

Belowground structure and determinants of woody plant height at a tropical dry forest site in Zambia, southern Africa

Research Article

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Abstract

Root metrics and plant height for 256 excavated saplings and small trees of 27 species, including sown plants, were used to describe belowground structure and assess factors that influence shoot growth in a tropical dry forest (TDF) in Zambia. Models were developed to (i) estimate taproot depth from incomplete excavations and (ii) coarse lateral root biomass from proximal diameter data. The majority of the species studied are slow-growing and had a median height of <200 cm at the age of 16 years. Root development advanced sequentially from taproot elongation to thickening to coarse lateral root development. Shrubs in shallow soil had short taproots with a lower wood density. Plant age explained <10% of the variance in shoot height. Root variables explained the majority of the variance in shoot height. More research is needed to improve our knowledge about how belowground structures influence shoot growth and tree recruitment in TDFs of southern Africa.

Introduction

Tropical dry forest (TDF) is defined as forest in a tropical region that experiences alternating rainy and dry seasons (Sankaran & Ratnam 2013). In east and southern Africa, TDFs include extensive areas of *Brachystegia-Julbernardia* (miombo) woodlands, undifferentiated woodlands and wooded grasslands that make up the Zambebian regional centre of endemism (White 1983). Seedlings and saplings in TDFs allocate more resources to root than shoot growth, which results in high root/shoot (R/S) ratios. At the seedling stage, the primary functions of roots are water and nutrient uptake; the anchorage function plays a minor role because of the diminutive size of the shoot. The anchorage role of roots becomes increasingly important in the sapling and tree phases as the aboveground components attain greater stature and the R/S ratios reach their lowest values. However, very little is known about the age and size at which the shift from high R/S to low R/S ratio occurs in TDFs of east and southern Africa.

The development and structure of woody plant roots are regulated by both abiotic (such as soil texture and depth) and biotic (e.g., phylogeny and ontogeny) factors. In spite of the ecological and physiological importance of woody plant roots in ecosystem functioning, little is known about the development and growth of root systems and how root traits relate to plant height in TDFs in east and southern Africa. Knowledge about root growth and traits is important in understanding the evolution and adaptation of these forests and their constituent species. Since saplings initially invest more resources in root development, it is hypothesized that variation in sapling height should be explained more by root variables (such as (i) taproot size, (ii) taproot depth and (iii) lateral root size) than by age and shoot variables (such as diameter and height). This hypothesis was tested using field measurements of plant height, taproot and lateral root sizes of 256 excavated saplings and small trees belonging to 27 species at a TDF site in central Zambia. The data were also used to assess the relationships between root traits/variables and plant height and how belowground structures influence the recruitment of trees from the sapling pool. The results have implications for the management of TDFs in east and southern Africa.

Materials and methods

Study site

The study was conducted in a 5.0-ha plot (15.47° S, 28.18° E, altitude 1260 m asl, [Figure 1](#)) at a previously disturbed TDF site (Chidumayo 2013a) in the Makeni area, about 15 km south of Lusaka city, Zambia, southern Africa. The climate at Mt Makulu (15.55° S, 28.27° E, 1240 m asl), 13 km south of the study site, is subtropical with alternating dry (mid-March to mid-November) and wet (mid-November to mid-March) seasons and a mean annual precipitation of 796 mm. Mean monthly daily minimum and maximum temperatures are 15.7° and 24.8° C,

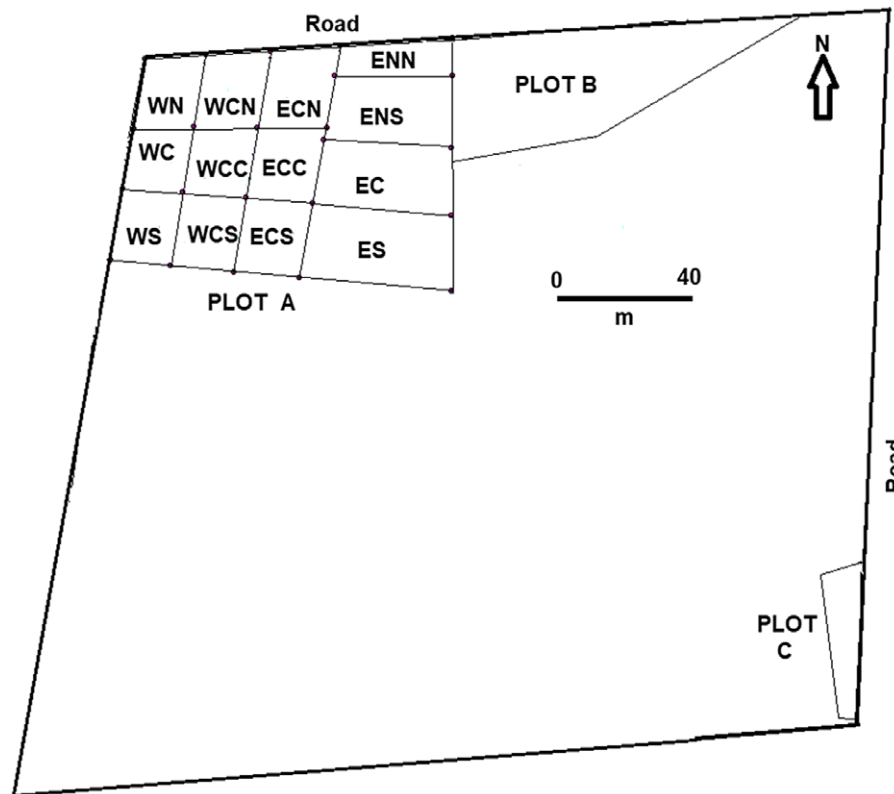


Figure 1. Layout of study plots and blocks at the study site

respectively. The lowest and highest temperatures are experienced during May–August and September–November, respectively. The soil at the study site is predominantly sand clay loam derived from limestone rocks and average texture composition in the top soil (0–30 cm depth) is 47% sand, 34% clay and 19% silt with a pH of 5.4 (Chidumayo 2013a). Soil nitrogen (N) and organic matter (OM) content is 0.10% and 3.7%, respectively, while the concentration of available phosphorus (Av. P) is 2.7 mg kg⁻¹ soil (Chidumayo, unpubl. data).

