



ROOT STRUCTURE OF SHRUB ENCROACHING PLANTS IN THE AFRICAN SAVANNAS: INSIGHTS FROM *TERMINALIA SERICEA* (BURCH. EX DC) ACROSS A CLIMATE GRADIENT IN THE KALAHARI BASIN

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Abstract.

The competitive exclusion of grasses by shrubs in the African savannas is an elusive phenomenon. The popular concept, Walter's two-layer hypothesis is still inconclusive. This concept suggests that trees and shrubs in the savannas develop deeper roots to avoid competition with grasses. This study was designed to test this hypothesis by investigating the root system of *T. sericea*, one of the common encroaching species in the Kalahari Basin. Using direct excavation method, 39 shrubs were randomly excavated across the Kalahari Basin. Results revealed contrasting rooting strategies by *T. sericea* under varying climatic conditions. Drier areas exhibit largely lateral roots, whereas moist sites were dominated by dual root systems. These findings are not consistent with the existing framework which argues that savanna shrubs are essentially deeper rooted. Instead, results support an emerging hypothesis that certain savanna shrubs opportunistically adapt their root systems in response to the prevailing environmental constraints such as water availability. A shrub such as *T. sericea* with lateral roots abundantly deployed in shallow soil depth points to a direct competition exclusion with grasses in the Kalahari Basin. It is probable that the occurrence of shrub encroachment by *T. sericea* is a manifestation of this competitive interaction, contrary to the root niche partitioning hypothesis. Future savanna models need to be cognizant of the variation in savanna shrubs roots system architecture and its potential implications on tree-grass coexistence and competition.

Key words: Competition; interspecific variability; root trait; shrub; terminal depth.

INTRODUCTION

The encroachment of shrubs, considered as a conversion of open grass savannas to shrub-dominated thickets, is a major socio-economic and ecological problem in Southern African savannas, a biome where both shrubs and grasses coexist harmoniously under natural settings (Angassa 2014; Eldridge et al. 2011; Kgosikoma and Mogotsi 2013; Kulmatiski and Beard 2013; Van Auken 2009). The ecological mechanisms which underpin the competitive interactions between shrubs and grasses resulting in shrub encroachment are not well understood. Various contrasting and diverging theories (Accatino et al. 2010; Gil-Romera et al. 2010; Jeltsch et al. 1996; Jeltsch et al. 2000; Sankaran et al. 2004; Scholes and Archer 1997) have been proposed, but the mechanisms under which shrub encroachment occurs are still inconclusive.

Probing into the belowground ecology of savanna plants, particularly those responsible for shrub encroachment, such as *Terminalia sericea* Burch. ex

DC, may reveal critical insights into understanding shrub encroachment. Earlier studies (Scholes and Walker 1993; Walker et al. 1981; Walker and Noy-Meir 1982; Ward et al. 2013) argued that under natural settings, shrubs and grasses coexist harmoniously because of a natural regulating mechanism of vertical root niche partitioning, such that shrubs develop deeper root systems to tap water from the groundwater aquifer, while grasses extract water from the shallow soil subsurface creating an equilibrium coexistence. Collectively known as "Walter's two-layer hypothesis" or alternative "root niche-partitioning hypothesis" (Ward et al. 2013), this concept further argues that overgrazing, a human-induced activity, disrupts this harmonious coexistence by reducing grass cover, which consequently create a competitive advantage for shrubs because of increases in water percolation to recharge the water table. This hypothesis put root systems of savanna shrubs at the centre of the savanna debate and effectively to continued scrutiny. Although studies (Hipondoka et al.

2003; Hipondoka and Versfeld 2006; Kulmatiski and Beard 2013; Smit and Rethman, 1998) that followed to interrogate this hypothesis, scant attention has been devoted to the role of the lateral roots of savanna shrubs, particularly those responsible for shrub encroachment. Knowledge of lateral roots may provide clues to the below-ground interactions between shrubs and grasses that may influence the long-term behaviours of the savannas.

This paper assessed how *T. sericea*, one of the most frequent encroaching shrubs in Namibia, develops its root system along the rainfall gradient of the Kalahari Basin in Southern Africa. This study test the hypothesis that *T. sericea* adapt its root system in accordance with the prevailing sub-climatic setting.

