

Root characteristics of C₄ grasses limit reliance on deep soil water in tallgrass prairie

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Abstract

Background C₄ grass species in the mesic tallgrass prairie of central North America can exhibit both high root production and deep rooting in the soil profile (>2 m). Differences in root growth and the types of roots produced vary according to local environmental gradients and management practices. The production of deep roots in tallgrass prairie has been historically presumed as a mechanism for water uptake when surface soils are dry.

Methods We examined changes in root biomass, total root length, root width, and theoretical hydraulic conductivity using roots collected from deep soil cores in upland and lowland topographic positions in grazed and ungrazed watersheds of the Konza Prairie Biological Station in north-eastern Kansas, USA.

Results Root biomass, total root length, and theoretical hydraulic conductivity were highest in roots found in the top 20 cm of the soil profile, and then declined exponentially with increasing soil depth. Compared to grazed areas, ungrazed locations had more root biomass and total root length of roots in the most superficial soil layers. No differences in rooting profiles were present among topographic contrasts. Theoretical hydraulic conductivity of axial root xylem did not vary by topographic

position or grazing contrasts, and declines in conductivity by depth were driven by changes in the number of vessels per stele, rather than changes in vessel size.

Conclusions Irrespective of differences by grazing treatment or topographic position, significant reductions in root biomass, total root length, and theoretical hydraulic conductivity of grass roots at soil depths greater than 1 m suggest deep roots in this grassland have limited functional significance for water uptake.

Keywords *Andropogon gerardii* · C₄ grass · Mesic grassland · Root biomass · Theoretical hydraulic conductivity · Total root length

Introduction

In the mesic tallgrass prairie of central North America, net primary productivity reflects shifting resource availability imposed by the interactive effects of a variable climate, ungulate grazers, and the regular occurrence of fire (Kucera et al. 1967; Sims and Singh 1978; Knapp et al. 1998). Ecosystem dynamics largely reflect the highly productive perennial C₄ grasses *Andropogon gerardii* (big bluestem), *Sorghastrum nutans* (Indiangrass), and *Schizachyrium scoparium* (little bluestem) (Smith and Knapp 2003). While aboveground growth responses to landscape gradients of resource availability and disturbance are well-documented (Schimel et al. 1991; Briggs and Knapp 1995; Craine et al. 2010; Nippert et al. 2011), our understanding of the variability in root dynamics (form and function) is incomplete. Specifically,

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how do changes in root biomass and root structure (root length, width and hydraulic conductivity) vary across the entire rooting profile as a function of topographic location and grazing history?

Peak root biomass in tallgrass prairie can range from 800 to 1,200 gm^{-2} in surface soils (top 40 cm) (Seastedt and Ramundo 1990; Rice et al. 1998). Biomass estimates that include roots and rhizomes to 60 cm depth have root:shoot ratios >3.0 (Rice et al. 1998). For C_4 grasses, the distribution of root biomass by soil depth is exponential, with the highest concentration of biomass (70–80%) in surface soils (top 30 cm) (Weaver and Darland 1949; Kucera and Dahlman 1968; Kitchen et al. 2009). Annual differences in root biomass reflect environmental variability, as dry years reduce root growth and biomass (Hayes and Seastedt 1987). Spatial variability reflects landscape management including grazing ($\sim 25\%$ decrease in root biomass for grazed versus ungrazed prairie: Vinton and Hartnett 1992; Johnson and Matchett 2001), and fire ($\sim 20\%$ increase in root biomass in annually burned versus unburned: Johnson and Matchett 2001; Kitchen et al. 2009) as well as edaphic differences (reduced biomass in clay versus silty soils: Weaver and Darland 1949). It has been shown previously that mowing (simulated grazing) in annually-burned plots reduced root biomass in the top 10 cm of the soil compared to unmowed treatments, but biomass did not vary between mowing treatments at depths >10 cm (Kitchen et al. 2009). Differences in root biomass between grazed and ungrazed areas can reflect differences in species composition (Gibson et al. 1993), but if species composition is similar across sites, differences in allocation of root biomass by soil depth reflect reduced allocation of carbon belowground due to repeated defoliation of the aboveground canopy (Johnson and Matchett 2001).