The study site consists of three plots (A, B and C, Figure 1). Plot A is made up of 13 blocks of about 0.062 ha each, and each block is surrounded by firebreaks (≈3.0 m wide) that are annually cleared of herbaceous vegetation during April or May to prevent the spread of fire between blocks. The blocks in Plot A were periodically burnt in July or August as part of the study design whose main objective was to monitor forest development under different fire frequencies following degradation by charcoal production. Over the period 1996 to 2021, the average fire return period in plot A blocks was 6 y; plot B was burnt annually while plot C was fire protected. The soil at plots A and B is deep with a concretionary layer at an average depth (mean ± 1 SE) of 100 ± 8.0 cm compared to the shallow soil at plot C that has a concretionary layer at an average depth of 65 ± 7.0 cm. The weathering of the concretionary zone at plots A and B is very advanced compared to that at plot C (see Figure 2). The site was fenced off in 1994 to keep out livestock and to minimize undesirable human disturbances in the re-growth forest.

Definitions

Sapling is here defined as a woody plant that is >1.0-y-old, <2.0 m tall and with a diameter at breast height (1.3 m aboveground, dbh) of

<3.0 cm that originated from seed and tree as a plant that is >1.0-y-old, >2.0 m tall and with a dbh of >3.0 cm. A shrub is a woody plant that is multi-stemmed close to the ground or single-stemmed with branches at or below 130 cm aboveground, and often with no dominant branch. A description of the terms used in this study in relation to the structure of woody plants at the study site is given in Table 1 and follows Freschet *et al.* (2021a, 2021b).

Plant data

Data were obtained from 256 sample plants: 141 raised from seed and 115 naturally recruited at the study site (Table 2). Seeds of raised plants were sown in shallow holes (2–3 cm deep) and covered with soil, in rows at plot C and in firebreaks (protected from fire through annual clearing of herbaceous material, see above) at Plot A from 1996 to 2012. Seeds were sown in November of each year. Two to four seeds were sown per planting station and a station covered 50 x 50 cm and consisted of separate sowing holes, 5 cm apart. The stations were 1 to 1.5 m apart along rows ranging from 20 to 60 m long. All the stations where seeds were sown were mapped for easy re-sighting and identification of sown plants in subsequent years.

In March and April 2012, 2019, 2020 and 2021, data were obtained from the 256 sample plants belonging to seven shrub and 20 tree species. For each plant, the following data were obtained: (i) plant height, taproot length, taproot top and distal diameters and lateral root proximal and distal diameters, (ii) biomass of shoot wood, leaves, taproot and lateral roots and (iii) number of lateral roots.

First, each plant was cut at ground level and the height measured in cm using a tape. The wood was then separated from leaves



Figure 2. Trenches used in excavating taproots at the study site. Note the deep soil profile in (a) found at plots A and B in contrast with the shallow soil in (b) found at plot C. Also note taproot deformation in (b) along the stone line.

and the fresh mass of the two components weighed with spring balances to the nearest gramme and recorded. Second, the soil in the root collar region was removed with a hole and spade to expose the root crown and lateral roots near the soil surface. The diameter at the root top and the proximal diameter of the largest lateral root near the soil surface were measured with a caliper and recorded.

A rectangular trench was then dug to expose the total taproot length and all lateral roots along the taproot length (Figure 2). For each trench, the depth at which the stone and/or concretionary layers were encountered were recorded. The taproot was then examined for any deformities and physical surface root deformation, and if present recorded. After this, the taproot was cut into 20 cm segments from top to the distal end and the top diameter of each segment measured and recorded and the number of lateral roots per segment counted and recorded. The proximal diameter of each coarse lateral root was measured and recorded. The soil on each taproot segment was then cleaned-off before weighing and recording the fresh weight of the segment. Fine roots attached to taproot segments were weighed together with the taproot. To avoid too much disturbance to the plots, only 1–3 coarse lateral roots, of variable proximal diameters, within the top 0–30 cm of soil surface were excavated up to their distal end and cleaned before measuring fresh weight and distal diameter.

Subsamples of each plant biomass component (shoot wood, leaves, taproot and lateral roots) for each species were obtained and measured immediately at the time of excavation and cutting and saved for moisture content analysis. These subsamples were oven-dried for 48 h at 105 °C and re-weighed in order to calculate oven-dry/fresh weight ratios which were used to convert measured biomass in the field to dry weight biomass.

Data analysis

One-way analysis of variance (ANOVA) was used to compare differences in the size of lateral roots between shrub and tree species at a significance level (P) of 0.05. Simple linear regression analysis was used to determine the significance of the relationships between belowground plant variables based on the coefficient of determination (R^2). The significance of interspecific differences in plant height between cohorts of the same age was determined

using the non-parametric Kruskal–Wallis one-way analysis of variance test (H) at $P = 0.05$ using ranks. This was adopted because sample sizes were small and the assumptions of parametric tests could not be met.

