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RESEARCH ARTICLE

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Root-niche separation between savanna trees and grasses is greater on sandier soils

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Abstract

1. In savannas, partitioning of below-ground resources by depth could facilitate tree–grass coexistence and shape vegetation responses to changing rainfall patterns. However, most studies assessing tree versus grass root-niche partitioning have focused on one or two sites, limiting generalization about how rainfall and soil conditions influence the degree of rooting overlap across environmental gradients.
2. We used two complementary stable isotope techniques to quantify variation (a) in water uptake depths and (b) in fine-root biomass distributions among dominant trees and grasses at eight semi-arid savanna sites in Kruger National Park, South Africa. Sites were located on contrasting soil textures (clayey basaltic soils vs. sandy granitic soils) and paired along a gradient of mean annual rainfall.
3. Soil texture predicted variation in mean water uptake depths and fine-root allocation. While grasses maintained roots close to the surface and consistently used shallow water, trees on sandy soils distributed roots more evenly across soil depths and used deeper soil water, resulting in greater divergence between tree and grass rooting on sandy soils. Mean annual rainfall predicted some variation among sites in tree water uptake depth, but had a weaker influence on fine-root allocation.
4. *Synthesis*. Savanna trees overlapped more with shallow-rooted grasses on clayey soils and were more distinct in their use of deeper soil layers on sandy soils, consistent with expected differences in infiltration and percolation. These differences, which could allow trees to escape grass competition more effectively on sandy soils, may explain observed differences in tree densities and rates of woody encroachment with soil texture. Differences in the degree of root-niche separation could also drive heterogeneous responses of savanna vegetation to predicted shifts in the frequency and intensity of rainfall.

KEYWORDS

niche partitioning, plant–climate interactions, rooting depths, savanna, soil texture, stable isotopes, tree–grass coexistence

1 | INTRODUCTION

Shifts in the frequency and intensity of rainfall are widely predicted as an outcome of global climate change, even where mean annual rainfall does not change (Fischer, Beyerle, & Knutti, 2013; Westra et al., 2014), with impacts on diverse ecosystems (Knapp et al., 2008). Savannas—defined by the co-dominance of trees and grasses—could be particularly responsive to changes in rainfall patterns, because below-ground competition for water has been widely observed to mediate productivity in these systems (February, Higgins, Bond, & Swemmer, 2013; Holdo & Nippert, 2015; Kulmatiski & Beard, 2013b; Riginos, 2009). Shifts to fewer, larger rain events could change the vertical distribution of soil moisture to the potential benefit of deeper-rooted plants (Knapp et al., 2008). As a result, rooting patterns could be key to predicting competitive outcomes between plant species and functional groups. If trees have access to deeper soil water than grasses, then rainfall intensification could favour savanna trees (Berry & Kulmatiski, 2017; Holdo & Nippert, 2015; Kulmatiski & Beard, 2013b). Conversely, if trees are competing directly with grasses for resources within the same soil layers, infrequent, intense rainfall may instead competitively favour grasses, which are often the more aggressive water users (O'Keefe & Nippert, 2018; Xu, Medvigy, & Rodriguez-Iturbe, 2015). Variation in the degree of root-niche separation along environmental gradients could lead to heterogeneous responses to rainfall intensification. However, while root-niche separation has been widely hypothesized as a process underlying savanna vegetation dynamics (Walker & Noy-Meir, 1982; Walter, 1939, 1971; Ward, Wiegand, & Getzin, 2013), comparative studies of root-niche separation across more than a single site are rare, and the environmental determinants of tree and grass rooting strategies remain poorly constrained.

The idea that savanna trees use deeper water than grasses is an old one: Walter's two-layer hypothesis (Walter, 1939) and later interpretations (Walker & Noy-Meir, 1982; Walter, 1971; Ward et al., 2013) proposed that vertical resource partitioning between shallow-rooted grasses and deeper-rooted trees could promote their coexistence by minimizing direct competition for water and nutrients. Evidence for below-ground resource partitioning has been mixed, with some studies claiming that substantial overlap between tree and grass rooting strategies refutes the two-layer hypothesis (Hipondoka, Aranibar, Chirara, Lihavha, & Macko, 2003; Le Roux & Bariac, 1998; Mordelet, Menaut, & Mariotti, 1997; Verweij, Higgins, Bond, & February, 2011) and others emphasizing differences between trees and grasses, even where some overlap is present (Holdo, 2013; Holdo & Nippert, 2015; Holdo, Nippert, & Mack, 2018; Kambatuku, Cramer, & Ward, 2013; Knoop & Walker, 1985; Kulmatiski, Beard, Verweij, & February, 2010; Ward et al., 2013). Experiments have consistently shown that grasses do competitively suppress trees (February, Higgins, et al., 2013; Kraaij & Ward, 2006; Riginos, 2009; Vadigi & Ward, 2014; Ward & Esler, 2011), suggesting that their resource-use niches are not completely separate, but even some degree of niche partitioning by depth could still contribute to tree growth and establishment in a grass-dominated environment (Holdo, 2013).

