



Vertical distribution of grass and tree roots in arid ecosystems of Southern Africa: niche differentiation or competition?

M.H.T. Hipondoka^{★*}, J.N. Aranibar[†], C. Chirara[‡], M. Lihavha[¶],
& S.A. Macko[†]

[★]*Etosha Ecological Institute, Namibia*

[†]*Department of Environmental Sciences, University of Virginia, U.S.A.*

[‡]*University of Zimbabwe, Zimbabwe*

[¶]*University of Venda, South Africa*

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A distinguishing, co-dominance feature of trees and grasses in Savannas was prominently explained by Walter. He hypothesized that water is the limiting factor and grasses are superior competitors for water in the upper soil, while trees have exclusive access at deeper layers. However, a new field evidence from the Kalahari, where the water table is too low for the tree roots' tapping, revealed that both plant types invest the bulk of their roots in the surface horizons. Further investigation should consider focusing on determining the co-dominance mechanism of both plant types without the displacement of the less-efficient species.

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Introduction

Unlike other biomes, savannas are characterized by a strong interaction between trees and grasses. Several investigations, such as those of Walter (1971), Knoop & Walter (1984) and Sarmiento (1984) probed into this phenomenon. Results from such studies provided various theories and findings. Walter (1971) in particular, suggested that as water is the limiting factor in semi-arid savannas, grasses are better competitors for this resource in the surface horizons of the soil, while trees have sole access of water at the deeper soil layers. However, more recent studies (Knoop & Walker, 1984; Sala *et al.*, 1989; Belsky, 1994) suggest that tree and grass roots exploit essentially the same soil volume. In the Kalahari sands of Botswana, the water table is located at considerable depths, which are not expected to be reached by tap roots of most of the local trees and shrubs. Although farmers have long known that some species, such as *Acacia karoo*, *Acacia erioloba* and *Ziziphus mucronata* growing along dried riverbeds extend their roots to the water table, this is not always the case. Ringrose *et al.* (2000), for example, drilled two *A. erioloba* trees to 60 m (the known local ground-water depth) in Southern Botswana, and found no evidence of roots appearing deeper than

*Corresponding author. E-mail: mhipondoka@unam.na, mhipondoka@yahoo.com

6 m. As part of SARARI 2000 Southern African Regional Science Initiative, which aims to understand the functioning of the savanna ecosystem, this study was carried out for its importance in contributing into the tree–grass dynamics.

In this study, the competitive interactions of trees and grasses for water in a spatial dimension were analysed, using indicators of water absorption—the root profile technique; and indicators of tree and grass root biomass— ^{13}C natural abundance ($\delta^{13}\text{C}$). We hypothesized that deep soil layers are not important in providing water for plants in the drier part of the Kalahari sands, because of the scarce rains (Scholes & Parsons, 1997), high evaporation (Tyson & Crimp, 2000) and deep location of the water table (Ringrose *et al.*, 2000). Thus, the expectation was that trees and grasses would compete for surface water, by among others, showing higher values of root density in the upper soil layers.

Methods

Devoid of permanent surface water, the field sites are located in the deep Kalahari Sandveld of Botswana. The first site is approximately 80 km south of Ghanzi. With an average annual rainfall of 400 mm, this site is characterized by topographic variation, dominated by *Acacia mellifera* and *Grewia flava* shrubs, and interspersed with scattered short trees. The second site is located further south, near Tshane. Here, the open savanna, receiving an average annual rainfall of 365 mm, is dominated by *Acacia luederitzii* and *A. mellifera*, the later being considered as a shallow-rooted species (Tolsma *et al.*, 1987). Both sites showed a healthy grass cover, with no sign of overgrazing.

The vertical distribution of tree and grass roots was measured using the profile count technique (Böhm, 1979). Soil pits, 120 cm deep and 100 cm wide was dug to expose the vertical section of the soil. Two of the soil pits were purposely dug under the dominant shrub canopies (*A. mellifera*), while the other two were randomly selected between canopies. At each pit, a grid 50 cm wide and 110 cm deep, sub-divided into $10 \times 10 \text{ cm}^2$ grids, was constructed on four replicate wall flanks (north, south, east, and west). Vertical fine root distribution of both trees and grasses was then counted and recorded, grid by grid. Additional 10 (five from each site) root exposures of *Terminalia sericea* were carried out to the corresponding depth and length of the ‘tap root’.