In order to determine factors that might explain variations in plant height, best subset regression analysis was used to evaluate the strength of five predictor variables (root top diameter, vertical taproot length, proximal diameter of the largest lateral root, taproot dry mass and lateral root dry mass (RDM)). Correlation and regression analyses were carried out in two phases. First, the best subset regression analysis was undertaken to select predictor (independent) variables that explained the largest variation in plant height. When two independent variables are highly correlated, the analytical procedure used automatically drops one of the independent variables to avoid problems of collinearity. Best subset regression analysis simultaneously compares models with single variables and all their possible combinations. The model with the lowest Akaike's Information Criterion for small samples (AICc) was selected as the best model (Burnham & Anderson 2002). Second, the predictor variable(s) in the selected best model was/were used to develop predictive models using ordinary linear regression analysis after excluding variables that had a high variance inflation factor of more than 5 in order to minimize the risk of overfitting.

All statistical analyses were done in Statistix 9.0 (Analytical Software 1985–2008). Nomenclature of woody plants follows White (1962).

Results

Taproot structure

Out of 253 uprooted plants, taproot excavation was complete for 229 and incomplete for 21 plants, the remaining three (all *D. cinerea*) had no taproots. Among plants with incomplete excavations, one was a shrub and the other 20 were tree species. The taproot distal diameter for plants with complete excavations was 3.3 ± 0.4 mm (range, 0.5–34.0 mm) compared to 8.7 ± 1.0 mm (range, 6.0–19.0 mm) for incomplete excavations and the difference was significant ($F_{1,126} = 24.32$, $P < 0.0001$). Five percent of the taproots with complete excavations ended

Table 1. Description of terms used in relation to woody plants at the study site (based on Freschet *et al.* 2021a, 2021b)

Term	Description
Proximal diameter (mm)	Diameter at the origin of a lateral root on the taproot
Distal diameter (mm)	Diameter at the end or terminus of a root
Root top diameter (mm)	Diameter at the root collar region
Plant height (cm)	Length of the shoot from the soil surface to the tip of the canopy
Vertical taproot length (cm)	Distance from the root collar to the bottom end of the taproot, excluding the horizontal distal portion of the root
Total taproot length (cm)	Distance from the root collar to the bottom end of the taproot, including the horizontal distal portion of the root
Coarse root	Lateral root with a diameter ≥ 2.0 mm
Fine root	Lateral root with a diameter < 2.0 mm
Root collar	Woody portion of the plant from which the shoot(s) and root(s) originate, sometimes also referred to as root crown
Plant dry mass (g)	Total dry mass of leaves, stems and roots
Shoot dry mass (g)	Dry mass of stems and leaves
Taproot dry mass (g)	Dry mass of taproot
Root dry mass (g)	Dry mass of taproot and lateral roots
Root mass fraction	Root dry mass/total plant dry mass
Root to shoot ratio	Root dry mass/leaf and stem dry mass
Taproot dry mass fraction	Taproot dry mass/total root dry mass
Lateral root dry mass (g)	Dry mass of lateral roots
Specific root length (m g^{-1})	Specific taproot length/taproot dry mass

abruptly at a distal diameter of > 6.0 mm but the majority (74%) ended at < 4.0 mm. The mean vertical taproot length among plants with complete excavations was 57.9 ± 7.2 cm for shrubs and 107.4 ± 4.7 cm for tree species. Shrubs growing on shallow soil at plot C had shorter taproots at 40.9 ± 8.3 cm than that of 86.9 ± 10.8 cm on deep soil at plots A and B. Similarly, tree species growing on shallow soil had a vertical taproot length of 84.0 ± 8.9 cm that was shorter than that of 115.9 ± 5.4 cm. In 2.4% of the plants with complete excavations, the taproot had a distal horizontal portion with an average length of 49.8 ± 15.9 cm; the mean vertical taproot length in these plants was 107.8 ± 42.4 cm compared to that of 157.6 ± 35.8 cm for total taproot length.

For plants with complete excavations, the overall taproot specific root length (SRL) averaged 0.07 ± 0.008 m g^{-1} with shrub species having a significantly higher value of 0.13 ± 0.024 m g^{-1} than that of 0.05 ± 0.008 m g^{-1} for tree species ($F_{1,213} = 18.40$, $P < 0.0001$). Among tree species, there was no significant difference in taproot SRL between deep and shallow soil types ($F_{1,162} = 1.70$, $P = 0.19$). In contrast, shrubs had a significantly higher taproot SRL in shallow soil (0.18 ± 0.03 m g^{-1}) than in deep soil (0.04 ± 0.008 m g^{-1}): $F_{1,49} = 9.14$, $P = 0.004$.

Lateral root structure

There was a clear difference in the distribution of lateral roots along the vertical taproot length between shrub and tree species (Figure 3). Shrubs had more lateral roots in the top 60 cm than trees but in deep soil lateral roots in trees occurred at deeper layers than in shrubs. Trees also had more lateral roots at a given vertical taproot length in deep soil than in shallow soil (Figure 3). Sample size of shrubs in shallow soil was too small to be shown in Figure 3. Among the most abundant shrub species, *L. camara* had more

lateral roots (13.8 ± 1.4) in the top 20 cm of soil than *D. cinerea* (10.7 ± 2.0) but the latter had a steady decrease in the density of lateral roots up to a depth of 100 cm. This was in contrast with *L. camara* that had a sharp decrease in lateral roots from 13.8 ± 1.4 in the top 20 cm to 1.0 ± 1.0 at a depth of 60 cm. Among the most abundant tree species, there was a gradual decrease in the density of lateral roots from the top (5.7 ± 0.4) to 0.2 ± 0.1 at a depth of 200 cm.

