Rooting depth as a key woody functional trait in savannas

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Summary

- Dimensions of tree root systems in savannas are poorly understood, despite being essential in resource acquisition and post-disturbance recovery. We studied tree rooting patterns in Southern African savannas to ask: how tree rooting strategies affected species responses to severe drought; and how potential rooting depths varied across gradients in soil texture and rainfall.
- First, detailed excavations of eight species in Kruger National Park suggest that the ratio of deep to shallow taproot diameters provides a reasonable proxy for potential rooting depth, facilitating extensive interspecific comparison. Detailed excavations also suggest that allocation to deep roots traded off with shallow lateral root investment, and that drought-sensitive species rooted more shallowly than drought-resistant ones.
- More broadly across 57 species in Southern Africa, potential rooting depths were phylogenetically constrained, with investment to deep roots evident among *miombo* Detarioids, consistent with results suggesting they green up before onset of seasonal rains. Soil substrate explained variation, with deeper roots on sandy, nutrient-poor soils relative to clayey, nutrient-rich ones. Although potential rooting depth decreased with increasing wet season length, mean annual rainfall had no systematic effect on rooting depth.
- Overall, our results suggest that rooting depth systematically structures the ecology of savanna trees. Further work examining other anatomical and physiological root traits should be a priority for understanding savanna responses to changing climate and disturbances.

Introduction

The mechanisms of tree–grass coexistence in savannas are of longstanding interest to ecologists (Walter & Mueller-Dombois, 1971; Beckage *et al.*, 2019; Higgins *et al.*, 2000; Sankaran *et al.*, 2004). Multiple hypotheses for tree–grass codominance in savannas have been proposed, divided thematically into: those involving differentiation in water and nutrient use (i.e. bottom-up limitation) vs those involving differential responses to disturbances such as fire and herbivory (i.e. top-down limitation). Aboveground, disturbance-related traits have been well-studied to show that fire and herbivory strongly structure tree function (Hoffmann *et al.*, 2003; Staver *et al.*, 2012; Charles-Dominique *et al.*, 2015). By contrast, root traits have proven more difficult to quantify, and even the basics, for example, rooting depths of savanna trees (Oliveira *et al.*, 2005; Cramer *et al.*, 2007; Fensham & Fairfax, 2007; Nippert & Holdo, 2015), remain largely unknown. This hampers our fundamental understanding of tree–grass coexistence in savanna and therefore our ability to predict savanna responses to changing climate and disturbance.

Roots are essential for acquiring limiting nutrients and water (Pregitzer, 2002), making it therefore reasonable to hypothesize that resource limitation should act as a primary determinant of root proliferation and structure (Mokany *et al.*, 2006; Dybzinski *et al.*, 2011). Savannas are characterized by variable rainfall during the wet season, further punctuated by a pronounced dry season (Rodríguez-Iturbe & Porporato, 2007), suggesting that savanna trees might benefit from adapting to water limitation (Sankaran *et al.*, 2005; Good & Caylor, 2011; Case *et al.*, 2019). Periodic droughts also can have major effects on savanna trees, with some species especially vulnerable to severe droughts (Fensham *et al.*, 2009, 2015; Case *et al.*, 2019).

Water uptake of trees depends on the dimensions of their rooting systems, which at the most basic level usually consist of two fundamental components – rooting depth and lateral extent (Schenk & Jackson, 2002) – although note that root mass (contributed largely by coarse roots) can under- or overestimate the role of root activity in water uptake, a function performed mostly by fine roots (Kulmatiski *et al.*, 2010). Savannas are among the most deeply rooted biomes (Canadell *et al.*, 1996; Jackson *et al.*, 1996), but are characterized by substantial variation within the biome (O'Donnell *et al.*, 2015). We expect more deep-root investment in arid environments (Schenk & Jackson, 2002), where access to permanent water allows trees to avoid water stress, for example, during droughts (Padilla & Pugnaire, 2007). We also expect responses especially to soil texture (Seghieri,

1995), because water percolates more readily into deeper soil layers on sandy soils and because the adsorptive forces which make water extraction by trees more difficult increase on clay-rich soils (Fernandez-Illescas *et al.*, 2001). Thus, sandy soils promote tree growth and establishment (Staver *et al.*, 2017; Zhou *et al.*, 2017; Case & Staver, 2018), in part because stronger root niche differentiation favors deeper rooting trees (Holdo, 2013). These predictions are loosely borne out in responses of tree rooting depth to soil physical properties and resource availability (Seghieri, 1995; Schenk & Jackson, 2002; Laio *et al.*, 2006; Fan *et al.*, 2017), but patterns documented to date are relatively weak (Wigley *et al.*, 2019), with substantial variation even within the same site (Seghieri, 1995; O'Donnell *et al.*, 2015).

Meanwhile, the spatial extent of lateral roots determines the horizontal soil space over which trees acquire and compete for belowground resources (Casper & Jackson, 1997; O'Donnell *et al.*, 2015). For example, savanna trees that allocate more lateral roots in the upper soil horizons effectively capitalize on water from small rainfall events, but also face more competition from grasses (Verweij *et al.*, 2011; Holdo *et al.*, 2018). This suggests a likely tradeoff between deep vs lateral rooting (O'Donnell *et al.*, 2015), which, while logical, has never been examined in detail across savanna species.

Curiously, syntheses of rooting depth in water-limited ecosystems have generally reported no obvious relationship between maximum rooting depth and mean annual precipitation for trees and shrubs (Schenk & Jackson, 2002; Bhattachan *et al.*, 2012). One possibility is that we have simply not studied the problem with sufficient consistency to detect patterns, or that comparisons of maximum rooting depth alone may not capture functionally relevant variation in biomass allocation and root physiology (Nippert & Holdo, 2015). Alternatively, real ecological processes may confound expectations of rooting strategies. First, tree–grass competition structures tree growth more strongly than rainfall, at least in an experimental setting, where trees have not acclimated to higher rainfall (Riginos, 2009; February *et al.*, 2013), although note that tree–grass interactions may shift from competition to facilitation in more arid environments (Dohn *et al.*, 2013). Secondly, rainfall is highly variable in time and space across aridlands (Knapp *et al.*, 2008); the role of this variation in defining tree growth dynamics and, worse yet, tree rooting dynamics, is unknown. And thirdly, because chronic disturbances from fire and herbivory vary systematically with rainfall in savannas (Archibald *et al.*, 2009; Hempson *et al.*, 2015), predictions are complicated of how rooting depths should vary with rainfall and other environmental gradients. We know that woody plants growing in frequently burnt (wetter) savannas invest more heavily in belowground reserves and biomass to aid with postfire recovery (Bhattachan *et al.*, 2012; Wigley *et al.*, 2019), potentially counteracting the expectation that trees invest in more roots in arid environments; what this means for rooting strategies beyond overall belowground allocation, however, is less clear.