In addition to high belowground root biomass, C_4 grasses in tallgrass prairie can be rooted deeply in the soil profile (Weaver 1968). For example, *Andropogon gerardii* roots have been reported to depths of 2.1 m, and *Sorghastrum nutans* to 1.8 m depth in south-central Nebraska and north-central Kansas (Weaver and Darland 1949). The production of deep roots by the dominant C_4 grasses has long been speculated as a mechanism to avoid drought (Albertson and Weaver 1944; Weaver 1968; Craine et al. 2002). In a tallgrass prairie in eastern Kansas, soil moisture at depths greater than 1 m in tallgrass prairie is relatively static between 30 and 40% volumetric content. Yet,

seasonal and inter-annual periods with low rainfall commonly reduce soil moisture in the top 30 cm between 10 and 20% volumetric content, with soils in upland locations experiencing both drier soils and a faster rate of drying than lowland topographic locations (Nippert and Knapp 2007b; Nippert et al. 2011).

Despite the assumed function of deep roots to supply water allowing the grass canopy to persist through drought, few studies have analyzed the source of water uptake or changes in root distribution and form across the entire rooting profile. Previously, Nippert and Knapp (2007a, b) used the stable isotopic signature of water in plants and soils to show a common reliance on surface soil moisture (top 30 cm) by the three dominant C_4 grasses irrespective of seasonal and inter-annual wet/dry periods, while C_3 herbaceous and C_3 shrub species showed greater flexibility to switch water sources in response to wet/dry periods. Similarly, a reliance on soil water in the upper 20 cm was reported for *A. gerardii* in an agricultural landscape in central Iowa, highlighting the low ecological plasticity in depth of water uptake for this C_4 perennial grass (Asbjornsen et al. 2008). Thus, the presence of roots at depth does not signify functional contributions of water uptake from depth if the biomass and length are a small fraction of the total root network and the capacity to move water (conductivity) is negligible. Typically, anatomical characteristics of roots are not reported even though anatomical structure of roots can reflect function and whole-plant ecological strategies (Wahl and Ryser 2000).

To link changes in root form with root function by depth, we examined root biomass, total root length, root width, and hydraulic characteristics using deep soil cores from locations in upland and lowland topographic positions in grazed and ungrazed watersheds from the Konza Prairie Biological Station in north-eastern Kansas, USA. Specifically, we hypothesized that root biomass and length would vary between upland and lowland topographic regions on site because shallow, rocky upland soils are characteristically more water-limited depending on seasonal precipitation (Craine et al. 2010; Nippert et al. 2011), and comparatively, dry soils have lower total root biomass per unit soil volume (Hayes and Seastedt 1987). Similarly, we predicted that grazing would reduce overall root length similar to changes in growth and biomass, as more carbon is allocated aboveground for leaf and shoot regrowth (Johnson and Matchett 2001).

Method

Site description

Research was conducted at the Konza Prairie Biological Station (KPBS), a 3,487 ha native tallgrass prairie located in eastern Kansas, USA (39°05', 96°35'W). This region has a continental climate, with mean (1982–2009) January and July daily air temperatures between -1.2°C – 26.1°C , and an annual mean precipitation of 844 mm, 75% of which occurs between April and September. KPBS is divided into 52 experimental manipulations (watershed-level) of varying fire frequency (1, 2, 4, 20 years) and grazing (bison or cattle and ungrazed). The site-level experimental design overlays a natural topographic gradient on site with uplands composed of thin loess soils overlain on Permian chert-bearing shales and limestones, while lowlands are typically deep-soil undifferentiated Quaternary alluvial-colluvial deposits (Ransom et al. 1998). The depth of soil in uplands is highly variable, ranging from 5 cm to 2 m, while lowland soils typically exceed 2.5 m depth.

Sampling protocol

Soil cores were collected in June, 2010, from four upland and four lowland locations per watershed, each separated by >50 m. Samples were collected from a long-term annually-burned, ungrazed watershed (1D), and an annually-burned, bison-grazed watershed on site (N1B) (16 cores total). Soil cores of 8 cm diameter were collected using a 540MT Geoprobe Systems hydraulic-push corer (Salina, KS, USA) taken to the deepest depth possible, commonly past 2 m depth. Soil cores were washed of large soil particles using 2 mm mesh sieves and divided into depth increments including 0–10, 10–20, 20–35, 35–50, 50–75, 75–100, 100–150, 150+ cm, and then further processed using a 1 mm mesh sieve. Soil C and N concentrations as well as particle size evaluation via the hydrometer method were conducted by the Soils Testing Laboratory in the Department of Agronomy, Kansas State University (Table 1).

Root analysis

To measure changes in total root length and root size distribution by soil depth, roots were imaged using a flatbed scanner at 4,800 dpi (Epson Perfection 4870) and analyzed using WinRhizo Pro software (Regent

Instruments, Quebec, ON, Canada). Using these root images, we calculated total root length by depth increment and classified roots into 3 diameter classes: <0.15 mm, 0.15–0.30 mm, >0.3 mm. Roots were subsequently dried at 60°C for 72 h and weighed to determine dry biomass by soil depth increment.