Crucially, if the degree of overlap in rooting niches varies with environmental factors such as soil texture and rainfall, we could expect context-dependent responses to environmental change. Indeed, our previous work has found that savanna tree cover is higher under infrequent, intense rainfall on sandy soils and at low mean annual rainfall, but decreases with rainfall intensity on clayey soils (Case & Staver, 2018). One hypothesized mechanism for this pattern is that trees have deeper roots on sandy soils (Zhou, Wigley, Case, Coetsee, & Staver, 2020) such that they overlap less with grasses and may more effectively exploit deep percolation during larger rainfall events (Case & Staver, 2018). It makes sense theoretically that rooting depths and the extent of root-niche differentiation between trees and grasses would vary with soil texture and rainfall (Holdo, 2013)—and a few studies have found empirical support for this (Holdo et al., 2018; Knoop & Walker, 1985; Schenk & Jackson, 2002b; Zhou et al., 2020). One experimental comparison between two sites under identical climates found that trees on the sandier site were less limited by competition from grasses and used more subsoil water (Knoop & Walker, 1985), while another experiment found that *Acacia mellifera* seedlings reached greater biomass on sandy than rocky soils (Ward & Esler, 2011). However, most studies evaluating below-ground niche partitioning in savannas have been conducted at just one or two sites at a time—or, in previous work by Holdo et al. (2018), across variation in rainfall but not soils—making broad generalization challenging. A rigorous comparative approach employing the same methods across several sites at once is necessary to reach broader conclusions about how root-niche partitioning varies across environmental gradients, especially with respect to soil texture.

Studies also vary in terms of the metrics used for determining and comparing tree and grass rooting niches. The most extensive global syntheses have emphasized maximum rooting depth (Schenk & Jackson, 2002a, 2002b), although this can present a limited picture of the overall pattern of root distribution throughout the soil column. Many site-specific studies in savannas, by contrast, have considered an integrative picture of fine or coarse root biomass allocation by depth (February, Cook, & Richards, 2013; February & Higgins, 2010; Hipondoka et al., 2003; Mordelet et al., 1997; Zhou et al., 2020). Still others have pointed out that the distribution of root biomass does not necessarily match the functional rooting depth, which describes actual water uptake patterns (Holdo et al., 2018; Kulmatiski et al., 2010; Nippert & Holdo, 2015). Variation in root functional traits, such as specific root length, root tissue density and hydraulic conductivity, further determines variation in root function with depth (McCormack & Iversen, 2019; Nippert & Holdo, 2015; Valverde Barrantes, Freschet, Roumet, & Blackwood, 2017). Measurements of water uptake and biomass allocation are both relevant to understanding and contrasting tree and grass rooting strategies and can illuminate different time scales of observation. Water uptake depths, measured here using natural-abundance stable isotopes of water as tracers, provide a snapshot of where plants are actively obtaining water at the time of sampling. Fine-root biomass distributions, measured here using root cores, indicate longer-term patterns of carbon allocation and investment.

In this study, we asked whether soil texture and rainfall influence the degree of root-niche separation between trees and grasses in savannas. Our comparative approach utilized a naturally occurring rainfall gradient crossed with a soil texture contrast in Kruger National Park in South Africa, with a total of eight study sites paired by mean annual rainfall and distributed across sandy and clayey soils. We used stable isotope techniques to characterize water uptake depths and fine-root biomass distributions of the dominant tree and grass species at each site, and compared across sites to determine whether rooting patterns and the degree of root-niche overlap varied predictably with environmental context.

2 | MATERIALS AND METHODS

2.1 | Study sites

Kruger National Park (hereafter, Kruger) is a large protected area in northeastern South Africa (22°20′–25°30′S; 31°10′–32°00′E). Kruger comprises nearly 20,000 km^2 of tropical and subtropical savanna. Rainfall is concentrated mainly between November and April, with a gradient of mean annual rainfall spanning approximately 350 mm in the north to over 750 mm in the south (Figure 1). The park is dominated by two major soil types, largely orthogonal to the north-south rainfall gradient, which differ markedly in texture, hydraulic properties and nutrient content. Granite-derived soils in the west are sandy and nutrient-poor, whereas basalt-derived soils in the east are clayey and nutrient-rich (Figure 1; Buitenwerf, Kulmatiski, & Higgins, 2014; Staver, Botha, & Hedin, 2017). Fires are frequent, with an average return interval of about 3.5 years (Govender, Trollope, & van Wilgen, 2006), and the park is home to a diverse community of African savanna wildlife. Tree densities are variable but tend to be higher on the sandy granitic soils and where maximum intervals between fires have been longest, while grass biomass is higher on clayey basaltic soils and increases with mean annual rainfall (Staver et al., 2017). The flora of the park comprises >200 C$_4$ grass species and >400 tree and shrub species, with dominant woody species including several within the Fabaceae (e.g. *Senegalia* and *Vachellia* spp., *Dichrostachys cinerea* and *Colophospermum mopane*) and Combretaceae (*Terminalia* and *Combretum* spp.).

