

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

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19  
20 **Abstract**

21  
22 **Aims**

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

25  
26 **Methods**

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

33  
34 **Results**

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

39  
40 **Conclusions**

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

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45 **Keywords:** belowground biomass; grass; minirhizotron; rainfall; root; savanna; tree

46 **Abbreviations:** Mean annual precipitation (MAP), Kruger National Park (KNP).

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## 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, especially for Africa (Hendricks et al. 2006; Jackson et al. 1997). This is due primarily to the difficulty of collecting belowground data (Metcalf 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<sup>-1</sup> (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

93 distributions using a factorial design across four sites: two ‘Clay’ and two ‘Sand’ sites, as well as  
 94 two ‘Dry’ and two ‘Wet’ sites (Venter 1986; Venter et al. 2003). Minirhizotron tubes were used  
 95 to measure fine roots at soil depths from 0 to 75 cm, in the middle of three growing seasons.

96

97 **Methods**

98 Kruger National Park (KNP) encompasses 19,485 km<sup>2</sup> in north-east South Africa between 30.9–  
 99 32.0 °E and 22.3–25.5 °S. A rainfall gradient from north to south in the park produces a range of  
 100 mean annual precipitation (MAP) from 450 mm to 750 mm yr<sup>-1</sup> (Table 1). This range of  
 101 precipitation represents a large portion of savanna ecosystems (Sankaran et al. 2005) and also  
 102 covers the range of precipitation under which there is likely to be a switch from increased  
 103 precipitation intensity causing either increases or decreases in plant productivity (Kulmatiski and  
 104 Beard 2013b). Over 80% of annual precipitation falls from November through April. Most of  
 105 the eastern half of KNP is underlain by basaltic rock that weathers into nutrient-rich, clay-rich  
 106 soils, while the western half is underlain by granitic rock that weathers into nutrient-poor, sandy  
 107 soils (Buitenwerf et al. 2014; Venter et al. 2003). Both of these dominant parent materials are  
 108 old: the basaltic rock was formed ~190 million years ago, and the granite was formed ~3200  
 109 million years ago (Venter et al. 2003).

110

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

117

118 All four sites are considered savanna ecosystems and are dominated by a mix of woody plants  
 119 and C4 grasses (Scholes et al. 2003; Venter et al. 2003). Standing grass biomass in March  
 120 samplings has been estimated at roughly 2.2 Mg ha<sup>-1</sup> in the Sand/Dry site, 4.1 Mg ha<sup>-1</sup> in the  
 121 Clay/Dry site, 5.1 Mg ha<sup>-1</sup> in the Sand/Wet site and 6.3 Mg ha<sup>-1</sup> in the Clay/Wet site (Wessels et  
 122 al. 2006). The sand sites are dominated by trees from the Combretaceae family (*e.g.*, *Combretum*  
 123 and *Terminalia* spp.) and C4 grasses *Hyparrhenia* spp. to the south, and *Panicum* spp. and  
 124 *Urochloa* spp. to the north (Scholes et al. 2003; Venter et al. 2003). The clay sites are dominated  
 125 by more palatable C4 grasses, *Cenchrus* spp., *Digitaria* spp. and *Bothrichloa* spp., and fine-  
 126 leaved woody plants, such as *Acacia* spp and *Dichrostachys* spp (Scholes et al. 2003; Venter et  
 127 al. 2003). There is a general pattern of greater woody plant biomass on sand than clay soils  
 128 (Colgan et al. 2012).

129

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

Site Name	Soil Type [Sand/Silt/Clay (%)]	Mean annual precipitation (mm) <sup>a</sup>	Observed annual precipitation (mm)	Soil description
Lower Sabie	Clay (42/26/32) <sup>b</sup>	730 (Wet)	732	Pedocutanic clay
Phalaborwa	Sand (83/9/8)	475 (Dry)	481	Coarse fersiallitic sand

Pretorioskop	Sand (85/10/5)	746(Wet)	820	Coarse fersitillitic sand
Satara	Clay (46/37/17)	547(Dry)	577	Pedocutanic clay

133 <sup>a</sup>Mean annual precipitation (September through August) for the 2010/2011, 2011/2012 and  
134 2012/2013 growing seasons during which root measurements were made.

