

Rooting depth and above-ground community composition in Kalahari sand woodlands in western Zimbabwe

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Abstract: The pattern of coarse-root distribution was analysed in the woody plant community along a 200-m edaphic gradient on a Kalahari sand woodland catena in Zimbabwe. The root systems of 45 trees and shrubs were excavated, mapped, and digitized to analyse rooting depth and architecture. Patterns of change in the above-ground community were also identified along this transect. Rooting depth increased, and the centre of mass of the root profile shifted towards the maximum rooting depth as a function of distance up the catena. The data also suggest that interspecific variation in rooting depth may increase up the catena. The below-ground pattern was accompanied by above-ground changes: species richness and basal area also increased up the catena. It is hypothesized that increasing soil depth allows greater coexistence of alternative water-use strategies, resulting in the observed increase in species richness up the catena.

Key Words: *Baikiaea plurijuga*, *Brachystegia spiciformis*, catena, community assembly, root architecture, rooting profiles, soil depth, species turnover, tree diversity

INTRODUCTION

Although a wealth of information has been compiled on above-ground vegetation structure across a wide range of biomes, our knowledge of below-ground structure remains rather limited (Schenk & Jackson 2002a). Many studies have shown that plant species and functional groups differ in rooting depth and root architecture (Jackson *et al.* 1996, McKane *et al.* 1990, Parrish & Bazzaz 1976, Timberlake & Calvert 1993), but relatively few (Schenk & Jackson 2002a, Schulze *et al.* 1996, Zerihun *et al.* 2006) have investigated general patterns of below-ground structure as a function of environmental gradients and the above-ground community, particularly for trees. This information may be of fundamental importance for understanding community assembly in water-limited environments, where access to soil water depends to a significant extent on the size and shape of root systems (Dimitrakopoulos & Schmid 2004, Schenk & Jackson 2002b). Quantifying patterns of variation in rooting strategies across environmental gradients and among species may therefore be fundamental for understanding

the role of water and nutrients in regulating ecosystem function and facilitating species coexistence in these environments.

Rooting strategies have been proposed to be of major significance in determining vegetation dynamics and tree-grass coexistence in savannas (Walker *et al.* 1981, Walter 1971), but few studies have characterized the rooting strategies of savanna trees, the focus of this study. Recent studies have shown that interspecific variation in rooting depth may be an important axis of niche differentiation and thus a driver of species coexistence in herbaceous communities (Fargione & Tilman 2005, Stubbs & Wilson 2004). In savanna ecosystems, discussion of rooting niches has primarily been limited to the two-layer model of soil depth partitioning (Walker & Noy-Meir 1982, Walter 1971), proposed to explain the stable coexistence of woody and herbaceous plants. Such vertical stratification of the soil profile might potentially explain the coexistence of multiple tree species, each preferentially exploiting particular soil layers (Dimitrakopoulos & Schmid 2004), but this has not been investigated. The Kalahari sands of southern Africa, with their marked catenas of increasing effective rooting depth, provide an ideal system to investigate this question. The Kalahari sand catenas occur along fossil Pleistocene dune systems, and range from shallow,

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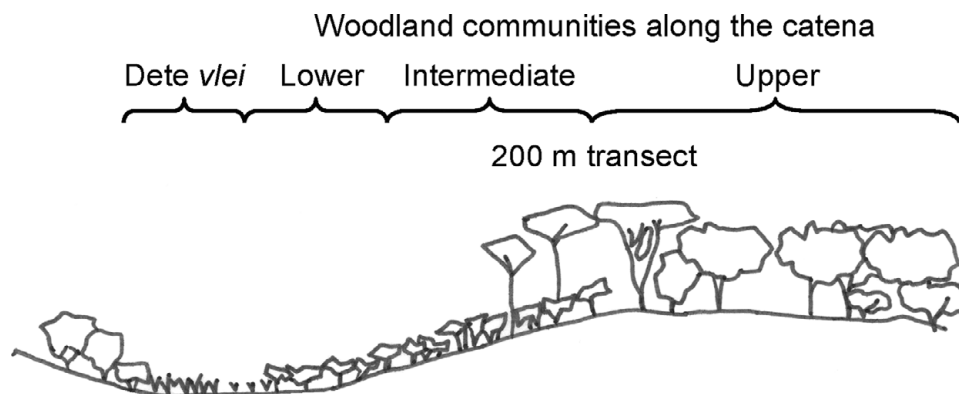


Figure 1. Schematic diagram of the Dete vlei 200-m catena transect. Kalahari sand woodland vleis are shallow, seasonally waterlogged valleys or drainage lines dominated by grasses. At the margin of these vleis, the lower catena community is dominated by low open scrubby woodland. In the intermediate-catena community, woody cover is thicker with numerous shrubs and taller trees up to 5 m in height, and the upper catena is characterized by tall woodland dominated (up to 15 m). The difference in elevation between the upper and lower catenas between 5 and 10 m (not shown to scale).

grassland-dominated soils with impediments to rooting at one extreme (due to hardpan layers or anaerobic conditions), to deep, unstructured, sandy soils dominated by woodland at the other (Flint & Bond 1968). The gradual increase in tree cover up the catena appears a priori to be accompanied by an increase in species diversity.