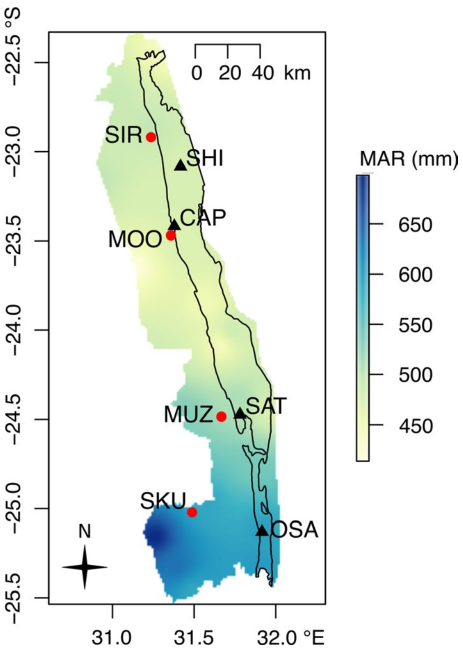

FIGURE 1 Map of study sites within Kruger National Park. Samples were collected at four sites on sandy granitic soils (red circles) and four sites on clayey basaltic soils (black triangles), paired along the rainfall gradient, which are labelled here with three-letter location codes (Table 1). The black outline denotes areas with clayey basaltic soils within the park. Yellow-to-blue shading shows mean annual rainfall, from an inverse-distance-weighted interpolation of long-term rain gauge records (Staver et al., 2019)

For this study, we examined tree and grass rooting depths at a total of eight sites: four on sandy granitic soils and four on clayey basaltic soils, paired by mean annual rainfall. Sites on granitic soils were a subset of those established for a previous study of functional rooting depths along the rainfall gradient (Holdo et al., 2018). We paired these locations with sites on basaltic soils at equivalent mean annual rainfall, as near to the granitic sites as permitted by road access and the spatial distribution of soils and rainfall. All sites were located on topographic crests and were 100–200 m from roads. Mean annual rainfall at sites ranged from ~470 mm for the driest pair to ~600 mm for the wettest pair, with site-specific rainfall values extracted from inverse-distance-weighted interpolation of long-term rain gauge records (Staver, Wigley-Coetsee, & Botha, 2019). Although there are wetter areas in Kruger, they are restricted to granitic soils, so 600 mm was the highest mean annual rainfall where a site pair across soil types could be sampled. Sampling occurred in May and early June 2018, just as wet-season rains were ending, with all sites sampled at least a week after the most recent rainfall event to allow for evaporative enrichment and the development of gradients in soil water isotopes with depth.

2.2 | Field collection

At each site, we identified individuals of the 2–3 dominant grass species and 2–4 dominant tree species within our target size (trees between 1.5 and 2.5 m in height) for collection of xylem water. We clipped fresh twig samples from three individuals of each tree species and immediately placed them inside 12-ml Exetainer vials (Labco), with each vial containing several twigs from multiple branches of a single individual. For grasses, we clipped non-photosynthetic aboveground stems (culms), and pooled samples from several grass tufts into two vials per species. To minimize the occurrence of evaporative fractionation, we immediately sealed vials with parafilm, placed them on ice and kept them frozen until water extraction could be conducted in the laboratory. To obtain end-member values for fine roots of C_4 grasses and C_3 trees to parameterize carbon-isotope mixing models, we excavated and clipped representative fine-root samples from each dominant tree and grass species at each site.

We collected soil samples and fine-root depth cores from soil pits. At each site, we dug three soil pits to a depth of at least 50 cm below the surface, unless soils were too shallow or stony to reach that depth. We collected soil samples for soil water extraction from depths of 5, 15, 30 and 50 cm (or 40 cm in shallower pits), sealed them in Exetainer vials and placed them on ice. We chose these sampling depths based on previous work in the region showing that the gradient of evaporative enrichment is steepest near the soil surface (Holdo & Nippert, 2015; Holdo et al., 2018). We collected soil cores for fine-root quantification by pounding a metal soil corer (AMS 2″ diameter × 6″ long cylindrical soil core sampler [5.08 cm diameter × 15.24 cm long], for a fixed soil volume of 308.9 cm^3 per sample) horizontally into the wall of each pit at depths of 5, 15, 25, 35 and 45 cm.

2.3 | Sample processing and laboratory analysis

After field collection, we removed and washed all fine roots from each soil core, and dried these samples in a drying oven at 65°C. In the laboratory at Yale University, root samples were further rinsed with deionized water, dried again at 65°C and ground to a fine powder with a mortar and pestle (homogenizing all root fragments found within a single core). This yielded a total of 104 mixture samples from soil cores and 49 end-member samples for stable carbon-isotope analyses. We analysed these samples for $\delta^{13}C$ values using a Costech ECS 4010 Elemental Analyzer with Conflo III interface in the Yale Analytical and Stable Isotope Center. The $\delta^{13}C$ values were expressed as deviations from an international standard (VPDB) in parts per thousand (‰) using δ-notation:

$$\delta = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \right],$$

where R is the ratio of the rare to the common isotope for the sample and standard. The long-term standard deviation measured for in-house quality-control standards was 0.2‰ for $\delta^{13}C$.

We used cryogenic vacuum distillation to extract water from all stem and wet soil samples. We conducted water extractions at Kansas State University using an open manifold system that allowed for removal of non-condensable gases and organic contaminants under vacuum (Holdo et al., 2018; Nippert & Knapp, 2007). Water extractions yielded a total of 76 xylem water samples from trees, 44 from grasses and 92 soil water samples. We analysed these samples for δD and $\delta^{18}O$ values using a Picarro L1102-*i* CRDS analyzer at the Stable Isotope Mass Spectrometry Laboratory at Kansas State University. Of the soil water samples, 14 could not be analysed reliably due to insufficient sample amount, but we still had at least duplicate coverage of each standard soil depth sampled at each site. We assessed the potential for organic contamination of plant water samples using ChemCorrect software, and discarded any flagged samples. The δD and $\delta^{18}O$ ratios were calculated as deviations from an international standard (V-SMOW) in parts per thousand (‰) using δ-notation, as above. The long-term standard deviation for these measurements using in-house quality-control standards was <0.3‰ for δD and <0.15‰ for $\delta^{18}O$.