Soil samples of two pits, one under *A. mellifera* and the other between the canopies, were taken at 0–30, 30–60 and more than 60 cm depth. The samples were sieved through a 2-mm sieve to separate the roots, and these soils were treated with HCl to remove the carbonates. The total organic matter was analysed for $\delta^{13}\text{C}$ and %C in an Optima Isotope Ratio Mass Spectrometer coupled to an Elemental Analyzer. Roots of plants with the C_3 and C_4 photosynthetic metabolism, which correspond with trees and grasses respectively, were grounded and equally analysed for $\delta^{13}\text{C}$. These data provided the isotopic signatures of the two end members, trees and grasses. The proportion of organic matter derived from C_3 and C_4 plants (trees and grasses, respectively) for each soil sample was obtained using the following mixing equation

$$\delta^{13}\text{C}_{\text{C}_3}\text{fc}_3 + \delta^{13}\text{C}_{\text{C}_4}\text{fc}_4 = \delta^{13}\text{C}_{\text{totalOM}}$$

where fc_3 and fc_4 are the proportions of C_3 and C_4 derived soil organic matter, respectively, $\delta^{13}\text{C}_{\text{C}_3}$ is the isotopic composition of tree roots, $\delta^{13}\text{C}_{\text{C}_4}$ is the isotopic composition of grass roots and $\delta^{13}\text{C}_{\text{total OM}}$ the isotopic composition of the soil organic matter.

Results

Figure 1 presents the results of the root distribution in all four pits. At the two sites near Ghanzi, it is clear that both grass and tree invest the bulk of their roots within the

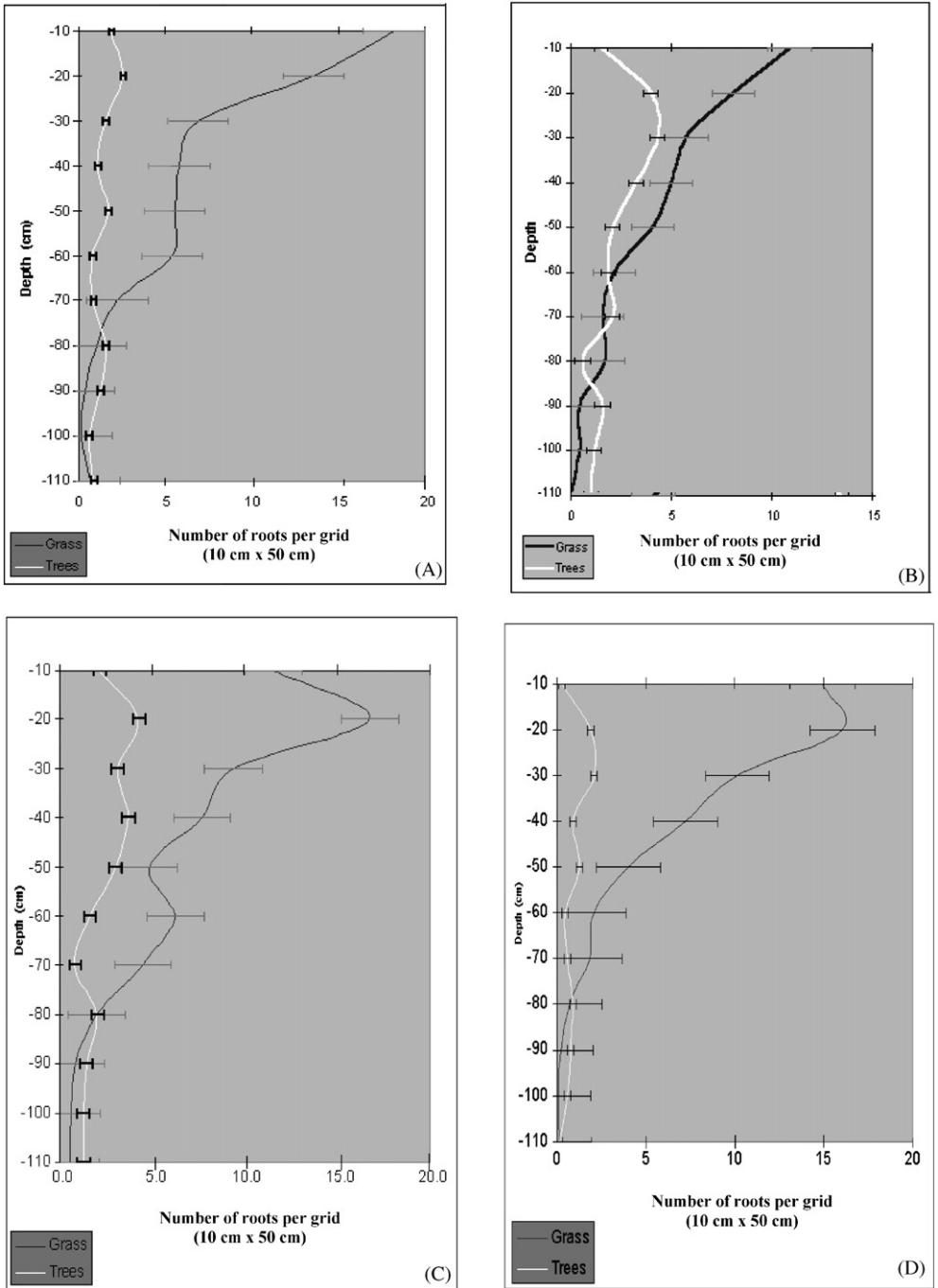
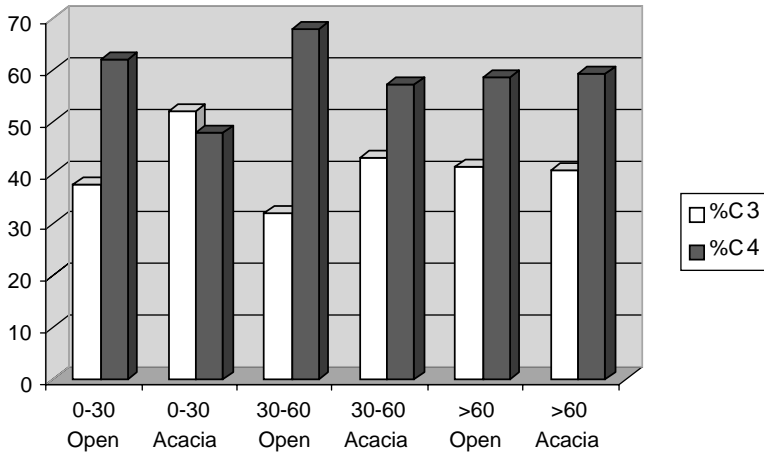


