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Root vascular anatomy predicts maximum growth rates in savanna trees and grasses

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Abstract

Root-based functional traits are relatively overlooked as drivers of savanna plant community dynamics, an important gap in water-limited ecosystems. Recent work has shed light on patterns of trait coordination in roots, but less is known about the relationship between root functional traits, water acquisition, and plant demographic rates. Here, we investigated how fine-root vascular and morphological traits are related in two dominant PFTs (C_3 trees and C_4 grasses from the savanna biome), whether root traits can predict plant relative growth rate (RGR), and whether root trait multivariate relationships differ in trees and grasses. We used root data from 21 tree and 18 grass species grown under greenhouse conditions, and quantified a suite of vascular and morphological root traits. We used a principal components analysis (PCA) to identify common axes of trait variation, compared trait correlation matrices between the two PFTs, and investigated the relationship between PCA axes and individual traits and RGR. We found that there was no clear single axis integrating vascular and morphological traits, but found that vascular anatomy predicted RGR in both trees and grasses. Trait correlation matrices differed in trees and grasses, suggesting potentially divergent patterns of trait coordination between the two functional types. Our results suggested that, despite differences in trait relationships between trees and grasses, root conductivity may constrain maximum growth rate in both PFTs, highlighting the critical role that water relations play in savanna vegetation dynamics and suggesting that root water transport capacity is an important predictor of plant performance in the savanna biome.

KEYWORDS
ecohydrology, relative growth rates, root economics spectrum, root functional traits, savanna dynamics, tree–grass interactions

1 | INTRODUCTION

Roots play a fundamental role in water acquisition and transport, yet root functional traits remain relatively understudied compared to those of shoot components (Bardgett et al., 2014, Laliberté, 2017). This issue is particularly pressing in ecosystems such as tropical savannas, where plant growth is water-limited (Holdo & Nippert, 2023; Sankaran et al., 2005). In the savanna biome, two very dissimilar plant functional types (PFTs), namely C_3 trees and C_4 grasses, compete for water during the growing season (Xu et al., 2015). Despite this overriding importance of water, the root functional traits responsible for water uptake, transport, and plant performance have generally not been characterized in detail in savanna plant species, with the exception of tree-grass differences in rooting depth (Case et al., 2020; Kulmatiski & Beard, 2013).

Functional trait studies provide a link between form and function. In particular, functional traits play a key role in understanding variation in plant demography. Relationships between functional traits and demographic rates across species allow us to resolve the underlying mechanistic basis of processes such as survival and growth (Yang et al., 2018). Second, functional traits provide a tool for predicting complex dynamic outcomes (e.g., whole-plant growth) from simple plant attributes. Generally speaking, commonly measured plant functional traits often fail to effectively predict demographic rates (Paine et al., 2015; Rosas et al., 2021; Yang et al., 2018), and this may be for several reasons. First, species-level trait values ignore individual variation, and some functional traits may not scale well from the tissue or organ to the whole-plant level (Yang et al., 2018). Second, traits that are critical in some contexts may be less so in others. For example, Paine et al. (2015) found that trait data provided poor explanatory power for tree growth rates, but the study focused on aboveground traits. In ecosystems where belowground resources are important for limiting growth, belowground (i.e., root) traits may be of far greater importance.

Beyond the ability of individual traits for predicting (and explaining) demographic rates, it is important to understand the extent of trait coordination within individuals and species. Correlations among traits help identify evolutionary and developmental constraints in plant form, and allow us to map species onto a few axes of variation, simplifying the task of understanding plant strategies for coping with environmental variation. For aboveground traits, the leaf economics spectrum (Wright et al., 2004) identifies a single axis describing slow to fast return on leaf nutrient and mass investments. This axis allows ready inferences to be made about resource acquisition and life history strategies of individual species on the basis of a few readily measured functional traits. For belowground traits, similar efforts to identify a "root economics spectrum" (RES) have generally concluded that root functional traits fail to map clearly only a single axis of variation that reflects fast versus slow strategies analogous to the leaf economics spectrum (de la Riva et al., 2018; Kong et al., 2019;Kramer-Walter et al., 2016; Weemstra et al., 2016). These studies, however, have tended to focus on root morphological traits such as specific root density and root size (Kramer-Walter et al., 2016; Weemstra et al., 2016) rather than on root vascular anatomy, which plays a key role in distinguishing the contrasting plant water relations of trees and grasses in savannas (Wargowsky et al., 2021).