During the initial processing of soil cores, long roots (>10 cm length) from each core were collected for microscopy of root vasculature at the various soil depths. 1-cm sections of long roots were embedded with paraffin, stained using Toluidine Blue, and cross-sectioned using a microtome at the Kansas State Veterinary Diagnostic Laboratory. Prepared root sections were then imaged using a digital camera (Leica DFC 290, Leica Microsystems GmbH, Wetzlar, Germany) coupled to a light microscope (Leica DM1000, Leica Microsystems GmbH, Wetzlar, Germany). Vessel diameters, stele area and cortex area (when available) were measured on all root cross-sections using ImageJ processing software (NIH, Bethesda, MD, USA). To estimate the capacity for axial water transport through the xylem, theoretical hydraulic conductivity (k_t) of each root cross-section was calculated assuming the shape of each vessel to be an ellipse (Lewis and Boose 1995):

$$k_t = \sum_{n=1}^N \frac{\pi}{64\eta} \frac{a_n^3 * b_n^3}{a_n^2 + b_n^2} \quad (1)$$

where η is the viscosity of water and a_n and b_n are the diameters of the major and minor axes of vessel n , respectively. Not all soil cores collected had long roots, and the distribution of long roots at varying depths was unequal, resulting in unbalanced distribution among grazing treatment and topographic positions. In all, 64 different root cross-sections were obtained for imaging of the root vasculature.

Statistical analysis

Differences in total root length, biomass, and proportional root widths were compared according to grazing and topographic contrasts. Data were analyzed using a linear mixed-effects model where soil depth, grazing treatment (grazed or ungrazed) and topographic position (upland or lowland) were the fixed effects, and sample location within each watershed was a random effect fit with a random intercept. As appropriate, data were log +1 transformed to meet the assumptions of normality. Multiple comparisons tests to compare differences

Table 1 Soil characterization by grazing and topographic contrasts at KPBS

Location	Depth (cm)	Total C (%)	Total N (%)	Texture		
				Sand (%)	Silt (%)	Clay (%)
1D—upland	0–10	3.34	0.28	6	68	26
	10–20	2.51	0.23	4	64	32
	20–35	1.61	0.17	8	54	38
	35–55			Loose rock		
	55–75	0.15	0.08	x	x	x
	76–100	0.26	0.10	x	x	x
1D—lowland	0–10	4.13	0.30	10	70	20
	10–20	3.16	0.25	10	65	25
	20–35	2.37	0.21	8	62	30
	35–50	1.56	0.16	10	56	34
	50–75	0.94	0.13	4	54	42
	76–100	0.15	0.09	4	56	40
	100–150	x	x	4	60	36
	150+	x	x	4	48	48
N1B—upland	0–10	3.65	0.34	14	62	24
	10–55			Loose rock		
	55–70	0.79	0.04	x	x	x
N1B—lowland	0–10	4.93	0.32	22	54	24
	10–20	3.37	0.24	16	54	30
	20–35	2.46	0.20	16	44	40
	35–50	2.11	0.20	14	44	42
	50–75	1.55	0.16	x	x	x
	75–100	0.77	0.13	x	x	x
	100–150	0.20	0.09	x	x	x
	150+	1.48	0.06	x	x	x

Watershed 1D is ungrazed, while watershed N1B is grazed by bison. Both watersheds are burned annually in the spring. For samples where analysis was below the detection limit, or texture classification was not possible, an 'x' is reported

by soil depth across treatment contrasts (grazing or topography) were conducted using Tukey's HSD. To facilitate comparisons of vertical root distributions between the sites sampled, β values were calculated as a numerical index of rooting distribution using the protocol of Jackson et al. (1996). Data were analyzed using the lme function in R (www.r-project.org/) and JMP 9.0.2 (SAS Institute, Cary, NC, USA).