Lateral roots averaged 10.6 ± 0.76 per taproot in deep soil and 7.6 ± 0.77 in shallow soil among tree species. Among shrubs the average number of lateral roots was also different between deep (14.0 ± 2.0) and shallow (8.9 ± 0.9) soil. Coarse lateral roots made up 67% of the lateral roots in deep soil and 28% in shallow soil. There was no significant difference in coarse lateral roots per vertical taproot length between deep and shallow soil (5.6 ± 0.65) among tree species ($F_{1,113} = 0.10$, $P = 0.76$). However, among shrub species, the number of coarse lateral roots per vertical taproot length of 18.7 ± 3.25 in deep soil was significantly higher than that of 5.9 ± 2.4 in shallow soil ($F_{1,47} = 10.06$, $P = 0.003$).

Estimating root structure from incomplete sampling

For incomplete taproot excavations, the following model was used to estimate vertical taproot length (VTL_{est}) using the excavated portion of the taproot (VTL_{exc} , cm).

$$\text{VTL}_{\text{est}} = \text{VTL}_{\text{exc}} + ((\text{TRDD}/\text{RTD}) * \text{VTL}_{\text{exc}})$$

where VTL_{est} is estimated vertical taproot length (excluding the horizontal portion) in cm, TRDD is distal diameter of the taproot in mm at the end of the incomplete excavation and TRD is taproot top diameter in mm. A simple way of evaluating the performance of a model is by measuring the deviation of the predicted VTL_{est}

Table 2. Excavated and uprooted woody plants at the study site. Figures in brackets indicate plants raised from seed

Growth form	Species	Plot A		Plot B	Plot C
		Firebreaks	Blocks		
Shrub	<i>Senna singueana</i>	0	0	0	2
	<i>Dichrostachys cinerea</i>	9 (4)	0	0	3
	<i>Flueggea virosa</i>	0	2	0	7
	<i>Grewia sp.</i>	0	0	0	1
	<i>Lantana camara</i>	1	3	1	19
	<i>Phyllanthus engleri</i>	2	0	0	5
	<i>Phyllanthus muelleranus</i>	2	0	0	0
Tree	<i>Adansonia digitata</i>	0	0	0	3 (3)
	<i>Bauhinia petersiana</i>	21 (21)	1 (1)	0	4 (4)
	<i>Bridelia micrantha</i>	0	0	0	1
	<i>Combretum molle</i>	1	5	0	0
	<i>Combretum zehyeri</i>	1 (1)	1 (1)	1	0
	<i>Diplorhynchus condlycaporn</i>	5 (5)	0	0	0
	<i>Erythrina abyssinica</i>	1 (10)	9 (4)	0	0
	<i>Lanea stuhlmannii</i>	3	1	0	8
	<i>Piliostigma thonningii</i>	18 (13)	3 (1)	2	17 (17)
	<i>Securidaca longipedunculata</i>	2 (2)	0	1	0
	<i>Senegalia goetzei</i>	1	0	1	7 (7)
	<i>Senegalia polyacantha</i>	12 (6)	13 (13)	1	0
	<i>Steganotaenia araliacea</i>	3	4	0	8 (3)
	<i>Strychnos spinosa</i>	1 (1)	0	0	0
	<i>Tamarindus indica</i>	7 (7)	0	0	4 (4)
	<i>Terminalia brachystemma</i>	2 (2)	0	0	0
	<i>Vachellia amythetophylla</i>	2	2	0	0
	<i>Vachellia sieberiana</i>	8 (8)	2 (1)	0	10 (10)
	<i>Ziziphus abyssinica</i>	0	1 (10)	0	0
	<i>Ziziphus mucronata</i>	0	0	0	1 (1)
All plants		102 (71)	47 (22)	7 (0)	100 (49)

from measured observed VTL_{exc} for each sample taproot. This error (sometimes referred to as bias) is defined as (Chave *et al.* 2005):

$$\text{Bias}(\%) = ((VTL_{est} - VTL_{exc}) / VTL_{exc}) * 100$$

In order to evaluate the performance of the model, it was applied to data for complete excavations in which the taproot distal diameter was the proximal diameter of the last taproot segment (see above) and the estimate was compared to the observed vertical taproot length. The model tended to overestimate total taproot length by an average of $11 \pm 0.9\%$ and this bias decreased with increasing excavated depth from 30% at 10 cm depth to 20% at 25 cm, 12% at 80 cm and 8% at 200 cm depth.

For tree species with incomplete excavations, the model estimated a vertical taproot length of 196.7 ± 20.9 cm which was nearly 52.0 cm below the depth of the incomplete excavation of 144.7 ± 17.6 cm. Given that the model estimates have an average

bias of 11%, the vertical taproot length of plants with incomplete excavations was in the range of 175 cm to 220 cm depth.