In this study, we evaluate rooting depth and lateral extent of common trees in Southern African savannas to ask (1) how rooting strategies influence tree response to severe drought, and (2) how rooting depths vary with respect to rainfall climatology and

soil substrate. Overall, our understanding of root traits is limited despite their essential role in the ecological functioning of savannas (Laliberté, 2017) because of methodological challenges that have not changed substantially over the past decades (Canadell *et al.*, 1996). Historically, both manual and mechanical excavations have been applied to map root structure and measure biomass distribution for tree species in arid and semiarid regions (Kummerow *et al.*, 1977; Rutherford, 1983; Brisson & Reynolds, 1994; Holdo & Timberlake, 2008; O'Donnell *et al.*, 2015). However, full root-system excavations are laborious and expensive, and moreover are insufficient to trace the deepest root of individual trees (Rutherford, 1983; Holdo & Timberlake, 2008) and are limited in the number of tree species (O'Donnell *et al.*, 2015). We tackle this constraint by using detailed excavations of a few species in Kruger National Park, South Africa, evaluating deep vs lateral coarse root distributions and how these correspond with a simple ratio of deep : shallow taproot diameters. We show that this metric potentially serves as an easier-to-measure proxy for overall potential rooting depth and facilitates interspecific comparisons among savanna trees. We also used these detailed excavations to evaluate tree rooting depth variation across drought-sensitive vs -resistant tree species and hypothesized (1) that drought-resistant species invest more in deep roots than drought-sensitive ones, as they do in other biomes (Hoffmann *et al.*, 2011; Nardini *et al.*, 2016). Next, we evaluated variation in the rooting-depth proxy across 57 tree species at 14 sites in Southern Africa on gradients of rainfall climatological parameters and soil texture, and hypothesized (2) that rooting depths decrease with mean annual rainfall and increase on sandy, nutrient-poor soils relative to clayey, nutrient-rich ones. An earlier study at the same sites reported that leaf traits, including leaf nitrogen (N) concentration, N : phosphorus (P) ratio, and average leaf area, were phylogenetically constrained (Wigley *et al.*, 2016), and so we also consider the possibility (3) that potential rooting depths across 57 tree species are phylogenetically constrained.

Materials and Methods

Detailed root excavation in Kruger National Park

Kruger National Park (lat. 22°20′–25°30′S, long. 31°10′–32°00′E, hereafter, Kruger) is the largest protected area in South Africa (Supporting Information Fig. S1a), covering nearly 20 000 km² of subtropical and tropical savannas. Mean annual rainfall increases from 350 mm in the north to 750 mm in the south with most precipitation falling during the wet season from November to April. Elevation ranges from 260 to 839 m above sea level. Kruger is dominated by two underlying parent materials, a granite and a basalt, which have strong influences on soil and vegetation properties (Venter, 1990; Staver *et al.*, 2017). Soils on granite are generally sandy and nutrient-poor whereas those on basalt are clayey and nutrient-rich (Staver *et al.*, 2017). The average fire-return interval is *c.* 3.5 yr, although spatial variation is significant, ranging from one fire every year to one every three decades (Govender *et al.*, 2006). The flora of Kruger

includes over 400 woody species and 200 herbaceous species. Nomenclature of all woody species in this study follows Coates Palgrave (2015). Large parts of northern Kruger are dominated by *Colophospermum mopane* whereas tree communities in the southern part are more diverse.

Detailed root excavations of eight dominant tree species belonging to three families were conducted in the south of Kruger on the sandy granitic soils (Fig. S1a; Table 1). To avoid the impacts from soil excavations on natural reserved areas, six tree species (i.e. *Acacia nigrescens, Combretum apiculatum, Combretum hereroense, Dichrostachys cinerea, Sclerocarya birrea* and *Terminalia sericea*) were selected on firebreaks on the perimeter of the Kruger Experimental Burn Plots (EBPs) (Fig. S1a; Biggs *et al.*, 2003). The firebreaks have already been disturbed (e.g. burned frequently) and trees are allowed to be excavated. *Acacia grandicornuta* and *Philenoptera violacea* which were not well-represented on firebreaks were excavated in areas with a fire-return interval of *c.* 3–5 yr (Fig. S1a). Case *et al.* (2019) studied annual mortality rates of individual trees and changes in total tree densities following a major drought during 2015–2016 in Kruger, which we used to broadly categorize five of our excavated species into drought-resistant and drought-sensitive species (Case *et al.*, 2019, 2020) (Table 1). Among common species for which we had sufficient post-drought data, drought-sensitive species were characterized by high mortality rates documented in individual-level monitoring and/or by major declines in stem densities in community-level monitoring during drought. Conversely, drought-resistant species had low individual-level mortality and/or low net changes in stem densities relative to control plots in a region unaffected by drought (Case *et al.*, 2020).

In order to standardize across individuals, we selected trees with a single stem, with no sign of post-fire resprouting at the base, and of sufficient height (> 3 m) to render these trees relatively resistant to fire (Table 1). *Sclerocarya birrea*, which is a protected species in South Africa and heavily impacted by elephants, was sampled shortly after being pollarded by elephant, which tend to snap the tree stem without damaging the roots. All selected trees were located on landscapes that have been categorized as moderately undulating plains and on granite sandy soils (Venter, 1990), except for *C. hereroense* trees which occurred on sandy loam soils (Table 1). Based on field observations, gravel was present underneath *A. nigrescens, T. sericea* and *S. birrea*, starting from *c.* 30 to 40 cm below the soil surface (Table 1).

Fieldwork was performed during the dry season in August, September and October of 2019. We excavated five individuals for each tree species. If necessary, we first leveled the ground before marking the ground level on the stem, which standardized the location where the stem ends and root system begins. We recorded the basal diameter, diameter at breast height (DBH), and height of the selected individuals after trees were cut down.

Previous work from savannas (O'Donnell *et al.*, 2015; Zhou *et al.*, 2019) and our own application of ground penetrating radar to map root 3D distribution in Kruger (Y. Zhou & A. C. Staver, unpublished) have shown that most of the woody root biomass is in the top 50 cm, so we established a cylindrical coordinate system with 100 cm radius and 50 cm depth centered at the edge of each individual base for root excavation (Fig. S1b). Soils within this cylinder were carefully excavated using a trowel, spade and pick. Coarse roots > 2 mm in diameter were left intact during soil excavation (Fig. S2). Thereafter, lateral roots of all sizes were cut at 20 cm intervals along the 100 cm radius for each 10 cm depth increment to a total depth of 50 cm (Fig. S1b). Lateral roots belonging to the same depth increment and radial distance from stem were combined. Taproots were cut at 10 cm increments to a depth of 50 cm, except taproots of *S. birrea* which were cut to a depth of 70–90 cm. Within each cross-cut section of the tap root (i.e. 0, 10, 20, 30, 40, 50 cm, etc.), we measured the largest root diameter and its perpendicular diameter, and averaged these to obtain the diameter of taproots at each depth increment. All roots collected were oven-dried at 85°C for 1 wk, then weighed, to obtain their dry biomass; large roots were cut before drying.