Results

In uplands, roots were found as deep as 112 cm in the ungrazed watershed, and 46 cm deep in the grazed watershed (Fig. 1). In lowlands, roots were present at

250 cm depth for both ungrazed and grazed locations, the deepest sampling depth possible with our equipment. Across all samples, root biomass decreased exponentially with depth (Fig. 1a), such that cumulative biomass increased logarithmically with increasing depth ($P < 0.001$) (Fig. 1a inset panel). Total root biomass did not vary statistically by topographic contrasts ($P > 0.05$). Averaged across the two topographic positions, total root biomass was 22% higher in the ungrazed versus grazed watersheds (mean \pm SE: 615 ± 5 and 505 ± 10 g m^{-2} , respectively) ($P < 0.001$). For the ungrazed treatment, 71% and 78% of the total root biomass in the entire soil profile was located in the top 20 cm in lowlands and uplands, respectively. In the grazed treatment, 79% of root biomass was present in the top 20 cm for the

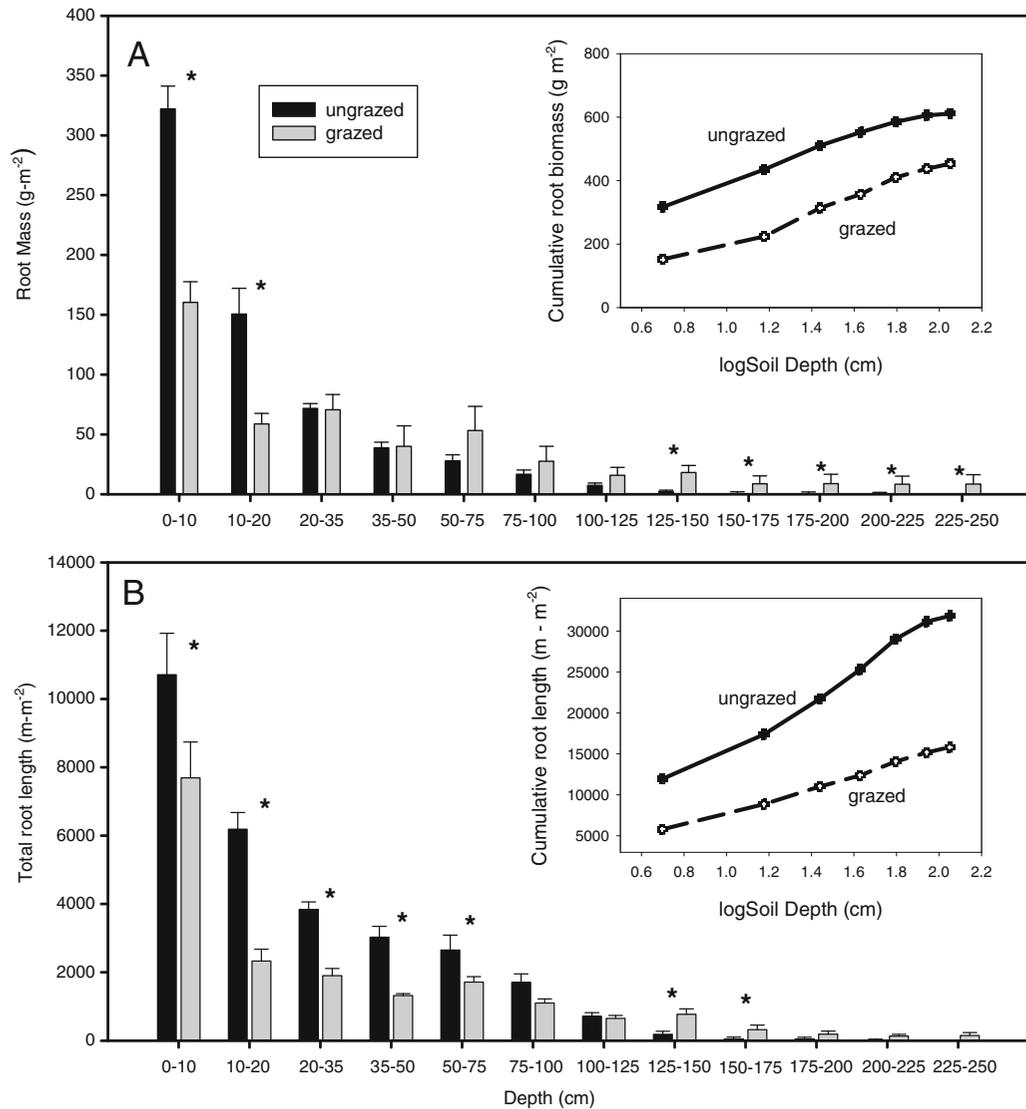


Fig. 1 Mean differences (\pm 1SE) in live root biomass (a) and total root length (b) by soil depth for grazed and ungrazed locations. Statistically significant differences ($P < 0.05$) between locations

within a given depth are denoted by an asterisk. Inset panels show the cumulative distribution of root biomass and root length per log soil depth for the grazing treatments

uplands sites, but lowland-grazed sites had lower total root biomass (45%) in the top 20 cm of soil.

