root length, but lower C: N and diameter than shoot-derived roots. Trait relationships between root N concentration and tissue density for the two root types differed from that reported among species. These traits in different types of roots were insensitive to resource addition. Furthermore, N concentration in shoot-derived roots was more strongly linked to aboveground plant N concentration than root-derived roots. The results of this study demonstrate structural differences within the root system that may reflect functional heterogeneity in grass roots.

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D. Kong (✉) · M. Wang · M. Simmons · X. Lü · Q. Yu ·
X. Han (✉)

Key Laboratory of Vegetation and Environmental Change,
Institute of Botany, Chinese Academy of Sciences,
No.20 Nanxincun, Xiangshan,
100093 Beijing, China
e-mail: deliangkong1999@126.com
e-mail: xghan@ibcas.ac.cn

H. Wu
Department of Horticulture,
Institute of Agricultural Sciences,
Nanyang 473000, China

D. Kong · M. Wang · X. Lü · Q. Yu
Graduate School of the Chinese Academy of Sciences,
100093 Beijing, China

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Introduction

Fine roots constitute an important component of carbon and nutrient cycling in terrestrial ecosystems (Jackson et al. 1997; Gordon and Jackson 2000; Silver and Miya 2001; Strand et al. 2008; Hodge et al. 2009). Although fine roots <2 mm in diameter have traditionally been treated as a homogenous unit, more and more evidence indicates that they are structurally and functionally heterogeneous within this root guild.

In many woody species, fine roots show significant differences in morphology, anatomy and chemicals within the branch system, e.g., roots of more distal orders have a thinner diameter, higher specific root length (SRL, root length per unit of dry mass), higher mycorrhizal colonization, higher N concentration, but lower root tissue density, lower C:N and short longevity (e.g., Pregitzer et al. 2002; Wells et al. 2002; Guo et al. 2008; Valenzuela-Estrada et al. 2008) than basal roots. These differences may suggest functional heterogeneity within fine roots, with distal roots serving mainly as water and nutrient uptake, and basal roots as anchorage, transport or storage (Pregitzer 2002; Guo et al. 2008).

Despite much progress, it remains unknown whether these patterns of fine roots in wood species can be generalized to other types of vegetation such as herbaceous species. In two perennial herbs, root N concentration was found to be relatively constant among orders (Pregitzer et al. 1997). This suggests that fine roots in herbaceous species may function differently from those in trees as nitrogen concentration is closely linked to respiration (Reich et al. 2008), which can fuel nutrient acquisition by roots. As for grasses, they lack a taproot, and their adventitious root system (shoot- and root-derived roots) is comprised chiefly of tissues with primary development (Eissenstat 2000; Wahl and Ryser 2000). This may be why grass roots are usually treated as a homogenous guild in structure and in their response to changes in environmental variables. Determining whether root structure is homogenous or heterogeneous among orders is important for understanding carbon and nutrient cycling since roots account for a great proportion of grass biomass and contribute the majority of total litter accumulation (Fornara and Tilman 2009). However, no studies to date have examined variation of root structure within a grass root system.

Root traits vary to a large extent with soil resource level. Despite the unresponsiveness of root traits to changes in soil resource availability in some studies (Pregitzer et al. 2002; Ryser 2006) it is possible that other morphological traits, and even traits related to anatomy and physiology, will change to allow nutrient acquisition (Ryser and Lambers 1995). In semi-arid grassland ecosystems, plant productivity is limited primarily by soil water and nutrient levels (Hooper and Johnson 1999; Bai et al. 2008). Plant responses to increased resource level may involve

changes of a suite of root traits (e.g., increase in SRL, root N concentration, or a decrease in root tissue density) for resource acquisition to support plant growth. Here, we also want to explore whether there are any differences in root responses to soil water and nitrogen addition within a grass root system.

Root and leaf N concentration are both important for their function as nutrient and CO₂ absorption. It has been demonstrated that N concentration in roots and leaves were correlated in many species even at large scale (Craine and Lee 2003; Craine et al. 2005; Tjoelker et al. 2005). In trees, the heterogeneity in structure and function within fine roots may be reflected by the different strengths of correlation of root N in different orders with leaf N. However, as suggested by Pregitzer et al. (1997), roots in herbaceous species may show a different functional structure, and root N within fine roots may be correlated with leaf N to a similar degree.