Table 1 Tree species excavated in Kruger National Park, South Africa, and associated characteristics and soil environments.

Species	Family	Drought response*	Basal diameter (cm)	DBH (cm)[†]	Height (m)	AGB (kg)[‡]	RS ratio[§]	Soil description
Acacia grandicornuta	Fabaceae	NA	15.1 ± 0.5	11.9 ± 0.7	6.4 ± 0.3	34.6 ± 2.9	0.22 ± 0.02	Sandy, no gravel
Acacia nigrescens	Fabaceae	NA	19.0 ± 1.3	12.2 ± 0.9	5.3 ± 0.5	40.2 ± 9.3	0.33 ± 0.04	Sandy, gravel at 30 cm
Dichrostachys cinerea	Fabaceae	Sensitive	13.8 ± 0.6	11.7 ± 1.6	4.1 ± 0.2	22.7 ± 4.5	0.27 ± 0.04	Sandy, no gravel
Philenoptera violacea	Fabaceae	Resistant	15.7 ± 0.7	11.7 ± 0.8	6.1 ± 0.3	32.8 ± 5.8	0.42 ± 0.03	Sandy, no gravel
Combretum apiculatum	Combretaceae	Sensitive	15.6 ± 1.0	10.7 ± 1.2	4.6 ± 0.3	24.6 ± 6.5	0.50 ± 0.12	Sandy, no gravel
Combretum hereroense	Combretaceae	NA	19.7 ± 1.2	10.2 ± 0.8	5.5 ± 0.5	23.8 ± 5.1	0.38 ± 0.04	Sandy loam, no gravel
Terminalia sericea	Combretaceae	Sensitive	14.0 ± 0.4	9.3 ± 0.3	5.1 ± 0.2	21.6 ± 2.0	0.37 ± 0.03	Sandy, gravel at 30 cm
Sclerocarya birrea	Anacardiaceae	Resistant	23.5 ± 1.5	19.3 ± 1.4	4.3 ± 0.3[¶]	NA[¶]	NA[¶]	Sandy, gravel at 30 cm

Values are mean ± SE (*n* = 5). NA indicates that data are inconclusive or not available.
*Drought-sensitive and -resistant species are based on Case *et al.* (2019, 2020).
[†]DBH, diameter at breast height (1.3 m).
[‡]AGB, aboveground biomass, calculated based on species-specific allometric models according to Colgan *et al.* (2014).
[§]RS ratio, root-to-shoot ratio, calculated by dividing total root biomass within the cylindrical pit (*c.* 100 cm in radius and 50 cm in depth) by aboveground biomass.
[¶]All selected *Sclerocarya birrea* trees in this study were recently toppled by elephants. For this reason, aboveground biomass and root-to-shoot ratio were not calculated for this species.

Potential rooting depth variation across Southern African savannas

In order to study potential rooting depth variation across Southern African savannas more broadly, we collected taproot diameters of 57 common tree species belonging to 23 families within 14 conservation areas in South Africa and Zimbabwe (Fig. S3; Table S1) (see also Wigley *et al.*, 2019). These sites are dominated by tropical and subtropical savannas, with mean annual precipitation ranging from *c.* 370 to 850 mm (Table S2). All sites experienced fire disturbances between 0 and 11 fires over a 12-yr period (Wigley *et al.*, 2019).

At each site, the woody species comprising > 80% of the standing woody biomass were identified and three replicate individuals per species were selected for sampling (0.5 m < height < 3.0 m). For each replicate, a cylindrical pit with a 30 cm radius and depth was excavated around the stem using a trowel, spade and pick. The majority of tree species had a main taproot, but when not present, then the largest vertical roots were selected. The diameters of the taproot were measured at depths of 30 and 15 cm. Soil samples at each site were taken for analysis of N, P and clay content, which has been used to broadly categorize these sites into nutrient-rich/clayey soils vs nutrient-poor/sandy soils (Table S1). A more detailed account of these methods and study sites can be found in Wigley *et al.* (2019). In addition, we extracted climatological parameters for each site from the Tropical Rainfall Measurement Mission (TRMM) 3b42-V7 daily gridded rainfall product (Huffman *et al.*, 2007). These parameters included mean annual rainfall, length of wet season, wet season rainfall, and wet season rainfall event intensity (i.e. amount of rainfall per individual day of rainfall) and frequency (i.e. return period of daily rainfall events) (Table S2); more details on calculation of each parameter can be found in Case & Staver *et al.* (2018).

Statistical analyses

All statistical analyses and figures were performed and generated using R v.3.6.1 (R Core Team, 2019). To facilitate comparisons among species, root biomass was presented in percentage allocation to each cylindrical quadrat for both lateral and taproots. For each tree, proportional lateral root biomass was calculated as: $p = B/TB \times 100$, where B is the root biomass at each depth and radial distance category, and TB is the total lateral root biomass retrieved within the cylinder. In the same way, proportional taproot biomass was calculated by dividing root biomass at each 10 cm increment by the total taproot biomass retrieved. In addition, to explore the relationships between tap and lateral roots, we computed biomass-weighted radial distance from stem and rooting depth for lateral roots, and biomass-weighted rooting depth for taproots: $W_b = \sum b \times d_i$, where W_b is the biomass-weighted radial distance from stem or rooting depth (cm), b is the proportional root biomass at a specific radial distance or depth, and d_i is the midpoint of the radial distance from stem or depth. Large values of W_b imply a greater proportion of root biomass allocated to areas either farther away from the stem or at greater soil depth.

Because taproots could potentially better characterize the maximal rooting depths of individual plants in water-limited environments (Schenk & Jackson, 2002), we used taproots to compare potential rooting depths among tree species in Kruger via three different metrics. First, we fitted our taproot biomass to the asymptotic equation $y = 1 - \beta^d$, where y is the cumulative root biomass fraction to a soil depth of d (in cm) and β is the fitted coefficient. This equation was initially proposed by Gale & Grigal (1987) and applied to the classic paper of global root distributions by Jackson *et al.* (1996). Lower β values (e.g. 0.92) correspond to more shallow-root allocation (Fig. S4), whereas higher β values (e.g. 0.96) correspond to deeper-root allocation (Fig. S4). Second, we further computed the ratio of taproot diameters at depths of 30 and 10 cm (hereafter, deep : shallow ratio) as a proposed proxy for root distribution with depth, with lower values implying potentially shallower rooting profiles, whereas larger values signify potentially deeper rooting profiles. Finally, we fitted an exponential decay distribution of diameters with depth to the individual taproot: $y = a \times e^{-b \times d}$, where y is the diameter at the depth d, and a and b are fitted parameters. Taproot diameters were exponentially fitted to a depth of 50 cm for all species except for those of *S. birrea* which were fitted to a depth of 70–90 cm; also note that, because they thinned only after first getting fatter with depth, taproot diameters of two *S. birrea* were fitted from the depth where peak diameter was observed to the depth of 90 cm (Fig. S5). After fitting the exponential decay function, we computed the potential depth when the diameter of each individual taproot reached 1 cm to facilitate interspecies comparisons, which we refer to as 'estimated rooting depth'. We used ANOVA to test the statistical significance of differences between tree species in β values, deep : shallow ratios, and estimated rooting depths. *Post hoc* comparisons of these variables were conducted using Tukey's correction and *P*-value < 0.05 was used as a threshold for significance.