In this study, we used a natural catena in Kalahari sand woodland to investigate patterns in below-ground coarse-root structure and their association with changes in the above-ground community. Kalahari sand catenas show consistent patterns of species replacement as one progresses along a topographic gradient of increasing soil depth from the hydromorphic grassland at the edge of the woody community to the crest. The following questions were addressed in the present study: (1) Does rooting depth increase as a function of distance up the catena? (2) How does the above-ground community change as a function of catena position? (3) Are there interspecific differences in rooting depth?

METHODS

Study site

The study area (18° 38'S, 27° 3'E,) is situated in the Dete vlei or valley on the north-eastern border of Hwange National Park in Matabeleland North province, Zimbabwe. It is at an altitude of 1050–1065 m, and the mean annual rainfall at the nearby park headquarters (15 km away) is 650 mm (parks records). Most rainfall occurs during the single rainy season, between November and March, with the bulk falling between December and February. The Dete vlei is a well-developed example of the valley grasslands that incise the Kalahari sand woodlands in this area. The soils are medium-textured, unconsolidated Kalahari sands, and tend to be deep

(>10 m) and lacking in well-defined horizons (Childes 1984). Mottling of the soil suggests the occurrence of seasonally anaerobic conditions that preclude root growth, especially at the low end of the catena. Much of this area is characterized by dense woodland 8–14 m tall dominated by *Baikiaea plurijuga* and *Brachystegia spiciformis* (Leguminosae: Caesalpinioideae), interspersed with broad grassy valleys fringed by *Terminalia sericea* and *Acacia erioloba*. Many woodlands have been exploited in the past for commercial timber (*Baikiaea plurijuga*, *Guibourtia coleosperma* and *Pterocarpus angolensis*) and for cattle grazing, but today wildlife utilization (e.g. hunting safaris, game viewing) is the predominant land use.

Data collection

A 200-m transect was set up in May 2002 from the woodland-grassland boundary upslope into the woodland, perpendicular to the boundary, traversing three distinct vegetation communities, which were designated lower-, intermediate- and upper-catena communities (Figure 1). Within each community type, trees of representative species were identified and tagged. Forty-five trees belonging to 15 species were sampled for the survey. For each tree, species, basal diameter of all stems, height and GPS position (Garmin eTrex, Garmin Corporation, Olathe, KS, USA) for determination of distance along the transect were recorded.

The root system of each tree was excavated with great care to avoid damaging small roots. The purpose of the excavation was to obtain a quantitative index of the vertical distribution of roots. For each tree, the central taproot was followed (when present), and excavation progressed until the maximum rooting depth was reached whenever possible. The depth of the excavated profiles ranged between 35 and 240 cm below ground level. In

almost all cases the profile was exposed to its maximum depth; in some cases it was not feasible to reach maximum depth and digging continued until as much of the root system as possible had been exposed. Lateral digging progressed to an extent that would allow most of the lateral root area to be recorded, but in most cases the full lateral extension of roots was not measured. Two-dimensional profiles of all roots ≥ 1 cm diameter were drawn on graph paper, with root length and branching depth measured to the nearest 5 or 10 cm. To minimize the misrepresentation of lateral roots, roots that were not on the plane of the profile were 'flattened' or projected onto two dimensions. The drawn profiles were then scanned and sharpened with Photoshop, and each file was digitized with Windig 2.5 (D. Lovy 1994). The digitized data were imported into spreadsheets as text files containing x-y coordinates, each coordinate representing a pixel digitized from a solid (filled) profile. The resulting profiles did not quantify root biomass or volume, but rather the area of the lateral root profile. The y coordinates were scaled to fall between 0 at ground level and the maximum measured profile depth in m. This allowed the cumulative profile area $r(D)$ to be reconstructed as a function of depth D by counting the number of pixels as a function of y in the digitized image.