Overall, when comparing root biomass to 1 m among treatments, there was no difference in the logarithmic rate of increase in cumulative root biomass with depth (Fig. 1a inset). Rates of biomass increase did not differ between uplands and lowlands ($P > 0.05$) nor between the grazed and ungrazed watershed ($P > 0.05$) in a single model of all root biomass to 1 m depth, nor for models where root biomass was collected to 2.5 m ($P > 0.25$ for both comparisons) or just the top 35 cm for which all

treatment combinations had soil ($P > 0.05$). Using the cumulative root fraction at specific soil depths, the extinction coefficient for root production (β) was calculated. For the ungrazed watershed, no differences by topography were present ($\beta = 0.90 \pm 0.02$ versus 0.89 ± 0.01 , for lowland and upland locations respectively, $P > 0.05$), but lowland locations in the grazed watershed had higher β values than upland locations (0.96 ± 0.01 versus 0.84 ± 0.02 , $P = 0.01$: Table 2).

Similar to root biomass, total root length at different depths varied by grazing treatment ($P < 0.001$), but not

Table 2 Statistical results for cumulative root biomass ($n=85$)

Source	SS	F Ratio	Prob > F
Watershed	7.99	131.9	<0.001
Position	0.04	0.6	0.44
logDepth	6.13	101.2	<0.001
Watershed*Position	0.22	3.7	0.06
Watershed*logDepth	0.03	0.5	0.48
Position*logDepth	0.00	0.1	0.79

Watershed refers to the grazed watershed (N1B) versus ungrazed (1D), Position refers to the upland or lowland topographic positions, and Depth refers to depth in soil

by topography ($P>0.05$). Total root length was high in the surface soils for both the ungrazed and grazed treatments (Fig. 1b). The majority of root length was in the top 10 cm for both grazing treatments, but decreases in root length by depth were more gradual in the ungrazed treatment. For example, 42% of the total root length was in the top 10 cm in the grazed treatment with 58% of root length distributed over the remaining 240 cm depth (Fig. 1b). In the ungrazed treatment, 97% of the total root length was in the top 1 m of soil.

The distribution of root biomass with depth followed patterns of soil carbon concentrations (Tables 1 and 3). Like root biomass, soil C declined exponentially with depth across all soil samples collected ($r^2=0.87$, $P<0.001$). For grazed lowlands and ungrazed uplands and lowlands, soil C explained 60% of the total variation in root biomass. Ungrazed uplands had a higher amount of biomass per unit soil C than grazed lowlands (16.2 ± 2.3 vs. 4.2 ± 2.1 [mg biomass cm^{-3} soil] [mg C g^{-1} soil] $^{-1}$) with ungrazed lowlands intermediate (9.1 ± 2.0 [mg biomass cm^{-3} soil] [mg C g^{-1} soil] $^{-1}$). The relationship between soil C and root biomass did not differ among treatment combinations ($P>0.05$).

Table 3 Statistical results for root biomass ($n=17$, $r^2=0.85$), predicted by soil C concentration and categorical expressions of three watershed and topographic position combined (WSPos: upland-ungrazed, lowland-ungrazed, lowland-grazed)

Source	SS	F Ratio	Prob > F
WSPos	3.44	7.3	0.01
SoilC	12.64	53.6	<0.0001
WSPos*SoilC	1.70	3.6	0.06

When roots were divided into three width classes, grazed locations had proportionally fewer of the finest root-width class in the top 1 m of soil, compared with ungrazed locations ($P<0.001$) (Fig. 2), but differences in root width class did not vary according to topographic contrasts ($P>0.05$). In the ungrazed treatment, ~60% of all roots in the top 125 cm had the finest widths (<0.15 mm). The proportion of the widest root-width class measured (>0.3 mm) increased from a minimum of 7% at 51–75 cm depth to 49% at the lowest depth sampled (Fig. 2). In the grazed treatment, the finest root-width class was highest at 0–20 cm depth (60%), but decreased proportionally thereon, with increases in the 0.15–0.30 width class up till 125 cm, and increases in the >0.3 mm width class from 125–250 cm (Fig. 2). At 250 cm, the widest root-width class accounted for 65% of the total in the grazed locations.

Similar to low amounts of root biomass and total root length at the deepest depths sampled, theoretical root hydraulic conductivity (k_t) declined with depth, reaching the lowest values at 1 m deep (Fig. 3a). No statistically-significant differences by grazing or topographic contrasts were present ($P>0.05$) (Fig. 3). k_t varied considerably among roots sampled in the top 30 cm, but roots below 50 cm depth had low values that continued to decline with depth (Fig. 3a). Changes in k_t by depth were not a function of changes in mean vessel area of the conduits (Fig. 3b), but rather changes in the number of vessels per stele (Fig. 3c). Changes in vessel number followed an exponential decay curve, with most roots sampled greater than 70 cm depth having but a single vessel in the stele.