The phylogenetic tree (81 species) reported by Wigley *et al.* (2016) for aboveground traits was trimmed to include only the 57 species sampled for the deep : shallow ratio using the function *drop.tip* in R/APE (Paradis *et al.*, 2004). To test for relationships among the root traits and between the root traits and environmental variables, we performed phylogenetic least squares (PGLS) regression on species means to account for phylogenetic dependence (Duncan *et al.*, 2007), using R/CAPER (Orme *et al.*, 2013). For PGLS analyses, λ (the extent to which covariance in potential rooting depth depends on phylogenetic branch length) was estimated using the Brownian Motion model of evolution (Pagel, 1999). Ordinary least squares (OLS) models, ignoring phylogenetic relatedness, and PGLS models were fitted for each comparison. We then tested for the most appropriate model using the Akaike Information Criterion (AIC).

Results

Rooting strategies of Kruger savanna trees

Excavations showed clear differences in tap and lateral rooting patterns among tree species in Kruger (Fig. 1), despite substantial

variation in the spatial distribution of root biomass within species (Fig. S6). *A. nigrescens*, *D. cinerea*, *C. apiculatum* and *T. sericea* tended to allocate more lateral coarse roots to the upper 20 cm soil layers, whereas *P. violacea* and *S. birrea* had more extensive lateral coarse roots in the deeper portions of the soil profile (Figs 1, S7). Taproot biomass was more concentrated near the soil surface for *D. cinerea*, *C. apiculatum*, *C. hereroense* and *T. sericea*, whereas it decreased more gradually with depth for the other four species (Fig. 1). Species that allocated more taproot biomass to deeper soil profiles tended to have lateral roots that extended less widely (Fig. 2a) but reached greater soil depths (Fig. 2b).

Estimated rooting depths exhibited significant interspecific differences (Table 2). Fitted β values indicated that *S. birrea* and *P. violacea* potentially had the deepest rooting profiles while *D. cinerea* and *T. sericea* had the shallowest (Fig. 3a; Table 2). The exponential decay distribution of taproot diameters with depths potentially predicted that *S. birrea* and *P. violacea* could reach > 3 m whereas *D. cinerea* and *T. sericea* could only extend to *c.* 1 m (Fig. S5; Tables 2, S3). The deep : shallow ratio presented similar patterns and was highly correlated to the fitted β value ($R^2 = 0.85$, $P < 0.0001$) (Fig. 3b), estimated rooting depth from an exponential decay function ($R^2 = 0.68$, $P < 0.0001$) (Fig. S8a), and biomass-weighted rooting depth for taproots ($R^2 = 0.88$, $P < 0.0001$) (Fig. S8b).

Compared to drought-resistant species, drought-sensitive species rooted significantly more shallowly, with lower values of β (Fig. 4a), deep : shallow ratios (Fig. 4b) and estimated rooting depths (Fig. 4c). In addition, lateral roots of drought-sensitive species extended farther but at much shallower depths than those of drought-resistant species (Fig. S9).

Rooting depth variation of Southern African savanna trees

The deep : shallow ratio was significantly correlated within the same species sampled both in Kruger and across Southern Africa despite differences in their sizes and locations ($R^2 = 0.56$, $P < 0.05$) (Fig. S10). Overall, deep : shallow ratios were phylogenetically constrained but varied substantially across the 57 woody species sampled across Southern African savannas (Fig. 5; Table S1). Despite variation, *miombo* specialists in the Detarioideae (including *Brachystegia* and *Baikiaea*) tended to invest heavily in deeper roots, whereas other taxa, most notably the Combretaceae (including *Combretum* and *Terminalia*), rooted more shallowly.

Controlling for phylogeny, deep : shallow ratios changed predictably only with soil substrate ($R^2 = 0.06$, $\lambda = 0.45$, $F = 4.34$, $P < 0.05$; Fig. 6a) and length of wet season ($R^2 = 0.19$, $\lambda = 0.29$, $F = 13.1$, $P < 0.05$; Fig. 6c), but not with mean annual rainfall ($R^2 = 0.01$, $\lambda = 0.39$, $F = 0.22$, $P = 0.64$; Fig. 6b) or other rainfall parameters (i.e. wet season rainfall, or wet season rainfall intensity or frequency; Fig. S11). Rooting depth increased on sandy, nutrient-poor soils relative to clayey, nutrient-rich ones, and decreased with increasing length of wet season. Although not significant, variance of deep : shallow ratios across species within a site was negatively correlated with mean annual rainfall ($R^2 = 0.22$, $P = 0.11$; Fig. S12).

Discussion

Our results suggest that the overall rooting patterns varied substantially across Southern African savanna trees and that the ratio of deep : shallow taproot diameter may be an easy-to-measure and repeatable proxy for rooting depth. Consistent with our hypothesis and results from other systems (Hoffmann *et al.*, 2011; Nardini *et al.*, 2016), drought-sensitive species generally rooted more shallowly than drought-resistant ones. Moreover, potential rooting depth responded strongly to soil texture, increasing on sandy, nutrient-poor soils relative to clayey, nutrient-rich ones. Although potential rooting depth decreased with increasing length of wet season, there was no predictable response of potential rooting depth to mean annual rainfall or other climatological parameters, in contrast with our *a priori* hypothesis. Finally, potential rooting depth was phylogenetically constrained across Southern African savanna trees, with the deepest rooting profiles most among *miombo* Detarioids.