Six 20×20 -m plots (two per community, set on opposite sides of the transect at random distances, from the transect and lower boundary of each community) were set up to record changes in above-ground community structure and composition along the transect. The presence of all woody species and basal diameter at 10 cm height of all stems > 3 cm were recorded. Species nomenclature follows Coates Palgrave (1977). Soil samples from three root profile excavations per community were also collected in cloth soil bags at depths of 10, 50 and 100 cm (if the profile was deep enough). Samples were analysed for texture at the Institute of Environmental Studies in Harare.

Five of the profiles were too deep to allow excavation to maximum root depth. The procedure of Schenk & Jackson (2002b) was therefore used to extrapolate the root distribution for these profiles, using a logistic-dose response curve:

$$r(D) = \frac{R_{\max}}{1 + \left(\frac{D}{K_{1/2}}\right)^c} \quad (1)$$

Here, $r(D)$ is the cumulative root profile area at depth D , R_{\max} is the total profile area, $K_{1/2}$ is the depth at which $r(D) = 0.5 R_{\max}$, and c is a shape parameter. Eqn 1 was fitted to the root depth data with a custom curve-fitting algorithm written in C, yielding values of R_{\max} , $K_{1/2}$, and c for each profile that were used to generate interpolated and extrapolated estimates of the 50% (D_{50}) and 95% (D_{95}) rooting depths (Schenk & Jackson 2002b).

For consistency throughout the analysis, the curve-fitting procedure was applied to all the root profiles, and the computed values of D_{50} and D_{95} were used as the primary dependent variables in subsequent analyses.

Statistical analysis

To test for an association between rooting depth and catena position, the SAS MIXED procedure (SAS v. 9.1, SAS Institute, Cary, NC) was used, with catena position as a fixed effect, species as a random effect, and D_{50} and D_{95} as dependent variables. Tree basal diameter was included in the regression models to test whether any relationship between rooting depth and catena position was associated with tree size, since tree size could change along the catena independently of below-ground factors and result in a potentially spurious relationship between rooting depth and catena position. Because it was assumed that rooting depth and basal diameter might be related by a power law, these variables were log-transformed prior to the analysis (this also homogenized the variance), but not position on the catena. To test for changes in root shape along the catena, the partial residual of D_{50} after controlling for D_{95} was regressed against catena position; two trees with equal values of D_{95} but different values of D_{50} root to the same depth, but allocate their roots along the profile differently.

Visual examination of the root profiles suggested that for cases in which trees had evidently resprouted following a major disturbance, most likely the removal of the original stem by elephants ($N = 10$), a large proportion of the below-ground mass was concentrated near the surface. This below-ground mass cannot be classified as root tissue. Trees that have been toppled, logged, or otherwise damaged often resprout from root collars, resulting in a new growth phase that has a higher root to shoot ratio than the undisturbed phase. Much of this below-ground mass is formed by a suffrutex that is largely dead (R. M. Holdo, pers. obs.) and therefore may differ functionally from root tissue. Since inclusion of these trees in the analysis may have added a potentially confounding factor, they were excluded, resulting in a final sample size of 35 trees.

RESULTS

The application of the curve-fitting procedure to the profiles where near-complete root data were available showed that it resulted in an unbiased and accurate representation of the root distribution, particularly for the interpolated estimates of D_{50} and D_{95} (interpolated D_{50} : $R^2 = 0.93$, slope = 1.03; interpolated D_{95} : $R^2 = 0.97$, slope = 1.02; extrapolated D_{50} : $R^2 = 0.60$, slope = 1.15; extrapolated D_{95} : $R^2 = 0.88$, slope = 1.12). The estimated

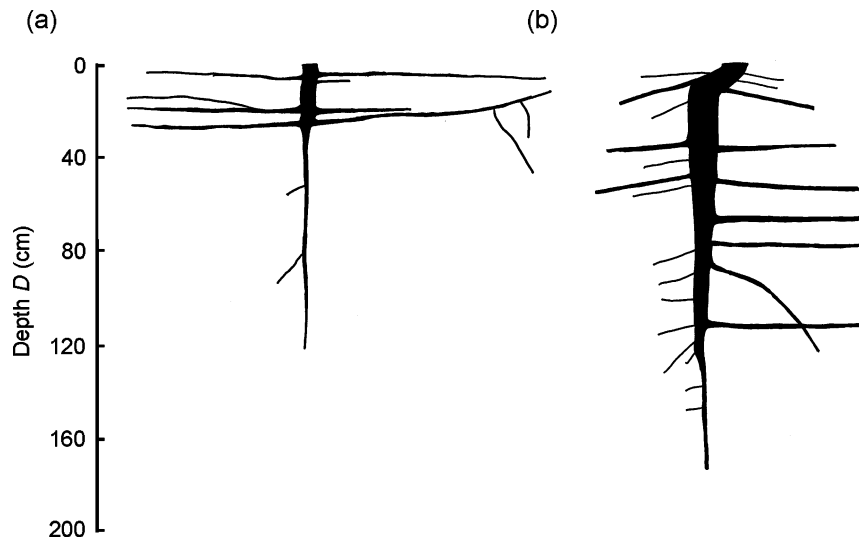


Figure 2. Digitized images of two excavated root profiles from a Kalahari sand woodland catena: a *Terminalia sericea* from the lower catena (a), and a *Baikiaea plurijuga* from the upper catena (b).

