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REGULAR ARTICLE

Soil type more than precipitation determines fine-root abundance in savannas of Kruger National Park, South Africa

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Abstract

Aims Our aim was to examine how soil type and precipitation affect fine-root abundance in savanna ecosystems across Kruger National Park (KNP), South Africa.

Methods Fine-root distributions were measured in four sites that represent the natural factorial combination of soil types (basalt-derived clay or granite-derived sand) and precipitation regimes [wet (~750 mm mean annual precipitation) or dry (~500 mm mean annual precipitation)] that occur in KNP. Root area and biomass (at soil depths of 0–75 cm) were estimated from measurements of root number, length and width in images from minirhizotron tubes at each site. Measurements were made during one mid-season sampling during three subsequent years.

Results Fine-root area was more than twice as large in clay (2.3 ± 0.0 mm^2 cm^{-2}) than sand (0.8 ± 0.3 mm^2 cm^{-2}) sites but did not differ between wet and dry sites. Root number, length and width, used to derive area, showed similar patterns to fine-root area. Fine-root biomass estimated from these values was 5.5 ± 0.6 Mg ha^{-1} in clay sites and 2.2 ± 0.9 Mg ha^{-1} in sand sites.

Conclusions Across the four sites, a change from sand to clay soils had a greater effect on fine-root abundance and distributions than a 50% increase in precipitation from dry to wet sites. Results highlight the importance of soil properties on root dynamics and carbon pools in the region.

Keywords Belowground biomass · Grass · Minirhizotron · Rainfall · Root · Savanna · Tree

Abbreviations

(MAP)	Mean annual precipitation
(KNP)	Kruger National Park

Introduction

There has been a significant effort to understand the abiotic and biotic drivers of savanna structure and function (Haverd et al. 2015; Sankaran 2008; Sarmiento 1984; Staver et al. 2011; Walter 1971). Nearly all of this work has emphasized the role of precipitation, herbivory and fire with some consideration of soil properties on aboveground growth (Bond 2008; Scholtz et al. 2014). Where it has been measured, belowground biomass has been found to be an important component of carbon stocks and also important to plant productivity and community composition in savannas (February and Higgins 2010; Jackson et al. 1997; Smithwick et al. 2014; Zeppel et al. 2008). Despite its importance, measurements of belowground biomass are uncommon,

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especially for Africa (Hendricks et al. 2006; Jackson et al. 1997). This is due primarily to the difficulty of collecting belowground data (Metcalfe et al. 2007). As a result, relatively little is known about the factors that determine patterns of root biomass in savannas, even though it is likely to represent half of the total biomass in this globally important ecosystem (Grace et al. 2006; Jackson et al. 2002).

Precipitation regimes are widely recognized to play a central role in aboveground growth in savannas, but the role of precipitation regimes on belowground growth is less clear. Within grasslands and forests, both above and belowground growth tends to increase with precipitation (Cairns et al. 1997; Leuschner et al. 2004; Parton et al. 1993; Weltzin and McPherson 2000). However, because grasses often produce more root biomass than woody plants within a particular precipitation regime, shifts in the relative abundance of grasses and woody plants can obscure relationships between precipitation and root biomass in systems where both plant types exist (Jackson et al. 1997; Mokany et al. 2006). Consistent with this, many studies in savannas have not documented relationships between precipitation and root biomass (Cairns et al. 1997; McNaughton et al. 1998; Zhou et al. 2009).

Soil properties can also affect grass and woody plant growth in savannas (Bond 2008; Bradford et al. 2006; Staver et al. 2011; Walter 1971). Root distributions can respond to soil texture, density, nutrient availability and hydraulic conductivity (Bréda et al. 1995; Hook and Burke 2000). For example, sandy soils are generally associated with large soil pores, high hydraulic conductivity and hence better drainage than fine-textured soils (Saxton et al. 1986). Sandy versus clay soils could be expected to result in deeper rooting distributions, but this effect has not been widely observed perhaps because many factors, such as nutrient availability also change with soil texture (Bradford et al. 2006; Colgan et al. 2012; Jackson et al. 2000; Schenk and Jackson 2002).