135 <sup>b</sup>Buitenwerf et al. 2014

136

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

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

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

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

148

149 At each site, four cellulose acetate butyrate tubes (5 cm diameter and 200 cm length) were  
150 installed at a 30° angle from the soil surface (Hendricks et al. 2006). To prevent light entry,  
151 exposed portions of tubes were painted opaque white. To prevent water entry into or around the  
152 tubes, caps were placed on either end of the tubes and a rubber collar that extended roughly 5 cm  
153 from the tubes was placed at the ground surface. Tubes were located at the cardinal points 20 m  
154 from a randomly-selected plot center. Each tube was installed into a 5-cm wide ‘pilot hole’  
155 established in otherwise undisturbed soils. Tubes were installed during the 2008/2009 growing  
156 season (henceforth, the 2009 season). Tubes were allowed to ‘equilibrate’ with the soils for  
157 more than one growing season prior to image collection (Joslin and Wolfe 1999). A  
158 minirhizotron camera (Bartz Technology, Santa Barbara, CA, USA) was used to collect 18.0 by  
159 12.5 mm images at 15x magnification.

160

161 Image collection occurred once each year at roughly peak growing season just before grass  
162 senescence (Wessels et al. 2006). Previous analyses of images at the Satara site indicated that  
163 root number and area increased by roughly 50% from the beginning of the growing season to a  
164 peak in March / April (Kulmatiski and Beard 2013b). In March 2011 roughly 60 images were  
165 collected every 25 mm down each tube. In March 2012 roughly 50 images were collected every  
166 12.5 mm down the top half of each tube in three sites due to sampler error. Due to logistical  
167 constraints, images in 2013 were collected in January. During this sampling roughly 120 images  
168 were collected every 12.5 mm down each tube. Previous research at the Satara site suggested  
169 that January values were likely to be roughly 15% smaller than peak-season values (Kulmatiski  
170 and Beard 2013b). Due to the length of time between samplings (*i.e.*, one year) data are used to  
171 estimate standing biomass and not to calculate root lifespan.

172  
173 To better understand fine-root dynamics across the growing season, images at the Sand/Wet site  
174 were collected four times during the 2011 season. Samples were collected prior to leaf-out  
175 (October 15, 2010), just after leaf-out (December 2, 2010), at the peak / end of the growing  
176 season (March 27, 2011) and late in the season after many grasses had senesced (May 1, 2011)  
177 (Archibald and Scholes 2007).

178  
179 We measured the length, width and number of living roots (*i.e.*, white or brown, not black) using  
180 Rootfly software (Version 2.0.2, Clemson University 2011; Hendrick and Pregitzer 1992; Wells  
181 and Birchfield 2008). One observer performed all image analyses to reduce sampler bias  
182 (Johnson et al. 2001; Kulmatiski and Beard 2004).

183  
184 Minirhizotrons are widely used and often considered a preferred approach for measuring fine  
185 roots (Yuan and Chen 2012), but roots may respond differently to access tubes than to  
186 surrounding soils (Rytter and Rytter 2012). Where this occurs, the absolute estimates of root  
187 parameters (*e.g.*, area) are likely to be biased. Similarly, an assumption of the depth of field of  
188 view (*i.e.*, 2 mm) may result in over- or underestimates of root biomass (Taylor et al. 2013).  
189 Therefore, conclusions based on inter-site comparisons (*i.e.*, the effects of soil type or  
190 precipitation regime) are likely to be more robust than absolute estimates of root biomass or  
191 distributions (Träger and Wilson 2016).

## 192 193 **Data analyses**

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

201  
202 Values from windows within 12.5 cm vertical depth increments were averaged prior to analyses.  
203 Root area, length and number are presented as mean values per  $\text{cm}^2$ . The volume of roots is  
204 reported for a 12.5 cm deep,  $\text{m}^2$  area (*i.e.*,  $\text{cm}^3$  of roots  $\text{m}^{-2}$  for a 12.5 cm depth strata). We  
205 included an analysis of root area as a proportion by depth to control for differences in the total  
206 amount of roots across sites. For this analysis, root area values are presented as the proportion of

207 root area per cm of soil depth. Root biomass is presented as a sum across depths (*i.e.*, Mg ha<sup>-1</sup> in  
208 the top 75 cm). For simplicity and because root parameters were similar across the three years of  
209 the study (Online Resource 1), values were averaged across years prior to analyses, with the  
210 exception that total biomass calculations did not include data from 2012 due to missing data  
211 from deeper depths. A separate set of analyses performed using only data from 2011 and 2013,  
212 for which a complete dataset of all soil depths at all sites was available, produced similar results  
213 to those reported here (Online Resource 2).