values of the LDR curve parameters, D_{50} and D_{95} are shown for all excavated individuals in Appendix 1.

Root profiles

The statistical tests from the regression analyses yielded the same conclusions regardless of whether the extrapolated profiles were included ($N = 35$) or not ($N = 30$). The extrapolated profiles are included here to ensure an adequate representation of all profile communities. There were marked differences in root-profile depth and shape among trees found in different catena communities (Figure 2). There was an increase in rooting depth up the catena (D_{50} : $F_{1,21} = 24.3$, $P < 0.0001$; D_{95} : $F_{1,21} = 8.3$, $P < 0.01$; Figure 3). This trend was unrelated to overall tree size, as the partial regression coefficient for basal diameter was not significant when it was included as a covariate (D_{50} : $F_{1,20} = 1.5$, $P > 0.1$; D_{95} : $F_{1,20} = 4.3$, $P > 0.05$). Given the lack of explanatory power provided by basal area, it was excluded from subsequent analyses. In the analysis of root shape, the partial regression coefficient for D_{50} vs. d was significant after controlling for D_{95} ($F_{1,20} = 9.3$, $P < 0.01$), suggesting that trees shift their relative root mass allocation to deeper soil as a function of distance up the catena (Figure 3). A mixed effects model that included species as a random effect was compared with a simpler fixed-effects model that ignored correlations within species. The mixed model clearly produced a better fit to the data than the fixed-effects model for D_{95} ($\Delta\text{AICc} = 9.1$), less so in the case of D_{50} ($\Delta\text{AICc} = 0.9$), indicating that species differ in terms of rooting depth after controlling for catena position.

Above-ground plots and soil analyses

The soil in the study site was heavily dominated by sand, with a silt plus clay content of $5.9\% \pm 1.9\%$ (mean \pm 1 SD) across all locations on the transect. There were no differences in soil texture along the catena, or as a function of depth between 10 and 100 cm. Although statistical analyses were not conducted on above-ground data (given the small sample size per community), there was a clear indication of increasing species richness and basal area up the catena (Figure 4), as expected. This increase in basal area appears to be driven primarily by an increase in stem density rather than tree size (Figure 4). Despite the lack of a clear trend in mean tree diameter, it was apparent through observation that maximum tree size increased up the catena: large (dbh > 40 cm) trees only occurred in the upper zone of the catena, but represented a minor fraction of stems sampled, so had a small influence on aggregate statistics.

An examination of species distributions in the three communities suggested also a sequence of species replacement associated with increasing rooting depths up the catena (Figure 5). At the woodland-grassland boundary, peat grasslands typified by *Aristida stipitata* began to give way to low (2–3 m high) individuals of *Terminalia sericea*, with scattered *Combretum collinum*, *Combretum psidioides* and *Ochna pulchra*. Further up the catena woody cover thickened visibly with shrubs of *Baphia massaiensis* and *Pseudolachnostylis maprouneifolia* and taller trees (3–5 m high) of *Combretum zeyheri*, *Erythrophleum africanum* and *Pterocarpus angolensis*. In the upper section of the catena tall (10–12 m high), dense *Brachystegia spiciformis* and *Baikiaea plurijuga* woodland dominated, with significant numbers of *Guibourtia coleosperma* and *Erythrophleum africanum*. There was a