In this study, root morphological traits (e.g., diameter, SRL and tissue density) and root N that were associated with plant growth and water and nutrient uptake (Eissenstat 1991; Ryser 1996; Wahl and Ryser 2000) were examined to explore structural and functional differences between shoot- vs root-derived roots in grasses. We predicted that, like the perennial herbs in Pregitzer et al. (1997), root N concentration and C:N in grasses will be similar between shoot- and root-derived roots because they are usually used for primary development and function mainly in resource absorption (Guo et al. 2008), which is related closely to root N concentration. Secondly, we hypothesized that there would be no difference in response of root traits to water and nitrogen addition between these two types of roots. Thirdly, we predicted that root N concentration in different types of roots is linked with similar strength to leaf N concentration.

Materials and methods

Study site

The study site is located in steppe grassland near the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences (116°42'E, 43°38'N). The site has been fenced from grazing since 1999, and is dominated by *Leymus chinensis*, *Agropyron michnoi*, *Achnatherum sibiricum*, *Cleistogenes*

squarrosa and *Stipa grandis*. The soil is dark chestnut with a loamy sand texture (Chen and Wang 2000) and corresponds to Calcis-orthic Aridisol in US Soil Taxonomy. Average annual precipitation is approximately 350 mm, most of which occurs from June to August. The mean growing season is about 150 days, and the long-term average annual temperature is 0.3°C.

Experimental design

This experiment consisted of 20 4×4 m plots, arranged in five blocks each with four plots. Treatments including control (C), nitrogen (N), water (W) addition, and both nitrogen and water (NW) addition were applied randomly to the four plots in each block. Nitrogen in the form of urea was added evenly in early June and July in 2008, respectively, to a total of 17.5 g N m⁻². It has been reported that fertilizer use efficiency can be maximized by this rate of N addition (Pan et al. 2004). Water was added at a rate of 10 mm per week from June to September in 2008. In total, 180 mm water, or about one-half of the average annual precipitation, was applied to each irrigation plot.

Root sampling and analysis

Aboveground and belowground parts of three perennial bunchgrasses—*Cleistogenes squarrosa*, *Achnatherum sibiricum* and *Stipa grandis*, which are common species in Inner Mongolia grassland—were removed from each plot in early August in 2008. A sharpened steel cylinder 22 cm in diameter was pushed into the soil to a depth of 20 cm to remove roots. During root sampling, aboveground parts of the same plant were also taken. Given the high density of the soil and the fragility of the grass roots, soil and plant roots were soaked in water to soften the soil. The soil was then carefully removed from the roots by hand. The roots were classified using a ‘developmental’ approach (Fitter 1982). They were defined as shoot-derived roots that were connected directly to shoots, and root-derived roots that emerged from shoot-derived roots. Since grass roots are fine, and separating the target roots from tangled grass roots is difficult, the terminal root-derived roots might be missed in this study.

For each order, a representative sub-sample of 15–20 roots was selected randomly and scanned on an Epson V100 scanner at 300 dpi in transparent mode.

Average diameter, total root length and root volume were determined using WinRHIZO (2004a, Regent Instruments, Quebec, Canada). In this version of WinRHIZO, improvements have been made to allow the estimation of root volume more precisely. Roots were then dried to constant weight at 70°C and weighed. SRL and root tissue density were calculated as the ratio of total root length to root mass, and the ratio of root mass to root volume, respectively (Craine et al. 2001).

Other root sub-samples were collected from each order to determine nutrient concentrations. Prior to analysis, root samples were ground and homogenized with a mixed mill (MM400, Retsch, Germany). To determine root C concentration, a small portion of root samples was digested with H₂SO₄-K₂Cr₂O₇ and titrated with FeSO₄ solution. Following Kjeldahl digestion, a semi-autoanalyzer (Kjeltec 2300 Analyzer Unit, Foss Tecator, Sweden) was used to determine root N concentration. In addition, aboveground plant N concentration was determined following the same method.