Two models were evaluated for their accuracy in estimating lateral root biomass: (i) a logarithmic linear model ($\ln(y) = \ln(a) + b \ln(x)$) and (ii) a Freundlich power model ($y = ax^b$) where y is lateral RDM in g and x is proximal diameter (PD) of the largest lateral in mm, as follows:

$$\ln(y) = \ln(-2.4257) + 2.1053 * \ln(\text{PD}) \text{ and}$$

$$y = 0.041 * \text{PD}^{2.3753}$$

The two models were tested for accuracy using the observed data (as explained above) before selecting the best model. Derived logarithmic data were back-transformed without application of a correction factor, because Chidumayo (2013b) found little difference in the estimates after applying a first-order correction factor (Chave *et al.* 2005). Across 239 sample laterals with biomass data,

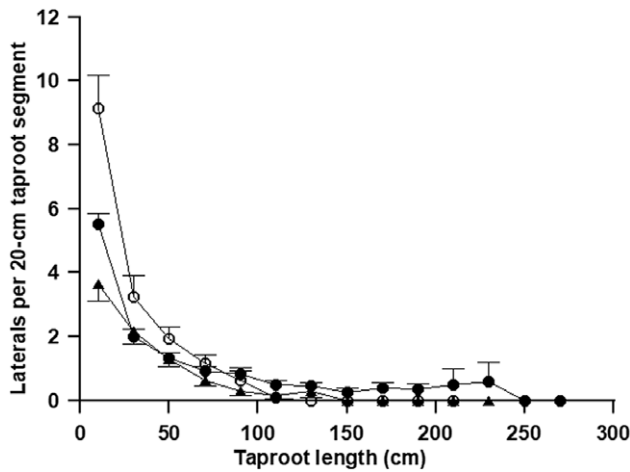


Figure 3. Average lateral roots per 20-cm segment along the vertical taproot length in shrub (empty circles) and tree (filled circles) species in deep soil type and in tree species in shallow soil type (filled triangles). Vertical lines show standard error of mean given in one direction only for clarity.

the mean bias of the logarithmic linear model was $28.9 \pm 7.9\%$ while the power model had a mean bias of $23.3 \pm 7.5\%$ and the latter model with a lower bias was selected for estimating biomass of coarse laterals of each excavated plant.

Belowground biomass relationships and plant height

The relationship between RDM and shoot dry mass (SDM) for plants with complete excavations was linear: $RDM = 106.2 + 0.28SDM$, $R^2 = 0.80$, $P < 0.0001$, indicating the influence of plant size on RDM. This relationship held for both shrub and tree species. The average R/S ratio for all plants was 1.52 ± 0.22 but this was higher among tree (1.81 ± 0.25) than among shrub (0.52 ± 0.46) species: $F_{1,234} = 5.98$, $P = 0.02$. Similarly, there was a significant difference in the root mass fraction (RMF) between shrub (0.31 ± 0.03) and tree (0.50 ± 0.02) species: $F_{1,235} = 34.96$, $P < 0.0001$. The relationship between root/shoot (R/S) ratio and RMF was curvilinear and was best described by an Asymptotic Regression: $RMF = 0.76 - 0.74 \cdot 0.342^{R/S}$, $AICc = -1884$, $RMSE = 0.0003$; the R/S ratio reached an asymptote at 8.0 when RMF was 0.84. There was no significant difference in R/S ratio between tree species growing in deep and shallow soil: $F_{1,181} = 3.31$, $P = 0.07$ but the difference was significant among shrub species with those on deep soil having an R/S ratio of 0.74 ± 0.10 compared to that of 0.40 ± 0.08 on shallow soil: $F_{1,51} = 7.07$, $P = 0.01$. Among shrub species the RMF of 0.37 ± 0.03 in deep soil was significantly higher than that of 0.27 ± 0.02 in shallow soil: $F_{1,51} = 8.49$, $P = 0.005$. Among tree species, RMF was also higher in deep (0.53 ± 0.02) than in shallow (0.40 ± 0.03) soil: $F_{1,182} = 12.79$, $P = 0.0004$.

The relationship between belowground and aboveground biomass (R/S ratio) was weakly related to plant height, root top diameter, vertical taproot length, proximal diameter of largest lateral root and plant age, either together or singularly. These predictor variables together only explained 33% of the variation in R/S ratio although the explanatory power was higher in shrubs (58%) than in trees (32%). In contrast, plant height, vertical taproot length and proximal diameter of largest lateral root explained 54% of the variance in RMF when all plants were considered. However, among shrubs this explanatory power was 68% compared to 54% among trees.

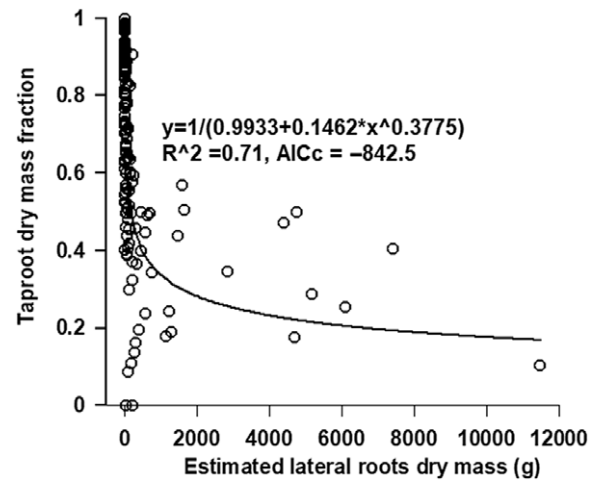


Figure 4. Curvilinear relationship between taproot dry mass fraction of root mass and estimated lateral root dry mass at the study site.