Due to the nature of the belowground environment, the particular problem of studying root functional traits, especially
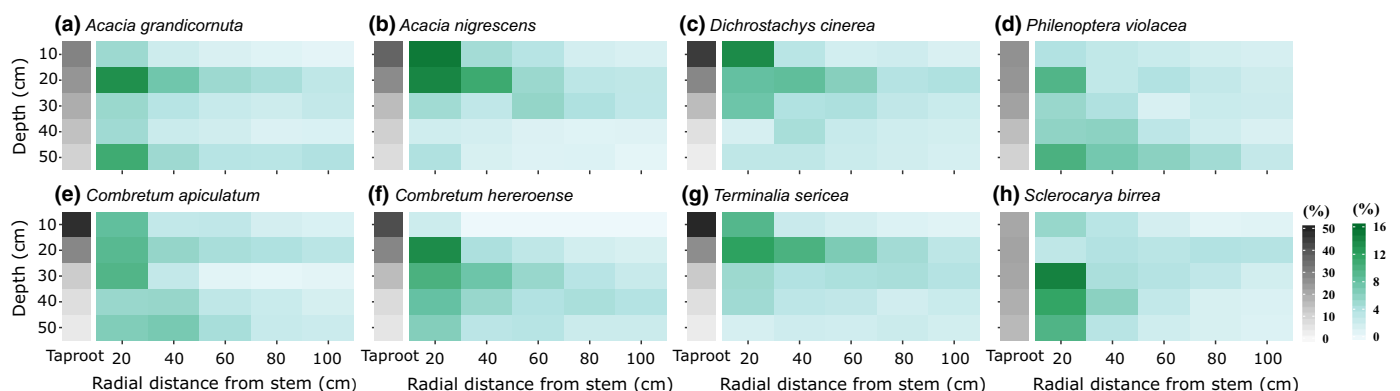

Fig. 1 Spatial distribution of taproot biomass with depth (in grey) and lateral root biomass with depth and radial distance from stem (in green) for each tree species in Kruger National Park, South Africa. Values are in percentage and averaged from five replicates. SEs for each grid can be found in the Supporting Information Fig. S6.
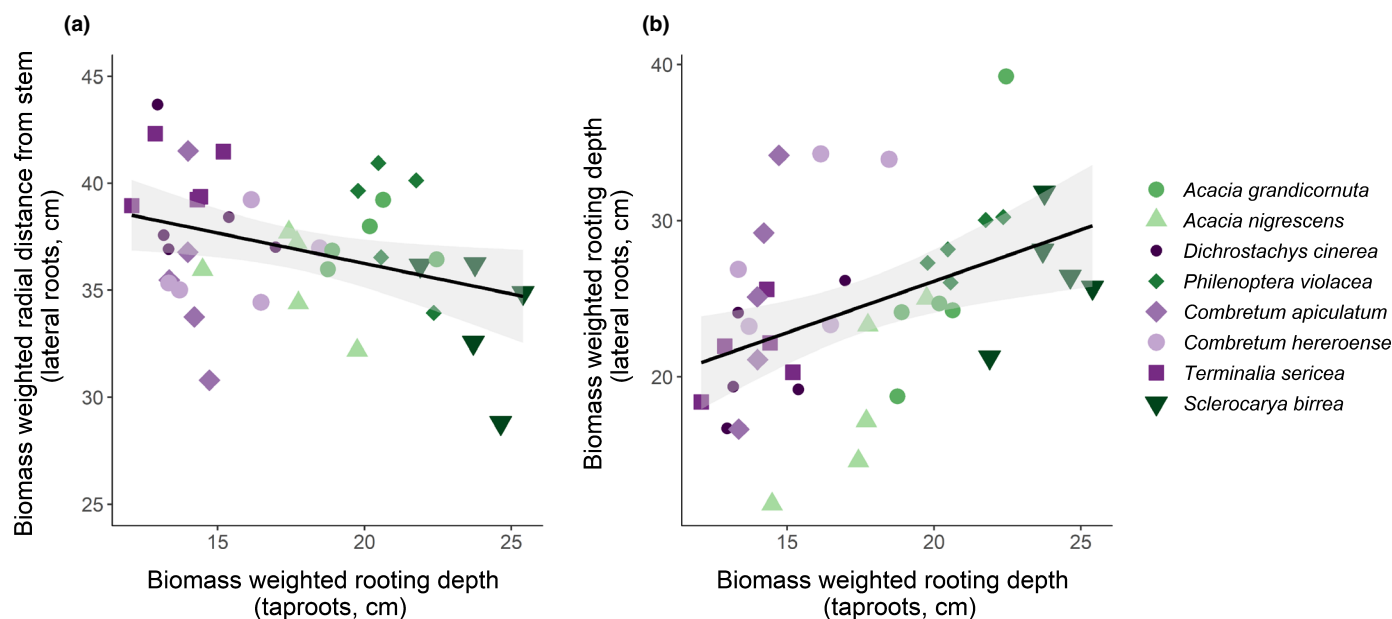
(a)

(b)

Fig. 2 Correlations between biomass-weighted radial distance from stem (lateral roots) and biomass-weighted rooting depth (taproots) ($R^2 = 0.12$, $P < 0.05$) (a) and between biomass-weighted rooting depth for lateral roots and taproots ($R^2 = 0.19$, $P < 0.01$) (b) in Kruger National Park, South Africa. The shaded areas indicate the 95% confidence interval. [Correction added after online publication 12 May 2020: Fig. 2(b) y-axis label inserted.]

Table 2 The fitted β value, deep : shallow ratio and estimated rooting depth (cm) for each tree species.

Tree species	β	Deep : shallow ratio	Estimated rooting depth (cm)
A. grandicornuta	0.957 ± 0.002 ab	0.77 ± 0.03 bc	255 ± 46 bc
A. nigrescens	0.947 ± 0.003 bc	0.65 ± 0.05 bcd	168 ± 22 bcd
D. cinerea	0.933 ± 0.004 cd	0.54 ± 0.06 d	87 ± 8 d
P. violacea	0.960 ± 0.001 ab	0.85 ± 0.03 ab	304 ± 24 b
C. apiculatum	0.932 ± 0.001 d	0.54 ± 0.04 d	110 ± 7 cd
C. hereroense	0.939 ± 0.005 cd	0.58 ± 0.05 cd	128 ± 21 cd
T. sericea	0.930 ± 0.004 d	0.53 ± 0.05 d	100 ± 11 d
S. birrea	0.967 ± 0.001 a	1.00 ± 0.03 a	458 ± 71 a

Values are mean ± SE ($n = 5$). Significant differences among tree species are indicated with different letters based on ANOVA and Tukey's honest significant difference test.

rooting depth and biomass allocation, is that only a fraction of the root system can typically be seen or sampled, using procedures that are often laborious, time-consuming and destructive. Maximum rooting depth is a desirable metric, but not practical to collect given that tree roots can reach > 50 m in water-limited environments (Phillips, 1963). Finding a 'soft' proxy that varies predictably with respect to a 'hard' trait of interest (in this case rooting depth) and that varies consistently across sites is sufficient for demonstrating its utility, especially given that, in most cases, functional traits are used only for comparative purposes (Franco *et al.*, 2005; Staver *et al.*, 2012). Here, we tested the use of the ratio of taproot diameters at deep (30 cm) : shallow (10 cm) depths as an easily measurable proxy for rooting depth, finding that the deep : shallow ratio was highly correlated with fitted β, estimated rooting depth based on exponential decay function, and biomass-weighted rooting depth (Figs 3b, S8), thus

summarizing not only maximum rooting depth, but also differences in biomass allocation with depth (Nippert & Holdo, 2015). We suggest a degree of caution, however, in examining woody species without taproots or with irregular shapes (e.g. with a lignotuber) (Wigley *et al.*, 2009; Pausas *et al.*, 2018). In addition, although our excavation of taproots to 50 cm depth suggest that the deep : shallow ratio has some validity, further work may be necessary to validate its correspondence with maximum rooting depths based on full excavation of the entire rooting zone. Overall, however, this proxy, obtainable by excavating no further than 30 cm along the taproot, should facilitate the collection of meaningful rooting depth data across a wider range of savanna sites and species to elucidate ecological patterns.