While precipitation regimes and soil types are likely to affect root biomass distributions, a general lack of data and potentially complex interactions among factors make estimating root biomass across savanna landscapes difficult. The few studies that have measured root biomass in or near Kruger National Park (KNP), South Africa, have produced widely variable estimates from 1 to 17 Mg ha^{-1} (February and Higgins 2010; Koerner and Collins 2014; Smit and Rethman 1998; Snyman 2005). The objective of this research was to examine how soil type and precipitation regimes affect fine-root abundance in KNP. Because the park naturally encompasses a factorial combination of precipitation regimes and soil type, we measured root distributions using a factorial design across four sites: two 'Clay' and two 'Sand' sites, as well as two 'Dry' and two 'Wet' sites (Venter 1986; Venter et al. 2003). Minirhizotron tubes were used to measure fine roots at soil depths from 0 to 75 cm, in the middle of three growing seasons.

Methods

Kruger National Park (KNP) encompasses 19,485 km^2 in north-east South Africa between 30.9–32.0 °E and 22.3–25.5 °S. A rainfall gradient from north to south in the park produces a range of mean annual precipitation (MAP) from 450 mm to 750 mm yr.$^{-1}$ (Table 1). This range of precipitation represents a large portion of savanna ecosystems (Sankaran et al. 2005) and also covers the range of precipitation under which there is likely to be a switch from increased precipitation intensity causing either increases or decreases in plant productivity (Kulmatiski and Beard 2013b). Over 80% of annual precipitation falls from November through April. Most of the eastern half of KNP is underlain by basaltic rock that weathers into nutrient-rich, clay-rich soils, while the western half is underlain by granitic rock that weathers into nutrient-poor, sandy soils (Buitenwerf et al. 2014; Venter et al. 2003). Both of these dominant parent materials are old: the basaltic rock was formed ~190 million years ago, and the granite was formed ~3200 million years ago (Venter et al. 2003).

Four research sites in the park were chosen to represent the dominant soil types and precipitation regimes: Lower Sabie (Clay/Wet), Phalaborwa (Sand/Dry), Pretoriuskop (Sand/Wet) and Satara (Clay/Dry; Table 1). Precipitation regimes during the three growing seasons of this study were similar to long-term patterns (Table 1; South African National Parks, Scientific Services). Mean annual temperatures are similar among sites and range from 21.1 °C in Pretorioskop to 22.9 °C in Satara.

All four sites are considered savanna ecosystems and are dominated by a mix of woody plants and C4 grasses (Table 2; Scholes et al. 2003; Venter et al. 2003). Standing grass biomass in March samplings has been estimated at roughly 2.2 Mg ha^{-1} in the Sand/Dry site, 4.1 Mg ha^{-1} in the Clay/Dry site, 5.1 Mg ha^{-1} in the Sand/Wet site and 6.3 Mg ha^{-1} in the Clay/Wet site

Table 1 Environmental conditions at the four study sites. Mean annual precipitation data collected for roughly 50 years from sites within 5 km of the study sites. Observed annual precipitation data collected at the field site

Site name	Soil type [Sand/Silt/Clay (%)]	Mean annual precipitation (mm)[a]	Observed annual precipitation (mm)	Soil description
Lower Sabie	Clay (42/26/32)[b]	730 (Wet)	732	Pedocutanic clay
Phaloborwa	Sand (83/9/8)	475 (Dry)	481	Coarse fersiatillitic sand
Pretorioskop	Sand (85/10/5)	746(Wet)	820	Coarse fersiatillitic sand
Satara	Clay (46/37/17)	547(Dry)	577	Pedocutanic clay

[a] Mean annual precipitation (September through August) for the 2010/2011, 2011/2012 and 2012/2013 growing seasons during which root measurements were made.

[b] Buitenwerf et al. 2014

(Wessels et al. 2006). The sand sites are dominated by trees from the Combretaceae family (e.g., *Combretum* and *Terminalia* spp.) and C4 grasses *Hyparrhenia* spp. to the south, and *Panicum* spp. and *Urochloa* spp. to the north (Scholes et al. 2003; Venter et al. 2003). The clay sites are dominated by more palatable C4 grasses, *Cenchrus* spp., *Digitaria* spp. and *Bothrichloa* spp., and fine-leaved woody plants, such as *Acacia* spp. and *Dichrostachys* spp. (Scholes et al. 2003; Venter et al. 2003). There is a general pattern of greater woody plant biomass on sand than clay soils (Colgan et al. 2012).