MATERIALS AND METHODS

2.1 Study area

This study was conducted in the Kalahari Basin (KB), a semi-arid to sub-humid environment covering approximately 2.5 million km² (Thomas and Shaw 1991). The KB is found in Southern Africa, extending from 14° to 28° S and from 21° to 28° E (Thomas and Shaw, 1991). The KB is dominated by a thick layer of arenosol sand of both fluvial and aeolian origin, known for its coarse texture, low water-holding capacity, rapid permeability, and low nutrient content (Thomas and Shaw, 1991). The climate of the KB is described as arid along the south-eastern edge, to semi-arid along the central part of the basin (Frssaf and Crimp, 1998). Sub-humid and humid cli-

matic conditions are found in the northern parts of the basin covering parts of northern Zambia and the southern Democratic Republic of Congo (DRC). The climate of the Kalahari Basin follows both a north-south and east-west gradient. Its climate is regulated by several atmospheric circulations, such as the migration of the Inter-tropical Convergence Zone (ITCZ) and its interaction with the Congo Air Boundary (CAB) over the subcontinent, which brings convective summer rainfall between October and March, and the high-pressure system responsible for the dry conditions during winter (Frssaf and Crimp, 1998). Rainfall variation is the most conspicuous indicator of the KB’s climate gradient. For example, the northern edge of the basin, south of the DRC, receives mean annual precipitation of approximately 1500 mm annually, whereas the southernmost edge of the basin along the Orange River receives less than 200 mm annually. The eastern edge of the basin located in Zimbabwe receives mean precipitation of 700 mm annually, while the western edge of the basin in Namibia, located just before Kaokoveld, receives precipitation of approximately 250 mm annually. Such harsh climatic conditions indicate that the Kalahari Basin is a dry environment in which plants grow. Within the Kalahari Basin, this study was conducted along the east-west Kalahari transect in Namibia (Fig. 1). For the purpose of this study, sites 1,2 and 3 were classified as “drier sub-climatic zone”, while sites 4 ,5 and 6 were classified as “mesic sub climatic zone”. Lastly, sites 7 and 8 were classified

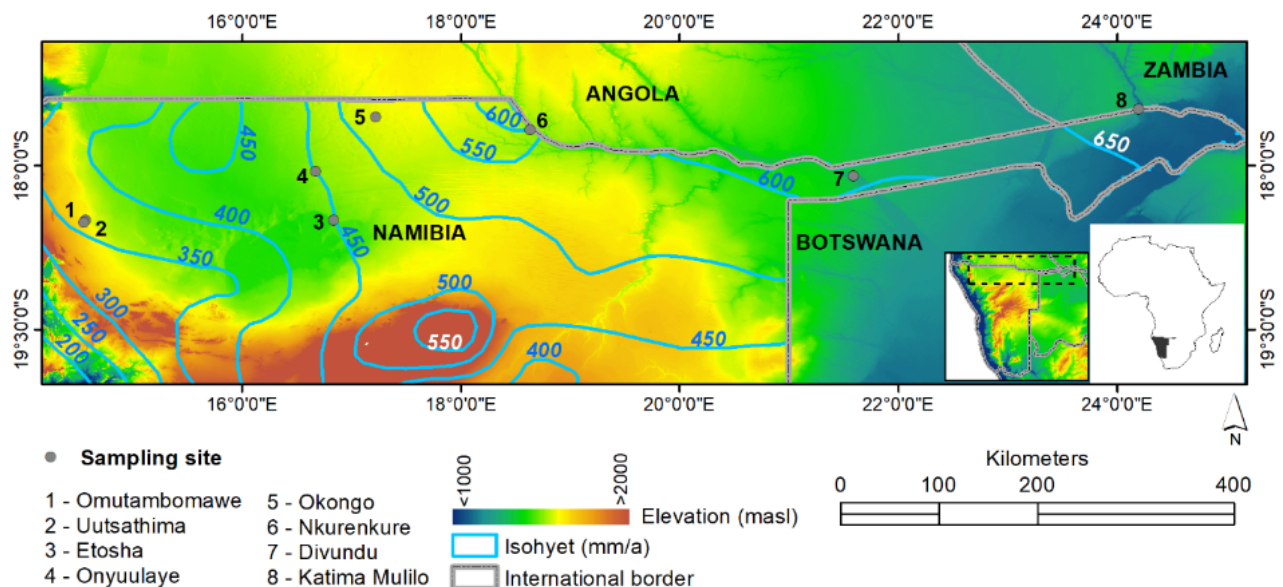


Figure 1: Map showing the study sites along the east-west Kalahari rainfall gradient.

as “wetter sub climatic zone”. All these zones were classified based on the mean annual precipitation.