Figure 1. Root distribution per depth: (A) site 1—Ghanzi, (B) site 2—Ghanzi (under tree canopy), (C) site 3—Tshane (under tree canopy); (D) site 4—Tshane. Note: horizontal bars denote standard error.

first 30-cm of the soil. Under the tree canopy, however, the tree and grass roots intertwine in a rope-like fashion after 60-cm depth. In addition, the two pits at Ghanzi depict that the grass root biomass dips from the start, and attained a gentle curve after

Table 1. Depth and length of *T. sericea*'s tap root (Note that at trees 3 and 10, the end of the root was not reached)

Tree number	Root depth before horizontal turn (cm)	Horizontal length of root (cm)	Depth at end of root (cm)
1	11	330	42
2	5	550	4
3	15	> 950	70
4	3	400	56
5	10	570	60
6	10	812	5
7	4	400	4
8	5	500	4
9	10	400	40
10	12	> 900	60
Average	8.5		

**Figure 2.** Proportion of C₃ (shrubs or trees) and C₄ (grasses) derived organic matter in different soil layers of pits under *A. mellifera* and between the canopies.

30 cm. Further south, at the site near Tshane, a distinctive peak both for the tree and grass is discernable at 20 cm. At around 80 cm, the tree curve surpasses the grass curve with a small margin, averaging 0.5 and 0.3 roots per 500 cm² (10 cm × 50 cm) at sites 3 and 4, respectively. Two-thirds of the grass roots are found between the surface and the depth of 36 cm, while trees deploy nearly half (48%) of their roots at the same depth range. In comparison, two-thirds of the tree roots are distributed within the first 62-cm depth, where grasses dispense a total of 86% of their roots.

The root exposures of the *T. sericea* showed that what initially started as, and ought to be tap roots ended their vertical rooting at a depth ranging between 3 and 15 cm and turned approximately 90° angle to become regular lateral roots. The roots have a horizontal extend ranging between 3.3 m to more than 9.5 m, and a depth at the root's end of 4–70 cm (Table 1). This pattern of tap rootless was found in all 10 root exposures carried out at both sites.

The results from the mixing equation show that tree-derived soil organic matter (SOM) is more abundant only in the surface soil under *A. mellifera*. In all the other

Table 2. $\delta^{13}\text{C}$ of C_3 (shrubs or trees) and C_4 (grasses) roots, and total organic matter in different soil layers of pits under *A. mellifera* and between the canopies

	$\delta^{13}\text{C}$ Acacia pit	$\delta^{13}\text{C}$ Open pit	%C Acacia pit	%C Open pit
Soil depth				
0–30 cm	–18.4	–16.8	0.27	0.17
30–60 cm	–17.3	–16.1	0.19	0.15
> 60 cm	–17.1	–17.1	0.15	0.12
End members				
C_4 : grass root	—	–12.8	—	—
C_3 : <i>A. mel.</i> Root	–23.9	—	—	—

samples, grass-derived SOM dominates (Fig. 2). The $\delta^{13}\text{C}$ values used for the mixing equations are shown in Table 2. The percent carbon data indicates a higher C content in the surface soil under *Acacia*, and decreasing C content with depth in both pits (Table 2).