Statistical analysis

In each type of roots, two-way ANOVA was employed to analyze the effects of water addition and nitrogen addition on root N concentration, C: N and morphological traits (root diameter, SRL and root tissue density). When a root variable was unresponsive to water and nitrogen addition in the two-way ANOVA analysis for each type of roots, data were pooled across treatments and comparison between the two types of roots was made by one-way ANOVA. Relationships between aboveground plant N concentration and root N concentration in each type of roots were determined by linear regressions. Data are transformed when necessary to meet the normal distribution and equal variance assumptions for ANOVA. All analyses were conducted using SPSS 12.0 (SPSS, Chicago, IL) with a significance level of $P < 0.05$.

Results

In each grass tested, root N concentrations were all higher in root-derived than in shoot-derived roots (all P values < 0.001, Table 1; Fig. 1a–c). For each grass, neither water addition nor nitrogen addition

Table 1 One-way ANOVA analysis of fine root traits between shoot- and root-derived roots in three grasses. *SRL* Specific root length

Fine root trait	<i>Cleistogenes squarrosa</i>			<i>Achnatherum sibiricum</i>		<i>Stipa grandis</i>	
	df	F	P	F	P	F	P
Root N	1	31.2	<0.001	87.14	<0.001	107.99 ^a	<0.001
Root C:N	1	9.59	0.005	81.05	<0.001	48.15	<0.001
Root diameter	1	622.91 ^b	<0.001	698.12 ^a	<0.001	1,145.86 ^a	<0.001
Root tissue density	1	22.37 ^b	<0.001	4.19	0.048	7.10 ^b	0.001
SRL	1	523.18 ^c	<0.001	1,024.71 ^c	<0.001	823.98 ^c	<0.001

^aData were root square transformed for equal variances

^bData were 1/ \times transformed for equal variances

^cData were logarithm transformed for equal variances

significantly increased root N concentration in either type of roots (see electronic supplementary material Table S1).

Root C: N ratios were all higher in shoot-derived than in root-derived roots (all P values < 0.001, Table 1; Fig. 2a–c). Within each type of roots, nitrogen addition reduced root C: N in root-derived roots of *C. squarrosa* ($P=0.008$), whereas there were no effects of water addition and interaction of water and nitrogen addition on root C: N in each type of roots for the three grasses (see electronic supplementary material, Tables S1, S2).

For the three grasses, fine root diameters were all higher in shoot-derived than in root-derived roots (all P values < 0.001, Table 1; Fig. 3a–c), whereas fine root tissue density (all P values < 0.05, Table 1; Fig. 3d–f) and SRL (all P values < 0.001, Table 1; Fig. 3g–i) were both higher in root-derived than in shoot-derived roots. There was no treatment effect on any of these morphological traits for either type of roots in any of the three grasses (see electronic

supplementary material Table S1). Details of these morphological traits are presented in Table S3 in the electronic supplementary material.

Relationships between fine root N concentration in each type of roots and aboveground plant N concentration were both fitted by linear regressions with $y=0.25x+0.44$ for shoot-derived roots ($P<0.001$) and $y=0.20x+0.85$ for root-derived roots ($P=0.029$; Fig. 4). However, the variation in root N concentration explained by aboveground plant N concentration was much higher for shoot-derived ($R^2=0.35$) than for root-derived ($R^2=0.082$) roots.

Discussion

Fine root nitrogen and morphological traits in two types of grass roots

Our results revealed significant differences in morphology and chemical composition between two types