Groundwater aquifers around the study area are located at various depths, depending on the prevailing climate and local geological setting. For example, Omutambomawe and Uutsathima are located in the Omusati Multi-zoned Aquifer (KOM) with a water depth of 10 to 60 m, and contained within the major Formations of the Kalahari sequence, with rocks ranging from consolidated to semi-consolidated sediments made up of sand, clay, and calcrete/dolomite, but also of large evaporitic deposits (Bittner 2006). The Etosha site is located along the Oshivelo multi-layered aquifer located at a depth of 30 m to 150 m (Bittner 2006). Onyuulaye and Okongo are located in the middle of the Ohangwena multi-layered aquifer, with an estimated depth of 60 m to 160 m (Bittner, 2006). Nkurenkure, Divundu and Katima sites lies on top of a major Kalahari aquifer with an estimated average depth of about 20 m (Christelis and Struckmeier, 2001).

Vegetation in the Kalahari can be broadly classified as savanna, the diversity, structure and biomass of which change across the rainfall gradient (Scholes et al. 2002). Its arid western edge, where Omutambomawe and Uutsathima are located, is dominated by shrubs such as *T. sericea*, *S. mellifera*, *Senegalia nebrownii*, *Vachellia erioloba*, *Elephantorrhiza suffruticosa*, *Bauhinia petersiana*, *Albizia anthelmintica*, *Catophractes alexandri*, *Croton gratissimus*, *Grewia flavescens*, *Colophospermum mopane*, *Searsia marlothii* and *Vachellia reficiens*. Because of the low rainfall, these plants are predominantly multi-stemmed shrubs, up to about 3 m tall. Dominant grass species in these two study sites are *Antheophora schinzii*, *Heteropogon contortus*, *Tragus racemosus*, *Cynodon dactylon*, *Dactyloctenium aegyptium*, *Sporobolus ioclados*, and *Stipagrostis uniplumis*. Other dominant species known to occur in the area are *Eragrostis rotifer*, *Aristida adscensionis*, *Schmidia kalahariensis*, and *Eragrostis dinteri* (Klaassen and Craven 2003; Müller 2007). Most of these grass species are highly palatable and thus the study area serves as good grazing land for communal farmers from the Omusati Region. However, grazing pressure is kept low because of the absence of permanent water sources.

The Etosha site is located in the Kalahari sandveld along the northern boundaries of the Etosha National Park. Unlike Omutambomawe and Uut-

sathima, the vegetation structure at Etosha is shared between shrubs and trees and is dominated by *Commiphora glandulosa*, *Commiphora angolensis*, *G. flavescens*, *T. sericea*, *Ximenia americana* and *C. gratissimus*. The Etosha site receives more rainfall than Omutambomawe and Uutsathima, and thus the density of woody species is higher. Onyuulaye and Okongo sites are located in the north-eastern Kalahari woodland, which is characterised by dense deciduous tree species, such as *T. sericea*, *Burkea africana*, *V. erioloba*, *C. gratissimus*, *B. albitrunca*, *Dichrostachys cinerea*, *B. petersiana* and *Mundulea sericea*. Compared to the previously discussed sites, vegetation growth form here demonstrates a change from dominant shrubs to trees.

The dominant grass species found in the aforesaid areas are *A. schinzii*, *H. contortus*, *Tragus racemosus*, *C. dactylon*, *D. aegyptium*, *Sporobolus ioclados*, and *Stipagrostis uniplumis*. Both Onyuulaye and Okongo are densely populated and support a large number of livestock, resulting in noticeable overgrazing. Further eastward, toward Nkurenkure, Divundu, and Katima Mulilo, vegetation changes in terms of dominant deciduous species. For example, Divundu is dominated by *B. albitrunca*, *B. africana*, *B. petersiana*, *Baphia massaiensis*, *P. angolensis*, *Philenotera nelsii*, *C. angolensis*, *C. gratissimus*, *Ochuna pulchra* and *Combretum imberbe*. The Katima Mulilo and Divundu sites have the largest mean annual precipitation and these two sites are dominated by woody species such as *Schinziophyton rautanenii*, *T. sericea*, *P. angolensis*, *B. plurijuga*, *Combretum collinum*, *B. massaiensis*, and *T. sericea*. The grass layer is dominated by *Chloris virgate*, *Cynodon dactylon*, *Dactyloctenium giganteum*, *Panicum kalahariense*, and *Schmidia pappophoroides* Klaassen, *Andropogon spp*, *Heteropogon contortus*, and *Perotis patens*. Besides the rainfall gradient, the Kalahari Basin was selected as a suitable area for this study because the landscape satisfies Walter’s two-layer hypothesis preconditions such as aridity, flat topography, a sandy landscape, and limited edaphic factors (Walter and Mueller-Dombois 1971; Ward et al. 2013).