At each site, four cellulose acetate butyrate tubes (5 cm diameter and 200 cm length) were installed at a 30° angle from the soil surface (Hendricks et al. 2006). To prevent light entry, exposed portions of tubes were painted opaque white. To prevent water entry into or around the tubes, caps were placed on either end of the tubes and a rubber collar that extended roughly 5 cm from the tubes was placed at the ground surface. Tubes were located at the cardinal points 20 m from a randomly-selected plot center. Each tube was installed into a 5-cm wide 'pilot hole' established in otherwise undisturbed soils. Tubes were installed during the 2008/2009 growing season (henceforth, the 2009 season). Tubes were allowed to 'equilibrate' with the soils for more than one growing season prior to image collection (Joslin and Wolfe 1999). A minirhizotron camera (Bartz Technology, Santa Barbara, CA, USA) was used to collect 18.0 by 12.5 mm images at 15× magnification.

Table 2 Common plants at the four study sites listed in descending order of relative abundance within each plant type

Site	Grasses*		Woody plants**	
	Species	Growth form / Palatability	Species	Growth form
Lower Sabie	*URMO* *PAMA* *BORA*	Loosely tufted to 1 m / Palatable Tufted, productive to 2 m / Palatable Tufted, productive to 1 m / Unpalatable	*SEVI* *STSP* *DAME*	Shrub Tree Tree
Phaloborwa	*SCPA* *URMO* *ARTR*	Stoloniferous to 1 m / Palatable Loosely tufted to 1 m / Palatable Tufted to 0.7 m / Unpalatable	*COMO*	Tree
Pretorioskop	*CECI* *HYSP* *SEIN*	Tufted to 1 m / Palatable Tufted to 2 m / Palatable Rhizomatous, to 2 m / Palatable	*SCBI* *TESE*	Tree Tree
Satara	*BORA* *CECI* *DIER*	Tufted, shrub-like / Unpalatable Tufted to 1 m / Palatable Tufted to 1.8 m / Palatable	*DISI* *COIM*	N-fixing shrub Tree

*Grasses: ARTR = *Aristida transvaalensis, BORA = Bothrichloa radicans, CECI = Cenchrus ciliaris* (L.), *DIER = Digitaria eriantha*, HYSP = *Hyparrhenia spp.*, PAMA = *Panicum maximum, SCPA = Schmidtia pappophoroides* (Steud), *SEIN = Setaria incrassate, URMO = Urochloa mosambicensis* (Hack).

**Woody plants: COMO = *Colophospermum mopane* (Kirk ex Benth.), SEVI = *Securinega virosa* (Roxb.), STSP = *Strychnos spinosa* (Lam.), DAME = *Dalbergia melanoxylon* (Guill. and Perr.), SCBI = *Sclerocarya birrea* (A. Rich), TESE = *Terminalia sericea* (Burch ex. DC), DISI = *Dichrostachys sinerea* subsp. *africana* (Brenan & Brummitt), COIM = *Combretum imberbe* (Warwa)

Image collection occurred once each year at roughly peak growing season just before grass senescence (Wessels et al. 2006). Previous analyses of images at the Satara site indicated that root number and area increased by roughly 50% from the beginning of the growing season to a peak in March / April (Kulmatiski and Beard 2013b). In March 2011 roughly 60 images were collected every 25 mm down each tube. In March 2012 roughly 50 images were collected every 12.5 mm down the top half of each tube in three sites due to sampler error. Due to logistical constraints, images in 2013 were collected in January. During this sampling roughly 120 images were collected every 12.5 mm down each tube. Previous research at the Satara site suggested that January values were likely to be roughly 15% smaller than peak-season values (Kulmatiski and Beard 2013b). Due to the length of time between samplings (i.e., one year) data are used to estimate standing biomass and not to calculate root lifespan.

To better understand fine-root dynamics across the growing season, images at the Sand/Wet site were collected four times during the 2011 season. Samples were collected prior to leaf-out (October 15, 2010), just after leaf-out (December 2, 2010), at the peak / end of the growing season (March 27, 2011) and late in the season after many grasses had senesced (May 1, 2011) (Archibald and Scholes 2007).

We measured the length, width and number of living roots (i.e., white or brown, not black) using Rootfly software (Version 2.0.2, Clemson University 2011; Hendrick and Pregitzer 1992; Wells and Birchfield 2008). One observer performed all image analyses to reduce sampler bias (Johnson et al. 2001; Kulmatiski and Beard 2004).

Minirhizotrons are widely used and often considered a preferred approach for measuring fine roots (Yuan and Chen 2012), but roots may respond differently to access tubes than to surrounding soils (Rytter and Rytter 2012). Where this occurs, the absolute estimates of root parameters (e.g., area) are likely to be biased. Similarly, an assumption of the depth of field of view (i.e., 2 mm) may result in over- or underestimates of root biomass (Taylor et al. 2013). Therefore, conclusions based on inter-site comparisons (i.e., the effects of soil type or precipitation regime) are likely to be more robust than absolute estimates of root biomass or distributions (Träger and Wilson 2016).