There was no significant relationship between vertical taproot length and tap RDM, similarly there was no significant relationship between vertical taproot length and lateral RDM. However, taproot dry mass explained 56% ($F = 300$, $P < 0.0001$) of the variance in lateral RDM and this relationship was more pronounced among shrub species ($R^2 = 86\%$, $F = 319$, $P < 0.0001$) than among tree species ($R^2 = 48\%$, $F = 167$, $P < 0.0001$).

The relationship between taproot dry mass fraction and estimated lateral RDM was curvilinear and was best described by the Farazdaghi-Harris function (Figure 4). This curvilinear relationship suggests that woody plants at the study site initially invested more biomass in taproots until the taproot dry mass fraction approached 0.5, after which more biomass was allocated to coarse lateral roots, such that the latter made up more than 60% of the total RDM in large shrubs and trees.

There was a significant, albeit weak, correlation between age and plant height for all sown plants (Figure 5a). The studied species are slow-growing and had a median plant height lying at or below 200 cm, with the exception of *B. petersiana* and *S. polyacantha* at the age of 13 years (Figure 5b). Some cohorts grew faster than others. For example, in *P. thonningii*, the 2008 cohort at 11 years old was growing faster than that of the 2004 cohort at 16 years old ($H = 46$, $P < 0.0001$) and the average plant height for the cohorts was 143 ± 35.5 cm and 45 ± 3.1 cm, respectively. The mean plant height of excavated plants was 168.4 ± 10.8 cm (range, 5.0–990.0 cm) and there was no significant difference between shrub (145.9 ± 15.3 cm) and tree (175.4 ± 13.3 cm) species: $F_{1,227} = 1.36$, $P = 0.25$. Among the sown plants, plant height was 194.1 ± 15.7 cm (range, 15.0–990.0 cm) for trees aged 2–26 years. The sample of excavated sown shrubs was small ($n = 3$) but among natural recruits, average plant height was 137.7 ± 14.7 cm (range, 5.0–410.0 cm) for shrubs and 141.5 ± 23.0 cm (range, 6.5–960.0 cm) for trees.

Among shrub species, 82% of the variation in plant height was explained by root top diameter but among tree species it was the additive effects of vertical taproot length, root top diameter and proximal diameter of the largest lateral root that explained 75% of the variation in plant height (Table 3). However, the explanatory power of root top diameter varied among shrub species from 75% in *L. camara* to 92% in *F. virosa* and 95% in *P. engleri* (Table 3). In *D. cinerea*, it was the additive effects of proximal diameter and total RDM that explained 85% of the variance in plant height. There was

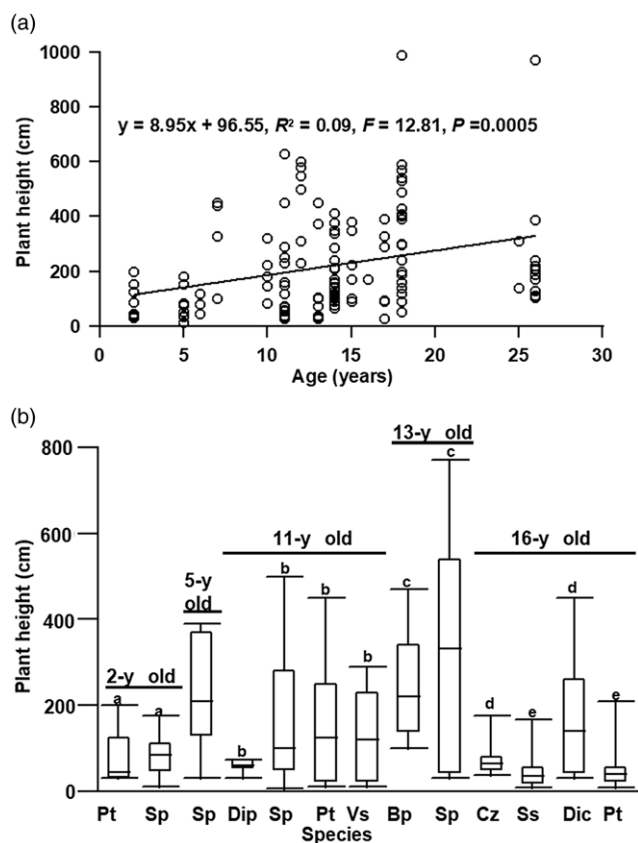


Figure 5. (a) Linear relationship between age and height for all sown plants with height measurements and (b) box-whisker plots of plant height for five selected cohorts aged 2, 5, 11, 13 and 16 y of eight species on Plot A. The box hinges in (b) represent the first and third quartiles, the centre horizontal line in the box is the median, and the vertical lines indicate the range of values that are within 1.5 of the hinges. Different letters above the boxes in (b) indicate significant differences for the age group. Species are abbreviated as follows: *Bauhinia pertesiana* (Bp), *Combretum zehyeri* (Cz), *Dichrostachys cinerea* (Dic), *Diplorhynchus condlycarpon* (Dip), *Piliostigma thonningii* (Pt), *Senegalia polyacantha* (Sp), *Strychnos spinosa* (Ss) and *Vachellia sieberiana* (Vs).

more diversity in the predictor variables of plant height among tree species, root top diameter explained a significant proportion of the variance in plant height in three species: *E. abyssinica* (92%) and *S. araliacea* (96%) and *V. sieberiana* (96%), vertical taproot length explained 77% of the variation in plant height in *D. condlycarpon* while the explanatory power of proximal diameter of coarse lateral roots ranged from 65% in *T. indica*, 71% in *P. thonningii* and 94% in *C. molle*. The combination of vertical taproot length and root top diameter explained 84% in *B. pertesiana* and 99% in *L. stuhlmannii* of the variance in plant height. The additive effects of root top diameter and proximal diameter of largest lateral root were significant only in *S. goetzei* in which they explained 99% of the variance in plant height. In *S. polyacantha*, the additive effects of taproot dry mass and total RDM explained 82% of the variance in plant height.