2.2 Studied species

The species *T. sericea* is small to medium sized deciduous woody plant which grow as a shrub and as a tree depending on the climate. It is usually 4-6 m in height, but may reach 10 m (Curtis 2005). It has

branches growing horizontally, giving such a plant's crown a layered appearance. Its bark is often dark grey and deeply fissured (Curtis 2005). Its leaves are clustered toward the end of each branchlet, and obovate-elliptic in shape, which are often four times longer than wide and occurs mainly between October and July (Curtis 2005). Such leaves are green in colour with silky hairs. It grow pink to rose-red fruits up to 35 mm long mostly between October and November each year, continuing until April the following year. *T. sericea* is widespread in sandy plains of Southern Africa often along dry watercourses, where it is considered a pioneer species. Parts of *T. sericea* are used for several purposes. This species is the preferred timber for poles used in construction of traditional houses and fencing because it is resistant to termites (Maesen et al. 1996). Such poles are soaked in water for several weeks to remove the sap, to increase the durability. The timber is also used to manufacture ox yokes (Maesen et al. 1996). Its roots are used for various medicinal purposes (Curtis 2005; Maesen et al. 1996). In Namibia *T. sericea* is considered as an encroacher species, responsible for thickening up of large track of land in the Kalahari (De Klerk 2004) to the detrimental of rangeland productivity.

2.3 Data collection

A total of 39 *T. sericea* shrubs, representing a total of 13 individual shrubs from each-sub climatic zone, were randomly selected, and their roots were excavated using a spade, a method described by Böhm (1979) from three sub climatic zones in the Kalahari Basin. Prior to excavation, above-ground measurement of attributes such as canopy diameter, standing height, and stem diameter were captured. Stem diameter was measured as the thickness of the stem at the base, measured using Vernier callipers. Canopy diameter was measured using flexible measuring tape along the canopy's widest sides. Excavation started with direct mechanical removal of soil covering the root system by digging with a spade to expose the root system. In order to make sure that lateral roots were not cut during the excavation process, excavation started at the stem base to identify the number of lateral roots present. Thereafter, each identified lateral root was excavated to its full horizontal extent. A trench was also dug to determine the tap root depth. Where appropriate, the taproot was excavated to a maximum depth of 1 m owing to the laborious nature of the exercise. The exposure of the

excavated shrub's root system allowed morphometric measurement of attributes such as lateral rooting depth lateral root diameter and lateral root's terminal depth.

Data analysis was done in R 3.3.1 (R Development Core Team 2019), using a one-way ANOVA. Prior to data analysis, and as a prerequisite for parametric tests, a normality test was done using the Shapiro-Wilk test. Results were considered significant at $p < 0.05$ alpha level. For ANOVA, F statistics reported include degree of freedom and residual. All post hoc pairwise comparisons were done using Tukey's honest significant difference test. Chi square test of association was also used test the association between root system architecture type and sub climatic zone.

RESULTS

3.1 Shrub height, canopy diameter and stem diameter

The above-ground morphometric properties of the excavated shrubs varied between the three sub-climatic zones. For example, shrub height was significantly different between the drier, mesic and wetter sub-climatic zones ($F_{(2,115)} = 5.16, p < 0.001$). Similarly, canopy diameter was significantly different between the drier, mesic and wetter sub-climatic zones ($F_{(2,115)} = 16.87, p < 0.001$). In addition, stem diameter was significantly different between the sub-climatic zones ($F_{(2,115)} = 5.96, p < 0.001$). Pairwise post hoc comparisons using Tukey's honest significant difference test revealed that the mean height for mesic (201.2 ± 13.4 cm) was significantly higher than that of wetter (139.8 ± 6.4 cm) so is the mean height for drier (189.0 ± 6.4 cm) compared to wetter sub climatic zones. Unlike mean height, pair wise comparison showed that the mean canopy diameter for drier (264.5 ± 26.0), mesic (180.0 ± 11.6 cm), and wetter (109.2 ± 8.1 cm) were each significantly different. Lastly, pairwise comparison indicated that mean stem diameter for wetter (43.8 ± 9.4 mm) was significantly higher than that of mesic (21.5 ± 0.7 mm). In terms of stem diameter, the mesic and drier sub-climatic zones so is the wetter and mesic, but there was no significant difference between the mean stem diameter for wetter and drier (34.4 ± 2.9 mm).