Data analyses

Fine-root length, number and width were measured directly from images. The following calculations were done to provide estimates area (total), area (proportion), volume and biomass. Root area was calculated as length multiplied by width for each individual root. Root volume was calculated assuming roots were cylinders (i.e., volume = length x πr^2). Root volume was converted to biomass assuming that images sampled a 2-mm deep field of view and that root biomass had a density equal to that of a mixture of grasses and woody plants of 0.26 g cm^{-3} (Jackson et al. 1997).

Values from windows within 12.5 cm vertical depth increments were averaged prior to analyses. Root area, length and number are presented as mean values per cm^2. The volume of roots is reported for a 12.5 cm deep, m^2 area (i.e., cm^3 of roots m^{-2} for a 12.5 cm depth strata). We included an analysis of root area as a proportion by depth to control for differences in the total amount of roots across sites. For this analysis, root area values are presented as the proportion of root area per cm of soil depth. Root biomass is presented as a sum across depths (i.e., Mg ha^{-1} in the top 75 cm). For simplicity and because root parameters were similar across the three years of the study (Online Resource 1), values were averaged across years prior to analyses, with the exception that total biomass calculations did not include data from 2012 due to missing data from deeper depths. A separate set of analyses performed using only data from 2011 and 2013, for which a complete dataset of all soil depths at all sites was available, produced similar results to those reported here (Online Resource 2).

To test for differences in root length, number, width, area (both absolute and proportional values) and volume by depth among sites, nested subsets of generalized additive mixed effects models (GAMMs) were fit using a beta likelihood with five “knots” (Burnham and Anderson 2003). A logit link was used for the proportion data. Akaike’s Information Criterion (AIC) was used to select the best models. As a rule of thumb, AIC values that differ by less than five are considered indistinguishable (Burnham and Anderson 2003). AIC values that differ by more than 10 are considered different (Burnham and Anderson 2003). Lower AIC values reflect a better fit to the data than higher values. AICs were used to compare the following: 1) a global model that did not distinguish any sites, 2) a model that separated all sites, 3) a model that separated wet and dry sites, and 4) a model that separated clay and sand sites. Models were fit using the 'gam' function from the 'mgcv' package in R (v3.1.3).

Because root biomass was calculated by adjusting root volume data by a fixed value (i.e., 0.26 g cm^{-3}), tests of volume and biomass produced the same results. However, because root biomass data is typically presented as a single value across depths (i.e., Mg ha^{-1}), we used a separate linear mixed model test for differences in total root biomass among treatments. Fixed effects were 'Soil Type' and 'Precipitation Regime' and random effects were 'tube' and 'year'. 'Year' effects were unimportant ($F_{1,18}$ = 0.46, P = 0.50) and did not interact with 'Soil Type' or 'Precipitation Regime' ($F_{3,18}$ = 0.33, P = 0.80) so data from years were combined in a final analysis. Treatments were considered different at the α = 0.05 level.

To test for differences in root length, number and width among dates within a growing season at the Pretorioskop site, we used a linear mixed model. The fixed effect was date and the random effect was 'tube'. Separate analyses were performed for each of the six soil depths. Treatments were considered different at the α = 0.05 level. All linear mixed models were performed in SAS v. 9.4 using proc. glimmix.

Results

All but three of 15,854 roots measured had widths less than 2 mm (2.7, 2.6 and 2.1) so we consider all roots to be fine roots. For root length, number and width, the model that separated all sites provided the best fit to the data (Table 3; Fig. 1). This largely reflected greater root length, number and width in the Clay/Wet site than other sites and less root length, number and width in the Sand/Dry site than other sites, particularly in the middle (i.e. 20–40 cm) depths.

For root area, the model that separated sites was best but not distinguishable from the model that separated clay and sand sites (Table 3; Fig. 2a). Both models were better than models that separated wet from dry sites or combined all sites. Differences among sites reflected greater root area in clay than sand sites. Averaged across depths, root area was 2.3 ± 0.0 mm^2 cm^{-2} in clay sites and 0.8 ± 0.3 mm^2 cm^{-2} in sand sites.

Analyses of the proportion of root area with depth produced similar results: the model that separated all sites was best (Fig. 2b). This reflected a greater proportion of root area in surface soils in sand sites than clay sites. The cumulative proportion of root area revealed that 50% of root area in the top 75 cm occurred above 37, 37, 33, and 27 cm in the Clay/Dry, Clay/Wet, Sand/Dry and Sand/Wet sites, respectively.