Discussion

Taproot structure

Data for complete excavations indicate that plant growth form and soil depth affect vertical taproot length. Overall, shrub species had shallower taproots than tree species but within each growth form,

plants growing on shallow soil had shorter taproots than those growing on deep soil at the study site. In shallow soils, mechanical impedance can retard root elongation and constrain plant growth (Bengough *et al.* 2011) and this may have contributed to the shallow vertical taproot length observed at plot C at the study site. The SRL is linked to vertical taproot length and root wood density and therefore low SRL signifies denser wood while high SRL signifies softer wood. Shrubs not only had lower SRL but also shallower roots in shallow soil but denser wood in deep soil while there was no such difference among tree species. It is not clear what drives this difference in shrub species growing on shallow and deep soil. The adaptive and functional significance of this differential between deep and shallow soils requires further research because it has implications for explorative and exploitative functions of roots (Freschet *et al.* 2021b).

Lateral root structure

There were more laterals in deep soil than in shallow soil, irrespective of growth form but tree species had larger coarse laterals based on proximal diameter measurements. Among shrub species, there were more coarse laterals per vertical taproot length in deep soil than in shallow soil which was not the case for tree species, suggesting differing anchorage strategies between the two growth forms. It is apparent, that vertical taproot length does significantly influence the deployment of coarse laterals in shrubs depending on soil depth. Given the lower SRL for shrub species, it is probable that physical soil impedance in shallow soil perhaps impairs the development of coarse laterals in shallow soil.

Estimating root structure from incomplete sampling

Maximum rooting depth is an important trait for determining the range of soil layers that can be colonized by roots (Freschet *et al.* 2021b). Recently Zhou *et al.* (2020) suggested that the ratio of taproot diameters at depths of 30 and 10 cm might be a good proxy for root distribution with depth but the accuracy of this model remains to be evaluated using data for complete taproot excavations. In this study, vertical taproot length for incomplete excavations was estimated by adding to the excavated depth the product of the quotient of distal diameter/root top diameter multiplied by excavated depth. The model estimates overestimated vertical taproot length by 11% and given the difficulty of complete excavations of taproots in TDFs of east and southern Africa, this model represents an important step in improving the estimation of vertical taproot length in the region and is therefore recommended. Since the model bias can be reduced by digging deeper, it is also recommended that excavations should be done up to at least 80 cm to achieve a bias of less than 11%. Consequently, the use of the Zhou *et al.* (2020) model would result in large biases, if excavations are limited to shallow depths.

Excavating all coarse laterals can be more destructive to the environment, especially for laterals located in deeper soil layers. The use of sample data on proximal diameter and lateral RDM to develop models for estimating total lateral RDM, as in this study, has been employed by other researchers (Kachamba *et al.* 2016, Mugasha *et al.* 2013). However, the selected power model used in this study tended to overestimate lateral root biomass by nearly 23%. Future research should aim at collecting more data in order to reduce this bias and perhaps using more species-specific data which was not attempted in this study due to data limitations.

Table 3. Best fit linear regression models for predicting plant height (y, cm) from (i) vertical taproot length (x_1 , cm), (ii) root top diameter (x_2 , mm), (iii) proximal diameter of the largest lateral root (x_3 , mm), (iv) taproot dry mass (x_4 , g) and (v) total root dry mass (x_5 , g) at the study site

Growth form/Species	Regression equation	R^2	ΔAIC_c	F-ratio	Significance level (P)
Shrubs					
All species	$y = 27.92 + 5.91x_2$	0.82	404.18	234.2	<0.0001
<i>D. cinerea</i>	$y = 45.2 + 3.82x_3 + 0.61x_5$	0.85	86.2	17.37	0.003
<i>F. virosa</i>	$y = 53.91 + 5.0x_2$	0.92	72.46	84.25	<0.0001
<i>L. camara</i>	$y = 28.5 + 5.28x_2$	0.75	151.47	55.04	<0.0001
<i>P. engleri</i>	$y = 17.47 + 6.1x_2$	0.95	59.58	96.98	0.0002
Trees					
All species	$y = 4.63 + 0.58 x_1 + 1.37x_2 + 4.59x_3$	0.75	1156.4	121.2	<0.0001
<i>B. petersiana</i>	$y = -10.53 + 0.59x_1 + 4.19 x_2$	0.84	209.28	60.81	<0.0001
<i>C. molle</i>	$y = 25.47 + 10.40x_3$	0.94	53.14	82.86	0.0003
<i>D. condlycarpon</i>	$y = -62.75 + 1.36x_1$	0.77	49.05	10.25	0.05
<i>E. abyssinica</i>	$y = -69.08 + 3.16 x_2$	0.92	76.56	94.14	<0.0001
<i>L. stuhlmannii</i>	$y = 22.11 + 10.78 x_2 - 1.03x_1$	0.99		99.58	0.01
<i>P. thonningii</i>	$y = 106.7 + 7.29x_3$	0.71	193.73	43.90	<0.0001
<i>S. goetzei</i>	$y = -33.65 + 7.34 x_2 - 3.06x_3$	0.99		211.40	0.005
<i>S. polyacantha</i>	$y = 159.2 + 0.12x_4 + 0.06x_5$	0.70	270.91	26.89	<0.0001
<i>S. araliacea</i>	$y = 3.32 + 4.28 x_2$	0.96	113.35	275.08	<0.0001
<i>T. indica</i>	$y = 164.06 + 7.05x_3$	0.65	109.17	16.45	0.003
<i>V. sieberiana</i>	$y = 8.72 + 4.6 x_2$	0.96	90.0	238.83	<0.0001