2.4 | Statistical analyses

We conducted all statistical analyses in R version 3.3.2 (R Core Team, 2016). To compare functional rooting depths based on water isotope values across sites, we modelled the relationship between soil water isotopes and depth, accounting for site-specific differences in soil water isotope profiles, to generate predicted estimates of mean water uptake depth from xylem water isotope values. This approach diverges from traditional isotopic mixing models (Ogle, Wolpert, & Reynolds, 2004; Parnell, Inger, Bearhop, & Jackson, 2010), but is nonetheless useful here, where the four 'sources' at each site (depths from 5 to 50 cm) are not independent pools but rather fall along a monotonic continuum of isotopic variation, and where some sample values fell outside of the bounds of the sources, suggesting water uptake that was either shallower than 5 cm or deeper than 50 cm (Holdo & Nippert, 2015; Holdo et al., 2018). Values of $\delta^{18}O$ and δD were highly collinear across soil water profiles (Figure S1) such that the first principal component (PC1) accounted for 91% of the variation in the two isotope values, so we used PC1 as a univariate indicator of isotopic variation (Holdo et al., 2018). PC1 declined linearly with log-transformed soil depth (Figure S2). We modelled soil water depth as a function of PC1, site, and the interaction between PC1 and site, in a generalized linear modelling framework with a Gaussian log link (Figure S3). By including both site and an interaction term between PC1 and site as predictors, we accounted for variation in the slope and intercept of enrichment profiles among sites. We used this model to infer average water uptake depth based on $\delta^{18}O$ and δD for all tree and grass xylem water samples.

Because of substantial species turnover among sites, and a flexible sampling strategy that focused on whatever the dominant species were at each site (Table 1), there was only limited overlap in species identities across environmental gradients; we also note that species turnover could in itself be a signal of shifts in dominant rooting strategies, though this is difficult to disentangle. We statistically analysed differences in plant water uptake depths across sites in two ways: first, a community-level approach ignoring species identity and analysing water uptake depth in a linear modelling framework as a function of plant type (tree vs. grass), soil type, mean annual rainfall, and interactions between all predictor variables; and second, as a linear mixed effects model considering the same suite of predictor variables as fixed effects but adding species as a random effect. For both approaches, we selected the best set of predictor variables by comparing second-order Akaike information criterion (AIC_c) values of models containing all possible

TABLE 1 Site characteristics and dominant species sampled at each site

Site code	Soil type	Mean annual rainfall (mm)	Tree species	Grass species
SIR	Sandy	494	*Colophospermum mopane* *Combretum apiculatum* *Terminalia sericea*	*Digitaria eriantha* *Eragrostis rigidior* *Urochloa mosambicensis*
SHI	Clayey	477	*Colophospermum mopane* *Flueggea virosa* *Terminalia prunioides*	*Bothriochloa insculpta* *Enneapogon cenchroides*
MOO	Sandy	472	*Colophospermum mopane* *Combretum apiculatum* *Terminalia sericea*	*Eragrostis rigidior* *Pogonarthria squarrosa*
CAP	Clayey	472	*Colophospermum mopane* *Combretum hereroense* *Combretum imberbe*	*Aristida congesta* *Panicum coloratum* *Themeda triandra*
MUZ	Sandy	515	*Senegalia nigrescens* *Combretum apiculatum* *Terminalia sericea*	*Panicum maximum* *Pogonarthria squarrosa* *Urochloa mosambicensis*
SAT	Clayey	508	*Combretum apiculatum* *Dichrostachys cinerea* *Lannea schweinfurthii*	*Bothriochloa insculpta* *Panicum maximum* *Urochloa mosambicensis*
SKU	Sandy	597	*Combretum apiculatum* *Euclea divinorum* *Peltophorum africanum* *Terminalia sericea*	*Aristida congesta* *Eragrostis rigidior* *Sporobolus panicoides*
OSA	Clayey	600	*Dichrostachys cinerea* *Grewia bicolor* *Grewia virosa* *Ziziphus mucronata*	*Bothriochloa insculpta* *Panicum maximum* *Urochloa mosambicensis*

subset combinations of predictors. Mean annual rainfall was treated as a continuous variable and centred on the mean for all analyses, whereas plant type and soil type were treated as categorical predictors.