214

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

226

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

235

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

241

## 242 **Results**

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

248

249 For root area, the model that separated sites was best but not distinguishable from the model that  
250 separated clay and sand sites (Table 3; Fig. 2a). Both models were better than models that  
251 separated wet from dry sites or combined all sites. Differences among sites reflected greater root

252 area in clay than sand sites. Averaged across depths, root area was  $2.3 \pm 0.0 \text{ mm}^2 \text{ cm}^{-2}$  in clay  
 253 sites and  $0.8 \pm 0.3 \text{ mm}^2 \text{ cm}^{-2}$  in sand sites.

254  
 255 Analyses of the proportion of root area with depth produced similar results: the model that  
 256 separated all sites was best (Fig. 2b). This reflected a greater proportion of root area in surface  
 257 soils in sand sites than clay sites. The cumulative proportion of root area revealed that 50% of  
 258 root area in the top 75 cm occurred above 37, 37, 33, and 27 cm in the Clay/Dry, Clay/Wet,  
 259 Sand/Dry and Sand/Wet sites, respectively.

260  
 261 For root volume, the model that separated clay from sand sites was best but not distinguishable  
 262 from the model that separated all sites (Table 1; Fig. 2c). Differences among sites reflected  
 263 greater root volume in clay than sand sites at most depths.

264  
 265 Root biomass was greater in clay than sand sites ( $F_{1,6} = 13.82, P = 0.01$ ) but did not differ  
 266 between wet and dry sites ( $F_{1,6} = 1.86, P = 0.22$ ), and there was no interaction between soil type  
 267 and precipitation regime ( $F_{1,6} = 0.36, P = 0.57$ ; Fig. 3).

268  
 269 With one exception, root length, number and width did not differ at any depth among the four  
 270 sampling dates in the 2011 growing season at the Sand/Wet site ( $P > 0.05$ ). The one exception  
 271 was that root width at 44 cm was smaller in May than October ( $F_{3,9} = 3.91, P = 0.05$ ; Fig. 4).

272  
 273 **Table 3.** Akaike's information criterion (AIC) values for General Additive Mixed Models of root  
 274 area ( $\text{mm}^2 \text{ cm}^2$  and as a proportion), length, number, volume and width with soil depth in four  
 275 sites in Kruger National Park. The Global model combined all sites into a single profile. The  
 276 Soil Type model separated clay from sand sites. The Precipitation model separated wet from dry  
 277 sites. The All Separate model separated all sites (*i.e.*, Clay/Wet, Clay/Dry, Sand/Wet,  
 278 Sand/Dry). Lower AIC values indicate a better model fit. The best models are highlighted in  
 279 bold. Values that differ by 10 or more are considered significantly different. Values that differ  
 280 by less than 5 are considered similar.

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

281  
 282  
 283 **Discussion**  
 284 Across four sites in Kruger National Park, South Africa, we found that fine-root biomass was  
 285 more than twice as great in two clay (basalt-derived) sites than two sand (granite-derived) sites.  
 286 In contrast, root biomass did not differ between the two wet (~750 mm MAP) and two dry (~500  
 287 mm) sites. Previous studies have failed to find large soil type effects on root biomass (Cairns et  
 288 al. 1997; Craine et al. 2008; February and Higgins 2010; Schenk and Jackson 2005). We suspect  
 289 that the paired sampling design, minirhizotron approach, and the particular soil types compared,

290 contributed to identifying soil type effects in this study. A larger response to soil type than  
291 precipitation regime was surprising but consistent with a recent study that found aboveground  
292 biomass in KNP was also better correlated with soil type than precipitation regime (Colgan et al.  
293 2012). Results were also consistent with a recent study that found no difference in shallow root  
294 biomass in nearby granite soils across a range of precipitation regimes from ~200 to 600 mm  
295 MAP (Priyadarshini et al. 2016). While precipitation is often considered a primary determinant  
296 of biomass in savannah ecosystems (Staver et al. 2011; Wessels et al. 2006), our results suggest  
297 that for belowground biomass, soil type can play a larger role than a 50% increase in mean  
298 annual precipitation. However, results must be taken with caution due to the limited number of  
299 sites and regional scope of sampling.