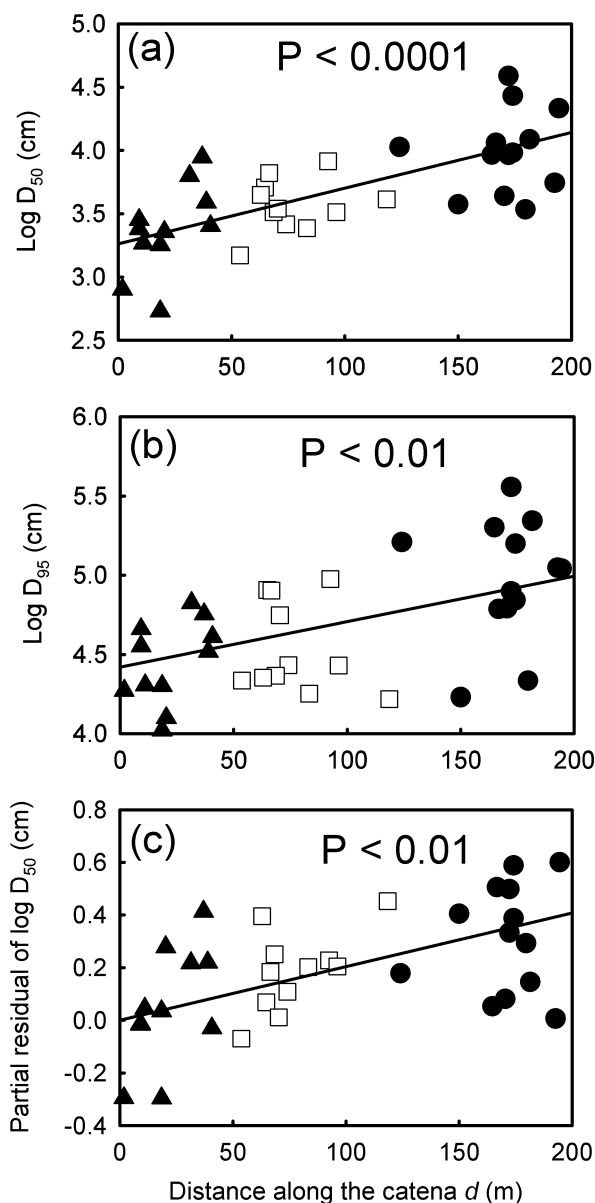


Figure 3. Rooting depth as a function of distance from the woodland–grassland boundary d along a catena on Kalahari sand: D_{50} (a), D_{95} (b), and partial residuals D_{res} of D_{50} after controlling for D_{95} (c) as a function of d . Observations are labelled according to our qualitative subdivision of the catena into three communities: lower (▲), intermediate (□), and upper (●). The P-values test the hypothesis that there is no relationship between rooting depth and distance along the catena using a mixed model with species as a random effect. The line equations are given by the equations $\log(D_{50}) = 3.26 + 0.0044d$ (a), $\log(D_{95}) = 4.42 + 0.0029d$ (b), and $D_{res} = 0.0021d$ (c).

low shrub layer of *Croton pseudopulchellus* and *Baphia massaiensis*.

DISCUSSION

The study suggests systematic patterns of below-ground structure associated with changes in tree diversity. The

marked pattern of species turnover and diversity along the catena, accompanied by the observed increase in rooting depth along the root-profile transect, suggests that the distribution and richness of tree species along this gradient may be strongly influenced by edaphic factors. Further work is required to determine the precise nature of the environmental gradient driving changes in rooting patterns along this catena. A plausible candidate is soil depth, as defined in this case by the depth of the hardpan layer or other impediments that frequently characterize the Kalahari sand environment (Childes & Walker 1987).

An assumption of the study is that the root profile area quantified is a reasonable representation of root mass distribution. The two-dimensional profile used here, although supported by previous work (Schenk & Jackson 2002a, b), is a relatively non-destructive method of assessing root allocation. Two assumptions of the method are that profile area is correlated with root volume and mass. A potential bias violating the latter assumption would result from differential tissue density as a function of root size. The method also ignores small roots and fine root biomass, which can form a substantial fraction of the total root biomass (Scholes & Walker 1993). Lateral root development was also not quantified to its full extent in all cases, leading to some potential bias in the determination of root distribution. It was assumed, however, that this bias was relatively minor in the determination of vertical (as opposed to horizontal) distribution. In general, the method provides an approximate index of rooting depth allocation, but further work is required to validate the approach by comparing profile-estimated depths with destructively sampled biomass estimates as a function of depth.

Previous work has suggested that tree species of the Kalahari sand differ in rooting depth and root morphology (Timberlake & Calvert 1993). Species such as *Baikiaea plurijuga* and *Brachystegia spiciformis* are deep-rooted, and tend to be absent from areas where a hardpan layer or seasonally anaerobic conditions impede root expansion (Childes 1984). The shallower potential rooting depth at the lower edge of the catena may thus be responsible for excluding these species, and shallow-rooted species like *Terminalia sericea* and *Combretum* spp. are favoured. The increasing species richness as a function of distance up the catena may thus be the result of increasing ‘biotope space’ (*sensu* Dimitrakopoulos & Schmid 2004), which permits species with a wider range of rooting strategies to coexist. Further study is required to investigate the extent to which increasing rooting space affects the ability of trees with contrasting rooting strategies to coexist, and to characterize interspecific differences in rooting niches. Although Figure 5 suggests that species occurrence patterns along the catena are correlated with rooting depth, the relative importance of other factors