For root volume, the model that separated clay from sand sites was best but not distinguishable from the model that separated all sites (Table 1; Fig. 2c). Differences among sites reflected greater root volume in clay than sand sites at most depths.

Root biomass was greater in clay than sand sites ($F_{1,6}$ = 13.82, P = 0.01) but did not differ between wet and dry sites ($F_{1,6}$ = 1.86, P = 0.22), and there was no interaction between soil type and precipitation regime ($F_{1,6}$ = 0.36, P = 0.57; Fig. 3).

With one exception, root length, number and width did not differ at any depth among the four sampling dates in the 2011 growing season at the Sand/Wet site (P > 0.05). The one exception was that root width at 44 cm was smaller in May than October ($F_{3,9}$ = 3.91, P = 0.05; Fig. 4).

Discussion

Across four sites in Kruger National Park, South Africa, we found that fine-root biomass was more than twice as great in two clay (basalt-derived) sites than two sand (granite-derived) sites. In contrast, root biomass did not differ between the two wet (~750 mm MAP) and two dry (~500 mm) sites. Previous studies have failed to find large soil type effects on root biomass (Cairns et al. 1997; Craine et al. 2008; February and Higgins 2010; Schenk and Jackson 2005). We suspect that the paired sampling design, minirhizotron approach, and the particular soil types compared, contributed to identifying soil type effects in this study. A larger response to soil type than precipitation regime was surprising but consistent with a recent study that found aboveground biomass in KNP was also better correlated with soil type than precipitation regime (Colgan et al. 2012). Results were also consistent with a recent study that found no difference in shallow root biomass in nearby granite soils across a range of precipitation regimes from ~200 to 600 mm MAP (Priyadarshini et al. 2016). While precipitation is often considered a primary determinant of biomass in savannah ecosystems (Staver et al. 2011; Wessels et al. 2006), our results suggest that for

Table 3 Akaike's information criterion (AIC) values for General Additive Mixed Models of root area (mm^2 cm^2 and as a proportion), length, number, volume and width with soil depth in four sites in Kruger National Park

	Models			
Variables	Global	Soil Type	Precipitation	All Separate
Area	1207	**1143**	1203	**1139**
Area (proportion)	454	373	440	**335**
Length	1920	1870	1904	**1845**
Number	1318	1285	1280	**1228**
Volume	861	**844**	861	**848**
Width	455	373	441	**335**

The Global model combined all sites into a single profile. The Soil Type model separated clay from sand sites. The Precipitation model separated wet from dry sites. The All Separate model separated all sites (i.e., Clay/Wet, Clay/Dry, Sand/Wet, Sand/Dry). Lower AIC values indicate a better model fit. The best models are highlighted in bold. Values that differ by 10 or more are considered significantly different. Values that differ by less than 5 are considered similar

belowground biomass, soil type can play a larger role than a 50% increase in mean annual precipitation. However, results must be taken with caution due to the limited number of sites and regional scope of sampling.

One potential explanation for greater fine-root biomass on clay than sand soils is that all plants are more productive on the more nutrient-rich clay soils (Fransen et al. 1998; Hook et al. 1991; Scholes et al. 2003; Venter