300  
301 One potential explanation for greater fine-root biomass on clay than sand soils is that all plants  
302 are more productive on the more nutrient-rich clay soils (Fransen et al. 1998; Hook et al. 1991;  
303 Scholes et al. 2003; Venter et al. 2003). An additional explanation is that grasses, which produce  
304 more root biomass than woody plants, may have greater abundance on clay than sand soils  
305 (February and Higgins 2010; February et al. 2013; Scholes 1988). There are several reasons  
306 grasses may have a greater abundance on clay than sand soils. Faster growth conditions (*i.e.*, due  
307 to nutrient availability), shallower water distributions, and greater fire and herbivory may all  
308 benefit grasses on clay soils (Bond 2008; Bond 2010; February et al. 2013; Groen et al. 2008;  
309 Hopcraft et al. 2010). Indeed, grass production (Scholes 1988), herbivore abundance (Mills and  
310 Fey 2005; but see Smit 2011), and fire frequency (Smit et al. 2013) are all greater on clay  
311 (basalt) than sand (granite) soils in KNP. Future research will be needed to identify the  
312 mechanism for greater root biomass found in clay than sand soils in KNP in this study, but it  
313 appears likely to be caused by greater growth of grasses, which produce more root biomass, on  
314 clay than sand soils (February and Higgins 2010).

315  
316 Recent isotope tracer experiments in KNP and other semi-arid sites in the USA indicate that a  
317 wide variety of grasses demonstrate consistently shallow rooting distributions at sites around the  
318 world (Kulmatiski et al. 2017; Kulmatiski and Beard 2013a; Mazzacavallo and Kulmatiski 2015;  
319 Warren et al. 2015). Therefore, while it is likely that grasses demonstrated similar rooting  
320 distributions with depth among sites, it remains possible that species differ in root production  
321 among sites within KNP. For example, some of the common grasses form tufts that grow to less  
322 than 1 m in height while others grow with rhizomes to over 2 m in height. It is reasonable to  
323 expect that the taller grasses produce more root biomass (Maire et al. 2009), unfortunately,  
324 relatively little is known about rooting patterns of different species or even relationships between  
325 aboveground plant traits and belowground plant traits (Franzen 2001; Picon-Cochard et al.  
326 2012). Future research is needed to distinguish the root biomass associated with different  
327 species.

328  
329 Colgan et al. (2012) found greater aboveground biomass (driven by woody plants) in sand (23  
330  $\text{Mg ha}^{-1}$ ) than clay sites ( $6 \text{ Mg ha}^{-1}$ ). We estimated fine-root biomass at  $2.2 \text{ Mg ha}^{-1}$  and  $5.5 \text{ Mg}$   
331  $\text{ha}^{-1}$ , in sand and clay sites, respectively. Consistent with global patterns, a study in a nearby  
332 system found that fine-root biomass represented roughly 29% of total root biomass (*i.e.*, fine and  
333 coarse roots; Jackson et al. 1997; Smit and Rethman 1998). Using this approximation, total root  
334 biomass in our study sites was  $7.5 \text{ Mg ha}^{-1}$  in sand sites and  $19.0 \text{ Mg ha}^{-1}$  in clay sites (Jackson et  
335 al. 1997; Smit and Rethman 1998). These values suggest a 10-fold difference in aboveground to



336 belowground ratios from 3 to 0.3 in sand to clay sites in KNP. Because aboveground to  
337 belowground biomass ratios are important to dynamic global vegetation models, the wide range  
338 of values found in this study highlights a potentially important role for soil type in understanding  
339 the carbon dynamics of the savannas in this region (Grace et al. 2006; Krinner et al. 2005).

340  
341 While the rhizotron technique may be susceptible to assumptions regarding the ‘field of view’  
342 and ‘root volume to biomass conversion’ (Taylor et al. 2013), several independent studies have  
343 produced similar estimates of root biomass in the region. Recent studies in Letaba (Clay/Dry)  
344 and Pretorioskop (Sand/Wet) reported 4 and 5 Mg ha<sup>-1</sup> of fine live roots in root cores,  
345 respectively (Kulmatiski et al. 2010; Mazzacavallo and Kulmatiski 2015). Another study  
346 reported 2.5 to 5.5 Mg ha<sup>-1</sup> for fine roots and 5 to 11 Mg ha<sup>-1</sup> for total root biomass at Satara  
347 (Clay/Dry) and Pretorioskop (February and Higgins 2010). Outside KNP values of 2-17 Mg ha<sup>-1</sup>  
348 were reported for sites with ~400-600 mm MAP (Smit and Rethman 1998; Snyman 2005).  
349 Changing assumptions of ‘field of view’ and ‘root volume to biomass’ to other common values  
350 of 0.68 mm and 0.2 g cm<sup>3</sup>, respectively, would change our estimates of total root biomass from  
351 7.5 to 18 Mg ha<sup>-1</sup> in sand sites and 19 to 45 Mg ha<sup>-1</sup> in clay sites (Träger and Wilson 2016). Thus  
352 the range of published estimates from roughly 5 to 45 Mg ha<sup>-1</sup> are broadly consistent with total  
353 root biomass values of 10 to 30 Mg ha<sup>-1</sup> which are often assumed for tropical savannas (Grace et  
354 al. 2006; Jackson et al. 1997; Rutherford 1993).