To determine proportional contributions of tree and grass fine roots to homogenized soil core samples, we used a simple two-end-member linear mixing model, calibrated for the dominant species present at each site. Within each site, all local grass and tree δ^{13}C values were averaged to yield one mean end-member value per functional type. We assumed that the isotopic signature of each homogenized core sample (M) was a mixture of mean tree (T) and grass (G) isotopic signatures associated with the site, and thus calculated the proportional contribution of each on the basis of the mixing equation:

$$M = pT + (1 - p)G,$$

where p is the proportion of the sample (by biomass) comprised of tree fine roots and $1 - p$ is the proportion comprised of grass fine roots. While nearly all of the mixture values fell within the bounds of the end-members, four were slightly outside the bounds of site-specific end-member means, yielding tree proportion values that were negligibly negative (between 0 and −0.032); these were set to zero (representing 100% grass content) for analysis. To estimate grass and tree fine-root biomass values, we multiplied these proportions by the total dry biomass found for each depth sample, and scaled up to units of g/m^3. We analysed determinants of fine-root depth distributions in a linear modelling framework, with sample biomass modelled as a function of depth, soil type, mean annual rainfall, and interactions between soil and depth and rainfall and depth. We constructed separate models for total biomass, tree root biomass only and grass root biomass only, and selected the preferred combination of predictor variables for each by comparing AIC$_c$ values of models.

3 | RESULTS

3.1 | Water uptake depths

At all sites, soil water isotope composition showed consistent patterns with depth. Water from deeper soil layers was isotopically lighter, with more depleted (more negative) values of both δ^{18}O and δD, while shallow soil water had higher values of δ^{18}O and δD, suggesting evaporative enrichment at the soil surface (Figure 2). These consistent, monotonic gradients allowed for the use of natural abundances of soil water isotopes as a tracer for water uptake by depth, as described in Methods. To compare tree and grass functional rooting depths across sites, we used the isotopic composition of tree and grass xylem water to infer mean depths of water uptake, based on our modelled log-linear relationship between soil water isotope composition and depth (Figures S2 and S3).

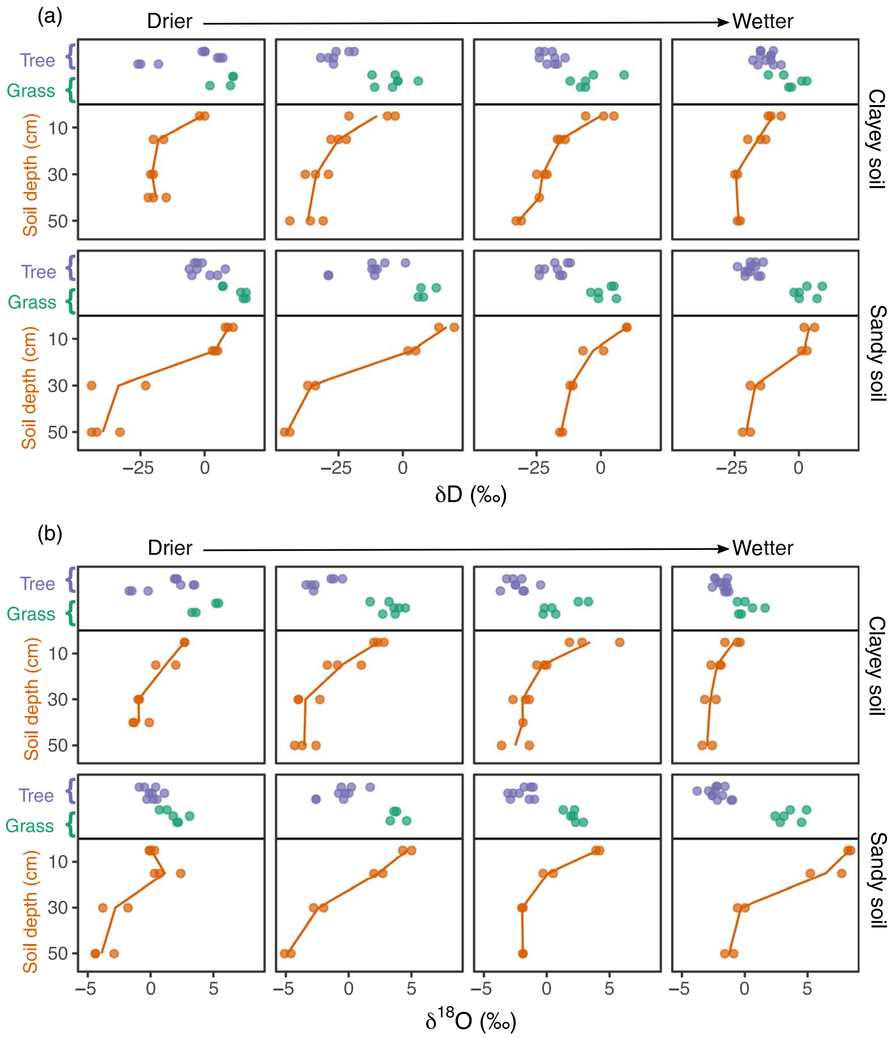

FIGURE 2 Hydrogen (a) and oxygen (b) stable isotopic composition of soil and xylem water samples. Each panel represents one site, with sites arranged by mean annual rainfall (increasing from left to right) and soil texture (clayey basaltic soils on top, sandy granitic soils below). Points correspond to tree species (purple), grass species (green) and soil layers by depth (orange), with tree and grass points horizontally aligned by species

At all eight sites, tree xylem water was isotopically lighter than grass xylem water, indicating deeper soil water uptake by trees (Figure 2). Analysed across sites, mean inferred tree functional rooting depths were always deeper than those of grasses, whether models explicitly accounted for species identity or not (Figure 3; Table 2; Table S1). For both trees and grasses, functional rooting depths were generally deeper on sandy than clayey soil (Table 2; Table S1). However, the degree of divergence between tree and grass roots varied with soil texture and mean annual rainfall. Tree water uptake was deeper and more distinct from shallow-rooted grass on sandy soils, and especially so at the wettest sites, as indicated by the three-way interaction between plant type, soil and rainfall in community-level analyses that ignored species identity (Figure 3; Table 2; Table S1). This three-way interaction term was not included in the best model when species identity was accounted for as a random effect, suggesting a potential confounding influence of species turnover on overall community-level patterns (Table S1; Figure S5). Both statistical modelling approaches favoured the inclusion of a two-way interaction between plant type and soil, indicating that trees consistently have a stronger deep-rooting response in sandy soils compared to coexisting grasses (Table 2; Table S1).