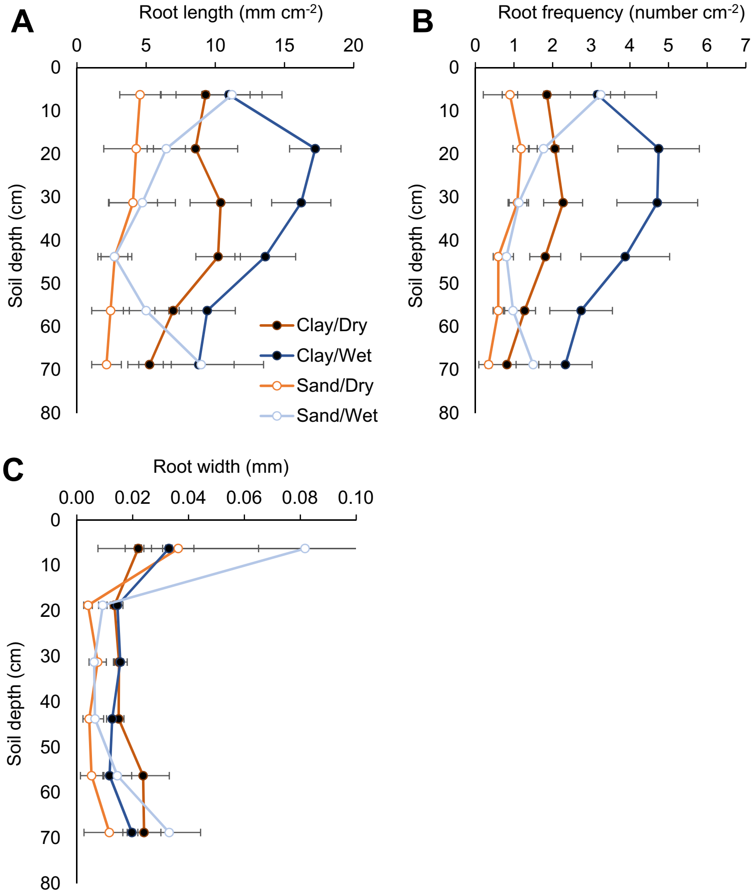

Fig. 1 (**a**) Root length, (**b**) number and (**c**) width by depth measured at four sites over three years in Kruger National Park, South Africa. The sites represent a natural factorial combination of soil type (Clay or Sand) and precipitation regime (Wet or Dry). Error bars represent the error associated with the four minirhizotron tubes at each site

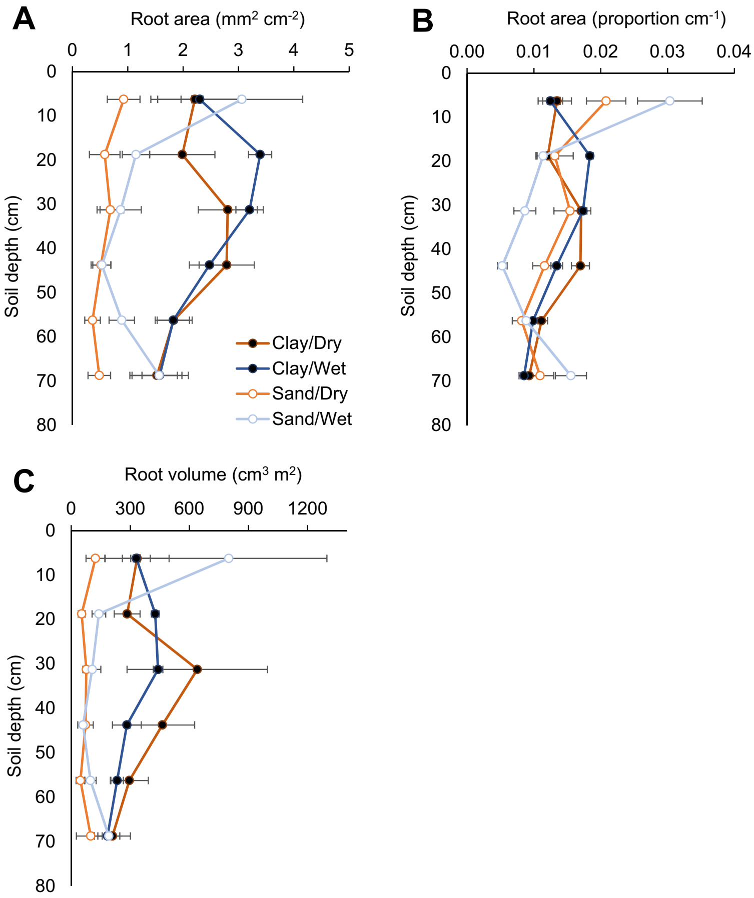

Fig. 2 (**a**) Root area (absolute), (**b**) root area (proportion) and (**c**) root volume by depth at four sites in Kruger National Park. The sites represent a natural factorial combination of soil type (Clay or Sand) and precipitation regime (Wet or Dry). Root area is reported as the mean area for a given depth. Root volume is the sum of root volume in the indicated 12.5 cm depth strata. Error bars represent the error associated with the four minirhizotron access tubes at each site

et al. 2003). An additional explanation is that grasses, which produce more root biomass than woody plants, may have greater abundance on clay than sand soils (February and Higgins 2010; February et al. 2013; Scholes 1988). There are several reasons grasses may have a greater abundance on clay than sand soils. Faster growth conditions (i.e., due to nutrient availability), shallower water distributions, and greater fire and herbivory may all benefit grasses on clay soils (Bond 2008; Bond 2010; February et al. 2013; Groen et al. 2008; Hopcraft et al. 2010). Indeed, grass production (Scholes 1988), herbivore abundance (Mills and Fey 2005; but see Smit 2011), and fire frequency (Smit et al. 2013) are all greater on clay (basalt) than sand (granite) soils in KNP. Future research will be needed to identify the mechanism for greater root biomass found in clay than sand soils in KNP in this study, but it appears likely to be caused by greater growth of grasses, which produce more root biomass, on clay than sand soils (February and Higgins 2010).