355  
356 Rhizotron data has the advantage of providing insight into root morphology. In this study,  
357 greater root biomass in clay sites reflected greater root number and root length. However, root  
358 biomass was not as large in wet clay soils as would be expected from root number and length  
359 because plants in wet clay soils produced narrower roots than in dry clay sites. Still, the  
360 dominant pattern in root distributions in our study sites was greater length, number, area and  
361 biomass in clay soils. Converting root area data to the proportion of root area by depth provided  
362 some insight into how plants distributed roots that was independent of total production. This  
363 data revealed similar root distributions among sites suggesting that plants, for the most part,  
364 maintained a consistent rooting strategy with depth across sites. The only notable difference in  
365 the proportion of root area with depth was that plants produced a greater proportion of fine-root  
366 area at the surface in sand than clay soils. This suggests that plants increased shallow root  
367 production to capture rapidly infiltrating water in sand soils.

368  
369 There are many approaches to measuring roots, each with their own strengths and weaknesses, so  
370 it is useful to compare estimates from different techniques. Data in this study were collected once  
371 each year and did not provide insight into root longevity or turnover, rather it provided insight  
372 into mid-season standing biomass of fine roots that grew along the access tubes during the five  
373 years of this study. These estimates, therefore, likely provide a good estimate of relatively short-  
374 term root growth but are likely to underestimate total root biomass because large roots were not  
375 observed (Taylor et al. 2013). Root growth can be affected by observation tube installation and  
376 presence, but roots in this study were allowed more than a full growing season to equilibrate with  
377 the tubes and did not show large differences in patterns between years (Online Resource 1; Joslin  
378 and Wolfe 1999). Also notable is the fact that previous measurements of root biomass taken  
379 from soil cores as well as from isotope tracer studies in these study sites have all documented a  
380 rapid decline in root biomass or activity with soil depth in the top meter of soil (Berry and  
381 Kulmatiski 2017; February and Higgins 2010; Kulmatiski and Beard 2013a; Mazzacavallo and

382 Kulmatiski 2015). Here, there was little change in root area with depth in the top 75 cm. We  
383 suspect this reflects, in part, the fact that soil coring techniques are more likely to measure larger  
384 suberized roots while the minirhizotron technique is more likely to capture the growth of smaller,  
385 faster growing roots. However, isotope tracer techniques should not be biased in this way and  
386 also showed decreasing root activity with depth (Berry and Kulmatiski 2017; Kulmatiski and  
387 Beard 2013a; Kulmatiski et al. 2010; Mazzacavallo and Kulmatiski 2015). This suggests that the  
388 minirhizotron approach may have underestimated root growth in the top ~12.5 cm. This could  
389 result from poor soil contact or frequent movement of the top of the tube against relatively loose  
390 soil near the surface, and may need to be considered in future minirhizotron studies.