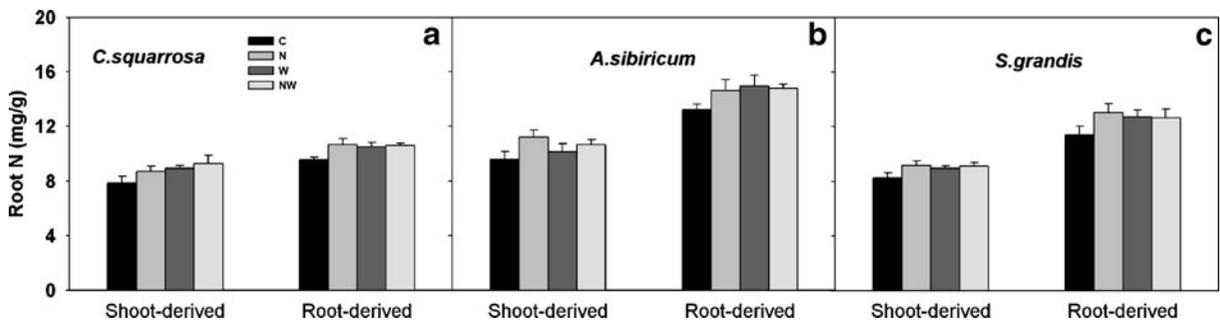


Fig. 1a–c Nitrogen concentration in shoot-derived and root-derived roots. Treatments: *C* Control, *N* nitrogen addition, *W* water addition, *NW* addition of both nitrogen and water. Bars

Means \pm SE ($n=5$). **a** *Cleistogenes squarrosa*, **b** *Achnatherum sibiricum*, **c** *Stipa grandis*

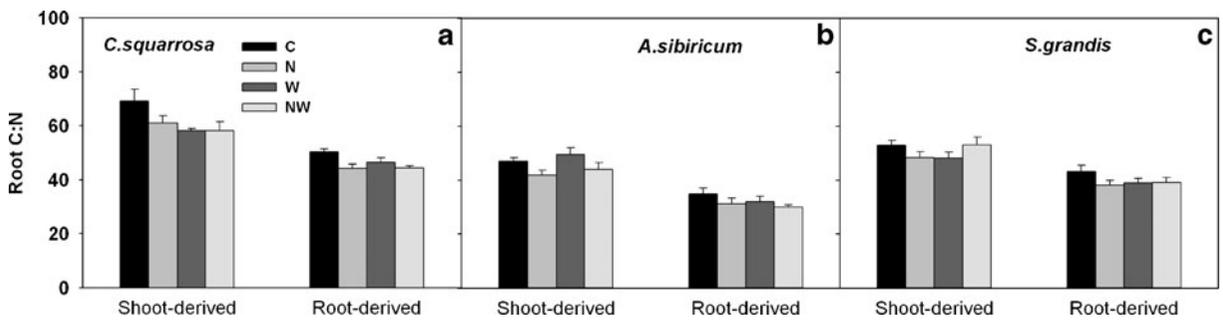


Fig. 2a–c C:N ratio in shoot-derived and root-derived roots. Treatments: *C* Control, *N* nitrogen addition, *W* water addition, *NW* addition of both nitrogen and water. Bars Means \pm SE ($n=5$). **a** *C. squarrosa*, **b** *A. sibiricum*, **c** *S. grandis*

of roots for all three grasses tested. Shoot-derived roots had lower N concentration, tissue density and SRL but higher C: N and larger diameter than root-derived roots, which is contrary to the hypothesis that

root N concentration and C:N remains constant between different types of roots.

Root N concentration has been linked to a suite of root traits, such as root respiration, resource uptake