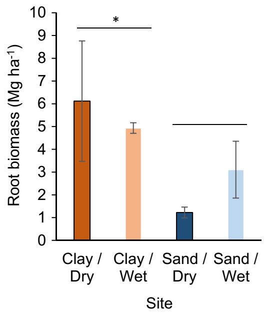

Fig. 3 Fine root biomass in the top 75 cm of soil at four sites in Kruger National Park that represent a two-way factorial combination of soil type (*Clay or Sand*) and precipitation regime (*Wet or Dry*). Error bars represent the error associated with four minirhizotron tubes. An asterisk indicates differences between indicated groups at the $\alpha = 0.05$ level

Recent isotope tracer experiments in KNP and other semi-arid sites in the USA indicate that a wide variety of grasses demonstrate consistently shallow rooting distributions at sites around the world (Kulmatiski et al. 2017; Kulmatiski and Beard 2013a; Mazzacavallo and Kulmatiski 2015; Warren et al. 2015). Therefore, while

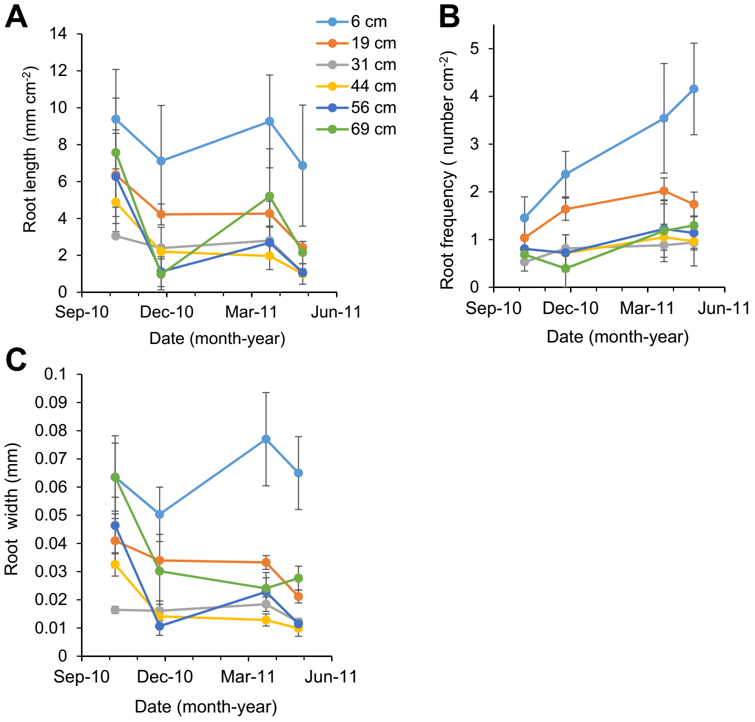

Fig. 4 (**a**) Root length, (**b**) number and (**c**) width at six soil depths on four sampling dates during the growing season ending in 2011. Samples taken at the Pretorioskop study site which was characterized as a Sand / Wet site. Error bars represent the error associated with the four minirhizotron tubes at each site. The only difference among any root parameter was that root width was smaller in May 2011 than October 2010 at the 44 cm depth

it is likely that grasses demonstrated similar rooting distributions with depth among sites, it remains possible that species differ in root production among sites within KNP. For example, some of the common grasses form tufts that grow to less than 1 m in height while others grow with rhizomes to over 2 m in height. It is reasonable to expect that the taller grasses produce more root biomass (Maire et al. 2009), unfortunately, relatively little is known about rooting patterns of different species or even relationships between aboveground plant traits and belowground plant traits (Franzen 2001; Picon-Cochard et al. 2012). Future research is needed to distinguish the root biomass associated with different species.