We found that the spatial distribution of tap and lateral coarse root biomass varied substantially among common tree species in southern Kruger, with marked tradeoffs between shallow- vs deep-rooting species. Moreover, shallow rooting tended to be associated with high mortality rates during a severe drought that extended from 2014 to 2016 (where *D. cinerea*, *C. apiculatum* and *T. sericea* were among the most drought-sensitive species; see Case *et al.*, 2019, 2020). Higher mortality with shallow rooting is consistent with results from other systems (Hoekstra *et al.*, 2015; Anderegg *et al.*, 2018). Previous work has suggested that drought-sensitive species in Kruger also have lower nonstructural carbohydrate reserves (Case *et al.*, 2020), which can be used to maintain respiration when stomata are closed to prevent hydraulic failure with extended periods of drought (McDowell, 2011; Dietze *et al.*, 2014). Here, we add another line of evidence by showing that drought-sensitive species in Kruger are generally shallow-rooted (Fig. 4). Anecdotally, we also observed that drought-resistant species *P. violacea* and *S. birrea* had higher water content in their roots than drought-sensitive ones, suggesting that high root xylem capacitance can aid in mitigating water
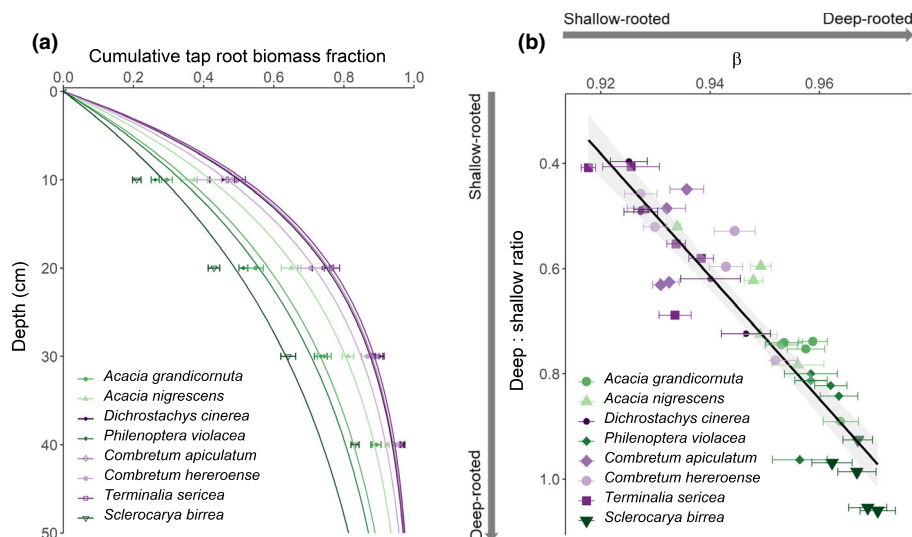
Fig. 3 Cumulative root biomass fraction as a function of depth for each tree species (a) and correlation between the deep : shallow ratio and the fitted β value ($R^2 = 0.86$, $P < 0.0001$) (b) in Kruger National Park, South Africa. Large values of β and deep : shallow ratio imply deeper rooting profiles. Error bars in panel (a) are SEs ($n = 5$), whereas in panel (b) are modelled SEs for β values. The shaded areas indicate the 95% confidence interval.
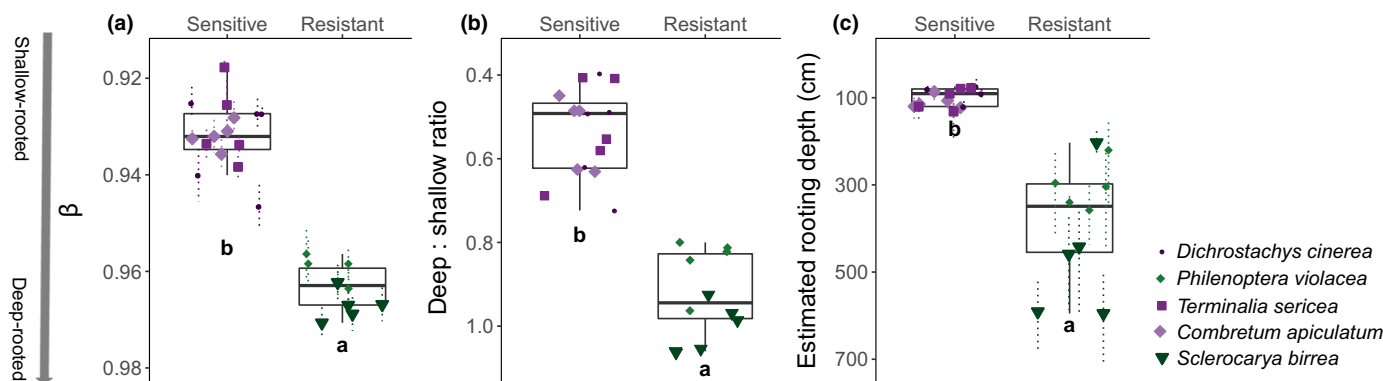

Fig. 4 Differences between drought-sensitive and -resistant species in the fitted β value (a), deep : shallow ratio (b), and estimated rooting depth based on exponential decay function (c) in Kruger National Park, South Africa. Significant differences between drought-sensitive and -resistant species were detected by unpaired two-sample Wilcoxon test, a nonparametric comparison. Dashed lines in panel (a) indicate modelled SEs for β while in panel (c) indicated modelled ranges for estimated rooting depth. The horizontal solid lines within boxes indicate median values, boxes and whiskers indicate 25–75% and 10–90% ranges, respectively.

stress during severe drought (Choat *et al.*, 2018), which may merit further quantitative study. In addition, drought-sensitive species tended to spread lateral roots nearer the soil surface but extending further away from the stem (Fig. S9), corroborating their proposed reliance on shallow soil moisture, which would be scarce during severe drought. It also may relate to the finding that drought-sensitive species were more likely to be root-suckering, which requires investment in lateral roots (Case *et al.*, 2020). However, the difference in rooting depth of taproots between drought-sensitive and -resistant species was more apparent than differences in lateral root distributions (Figs 4, S9), suggesting that deep rooting may be the more important trait for predicting drought survival.