Discussion

Contrary to expectations, the root metrics compared here (root biomass, total root length, root width classes, root vascular anatomy) did not vary by topographic contrasts (upland / lowland). Topographic variability is a strong driver of aboveground productivity at this site, with aboveground growth reduced in upland locations as a function of drier soils (Nippert et al. 2011). Thus, the lack of topographic differences for either grazing contrast may reflect the greater proportional allocation belowground in upland versus lowland sites, likely in response to greater soil moisture limitations on upland sites (Schimel et al. 1991; Craine et al. 2010; Nippert et al. 2011). For the grazing contrasts, our results were similar

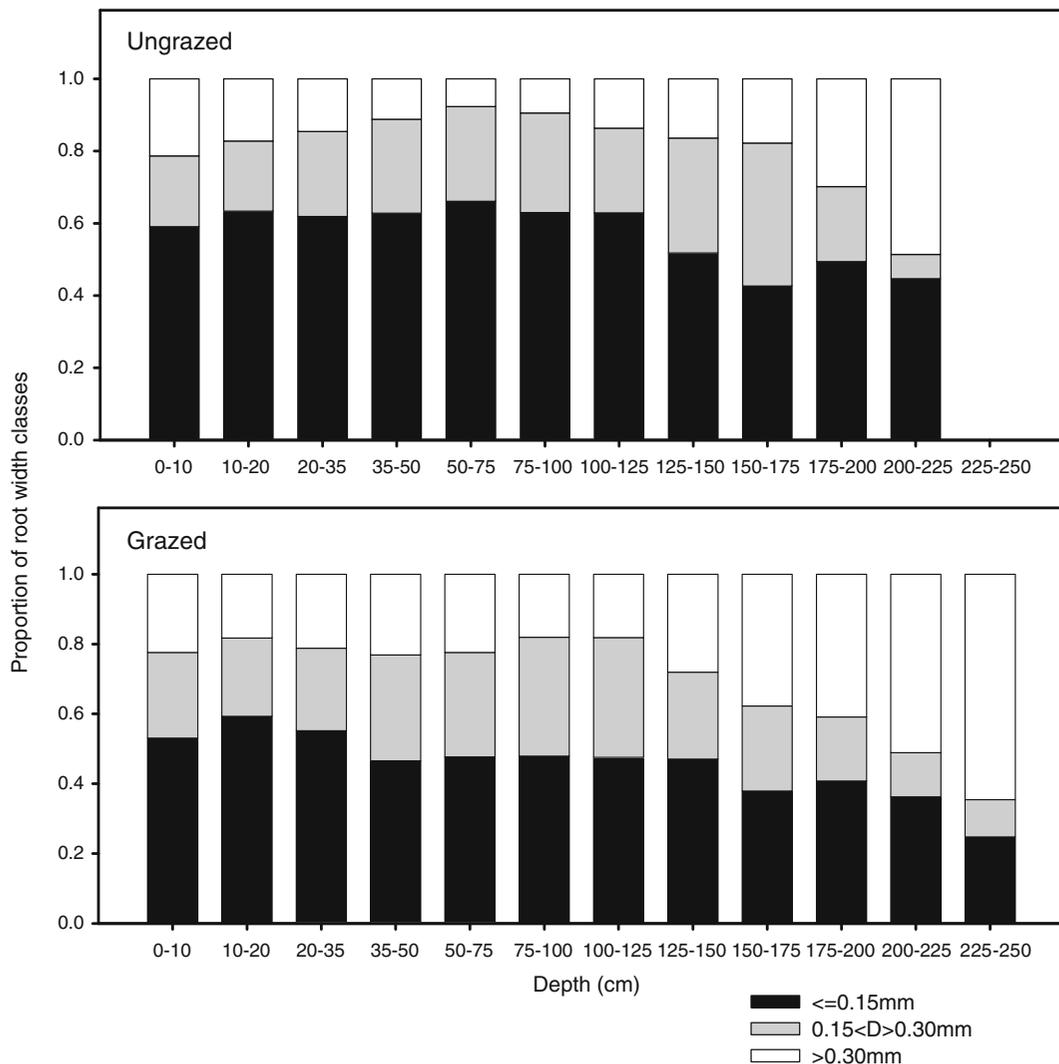


Fig. 2 Proportional distribution of root width classes by soil depth for grazed and ungrazed locations

to previous studies focused on shallower portions of the rooting profile, showing reduced biomass and root length in grazed versus ungrazed locations (Vinton and Hartnett 1992; Johnson and Matchett 2001). The exponential decline in root biomass, total root length, and low hydraulic conductivity with depth at all locations measured supports conclusions from previous analyses of functional water uptake and provides a structural mechanism for the lack of reliance on water sources below 30 cm depth among the dominant C_4 grass species (Nippert and Knapp 2007a, b; Asbjornsen et al. 2008).