In previous work, we showed that trees and grasses differ in their xylem vessel architecture and specifically, that grasses have greater theoretical axial conductivity than trees (Wargowsky et al., 2021). These findings improve our understanding of the root vascular anatomy of savanna plants, but it is still unclear to what extent variation in root anatomical and morphological traits explains plant demography. In this study, we used datasets consisting of root morphological and root vascular anatomy functional traits obtained under greenhouse conditions to explore the relationship between root functional traits and plant demographic rates for co-occurring savanna tree and grass species, and to investigate the degree of trait coordination within and between these two PFTs. We asked three main questions: (1) To what extent do morphological and vascular traits map onto a common axis of variation? (2) Do root traits predict potential growth rates in savanna trees and grasses? (3) Do trees and grasses show similar patterns of trait coordination?

2 | MATERIALS AND METHODS

2.1 | Trait measurements

We used data from seedlings of 21 tree and 18 grass species (*n* = up to 5 individuals per species) native to the southern African savanna biome, grown at the UGA Botany Greenhouse between January and October 2018. Our aim was to select representative co-occurring tree and grass savanna species (specifically, from the southern African lowveld savanna). We were guided in part by species abundance data from Kruger National Park from Venter (1990), and sought to collect common species from that ecosystem. We supplemented this list with common species from nearby Wits Rural Facility. A detailed description of greenhouse protocols and methods are provided in Wargowsky et al. (2021). Briefly, we grew five tree and grass seedlings per species in the Botany Greenhouse at the University of Georgia between January and October 2018. Weather station failure precluded analysis of growing conditions the year of the study, but the following year, conditions during the same period were as follows: mean daily minimum and maximum temperatures were 22.1 and 33.7°C, respectively, mean daily solar radiation from 8 a.m. to 8 p.m. was 540 W/m^2 (~ 2470 µmol m^{-2} s^{-1}), and relative humidity ranged between 32 and 98% (with a mean of 74%). At harvest (timed so that trees and grasses were of similar height, equal to the ~40-cm depth of the pot), we removed plants from containers and collected and washed 3–4 fine-root (<2 mm) segments, which we stored refrigerated in formaldehyde alcohol acetic acid (FAA:10% formaldehyde (37%), 50% ethanol (95%), 5% glacial acetic acid, and 35% DI water) until processing. We rinsed, dried, and froze the remaining root systems until further processing of root morphology could occur. During processing, we dehydrated fine roots in ethanol (70%), embedded them in paraffin, stained them using Safranin O and Fast Green, and then thinly cross-sectioned and mounted them on microscope slides (Wargowsky et al., 2021). We used ImageJ to identify and measure individual xylem vessels for each root cross section. We used this dataset to extract six anatomical variables, four of which were used in the current study to minimize redundancy: maximum xylem vessel diameter (D_{max}, in mm), vessel number per unit root cross-sectional area (N, in mm^{-2}), lumen fraction (F, in mm^2/mm^2), and theoretical axial conductivity (K_r, in kg m^{-1} MPa^{-1} s^{-1}), which represents flow per root cross-sectional area. We used the Hagen-Poiseuille equation to calculate K_r based on the number and diameter of individual vessels and root cross-sectional area (Tyree & Ewers, 1991; Wargowsky et al., 2021).

To measure morphological traits, we thawed and gently separated the frozen root samples. We divided roots into three components: a subset of intact fine root branches to be scanned, all remaining fine roots (<2 mm), and coarse roots. We scanned the root branch subsets with a flatbed scanner (Plustek OpticPro A230L, Santa Fe Springs, CA, USA). After scanning, we dried all components of the root system at 65°C for 48 h and weighed components separately using an analytical balance to 0.0001 g (AL104, Mettler-Toledo, Columbus, OH, USA). We used Smartroot for ImageJ (Lobet et al., 2011; Schneider et al., 2012) to trace all individual roots from scanned samples and collect data on three fine-root morphological traits: branching intensity (BI, in mm^{-1}), given by the number of nodes divided by the total root length; specific root length (SRL, in m/g), mean root diameter (RD, in mm), and root length per total root mass (RLM, in m/g).