Consistent with global synthesis and observational work (Schenk & Jackson, 2002; Bhattachan *et al.*, 2012), we found no overall trend in investment in potential rooting depth with mean annual rainfall (Fig. 6b) or other rainfall parameters (i.e. wet season rainfall, or wet season rainfall event intensity or frequency)

(Fig. S11), except that potential rooting depth increased with length of dry season (Fig. 6c). The response is easy to contextualize, as trees growing in an environment characterized by an extended dry season tend to have less opportunity to take up water from moist surface soils and stand to benefit more from foraging for water from deeper soils.

However, responses of potential rooting depth to other elements of rainfall climatology were nonexistent, which deviates from theoretical (Dybzinski *et al.*, 2011; Farrior *et al.*, 2013) and, in other systems, empirical expectations (Mokany *et al.*, 2006). One possibility remains that disturbances strongly influence belowground traits (Tomlinson *et al.*, 2012) as well as aboveground ones (Tomlinson *et al.*, 2013). Another is that grass competition, and not total water availability, most tightly constrain tree growth in savannas (Riginos, 2009; February *et al.*, 2013). Or alternatively, recent theory has argued that highly variable systems, where luck has as much to do with life history outcomes as adaptation, can yield unpredictable trait evolution (Snyder &
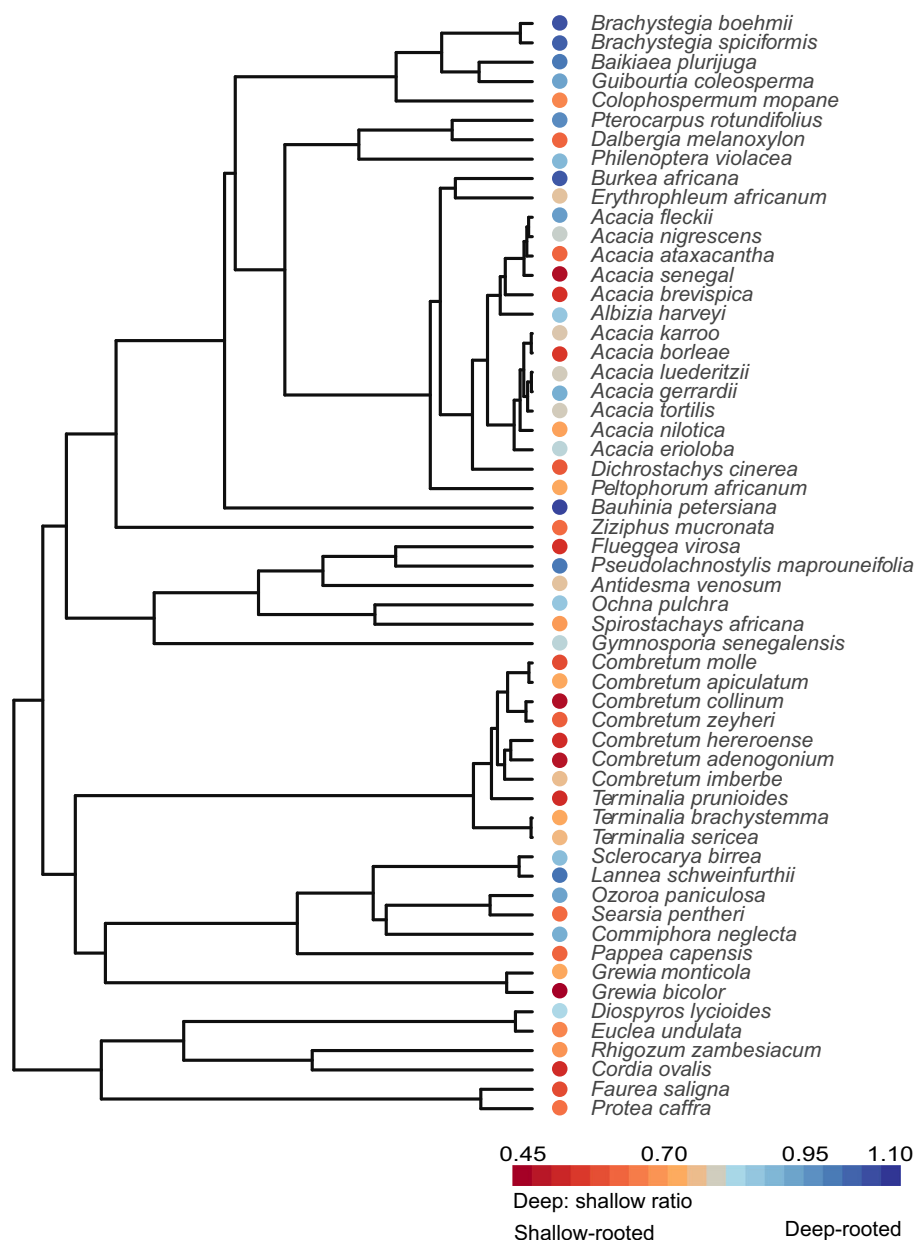
Fig. 5 Phylogenetic relationships among tree species and associated relative deep : shallow diameter across Southern African savannas.

Ellner, 2018). In savannas, this idea has been applied to trees escaping the effects of stochastic fires (Hoffmann *et al.*, 2020), but may as accurately apply to trait variation with rainfall, because variation in rainfall within a site can completely overwhelm spatial variation among sites in mean rainfall through time (Sala *et al.*, 2012).

Interestingly, although we found no trends in mean potential rooting depth with mean annual rainfall, we did find that variance in potential rooting depths within sites was negatively correlated with mean annual rainfall across these Southern African savannas (Fig. S12), suggesting greater diversity in rooting strategies in more arid sites. Broadly, tree species appeared to diverge at arid sites, where rainfall infiltration tends to be shallow. In the extreme, this suggests that trees were either (1) shallow-rooted,

mostly relying on direct rainfall inputs, or (2) deep-rooted, actively seeking groundwater that recharges elsewhere (e.g. wetter uplands) or infrequently (Guswa 2010; Schymanski *et al.*, 2009). Whether rooting strategies in arid systems are truly bimodal merits further direct evaluation.