3.2 Root structure of *T. sericea* shrub across the climate gradient

The excavated shrubs exhibited two types of root system architecture, a dual root system, comprising

both lateral roots and a taproot, and a lateral root system, comprising strictly lateral roots (Figure 2). The proportion of *T. sericea* shrubs with a dual root system as compared to those with a lateral root system (Table 1, Fig. 3). Among the 39 *T. sericea* shrubs excavated, 67% (n= 26) had a dual root system, while remaining 33% (n = 13) had a lateral root system. Of all the shrubs with a lateral root system, the majority (61.5%) were excavated from a drier sub climatic zone. This was dominantly found at Uutsathima and Omutambomawe, where all, but one shrub excavated exhibited lateral root system. Meanwhile, of all the shrubs with a dual root system, the majority (42.2%) were excavated from a wetter sub climate zone, followed by mesic (38.4%). For instance, at Nkurenkure, only two of the six shrubs excavated at each of the two study sites had a lateral root system. In the drier zone, only 19% of the shrubs with a dual root system were excavated. Those figures translate in a ratio of 2:1 in a drier sub climatic zone to 1:3 in a mesic, and 1:6 in a wetter sub climatic zone, a change in ratio between lateral rooted shrubs and dual rooted shrubs across the Kalahari rainfall gradient. A chi squared test found a significant association between root system type and sub-climatic zone $X^2 (2,39)= 7.15, p= 0.02$.

Fig. 4 illustrates the variation in lateral rooting depth and terminal depth across the three sub-climatic zones. ANOVA results revealed a significant difference in lateral rooting depth between the three sub-climatic zones ($F_{(2, 115)}= 6.97, p < 0.001$). Further pairwise comparison using Tukey’s honest significant difference test showed the significant difference ($p < 0.001$) between the wetter and drier zones. The shallowest individual lateral root development was recorded at a depth of 4 cm from the soil surface at Uutsathima, a drier site, while the deepest individual lateral root developed at a depth of 39 cm at Katima Mulilo, a wetter site. Similarly, the lowest mean lateral root depths (7.4 ± 1.0 cm) were recorded at Uutsathima, followed by Omutambomawe (9.6 ± 1.0 cm), then the depth increased progressively at Okongo, a mesic site, reaching a maximum mean depth of 17.8 ± 3.0 cm at Katima Mulilo, a wetter site (Fig. 4). Terminal depth exhibited a pattern similar to lateral rooting depth. Results showed a significant difference ($F_{(2, 115)} = 10.79, p < .001$) between the drier, mesic and wetter sub-climatic zones for terminal depth, of which the pairwise significant difference was between the mean diameter for wetter (9.2 ± 0.9 mm) and drier zones (12.3 ± 0.7 mm), as well as the mean diameter between wetter and mesic zones (12.4 ± 1.1 mm). No significant

Table. 1. Proportion of lateral rooted shrubs and dual rooted shrubs along the Kalahari Transect

Sub climatic zones	Lateral system	Dual system	Ratio
Drier	8	5	2:1
Mesic	3	10	1:3
Wetter	2	11	1:6
Grand Total	13	26	1:2
%	33.3%	66.7%	NA

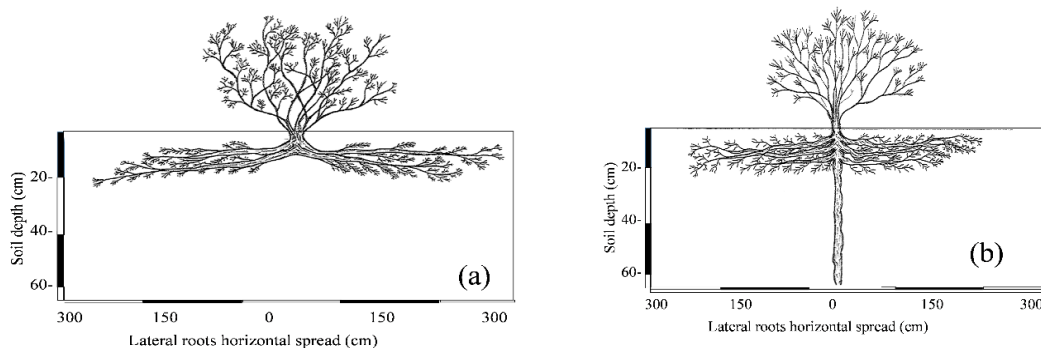


Figure 2: Various root system architecture exhibited by *T. sericea* shrubs (a) lateral root system, (b) dual root system.