2.2 | Relative growth rate measurements

We used two different metrics to calculate RGR for trees and grasses. For trees, we based RGR on stem basal diameter growth between transplantation and harvest. We used this size-based metric because it would have been difficult to obtain initial tree mass values without risking damage to transplants. We used the equation $\text{RGR}_{\text{diam}} = (\ln[D_h] - \ln[D_i])/(t_h - t_i)$, where D_i and D_h represent stem diameters (in mm) at initial and harvest times t_h and t_i, respectively. Since grass had negligible mass at the time of transplantation (in an unpublished dataset, we determined grass seedling dry transplant mass to have a mean value of 0.009 g, whereas our mean harvest dry mass here was 17.8 g, a 2000-fold difference), we ignored the contribution of initial mass to RGR and used a mass-based metric: $\text{RGR}_{\text{mass}} = \ln(M_h)/(t_h - t_i)$, where M_h represents mass at harvest (in g).

2.3 | Data analysis

We conducted all of our analyses in R version 4.1.2 (R Core Team, 2022). In a first analysis, we found that RLM was perfectly correlated with SRL in grasses (none of the grasses had coarse roots), and very highly correlated with SRL in trees, despite variation in coarse: fine-root biomass ratios in trees. We therefore omitted RLM from the analysis. We used the *prcomp* function to conduct a principal components analysis (PCA) to identify the dominant axes of variation for root functional traits, separately in trees (Table S1) and grasses (Table S2). We tested for statistically significant relationships between the original trait variables and the first two principal components using a bootstrapping method, resampling the plant trait dataset with replacement (Table 1). To examine the relationship between root functional traits and plant performance, we conducted phylogenetically weighted regressions (PGLS) between the dominant PCA axes and RGR. We conducted the PGLS with the *gls* function in the *nlme* package (Pinheiro & Bates, 2000). The PGLS allowed us to correct for nonindependence among observations caused by phylogenetic relatedness (Felsenstein, 1985). We obtained a phylogenetic tree of our species from the V.Phylomaker R package (Jin & Qian, 2019; Qian et al., 2019). We incorporated phylogeny into the *gls* analysis using the *ape* R package (Paradis & Schliep, 2018). We ran the regression between RGR and the trait PCA axes separately for trees (using RGR_{diam} as the dependent variable) and grasses (using RGR_{mass}), treating individual plants as units of observation and species as a random effect. We log-transformed trait values where necessary to meet the assumption of normality. We also conducted bivariate regressions between a subset of four functional trait variables (K_r, RD, SRL, and BI, i.e., one vascular trait and three morphological traits) and RGR to systematically identify individual traits that best explained RGR in each plant functional type. We focused on K_r as an integrative vascular trait that captures the joint effects of vessel size and number of root conductance. Finally, to test for differences in trait relationships within PFTs, we tested for differences between the tree and grass correlation matrices using confirmatory factor analysis using the R *lavaan* package (Rosseel, 2012).

TABLE 1 Principal components analysis loadings for the first two PC axes (PC1 and PC2) for seven root functional traits in two categories.

		Trees		Grasses	
Variable	Category	PC1	PC2	PC1	PC2
D_{max}	Vascular	**−.55**	.04	**.42**	−.17
N	Vascular	**.26**	.08	**.26**	−.20
F	Vascular	**−.54**	.05	**.52**	−.20
Kr	Vascular	**−.55**	.08	**.55**	−.19
RD	Morphological	−.01	**.62**	−.26	−.59
SRL	Morphological	.05	**−.51**	.08	.61
BI	Morphological	−.17	**−.58**	.33	.37

Note: Values in bold are significantly correlated with a given axis (alpha = .05).

3 | RESULTS

Our PCA of root-based functional traits showed that within both trees and grasses, PC1 was dominated by vascular anatomy variables, while PC2 was dominated by root morphological variables (Table 1). PC1 accounted for 42.4% and 41.4% of the overall variance in trees and grasses, respectively (Figure 1). PC2 explained 27.2% of the variance in trait variables for trees and only 19.3% in grasses (Figure 1), that is, not much more than might be expected from any individual raw variable. All of the vascular trait variables exhibited significant relationships with PC1 in both trees and grasses, and generally in the same direction (i.e., loadings with the same sign), with the exception of vessel number (N), which had the same positive relationship with