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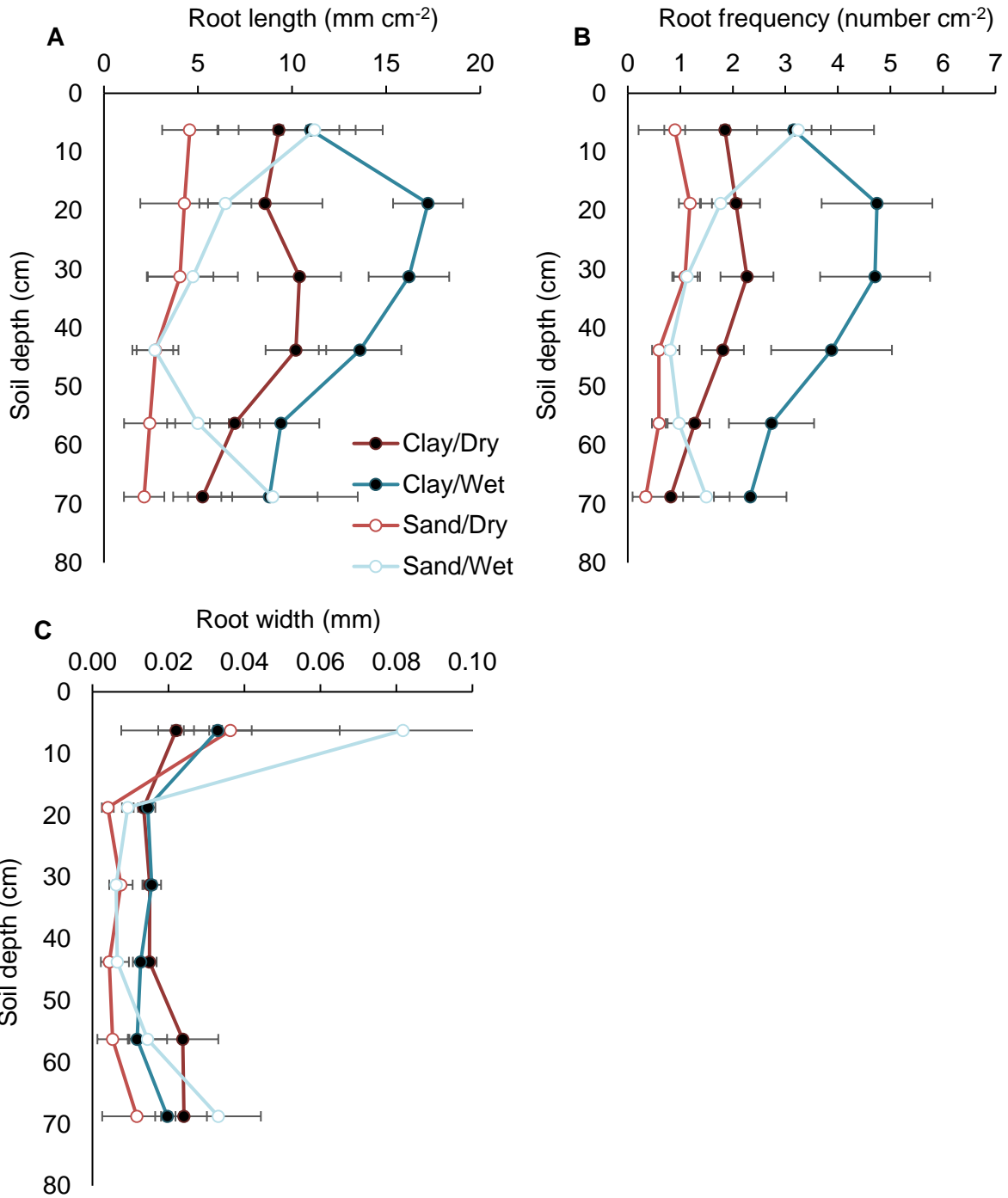
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580 **Fig. 1** (A) Root length, (B) number and (C) width by depth measured at four sites over three  
581 years in Kruger National Park, South Africa. The sites represent a natural factorial combination  
582 of soil type (Clay or Sand) and precipitation regime (Wet or Dry). Error bars represent the error  
583 associated with the four minirhizotron tubes at each site.  
584