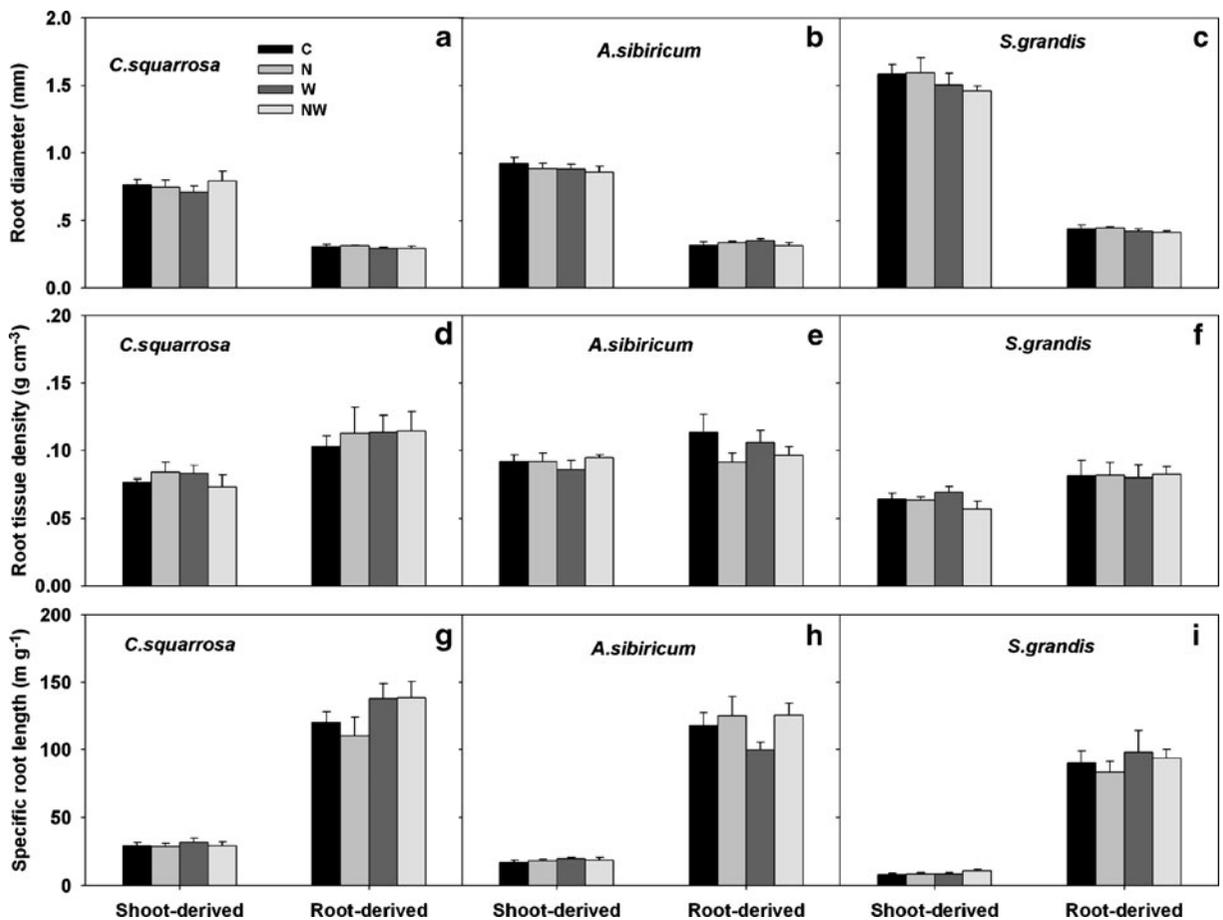
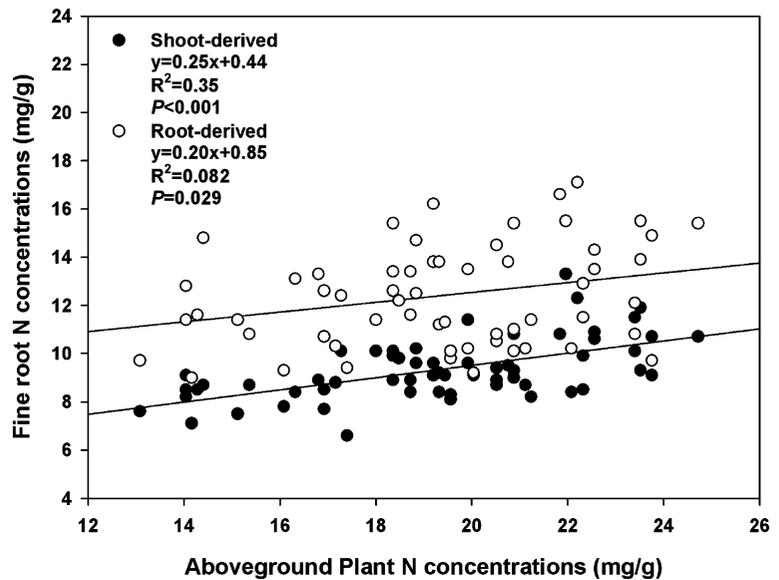


Fig. 3 Diameter (a–c), tissue density (d–f) and specific root length (SRL; g–i) in shoot-derived and root-derived roots. Treatments: *C* Control, *N* nitrogen addition, *W* water addition,

NW addition of both nitrogen and water. Bars Means \pm SE ($n=5$). **a, d, g** *C. squarrosa*; **b, e, h** *A. sibiricum*; **c, f, i** *S. grandis*