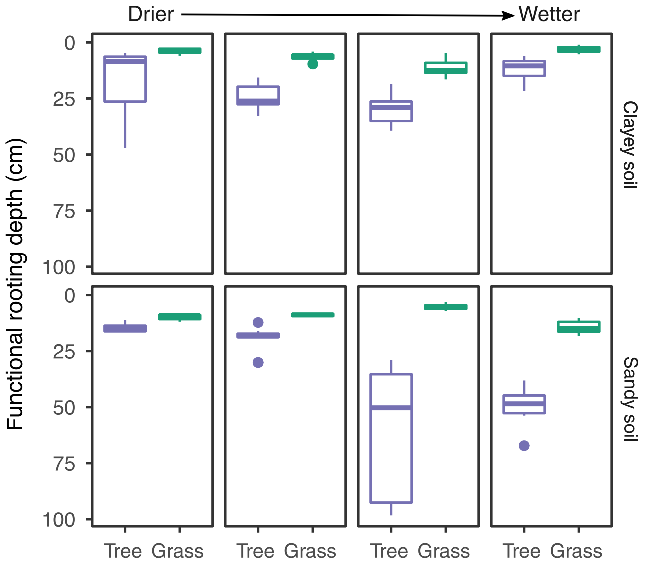

FIGURE 3 Inferred functional rooting depth values for trees and grasses across sites, from water isotope analyses. Each panel represents one site, with sites arranged by mean annual rainfall (increasing from left to right) and soil texture (clayey basaltic soils on top, sandy granitic soils below)

3.2 | Fine-root biomass allocation

Total fine-root biomass extracted from soil cores was higher per unit volume on clayey soils than sandy soils, but did not vary predictably with rainfall (Table S2). In general, total fine-root biomass declined substantially with depth, from a mean of 2,238 ± 217 g/m^3 at 5 cm depth to 885 ± 103 g/m^3 at 45 cm on clayey soils and from a mean of 1,742 ± 233 g/m^3 at 5 cm to 832 ± 115 g/m^3 at 45 cm on sandy soils.

TABLE 2 Estimated model coefficients for the top-ranked linear model describing functional rooting depths across sites (Table S1). Grass versus tree, and sandy versus clayey soil, were included as categorical predictors. Mean annual rainfall (MAR), a continuous variable, is in units of mm and was mean-centred to improve interpretability of interaction terms. Responses are in units of centimetres below the surface, where more *negative* numbers denote shallower functional rooting depths, and more *positive* numbers are deeper. For overall model, $R^2 = 0.51$, $F_{7,113} = 18.78$, $p < 0.001$

Variable	Coefficient	*SD*	*t*	*p*
Intercept	20.51	2.19	9.353	<0.001
Main effects				
Type = grass	−14.18	3.54	−4.002	<0.001
Soil = sandy	14.52	3.07	4.734	<0.001
MAR	−0.09	0.04	−2.179	0.031
Interactions				
Grass × sandy soil	−11.43	5.03	−2.273	0.025
Grass × MAR	0.06	0.07	0.953	0.342
Sandy × MAR	0.32	0.06	5.474	<0.001
Grass × sandy × MAR	−0.25	0.10	−2.481	0.015

Carbon-isotope signatures of homogenized roots collected from soil cores fell in between the isotopic values found for C_3 tree and C_4 grass end-members at each site, indicating a mixture of tree and grass fine roots throughout the soil column (Figure S4). However, the proportional contribution of tree versus grass varied widely across samples. We used these estimates of proportional contributions, multiplied by measurements of total fine-root biomass by depth, to generate estimates of tree and grass fine-root biomass in each sample (Figure 4).

Trees and grasses differed in how their fine-root distributions responded to soil texture. Regardless of soil texture or mean annual rainfall, grass fine-root biomass declined sharply with soil depth, with most grass roots concentrated close to the surface. Total grass fine-root biomass was higher on clayey soils than sandy soils, but soil texture did not meaningfully influence the slope of the biomass–depth relationship (Figure 4; Table S2). Total tree fine-root biomass was also higher on clayey than sandy soils. By contrast, however, while tree fine-root biomass showed a sharp decline from shallow to deep layers in clayey soils, similar to grass, tree fine roots were more evenly distributed throughout the soil column in sandy soils, indicating greater relative allocation of fine roots to deeper layers (Figure 4; Table S2). Neither tree nor grass fine-root distributions responded consistently to mean annual rainfall in the best statistical models, despite some apparent variation among sites (Figure 4; Table S2).