Curiously, soil properties structured potential rooting depth more directly than mean annual rainfall itself, likely due to the importance of soil substrate to belowground hydrology. Consistent with expectations, we found that potential rooting depth increased on sandy, nutrient-poor soils compared to clayey, nutrient-rich ones. This suggests that water, rather than nutrients, predominantly determines rooting strategies: If nutrient limitation were dominating savanna tree root strategies (Cramer *et al.*, 2007), we might expect a proliferation of roots near the surface
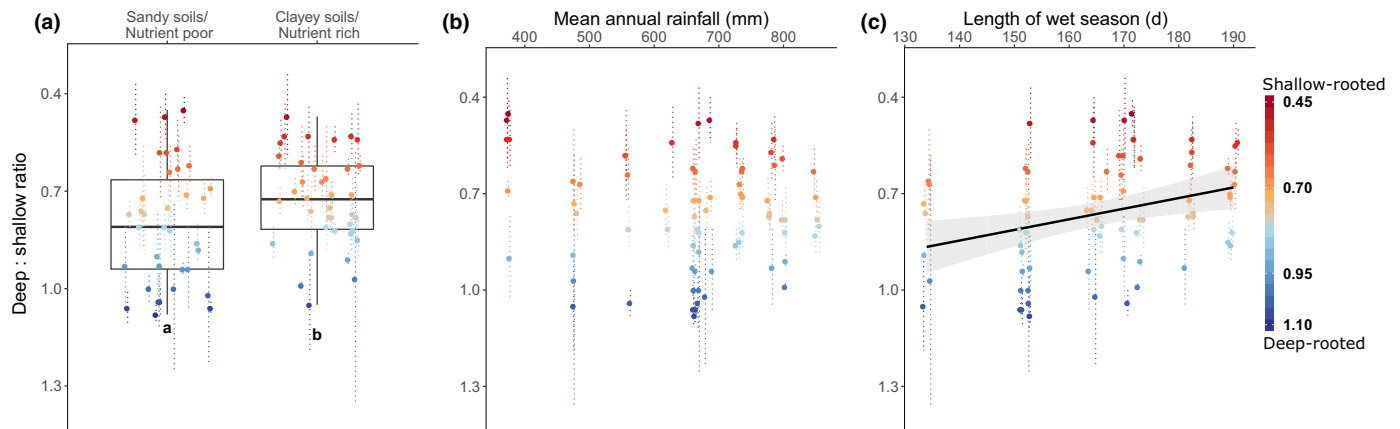
Fig. 6 Changes in deep : shallow ratio with sandy, nutrient-poor vs clayey, nutrient-rich soils (a), mean annual rainfall (mm) (b), and length of wet season (days) (c) across Southern African savanna trees. Points are jittered slightly in the X direction for legibility. Dashed lines indicate SEs ($n = 3$). In (a), the horizontal solid lines within the boxes indicate median values, boxes and whiskers indicate 25–75% and 10–90% ranges, respectively. In (b) and (c), a fitted relationship is shown only where it was statistically significant and shaded areas indicate the 95% confidence interval.

of nutrient-poor soils, because that is where nutrients are concentrated (Coetsee *et al.*, 2010; Zhou *et al.*, 2018). Instead, we observed that woody plants tended to root deeper on nutrient-poor sandy soils, consistent with the idea that water is strongly limiting in savannas (Sankaran *et al.*, 2005) and percolates more readily to deeper soil layers on sandier substrates (Rodriguez-Iturbe, 2000; Zhou *et al.*, 2017). Water-holding capacity may also play a role, because trees experience greater water stress at the surface of sandy substrates than clayey ones (Porporato *et al.*, 2002; D'Odorico *et al.*, 2019), forcing deeper rooting on sandy soils. Moreover, as discussed above, the stochasticity of rainfall could weaken relationships between mean annual rainfall and rooting strategies; soil texture effects on hydrology are comparatively time invariant, perhaps resulting in stronger selection for rooting strategies with more consistent constraints through time. Regardless, evidence is accumulating that soil hydrology must be a central component of any evaluation of savanna heterogeneity and any projections of savanna responses to global change (Holdo *et al.*, 2020).

A notable exception is that tree clades that dominate the *miombo*, an iconic wet savanna, had higher investments in deeper roots than other taxa (see also Ryan *et al.*, 2011; Mugasha *et al.*, 2013). Here again, there are a number of possibilities. One is that *miombo* Detarioids may invest heavily in roots to help them survive repeated disturbances from fire, elephants or human harvesting (Chidumayo, 1988, 2013; Ryan & Williams, 2011). If this is the case, strategic investment belowground suggests that disturbances have been an important feature of *miombo* systems on evolutionary timescales (but, also, see Finckh *et al.*, 2016; Syampungani *et al.*, 2016). Another possibility is that deep rooting among *miombo* species may facilitate other phenological adaptations. For instance, recent evidence suggests that pre-rain green-up is a key feature of some *miombo* systems, and probably necessitates accessing water during the dry season (Ryan *et al.*, 2017).

In conclusion, our findings emphasize that rooting depth is a key woody functional trait in savanna ecosystems. Although we found that drought-sensitive species were rooted relatively

shallower than drought-resistant ones, further work combining rooting depth with other anatomical (e.g. root xylem size and conductivity) and physiological (e.g. root hydraulic isolation) traits is needed to advance our mechanistic understanding of the role of roots in response to drought and other disturbances (Choat *et al.*, 2018). In addition, we found that potential rooting depth varied substantially across Southern African savanna trees, and particularly with respect to soil texture, with deeper roots on sandier soils where water percolates more rapidly. A more thorough understanding of root functional variation in savanna ecosystems will depend on a combination of greenhouse and common garden work (to disentangle rooting strategies from plastic responses, especially to disturbance; see Tomlinson *et al.*, 2012) with field experiments and much more extensive observational work across diverse savanna systems. The payoffs will be substantial, including improving our understanding of belowground carbon storage and dynamics, resource limitation, and the impacts of chronic disturbance in savannas.

Author contributions

YZ and ACS designed this study in conversation with CC and BJW; YZ conducted detailed excavations in Kruger National Park; BJW and CC provided the dataset across Southern African savannas; MFC provided data on drought sensitivity and rainfall climatology; YZ and BJW performed statistical analyses; and YZ

and ACS wrote the manuscript with extensive feedback from all authors.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Locations of sampling sites for each tree species within Kruger and the sampling regime for root excavations.

Fig. S2 Examples of root excavation for eight tree species in Kruger.

Fig. S3 Locations of sampling sites across Southern African savannas.

Fig. S4 Examples of cumulative root biomass fraction as a function of depth.

Fig. S5 Exponential decay functions fitted to diameters with depths for each individual taproot excavated in Kruger.

Fig. S6 The SEs for spatial distribution of lateral root biomass with depth and radial distance from stem and taproot biomass with depth for each tree species in Kruger.

Fig. S7 Sum of lateral root biomass with radial distance from stem and with depth increment for each tree species excavated in Kruger.

Fig. S8 Correlations between deep : shallow ratio and estimated potential rooting depth and biomass-weighted rooting depth for eight tree species excavated in Kruger.

Fig. S9 Differences between drought-sensitive and -resistant species in biomass-weighted radial distance from stem and biomass-weighted rooting depth for lateral roots.

Fig. S10 Correlation of deep : shallow ratio for eight tree species sampled both within Kruger and across Southern African savannas.

Fig. S11 Changes in deep : shallow ratio with wet season rainfall, intensity and frequency across Southern African savanna trees.

Fig. S12 Response of variance in deep : shallow ratio to mean annual rainfall across Southern African savannas.

Table S1 Site and species information and deep : shallow ratio across Southern African savannas.

Table S2 Rainfall parameters for each site across Southern African savannas.

Table S3 Parameters and model fits for exponential decay functions.

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