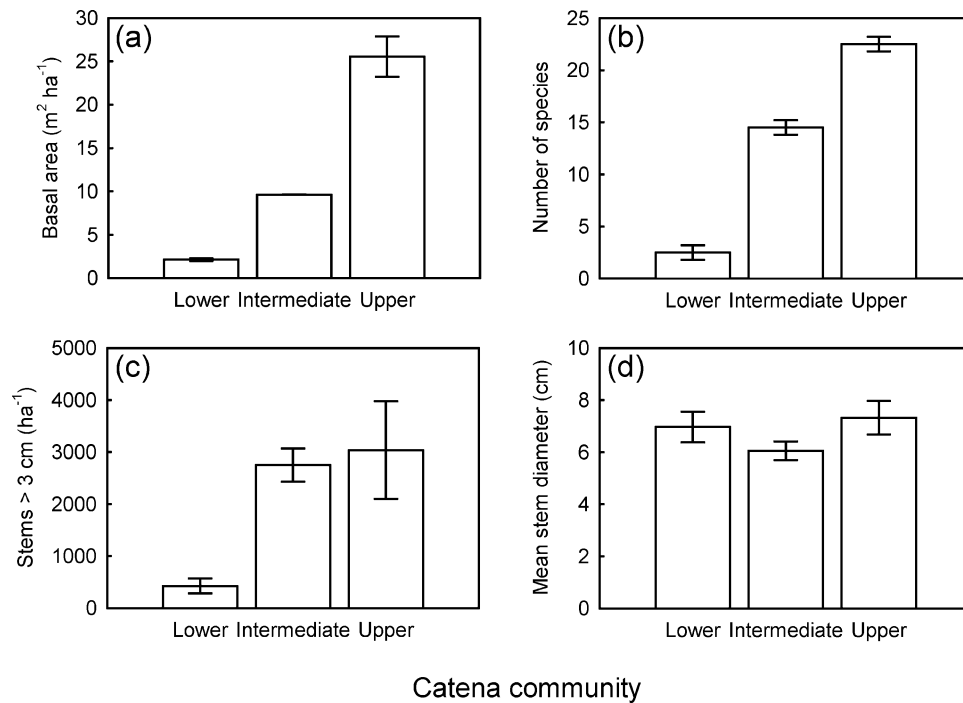


Figure 4. Above-ground measurements in 400-m² plots of three distinct communities along the woodland catena (N = 2; mean ± 1 SD): basal area (a), species richness (b), stem density (c), and mean stem diameter (d). Except for species richness (which includes all woody plants), calculations were performed on stems > 3 cm diameter.

(e.g. competition for light) in structuring the community has not been examined in this system.

Although effective soil depth was not directly measured in this study, it can be inferred from the marked increase in elevation (5–10 m) of the soil surface along the valley slope over the length of the catena transect. Soil texture, the only other covariate measured in the study, did not vary with catena position, although this may be due to the low resolution of the soil texture analysis: previous work has showed that soil texture variation along Kalahari sand catenas is driven by an increase in the size of sand particles up the catena (Flint & Bond 1968). Other unmeasured variables, such as nutrient availability and air temperature profiles, could also potentially play a role in determining community composition. Kalahari sand species show marked interspecific variation in frost sensitivity, for example, and night-time air temperature has been shown to be strongly affected by topographic position along Kalahari sand catenas (Childes 1984).

If effective soil depth is in fact the limiting factor restricting *Baikiaea* and other species to the upper reaches of the catena, this suggests the existence of constraints on root allometry, not surprising given that such species-specific constraints affect the allometry of above-ground structures (Niklas 1994). Whether these constraints are dictated by interspecific differences in water utilization strategies remains to be investigated. There is some indication of a relationship between water utilization

patterns and rooting depth from phenological studies, which show that deep-rooted species such as *Baikiaea* and *Guibourtia* retain their leaves far longer into the dry season than the shallow-rooted species like *Terminalia* and *Burkea* (Childes 1984). Childes & Walker (1987) showed that on dune ridges in Kalahari sand, soil water in deep layers (3.5 m) remains relatively constant throughout the annual cycle, whereas shallow layers fluctuate markedly. In areas with deep soils where these species coexist, *Terminalia* may be able to exploit an ephemeral resource immediately following a storm event (Scholes & Walker 1993), whereas *Baikiaea* may preferentially use deeper water layers. The fact that root allocation appears to shift to deeper layers in deep soils (i.e. controlling for rooting depth, there is a downward shift of the root centre of mass) suggests that trees may preferentially allocate roots to soil layers with more reliable water supplies as one progresses up the catena.