4 | DISCUSSION

We found predictable relationships between environmental context and tree and grass rooting niches across Kruger National Park. In

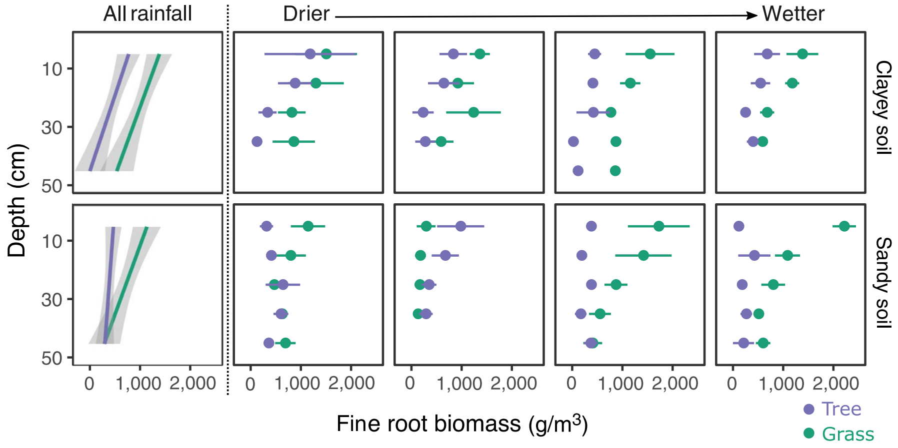

FIGURE 4 Vertical distribution of grass (green) and tree (purple) fine-root biomass across sites, as estimated from fine-root biomass measurements and $\delta^{13}C$ mixing-model analysis. Panels on the left summarize the overall relationship between depth and fine-root biomass, across all rainfall, as predicted by a separate linear model for each plant type; for grass, the best model (selected by AIC_c) is one where the biomass versus depth relationship differs in the intercept but not the slope when compared across soil textures ($R^2 = 0.2231$, $F_{2,98} = 15.36$, $p < 0.001$), while for trees the intercept and slope both vary between clayey soils (top) and sandy soils (bottom; $R^2 = 0.1268$, $F_{3,97} = 5.841$, $p = 0.001$). To the right, site-level data are shown, where each panel corresponds to a study site, arranged by soil texture (clayey soils on top, sandy soils below) and mean annual rainfall (increasing from left to right). Dots and lines depict mean and standard error of fine-root biomass at each soil depth

terms of functional rooting depth (corresponding to actual water uptake), trees consistently used deeper water than grasses, and trees and grasses both shifted their water use deeper on sandy soils. However, trees varied more with environmental context than grasses: on sandy soils and at wetter sites, trees used deeper water and differed more from grasses than on clayey soils and at drier sites. In terms of fine-root biomass allocation (i.e. where in the soil roots were located), soil texture determined not only the overall amount of fine-root biomass (with greater total biomass on clayey soils) but also patterns of allocation by depth. Grasses consistently allocated most fine roots to shallow soil layers regardless of soil texture. By contrast, tree rooting varied depending on soil type, with shallow allocation of fine roots on clayey soils but a more even distribution of fine roots across soil depths on sandy soils. Meanwhile, mean annual rainfall had little effect on total biomass or allocation of fine roots. In sum, our results suggest that, while grasses in this system largely take up shallow water, trees employ divergent strategies depending on soil texture: competing more directly with grasses for shallow soil water on clayey soils, but accessing deeper soil moisture when available on sandy soils (Knoop & Walker, 1985).

Savanna ecologists have long been interested in the extent to which trees and grasses overlap in their rooting niches. Though some studies have not found separation between tree and grass below-ground resource use, particularly in mesic savannas (Ward et al., 2013), a common finding in semi-arid savannas is that, while trees and grasses may overlap in root distributions and water uptake, trees tend to use deeper soil water on average (Holdo, 2013; Holdo & Nippert, 2015; Holdo et al., 2018; Kambatuku et al., 2013; Knoop & Walker, 1985; Kulmatiski et al., 2010; Ward et al., 2013). Theoretically, even subtle niche differences could stabilize coexistence (Adler, HilleRisLambers, & Levine, 2007; Chesson, 2000; Holdo, 2013). Here, our findings support the idea of niche differentiation between trees and grasses. Both water uptake and fine-root allocation suggest that trees exploit deeper soils than grasses do. Across clay soils, the average water uptake depth of grasses and trees was 6 and 20 cm, respectively, while across sandy soils it was 9 and 36 cm. Moreover, where most previous assessments of savanna tree and grass root-niche differentiation have focused on one or two sites, our more extensive comparative approach allowed us to assess how these patterns vary across environmental gradients. By systematically comparing across eight sites, we found that soil texture and, to a lesser extent, mean annual rainfall structured the relative rooting strategies of trees and grasses in semi-arid savannas. This suggests that some unexplained heterogeneity between previous studies, which have disagreed widely about the extent and importance of root-niche differentiation (Ward et al., 2013), could be attributable to soil texture. It also suggests that the importance of root-niche differentiation may vary substantially across sites as a mechanism stabilizing tree–grass coexistence.