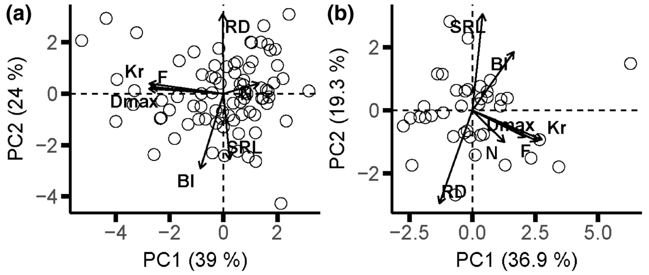

FIGURE 1 Principal components analysis for southern African savanna (a) tree seedlings and (b) grasses along the first two principal components, based on seven root functional traits. The proportion of the overall variance explained by each axis is shown in parentheses. Points represent individual plants.

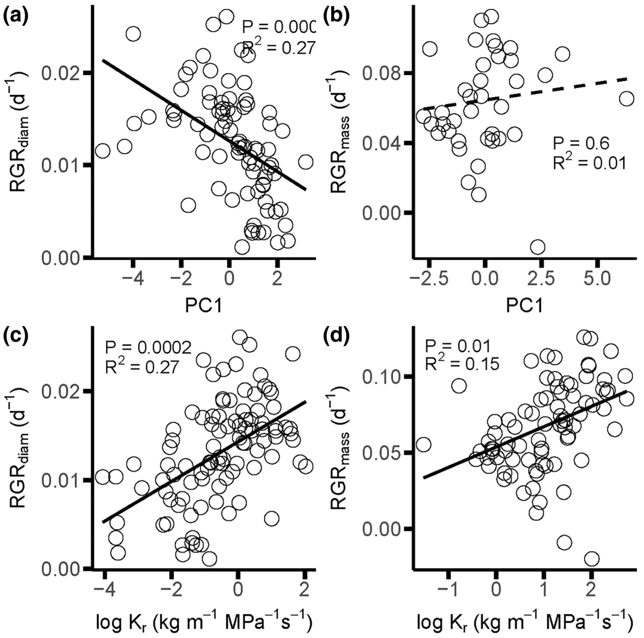

FIGURE 2 Relative growth rate (RGR) as a function of the first principal components axis PC1 for (a and b) root functional traits and (c and d) root theoretical axial conductivity per root cross-sectional area in (a and c) savanna tree seedlings and (b and d) grasses. Points represent individual plants. RGR_{diam}, RGR based on tree diameter increments; RGR_{mass}, RGR based on mass at harvest.

PC1 in grasses as the other vascular traits, but went against these other traits in trees (Table 1), suggesting a tradeoff between vessel size and number in trees but not in grasses (Figure 1). None of the morphological traits were significantly related to PC1 in either functional type. PC2 represented a "root morphology" axis in trees, with all variables exhibiting significant relationships. Whereas RD had a positive relationship with PC2, the relationship was negative for SRL and BI (Figure 1). This axis therefore contrasted species and individuals with denser, thicker, relatively unbranched (simple) roots from those with less dense but fine and more complex roots. For grasses, we found no statistically significant loadings on PC2, minimizing the importance of this axis (and therefore of variation in root morphology) within this functional type.

We found a significant relationship between RGR and PC1 in trees (*gls* fit by REML for RGR_{diam}: $F = 10.4$, $p = .002$, Figure 2a), but not in grasses (RGR_{mass}: $F = 0.26$, $p = .6$, Figure 2b). We did not examine the relationship between PC2 and RGR in grasses, given the low amount of variance explained by PC2 in this group. In trees, we found no relationship between RGR_{diam} and PC2 ($F = 0.26$, $p = .6$). For individual root traits, RGR was positively related to K_r in both trees (RGR_{diam}: $F = 14.5$, $p = .0002$, Figure 2c) and grasses (RGR_{mass}: $F = 6.2$, $p = .015$, Figure 2d), but there was no relationship between the respective RGR metrics and any of the three root morphological traits we tested (SRL, RD, and BI) in either functional type.

The confirmatory factor analysis showed that the differences between the tree and grass root trait covariance matrices were highly significant ($\chi^2 = 63.1$, $df = 28$, $p << .0001$), reinforcing the contrasting relationships in trees and grasses between the trait variables and PC1 and PC2 identified above, and suggesting that root traits in these two functional types are not necessarily coordinated in the same manner.