Belowground biomass relationships and plant height

Shoot and root growth is closely coordinated and therefore RDM can be influenced by plant size (Farrar & Jones 2000) and although Mokany *et al.* (2006) reported that for forests and woodlands the relationship between RDM and SDM is best described by a power function, in this study, this relationship was best described by a linear model confirming the influence of plant size on RDM. Root/shoot ratio reflects the differential biomass investment between the root and shoot organs (Mokany *et al.* 2006).

The RMF is an exploitative trait and increases when plants proportionately invest more in the root system (Freschet *et al.* 2021b). However, root variables, plant age and height together only explained a third of the variation in R/S ratio but $\geq 54\%$ of the variance in RMF was attributed to the additive effects of plant height, vertical taproot length and proximal diameter of the largest lateral. This suggests that these biomass quotients can be influenced by different plant variables. In this study, R/S ratio reached an asymptote of 8.0 when RMF was 0.84. RMF in shrub and tree species was 0.31 and 0.50, respectively, which are within the range of 0.16–0.63 reported for woody shrubs and small trees in *Banksia* woodland in Australia (Pate & Bell 1999). There was no significant relationship between vertical taproot length and taproot dry mass which suggests that taproot elongation may be decoupled from taproot thickening. The lack of a significant relationship between vertical taproot length and lateral RDM also indicates a de-linkage between taproot elongation and development of coarse laterals. However, taproot dry mass explained $>50\%$ of the variance in lateral RDM that may indicate a linkage between taproot thickening and the development of coarse laterals in both shrub and tree species at the study site.

Root biomass tends to be underestimated compared to above-ground biomass (Robinson 2004). This is partly because most

studies in TDFs in east and southern Africa only included coarse roots and even for these roots, excavations had high distal diameter cut-off points that ranged from 10 mm (Kachamba *et al.* 2016, Mugasha *et al.* 2013) to 20 mm and 50 mm (Chidumayo 2013b, Ryan *et al.* 2011). Only Ngoma *et al.* (2018) used a cut-off point of ≤ 5 mm. Obviously the exclusion of some coarse root material, due to the use of high diameter cut-off points, and fine roots, results in the gross underestimation of root biomass in TDFs of east and southern Africa and casts doubt on the validity of using R/S ratio for estimating root biomass (Mokany *et al.* 2006, Robinson 2004).

Wakeling *et al.* (2011) argued that in mesic savannas only the fastest growing saplings transit to trees after growing above the fire zone during the short fire-free intervals while Laris *et al.* (2016) observed that 2–3 years is what is needed for saplings to transit into trees. The objective of this study was to investigate root variables and traits and their role in determining plant height. The study area experiences surface fires that have, at best, indirect effects on early belowground plant development and so fire was not the main focus of this study. Further, the data could not be analyzed by the burned/deep and unburned/shallow dichotomy due to sample size constraints. The sample sizes were unbalanced for the species and plots (see Table 2). Hence, the adoption to analyze the data by growth form, soil depth and age that were assumed to impact more on early belowground plant development at the study site. Of course, fire is a major bottle-neck to shoot growth but it is apparent from the results of this study that fire impacts manifest only after overcoming early belowground constraints on plant height growth. Over 90% of the variation in plant height at the study site could not be explained by age. With the majority (70%) of sown plants in fire-protected firebreaks at Plot A, most sown plants would have

transited into trees within 10 years but this was not the case. The majority of sown plants were below 200 cm height, even at the age of 16 years. It is apparent therefore that the majority of woody plants in TDFs in east and southern Africa are slow growers, even in the absence of fire. This is partly because of the slow development and growth of the root system. This may also explain why plant height was not strongly correlated with plant age at the study site.

Root top diameter is a product of the development and growth of both taproot and coarse laterals, as is root biomass, while vertical taproot length and taproot dry mass are products of taproot elongation and thickening, respectively. Lateral root proximal diameter is a result of coarse lateral root growth. It is apparent therefore that root-associated variables, either singularly or severally, determined the plant height in shrubs and small trees at the study site, with age playing a minor role. The diversity of root variables determining plant height in tree species is perhaps a reflection of different growth strategies compared to shrubs.

Belowground structure and biomass therefore set the template for the early growth of woody species at the study site. Previous studies have tended to concentrate on factors affecting the shoot as determinants of plant height in TDFs (Bond 2008, Higgins *et al.* 2000, Laris *et al.* 2016, Sankaran *et al.* 2004) without consideration of the role of belowground factors. The present study has revealed the equally important roles played by belowground organs, and factors affecting them in determining the early development and growth of the shoot in TDFs shrubs and small trees. These observations have implications for the management of TDFs in east and southern Africa.

Conclusion

Belowground factors play a key role in determining early shoot growth in TDF woody plants. There appears to be a temporal sequencing of taproot elongation, thickening and development of coarse lateral roots and because of the co-existence fast- and slow-growing individuals within a species, age is not a major determinant of early shoot growth. Little is known about the effects of root damage on shoot growth and tree recruitment. More research is therefore needed to improve our knowledge of how belowground structures influence shoot growth rate in woody plants, especially in TDFs of east and southern Africa.

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