585 **Fig. 2** (A) Root area (absolute), (B) root area (proportion) and (C) root volume by depth at four  
586 sites in Kruger National Park. The sites represent a natural factorial combination of soil type  
587 (Clay or Sand) and precipitation regime (Wet or Dry). Root area is reported as the mean area for  
588 a given depth. Root volume is the sum of root volume in the indicated 12.5 cm depth strata.  
589 Error bars represent the error associated with the four minirhizotron access tubes at each site.  
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591 **Fig. 3** Fine root biomass in the top 75 cm of soil at four sites in Kruger National Park that  
592 represent a two-way factorial combination of soil type (Clay or Sand) and precipitation regime  
593 (Wet or Dry). Error bars represent the error associated with four minirhizotron tubes. An  
594 asterisk indicates differences between indicated groups at the  $\alpha = 0.05$  level.  
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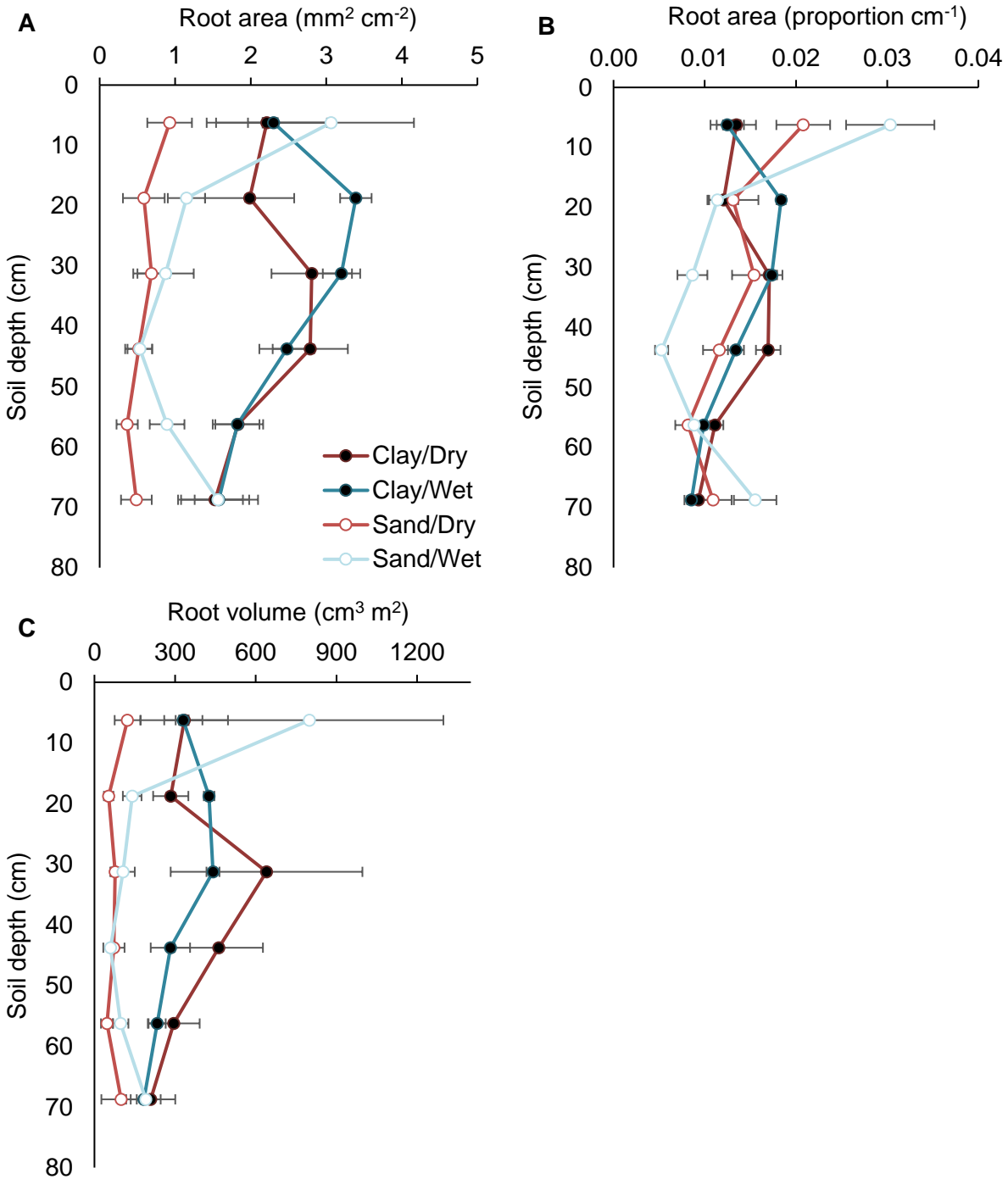
596 **Fig. 4** (A) Root length, (B) number and (C) width at six soil depths on four sampling dates  
597 during the growing season ending in 2011. Samples taken at the Pretorioskop study site which  
598 was characterized as a Sand / Wet site. Error bars represent the error associated with the four  
599 minirhizotron tubes at each site. The only difference among any root parameter was that root  
600 width was smaller in May 2011 than October 2010 at the 44 cm depth.  
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**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.