4 | DISCUSSSION

Our results did not support the existence of a single dominant axis that can integrate both anatomical and morphological root traits in savanna tree and grass species. This lack of clear trait coordination (as captured by the occurrence of main axes of variation: vascular vs. morphological) may suggest that root water transport and acquisition functions are decoupled to some extent. We propose that morphological traits are mainly related to the distribution of root length throughout the soil volume explored by a given plant, and should therefore primarily be associated with soil exploration and water acquisition capacity. By contrast, vessel anatomy should play a more important role in water transport ability from soil to shoot. Our results support the idea of a multidimensional (or nonexistent) RES, based on the idea that root traits exhibit a lower level of coordination than leaf traits, and are ultimately influenced by factors beyond resource acquisition (bergmann et al., 2020; Kramer-Walter et al., 2016; Weemstra et al., 2016). Further reinforcing this idea, we found that trait coordination patterns differ between the two functional types in our study, with grasses demonstrating weaker trait integration than trees. Previous work has shown clear root trait differences between trees and grasses (Ma et al., 2018; Wargowsky et al., 2021), so the fact that trait relationships also differ between the two functional types may not be surprising. Still, this result is consistent with the idea that tree and grass roots do not simply fall on opposite ends of a one-dimensional spectrum.

Our analysis of functional traits and growth showed that growth is correlated with root water transport capacity in both plant functional types. Although we did not find a significant relationship between RGR and PC1 in grasses, we did find a relationship between K_r and RGR. Our results also implied a stronger link between root functional traits and RGR in trees than in grasses, with vascular traits proving more important than fine-root morphology. Root morphological traits did not exhibit significant relationships with RGR in either trees or grasses. One interpretation of this result is that transport capacity may be more important than soil exploration and water acquisition capacity in dictating overall plant performance. It is important to note, however, that our measurements were conducted under well-watered conditions, when plants may be more limited by transport capacity than moisture availability in the rhizosphere. Under conditions of soil moisture limitation, we would expect that some of the morphological root functional traits would increasingly gain significance in terms of limiting growth. Regardless of which specific root traits are most predictive of growth, it is clear that variation in root characteristics can be linked to plant performance in both of these competing functional types, a novel result. It has been challenging to link plant functional traits to demographic rates in plants for a number of reasons (Paine et al., 2015; Rosas et al., 2021; Yang et al., 2018). Yang et al. (2018) focused on issues of scaling and context: functional traits are often quantified at the species level and measured at the tissue or organ scale, and fail to predict whole-plant demographic rates in individuals. Here, we were able to match functional trait values and growth rates in individual plants (while correcting for species effects) to show clear relationships between the two. Our functional traits are largely measured at the tissue and organ level, but our focus on vascular architecture represents a departure from most other analyses of savanna species, which have tended to focus on aboveground traits such as SLA and bark thickness, traits that are mostly relevant for light acquisition and resistance to disturbance (Higgins et al., 2012; Tomlinson et al., 2014). Since savannas are largely defined by soil moisture limitation (at least seasonally), we argue that a focus on water acquisition and transport traits should receive more attention in efforts to understand the mechanistic basis of variation in growth and survival.

Given that our study focused on plant performance under conditions of high resource availability, an important next step would be to explore how trait-performance relationships change under conditions of resource limitation, particularly in the field. Under field conditions, plants experience fluctuations in water availability as well as changing conditions of atmospheric demand and light availability, all of which exert an impact on water uptake (Sperry et al., 2016). Field conditions are also highly variable across seasons, making field predictions from a given set of greenhouse conditions challenging. Effectively connecting root traits to plant demography will thus require additional studies to quantify variation in plant performance as a function of variation in soil moisture and other key environmental variables.

Our analysis showed that root transport traits (as captured by vessel architecture) were largely decoupled from acquisition traits (represented by root morphological characteristics) in savanna tree and grass species. Our results therefore do not support the idea of a one-dimensional root economic spectrum that can be linked to plant demography in savannas, suggesting that multiple root functional trait axes need to be identified. However, we did find that root vascular traits, and thus root water transport capacity, show clear associations with potential growth rates of both trees and grass, emphasizing the key role played by water limitation in savanna tree-grass dynamics.

AUTHOR CONTRIBUTIONS

IKW and RMH conceived the study and conducted the analysis. IKW wrote the first draft of the paper. IKW, JEN, and NG conducted the greenhouse work and collected plant trait data. All authors contributed to the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.fbg79cp1q (Wargowsky et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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