The fact that deep-rooted species have access to deep water in the soil layer, however, does not imply that these species do not also exploit shallow soil layers as well, unless trade-offs impose limitations on the range of depths that can be exploited by any given species. Coexistence of shallow- and deep-rooted species at the top of the catena may occur through a variety of mechanisms, but one plausible one is vertical partitioning of soil water layers. Studies with herbaceous plants have identified vertical segregation in resource utilization as a mechanism

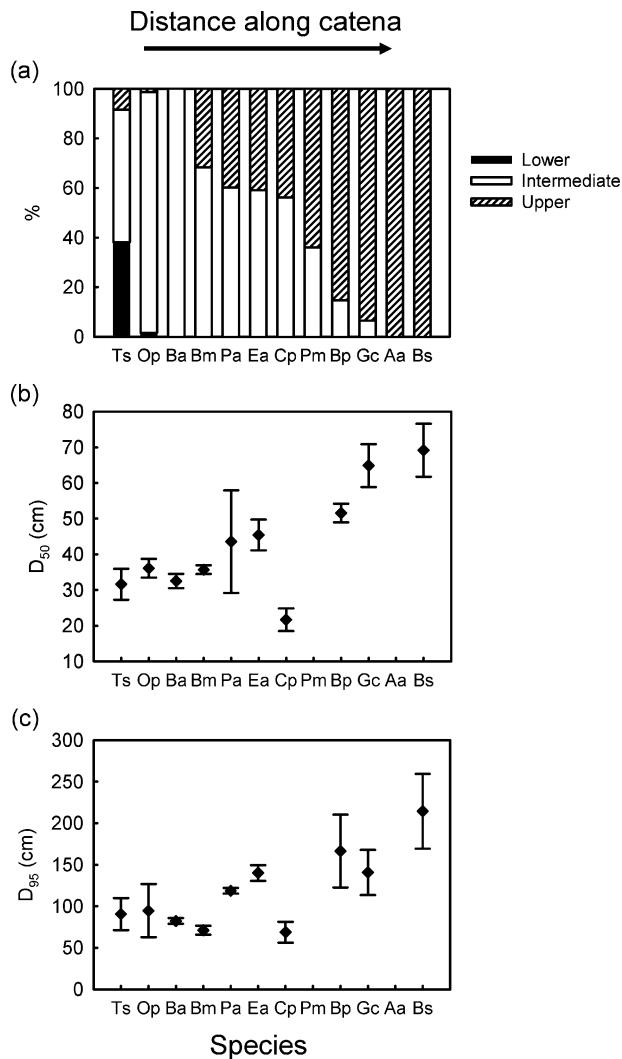


Figure 5. Basal area distribution (% of total along the transect) within each of three communities (a); D_{50} (b) and D_{95} (c) for 12 common species in the study (expressed as mean and 95% CI). Only species for which basal area was quantified are included (*Combretum collinum* is excluded because it was absent from the above-ground plots). The species have been arranged in order of their relative dominance up the catena, inferred from above-ground plot data. Species key: Aa = *Amblygonocarpus andongensis*; Bp = *Baikiaea plurijuga*; Bm = *Baphia massaiensis*; Bs = *Brachystegia spiciformis*; Ba = *Burkea africana*; Cp = *Combretum psidioides*; Ea = *Erythrophleum africanum*; Gc = *Guibourtia coleosperma*; Op = *Ochna pulchra*; Pm = *Pseudolachnostylis maprouneifolia*; Pa = *Pterocarpus angolensis*; Ts = *Terminalia sericea*.

allowing species coexistence (Fargione & Tilman 2005, Stubbs & Wilson 2004). Soil water availability appears to be a key resource partitioned along this axis, and thus a key environmental variable explaining patterns of species diversity (Silvertown *et al.* 1999). Although our study does not demonstrate such partitioning, it suggests that future research to investigate this possibility is warranted. An experimental approach that simultaneously monitors water uptake in tree species differing in rooting depth

and morphology and water availability as a function of soil depth could be used to estimate the degree of vertical stratification in soil water use in this system.

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Appendix 1. Variables and parameters for the data set used in the root profile analysis. The parameters c and $K_{1/2}$ indicate the shape of the curve relating cumulative root profile area versus depth and the depth at which 50% of roots have been reached, respectively, and are fitted parameters from the logistic dose response (LDR) curve fitted to $r(D)$, cumulative root profile area as a function of depth D . D_{50} and D_{95} were estimated from the LDR curve. For complete profiles they are interpolated, and for incomplete profiles they are extrapolated.