Theory predicts that mean annual rainfall should also influence optimal rooting strategies (Holdo, 2013; Laio, D'Odorico, & Ridolfi, 2006), so it is notable here that soil texture mattered more than mean annual rainfall in determining differences in rooting strategy, particularly fine-root allocation. This is consistent, however, with some other observations of Kruger vegetation, specifically that tree densities across the park vary predictably with soils but not with rainfall (Staver et al., 2017), and that total fine-root biomass responds much more strongly to soil type than to rainfall (Kulmatiski, Sprouse, & Beard, 2017). Recent observational work across southern Africa has also found that tree coarse root investment with depth responds to soil texture but not mean annual rainfall (Zhou et al., 2020). In our consideration of tree and grass rooting strategies here, it could be that the rainfall gradient sampled was simply too narrow to observe meaningful differences. Mesic savannas are more limited by disturbance feedbacks than by water availability (Bond, 2008; Sankaran et al., 2005; Staver, Archibald, & Levin, 2011) such that disturbances may play a stronger role in shaping rooting strategies (Bhattachan et al., 2012; Tomlinson et al., 2012; Wigley, Staver, Zytkowiak, Jagodzinski, & Wigley-Coetsee, 2019), likely resulting in departures in root allocation by depth from those we observed across this semi-arid rainfall gradient (Ward et al., 2013). But there are other possibilities. Given high inter-annual rainfall variability in savannas, soil texture is a more consistent feature of the environment from year to year than rainfall, and thus perhaps more likely to structure lasting community-level differences in root biomass allocation. The north of Kruger receives less rainfall on average, but rainfall is nonetheless highly variable, and some years, the rainfall gradient inverts (such as during the 2014–2016 drought but also within the bounds of more typical rainfall variation; Staver et al., 2019).

In contrast to the fine-root biomass results, we did find that water-uptake patterns varied along the rainfall gradient, with the deepest water uptake by trees at the wetter sites on sandy soils. It is worth considering in some detail the fact that this contrasts with previous work by Holdo et al. (2018) in Kruger, which examined water-uptake patterns across the rainfall gradient on sandy soils only, and found instead that trees used shallower water at sites with higher mean annual rainfall. A few factors could be driving these differences. First, the previous study sampled more extensively across the rainfall gradient, including sites in the wettest parts of the park, which were not considered here because they lacked a soil-texture contrast. That study also focused on intraspecific variation in three focal species, whereas the community-level approach used here incorporates turnover in dominant species between sites; when we accounted for species identity, the interactive effect of rainfall was less important. Temporal variability also likely contributes to divergent observations of rooting strategy, both between studies of water uptake conducted in different years, and between the water uptake and fine-root biomass observations reported here. Water-uptake measurements provide a snapshot of functional rooting depth (Nippert & Holdo, 2015), which depends on root activity and root traits as well as contemporaneous soil-moisture availability, and has been found to fluctuate seasonally in trees (Kulmatiski & Beard, 2013a). Though fine-root biomass distributions can also shift temporally, they integrate root allocation over longer time scales without distinguishing which roots are most often active, such that a mismatch between these measurements is not surprising

(Kulmatiski et al., 2010; Nippert & Holdo, 2015). In the long term, allocation of roots throughout the soil profile will constrain the extent to which plants can adopt a flexible strategy of shifting to deeper water uptake depending on soil moisture conditions (Kulmatiski & Beard, 2013a). Our results suggest that trees on sandy soils, which invest more heavily in an infrastructure of deep roots (Zhou et al., 2020), are best equipped to deploy such flexibility. Trees on clayey soils, and grasses at all sites, invested predominantly in shallower fine roots, and also varied less widely across sites in water uptake depths. Further monitoring of seasonal variation in root activity across sites, paired with explicit measurements of soil moisture and transpiration, could provide more detailed insight into these dynamics (Mazzacavallo & Kulmatiski, 2015).

The major finding here, that soil texture is a key determinant of root-niche separation between trees and grasses in savannas, can help explain existing savanna vegetation patterns while also improving predictions of vegetation change. A better ability to use deeper soil moisture and mitigate competition with grass could enhance tree performance on sandy soils, likely contributing to widely observed patterns of higher tree cover (Fensham, Butler, & Foley, 2015; Sankaran, Ratnam, & Hanan, 2008; Staver et al., 2017; Williams, Duff, Bowman, & Cook, 1996) and faster rates of woody encroachment (Case & Staver, 2017; O'Connor, Puttick, & Hoffman, 2014) on sandy soils, though rocky soils can also have higher rates of encroachment (Britz & Ward, 2007). Soil texture also mediates the relationship between tree cover and rainfall intensity, where trees respond more positively to infrequent, intense rainfall regimes on sandy soils (Case & Staver, 2018); this, too, could be an outcome of variation in the degree of tree versus grass root-niche differentiation with soil texture. As climate change causes shifts in the frequency and intensity of rainfall (Fischer et al., 2013; Westra et al., 2014), differences in rooting strategies could drive heterogeneous vegetation responses, with trees increasingly favoured on sandy soils, but less able to maintain populations on clayey soils where competition with grass is more intense.

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AUTHORS' CONTRIBUTIONS

All authors (M.F.C., J.B.N., R.M.H. and A.C.S.) contributed to conceiving ideas and designing methodology; M.F.C. collected field samples; M.F.C. and J.B.N. performed laboratory analyses; M.F.C. and A.C.S. analysed data; M.F.C. led the writing of the manuscript and all authors contributed feedback on drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the South African National Parks Data Digital Repository: http://dataknp.sanparks.org/sanparks/metacat/judithk.112281.1/sanparks (Case, Nippert, Holdo, & Staver, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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