These comparisons of root characteristics by depth clearly show that root biomass, length, and vascular capacity to conduct water are skewed towards a functional

reliance on resource availability in surface soils (top 20 cm) across a variety of environmental conditions. Similar to temperate grasslands worldwide (Jackson et al. 1996), the C_4 grasses sampled at the Konza Prairie are deeply rooted, but β values in this grassland reflect greater cumulative root distribution in surface soils. The majority of roots in the top 1 m of soil from each location sampled were of the finest width class, similar to other results from North American tallgrass prairie (Craine et al. 2002). Functionally, fine adventitious roots produced by grasses are a strategy to maximize belowground resource capture (water or nutrients) in systems that are commonly resource limited (Rice et al. 1998; Robinson et al. 2003).

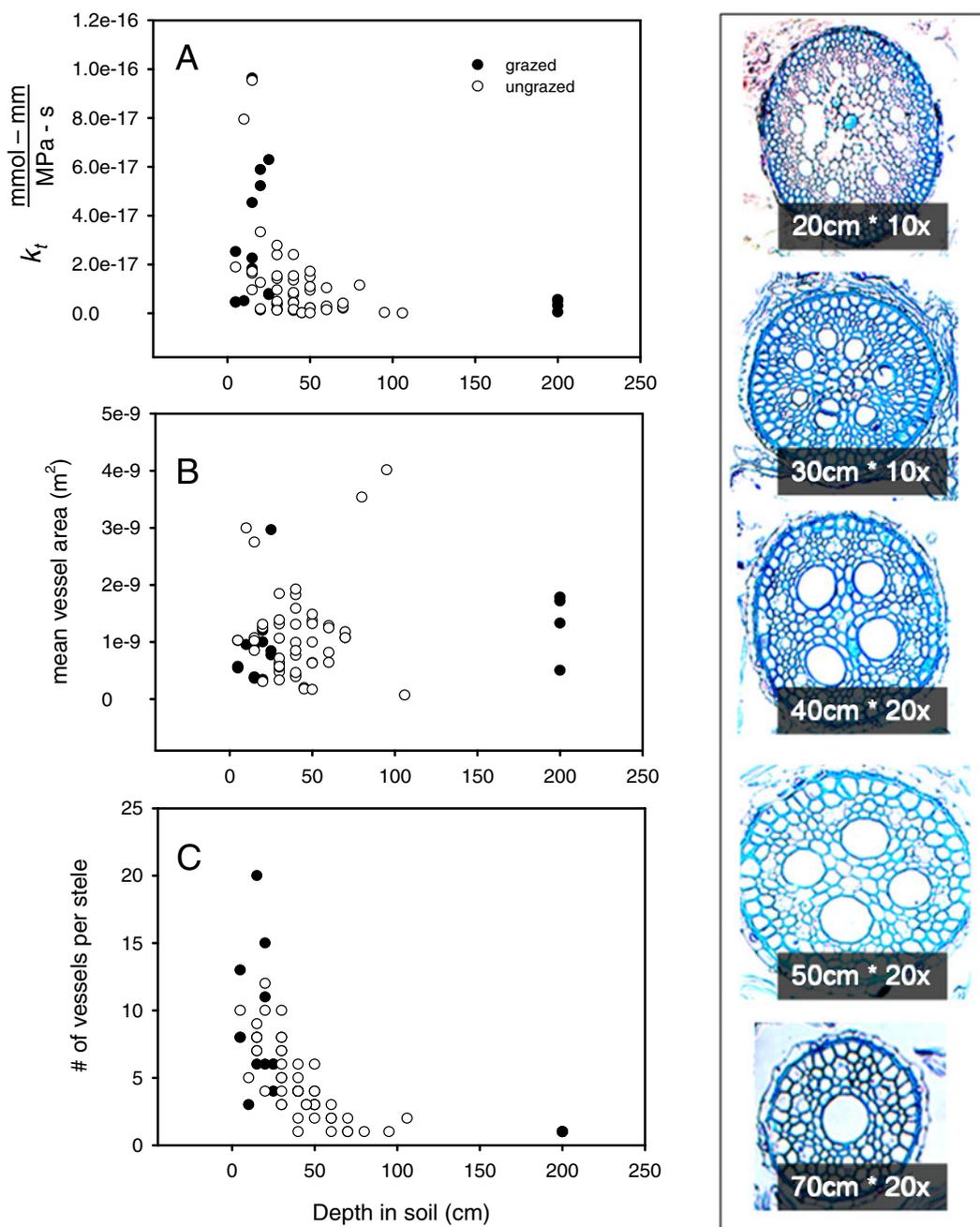


Fig. 3 Changes in theoretical root hydraulic conductivity (k_t), mean vessel area in the stele, and number of vessels in the stele according to root depth in the soil. No statistical differences by topography or grazing treatment were present. Images in the

right panel illustrate the stele from cross-sections of a single long-root measured at 20, 30, 40, 50, and 70 cm depth. Image magnification increases from 10 \times to 20 \times between the 30 and 40 cm depth

High root biomass and total root length in surface soils highlights the strategy of the C_4 grasses to respond to pulses in resource availability in surface soils or intense competition for soil resources (Jackson and Caldwell

1996; Craine et al. 2002). In maize, prodigious biomass production and root length in surface soils allow this species to quickly respond to rainfall events and thoroughly scavenge all available soil moisture between

rainfall events (Yu et al. 2007). Similarly, physiological performance and growth of C_4 grasses in tallgrass prairie species are linked to changes in water availability in surface soils (Nippert et al. 2011). Perennial grasses commonly exhibit root plasticity and alterations in root:shoot ratios in response to nutrient patchiness in surface soils (Benning and Seastedt 1997; Johnson and Biondini 2001). In this study, soil C and root biomass were tightly correlated ($r^2=0.87$; Table 3) as both declined exponentially with increasing soil depth (Table 1, Fig. 1). With lower soil %C and soil %N at deeper soil depths, there is presumably low mineralizable N available for root uptake at deep soil depths (Booth et al. 2005). Roots produced deeper in the soil profile had a proportionally greater width (Fig. 2). Soil texture changed with soil depth for all locations sampled, with increases in the proportion of clay, especially in the deepest soil layers (Table 1). The most parsimonious explanation for proportionally wider roots at depth, but with no change in mean vessel area (Fig. 3b), is the increased thrust potential required for roots to grow through dense soil (Fitter 1996).