Species	Catena community	Diameter (cm)	Distance along catena d (m)	c	$K_{1/2}$ (cm)	$D_{profile}$ (cm)	Profile complete?	D_{50} (cm)	D_{95} (cm)
<i>Terminalia sericea</i>	lower	3.9	1.9	-2.18	18.2	120	y	18.2	71.6
<i>Terminalia sericea</i>	lower	5.3	9.3	-1.26	42.3	120	y	29.4	94.9
<i>Ochna pulchra</i>	lower	3.3	9.3	-1.84	33.8	120	y	31.6	105.7
<i>Combretum collinum</i>	lower	14.8	11.1	-2.08	28.0	110	y	26.2	74.1
<i>Combretum psidioides</i>	lower	15.2	18.5	-0.94	33.5	70	y	15.3	55.8
<i>Combretum psidioides</i>	lower	13.5	18.5	-1.58	32.2	90	y	25.9	73.9
<i>Ochna pulchra</i>	lower	3.3	20.4	-2.39	32.3	70	y	28.7	60.3
<i>Terminalia sericea</i>	lower	10.1	31.5	-1.34	67.2	150	y	44.7	124.6
<i>Combretum collinum</i>	lower	5.7	37.0	-1.93	63.7	130	y	51.8	116.2
<i>Terminalia sericea</i>	lower	13.5	38.9	-1.59	48.4	110	y	36.2	91.6
<i>Acacia erioloba</i>	lower	2.9	40.7	-0.69	338.8	110	y	30.1	100.6
<i>Combretum psidioides</i>	intermediate	8.8	53.7	-0.99	54.8	90	y	23.8	76.3
<i>Ochna pulchra</i>	intermediate	1.4	63.0	-1.08	260.3	80	y	38.5	77.8
<i>Erythrophleum africanum</i>	intermediate	19.5	64.8	-0.87	131.0	160	y	40.7	135.2
<i>Ochna pulchra</i>	intermediate	9.1	66.7	-1.53	57.1	150	y	45.6	134.8
<i>Burkea africana</i>	intermediate	8.6	68.5	-1.04	132.3	100	y	33.6	78.7
<i>Pterocarpus angolensis</i>	intermediate	7.1	70.4	-1.06	62.9	140	y	34.4	115.3
<i>Burkea africana</i>	intermediate	6.6	74.1	-2.29	31.9	90	y	30.5	84.1
<i>Terminalia sericea</i>	intermediate	11.9	83.3	-2.24	32.5	90	y	29.6	70.3
<i>Erythrophleum africanum</i>	intermediate	7.7	92.6	-1.02	124.7	160	y	50.1	144.9
<i>Burkea africana</i>	intermediate	10.1	96.3	-1.93	38.9	110	y	33.5	84.0
<i>Baphia massaiensis</i>	intermediate	11.7	118.5	-2.81	41.6	80	y	37.1	67.9
<i>Brachystegia spiciformis</i>	upper	25.1	124.1	-1.89	59.9	170	n	56.2	183.1
<i>Baphia massaiensis</i>	upper	10.4	150.0	-1.20	172.4	80	y	35.7	68.8
<i>Brachystegia spiciformis</i>	upper	9.3	164.8	-1.39	63.1	240	y	52.9	200.9
<i>Pterocarpus angolensis</i>	upper	7.3	166.7	-2.02	73.5	140	y	58.1	120.1
<i>Pterocarpus angolensis</i>	upper	8.3	170.4	-1.60	44.7	100	n	38.1	120.6
<i>Brachystegia spiciformis</i>	upper	21.1	172.2	-1.62	125.9	200	n	98.5	259.2
<i>Baikiaea plurijuga</i>	upper	7.2	172.2	-1.62	69.2	170	y	52.8	134.0
<i>Guibourtia coleosperma</i>	upper	4.5	174.1	-1.01	236.9	150	y	53.6	126.9
<i>Dialium englerianum</i>	upper	5.8	174.1	-1.02	558.7	200	y	84.1	181.3
<i>Baphia massaiensis</i>	upper	3.5	179.6	-2.38	37.7	100	y	34.3	76.3
<i>Baikiaea plurijuga</i>	upper	37.1	181.5	-1.28	79.6	170	n	59.6	209.4
<i>Baikiaea plurijuga</i>	upper	12.7	192.6	-1.72	45.3	150	n	42.3	155.8
<i>Guibourtia coleosperma</i>	upper	11.3	194.5	-1.04	691.4	170	y	76.2	154.6