Fig. 4 Relationships between root N concentration in each type of root and aboveground plant N concentration



and root longevity (Pregitzer et al. 1998, 2002; Tjoelker et al. 2005; Volder et al. 2005). Higher N concentration in root-derived than shoot-derived roots (Fig. 1) may indicate higher respiration in root-derived roots, which in turn produces more energy (Wright and Westoby 2004) to support higher nutrient acquisition than in shoot-derived roots. Lower C: N in root-derived compared to shoot-derived roots (Fig. 2) suggests C invested in root-derived roots was more expensive to maintain but more profitable in resource acquisition than shoot-derived roots. The consistent differences of root N and C: N between orders could be associated with functional differences between shoot-derived and root-derived roots, which have been found frequently in trees but have been little investigated in grasses.

Pregitzer et al. (1997) reported a different pattern in two perennial herbs, *Viola pubescens* and *Hydrophyllum canadense*, with roots having constant N concentration among orders. The discrepancy of root structure in terms of branching order between perennial herbs in Pregitzer et al. (1997) and perennial graminoids in this study may be a result of differences in soil conditions or the arbuscular-mycorrhizae with which they are associated (Cornelissen et al. 2001). Alternatively, patterns of root traits among orders may be species-specific, with herbs and graminoids species associated with different root structure.

For each morphological trait examined, all three grasses followed a similar pattern for each of the two

types of roots. Root morphological traits between shoot-derived and root-derived roots were consistent with other studies reporting larger diameter and lower SRL in more basal branching orders (Pregitzer et al. 1997, 2002; Wang et al. 2006; Hishi 2007). Root tissue density was higher in root-derived than in shoot-derived roots for all three species (Fig. 3d–f), which contradicted findings indicating lower tissue density in more distal roots in the shrub *Vaccinium corymbosum* (Valenzuela-Estrada et al. 2008) and the tree *Fraxinus mandshurica* (Wang et al. 2006), but was similar to *Larix gmelinii* for the two distal roots (Wang et al. 2006). Previous studies have shown that tissue density is linked to N concentration, and species with lower root tissue density have higher root N concentration (Craine and Lee 2003; Craine et al. 2005). This may indicate a trade-off between absorptive capacity and longevity (Eissenstat and Achor 1999) as lower root tissue density is related to longer lifespan (Ryser 1996). However, little is known about whether this is the case among root branching systems. For each grass in this study, roots of higher tissue density in root-derived roots (Fig. 3d–f) had higher root N concentration (Fig. 1a–c) and lower root C: N (Fig. 2a–c). This suggested that there was no trade-off between root N concentration and tissue density between the two types of roots within species. For these grasses, roots with higher tissue density may be important in resisting mechanical stress or herbivory in the soil (Craine et al. 2001), and roots with higher N concentrations may be

related to a higher capacity for nutrient uptake (Scheurwater et al. 1998). Moreover, higher root tissue density was reported to be associated with higher root longevity (Ryser 1996; Eissenstat et al. 2000; Craine et al. 2001), which may suggest a longer duration of resource acquisition. Taken together, higher root N concentration with higher tissue density in lateral roots may serve as a strategy profitable for nutrient acquisition in these grasses. Although only three grasses were examined in this study, it is likely that other perennial grasses in this grassland share this pattern within their root systems because they all face poor soil fertility and a harsh environment. This speculation may be tested by sampling more species in future studies.

Responses of fine roots to nitrogen addition and water addition

Fine root traits are closely related to soil resource availability (Fitter and Stickland 1992; Pregitzer et al. 1993; Majdi et al. 2001; Comas and Eissenstat 2004). However, only a few studies have addressed responses to natural or manipulated resource gradients of fine roots in different orders. It is interesting to note that water and nitrogen addition had no influence on SRL and its two components—diameter and root tissue density—in each type of root. This is consistent with the hypothesis that root response will not differ between the two types of roots. Insensitiveness of SRL to resource addition has been found in other studies (Pregitzer et al. 2002; Ryser 2006), and may be due to counterbalancing changes in its components, root diameter and root tissue density (Ryser 2006). However, neither of the two components of SRL showed any response to resource addition. We speculate that the larger diameter of shoot-derived roots and higher tissue density in root-derived roots may underlie the insensitiveness of SRL in each type of roots within these species.