If deep roots for C_4 grasses in this tallgrass prairie don't serve as a mechanism to avoid the negative consequences of drought, what is the significance of producing deep roots at all? The low root length, biomass, and hydraulic conductivity at depths below 0.5 m reduces the amount of soil water available for transport, but it doesn't eliminate all water-use at depths below 0.5 m. Thus, these roots should be able to transport small amounts of water during a multi-year drought, even if the majority of the canopy senesces. During drought, root biomass and root length decline (Hayes and Seastedt 1987; Fiala et al. 2009) with the greatest proportional decline in root production in surface soils. Indeed, Weaver noted that following the prolonged droughts of the 1930's, rhizomes of the dominant C_4 grasses persisted for many years despite severely-reduced aboveground production (Albertson and Weaver 1944; Weaver 1968). Thus, one possible function of deep roots is as a survival mechanism to persist through extremely adverse drought conditions, by transporting the minimum amount of water necessary to support a reduced aboveground canopy and maintain the turgidity of meristematic tissues in the rhizomes. Estimates of hydraulic conductivity in this study are based on theoretical axial hydraulic conductivity in the xylem. It is currently unknown how closely radial

conductivity and water uptake capacity scale with axial conductivity within the xylem of grass roots.

Knowledge of the drivers of root growth, turnover, and distribution remains the least understood realm of terrestrial ecology because of the difficulty of assessing differences to environmental gradients or management practices in situ. This study provides further evidence that the roots of C_4 grasses in tallgrass prairie are functionally skewed towards water and nutrient uptake from surface soils, with deep roots providing a minor role for water uptake. The reduced functional significance on water at deeper soil depths by these C_4 grasses raises several questions. Specifically, is the physiological drought tolerance of these species sufficient to withstand seasonal or annual periods with low precipitation, minimizing the benefit of investing carbon in deep roots, or alternatively, is root type, production and distribution in these species phylogenetically constrained? These questions, as well as the role of deep roots for nutrient uptake (either macronutrients or trace mineral) and potential changes in dependence on soil water at deeper depths following an extreme drought (multi-year) requires further investigation.

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