Discussion

The root profiles exhibited more abundant and dominant grass roots in the surface soil, especially down to 30-cm depth, even in the pits located under the tree canopies (Fig. 1). However, trees do not have a clear dominance over grasses at deeper layers, refuting the hypothesis that trees are better competitors for water in the deeper soil layers. Moreover, the absence of tap roots in *T. sericea* and the dominance of the *A. mellifera*, a shallow-rooted species (Tolsma *et al.*, 1987) point out the importance of the upper soil layers for water resources. It is noteworthy that *Terminalia sericea* presents tap root beyond a depth of 80-cm in other Southern African ecosystems with relatively higher precipitation, such as South Africa (Lihavha, unpublished data) and Namibia (Hipondoka, unpublished data). Tree roots are more abundant under tree canopies than between the canopies, but even there, grass roots dominate. The data insinuate that grasses are spatially better competitors for water in the surface, and trees do not show a clear advantage at deep layers, given that the error bars of both overlap.

The isotopic data indicate proportion of biomass derived from each, trees and grasses, and suggest a pattern similar to the root profiles (Fig. 2). In all but one sample, SOM is derived from grasses in a higher proportion than from trees. The exception is the surface soil under *A. mellifera*, which also has the highest carbon content (Table 2). These values are possibly affected by the input of leaf litter from the surface, instead of reflecting exclusively the root biomass. The same is true for the surface of the pit between the canopies, which can be affected by grass litter fall. However, the SOM at deeper layers is likely to be derived mainly from roots, being a better indicator of tree–grass root dynamics. Overall, the $\delta^{13}\text{C}$ analysis points to a dominance of grass root biomass in all, but one, soil layers.

The root profile and isotopic data do not support Walter's (1971) hypothesis, given that trees do not seem to have a better advantage at deeper layers. The question arises as to how are trees still a typical feature of savannas, instead of being out-competed by grasses in water uptake. A model that introduces a third axis of niche separation—time, could better explain the co-dominance of trees and grasses in savannas. The largest degree of niche separation between trees and grasses could exist during the time at which their roots are active. Trees develop a full leaf canopy, and presumably a root system of similar extension, within weeks of the first rains, while grasses reach

their peak after only a few months (Scholes & Walker, 1993). The early growth of trees is permitted by a carry-over of carbohydrates, nutrients and water from the previous season, which gives trees previous access to water during the early wet season. However, trees must maintain a low stomatal conductance to be more water-use efficient, which results in a lower peak photosynthetic rate than that of grasses. Grasses have a much denser root network, which gives them a better access to water when it is present and grasses are fully developed (Scholes & Walker, 1993).

An engaging pattern observed in Botswana's overgrazed areas is the dominance of shallow-rooted shrubs, among which *A. mellifera* is very common, after the removal of the grass layer by cattle (Tolsma *et al.*, 1987; Skarpe, 1990; Ringrose *et al.*, 1996). This state, commonly called 'bush encroachment' is thought to be a self-sustaining system, which is not easily removed, even with the elimination of cattle. The current hypothesis suggests that once grass cover is decreased, shallow-rooted shrubs have better access to surface water and nutrients, and create areas of low nutrient and water availability between the canopies. This prevents the re-establishment of grasses, even when cattle are removed from the ecosystem (Skarpe, 1990; Schlesinger *et al.*, 1990). This notion concurs with our results on tree-grass root distribution, as it suggests that grasses out-compete shrubs and trees in respect to water uptake, and only when they are removed, can trees and shrubs dominate the ecosystem. There are other competitive interactions that maintain the balance between trees and grasses, which include competition for resources during seedling establishment and recruitment. Any change in the balance of tree-grass cover and resource availability during recruitment, could cause the system to move to a dominance of either grasses or trees.

Conclusions

In this study, the isotopic composition of soil organic matter and root profiles suggest that most of the activities regarding water uptake are performed near the soil surface. Moreover, the data revealed that grass roots are more abundant than tree roots in the surface layers, implying that the former are better competitors for water in the spatial dimension, particularly in mature communities. Subsequently, our hypothesis is partially supported, as there was no indication of trees exploiting better the water resources at deeper soil layers. Rather, even shrubs that have tap roots in areas of relatively higher precipitation, appeared to have adapted to a more drier climate by presenting an opportunistic phenomena of having no tap roots. The dominance of shallow root shrubs in overgrazed areas, would therefore mean that the best strategy for shrubs in these environments is to tap water from the surface soil layers, where grasses, if present and active, are more successful than trees. Thus, the co-existence of trees and grasses in Southern African savannas should be explained considering other factors, such as niche partitioning in the temporal dimension, capillary rise or competition during seedling establishment.

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