We also found that both root N concentration and C: N were unresponsive to treatments, with the exception of root C: N in root-derived roots of *C. squarrosa* upon nitrogen addition. The consistent unresponsiveness of root morphology and N concentration in each type of roots to treatments suggests that grass roots, especially root-derived roots with higher tissue density, might have adapted to the nutrient-poor soil and slightly altered their morphol-

ogy and physiology in response to a short-term increase in soil resource availability. Despite the insignificant responses of fine roots, plant growth has frequently been reported to be stimulated when soil water and nitrogen availability is increased (Chen and Wang 2000; Bai et al. 2008). Thus, more resources could be acquired by faster growth or proliferation in lateral roots due to their higher SRL (Eissenstat 1991) to meet the demands of nitrogen by higher aboveground plant productivity in response to water and nitrogen addition. Although the finest lateral roots may have been inadvertently excluded in this study, the unresponsiveness of these two types of roots means that they cannot be compared to each other. It has been reported that fine roots in different positions of the branching system vary in their root dynamics (Hishi and Takeda 2005). Thus, speculation about the greater dynamics of root-derived roots in response to treatments may be true and deserves investigation in future studies. As mentioned previously, it is difficult to sample the terminal root-derived roots and they may have been missed in this study. Since shoot- and root-derived roots are significantly different, it is reasonable to expect that these differences in morphology, chemicals and responses to changes in soil resource levels would be even greater if terminal roots were included.

Correlations between aboveground plant N and fine root N for different types of roots

Root traits have been reported to be associated with leaf traits in a number of species (Craine et al. 2001, 2005; Craine and Lee 2003; Tjoelker et al. 2005; Withington et al. 2006). In this study, root N concentration in both types of root exhibited a linear regression with aboveground plant N concentration (Fig. 4). Although leaf N was not assessed separately from stem N, this result was similar to other studies of leaf and root N concentration (Craine and Lee 2003; Craine et al. 2005; Tjoelker et al. 2005).

The functional similarity of leaves and roots in resource acquisition, which is closely correlated with N concentration, may underlie the correlation in their N concentration. It is expected that distal roots functioning mainly in resource acquisition could be more strongly related to leaves in terms of N concentration than basal roots. In this study, variation in root N concentration explained by aboveground

plant N concentration was much lower in root-derived ($R^2=0.082$) than in shoot-derived ($R^2=0.35$) roots despite the similar slopes of the two linear regressions (Fig. 4). This indicated that the strength of the relationship between leaf and root N was different between different roots, with the shoot-derived root N linked more strongly to leaf N. The closer association of N in shoot-derived roots with aboveground plant N may be a result of anatomical proximity of these roots to aboveground plant parts. However, it is more likely to result from a functional transition from resource acquisition (Guo et al. 2008) in the root-derived roots to storage in shoot-derived roots for these grasses as previously indicated by structural differences in the two types of roots. Consequently, this might explain the greater responsiveness of fine roots in more basal orders (Guo et al. 2004), or those with larger diameters (Kosola et al. 2001), to reductions in photosynthesis as a result of leaf scorching or insect defoliation.

In conclusion, this study demonstrated that, although shoot-derived and root-derived roots in grasses are relatively closely related, many of their characteristics diverge from one another. Trait relationships such as higher root N concentration associated with higher tissue density between orders was different from other studies reporting trade-off of these two traits among species. This contributes to our understanding of plant trait syndromes, which have been demonstrated clearly in leaves (Reich et al. 1997; Wright et al. 2004) but remain relatively little studied in roots. The insensitivity of root morphological traits and nitrogen in each type of roots to resource addition may be a result of adaptation of grass roots to nutrient-poor soil, and suggest nutrient acquisition may be enhanced through fast growth or proliferation of root-derived roots to support higher aboveground productivity. N concentration in shoot-derived roots was linked more strongly to aboveground plant N concentration than root-derived roots, which may reflect their functional difference. Taken together, we suggest that structural differences within root systems may be a reflection of functional heterogeneity in grasses, as has been demonstrated in trees. Future studies should concentrate on the comparison between adventitious roots in herbaceous species and roots in woody species by incorporating physiological and anatomical evidence and by sampling more species.

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