Colgan et al. (2012) found greater aboveground biomass (driven by woody plants) in sand (23 Mg ha^{-1}) than clay sites (6 Mg ha^{-1}). We estimated fine-root biomass at 2.2 Mg ha^{-1} and 5.5 Mg ha^{-1}, in sand and clay sites, respectively. Consistent with global patterns, a study in a nearby system found that fine-root biomass represented roughly 29% of total root biomass (i.e., fine and coarse roots; Jackson et al. 1997; Smit and Rethman 1998). Using this approximation, total root biomass in our study sites was 7.5 Mg ha^{-1} in sand sites and 19.0 Mg ha^{-1} in clay sites (Jackson et al. 1997; Smit and Rethman 1998). These values suggest a 10-fold difference in aboveground to belowground ratios from 3 to 0.3 in sand to clay sites in KNP. Because aboveground to belowground biomass ratios are important to dynamic global vegetation models, the wide range of values found in this study highlights a potentially important role for soil type in understanding the carbon dynamics of the savannas in this region (Grace et al. 2006; Krinner et al. 2005).

While the rhizotron technique may be susceptible to assumptions regarding the 'field of view' and 'root volume to biomass conversion' (Taylor et al. 2013), several independent studies have produced similar estimates of root biomass in the region. Recent studies in Letaba (Clay/Dry) and Pretorioskop (Sand/Wet) reported 4 and 5 Mg ha^{-1} of fine live roots in root cores, respectively (Kulmatiski et al. 2010; Mazzacavallo and Kulmatiski 2015). Another study reported 2.5 to 5.5 Mg ha^{-1} for fine roots and 5 to 11 Mg ha^{-1} for total root biomass at Satara (Clay/Dry) and Pretorioskop (February and Higgins 2010). Outside KNP values of 2–17 Mg ha^{-1} were reported for sites with ~400–600 mm MAP (Smit and Rethman 1998; Snyman 2005). Changing assumptions of 'field of view' and 'root volume to biomass' to other common values of 0.68 mm and 0.2 g cm^3, respectively, would change our estimates of total root biomass from 7.5 to 18 Mg ha^{-1} in sand sites and 19 to 45 Mg ha^{-1} in clay sites (Träger and

Wilson 2016). Thus the range of published estimates from roughly 5 to 45 Mg ha^{-1} are broadly consistent with total root biomass values of 10 to 30 Mg ha^{-1} which are often assumed for tropical savannas (Grace et al. 2006; Jackson et al. 1997; Rutherford 1993).

Rhizotron data has the advantage of providing insight into root morphology. In this study, greater root biomass in clay sites reflected greater root number and root length. However, root biomass was not as large in wet clay soils as would be expected from root number and length because plants in wet clay soils produced narrower roots than in dry clay sites. Still, the dominant pattern in root distributions in our study sites was greater length, number, area and biomass in clay soils. Converting root area data to the proportion of root area by depth provided some insight into how plants distributed roots that was independent of total production. This data revealed similar root distributions among sites suggesting that plants, for the most part, maintained a consistent rooting strategy with depth across sites. The only notable difference in the proportion of root area with depth was that plants produced a greater proportion of fine-root area at the surface in sand than clay soils. This suggests that plants increased shallow root production to capture rapidly infiltrating water in sand soils.

There are many approaches to measuring roots, each with their own strengths and weaknesses, so it is useful to compare estimates from different techniques. Data in this study were collected once each year and did not provide insight into root longevity or turnover, rather it provided insight into mid-season standing biomass of fine roots that grew along the access tubes during the five years of this study. These estimates, therefore, likely provide a good estimate of relatively short-term root growth but are likely to underestimate total root biomass because large roots were not observed (Taylor et al. 2013). Root growth can be affected by observation tube installation and presence, but roots in this study were allowed more than a full growing season to equilibrate with the tubes and did not show large differences in patterns between years (Online Resource 1; Joslin and Wolfe 1999). Also notable is the fact that previous measurements of root biomass taken from soil cores as well as from isotope tracer studies in these study sites have all documented a rapid decline in root biomass or activity with soil depth in the top meter of soil (Berry and Kulmatiski 2017; February and Higgins 2010; Kulmatiski and Beard 2013a; Mazzacavallo and Kulmatiski 2015). Here, there was little change in root area with depth in the top 75 cm. We suspect this reflects, in part, the fact that soil coring techniques are more likely to measure larger suberized roots while the minirhizotron technique is more likely to capture the growth of smaller, faster growing roots. However, isotope tracer techniques should not be biased in this way and also showed decreasing root activity with depth (Berry and Kulmatiski 2017; Kulmatiski and Beard 2013a; Kulmatiski et al. 2010; Mazzacavallo and Kulmatiski 2015). This suggests that the minirhizotron approach may have underestimated root growth in the top ~12.5 cm. This could result from poor soil contact or frequent movement of the top of the tube against relatively loose soil near the surface, and may need to be considered in future minirhizotron studies.

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