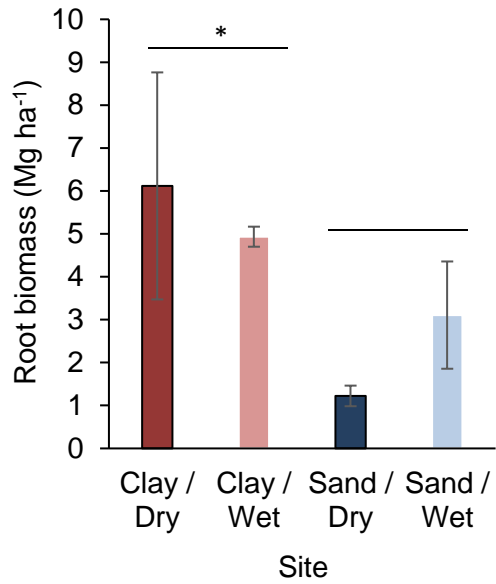


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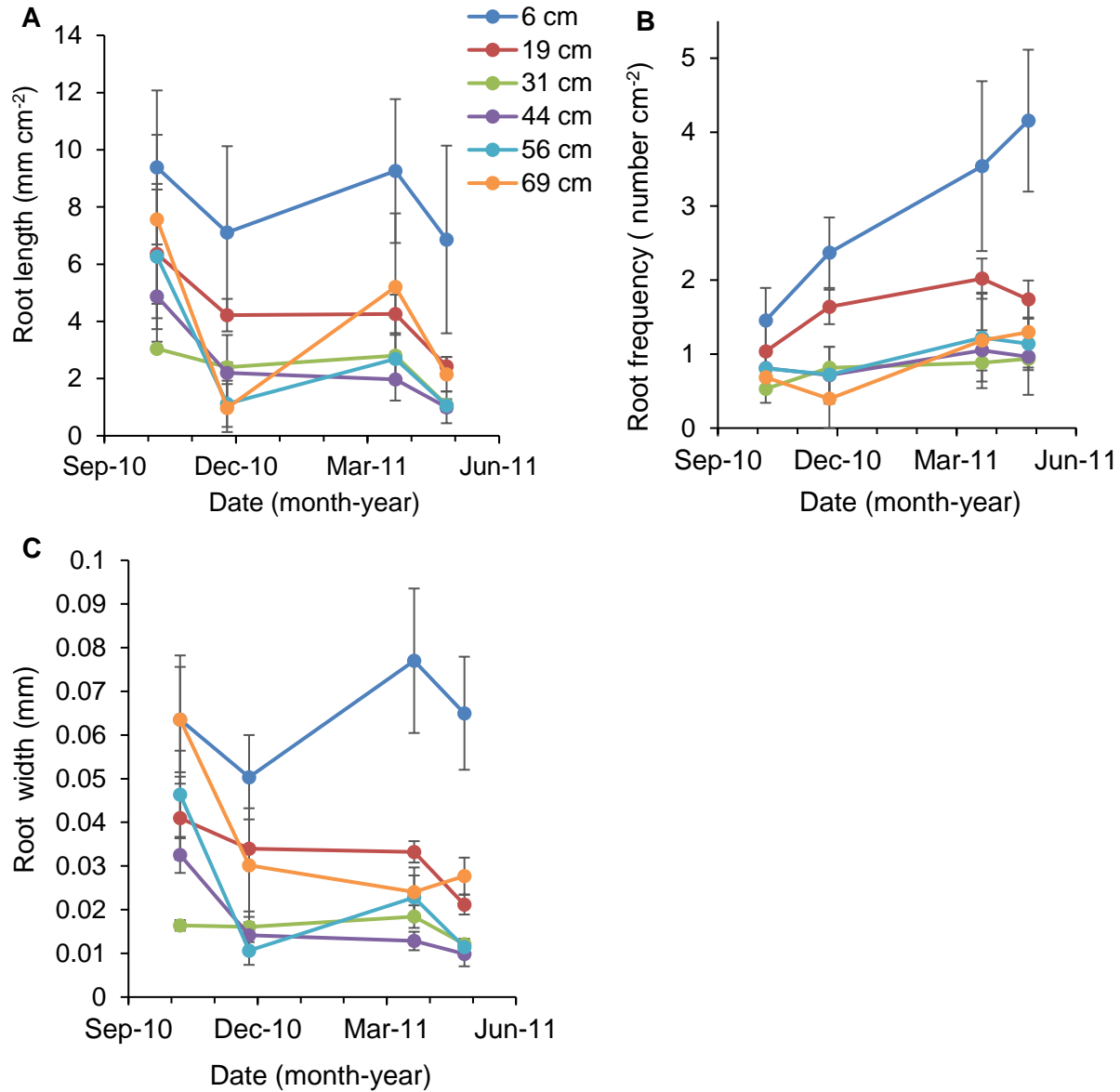
**Fig. 2** (A) Root area (absolute), (B) root area (proportion) and (C) root volume by depth at four sites in Kruger National Park. The sites represent a natural factorial combination of soil type (Clay or Sand) and precipitation regime (Wet or Dry). Root area is reported as the mean area for a given 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.





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**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.



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**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 the 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.