Figure 3: Excavated lateral roots of *T. sericea* shrub in the Kalahari.

difference was found between mesic and drier zones. The shallowest lateral root terminal depth was found at 6 cm at Okongo, a drier site, while the deepest lateral root terminal depth was found at 70 cm at Divundu, a wetter site. Equally the wetter sub climatic zone exhibited a higher variation in terminal depth as compared to the mesic and drier sub-climatic zones.

The morphometric structure of the *T. sericea* shrub’s lateral roots can also be described in terms of its lateral root diameter. ANOVA results showed that the excavated lateral roots varied significantly ($F_{(2, 115)} = 5.42, p < .001$) between the drier, mesic and wetter sub-climatic zones. Tukey’s honest significant difference test showed that the significant difference was found between the wetter and drier zones. The variation in lateral root diameter per each sub climatic zone is illustrated in fig. 5, which shows that the

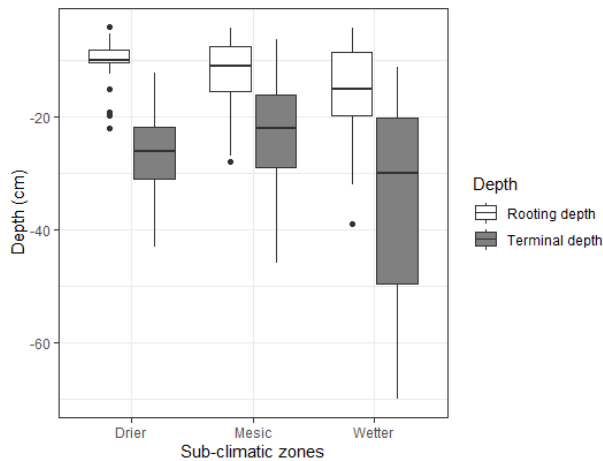


Figure 4: Lateral rooting depth at the base and an elongated terminal depth of *T. sericea* shrubs.

largest mean lateral root diameter was recorded in the drier zone, followed by mesic and lastly the wetter zone.

The thickness of lateral roots, using diameter as an indicator, was significantly influenced by the interaction ($F_{(2,113)} = 4.78, p < .01$) of the sub-climatic zone and terminal depth. Figure 6 illustrates the relationship between lateral root diameter versus lateral root depth and lateral root terminal depth, and how it interacts with the sub-climatic zones, drier (a), mesic (b) and wetter (c) zones. For all zone, such as that of drier, mesic and wetter, nearly all lateral roots, irrespective of diameter, developed within a depth range

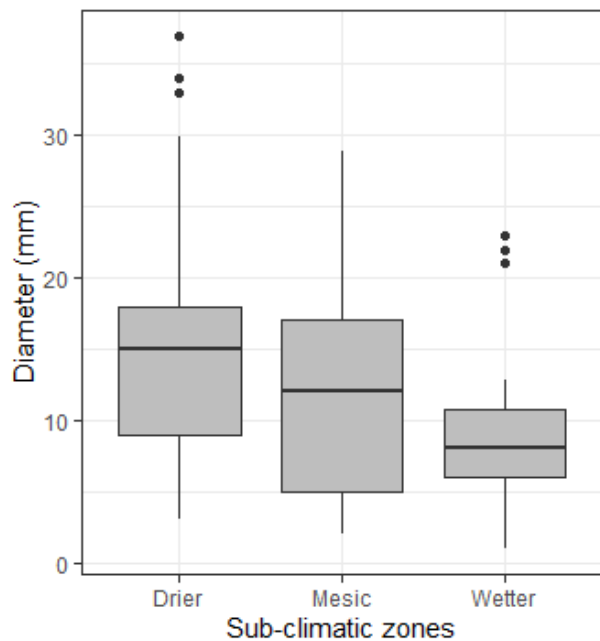


Figure 5: Variation in diameter for lateral roots measured at the base.

of 5 cm to 30 cm. However, an interaction between the terminal depth and sub-climatic zone yield a different pattern. For example, in the drier sub-climatic zones, lateral roots had various terminal depths, irrespective of their diameter. However, for a mesic sub-climatic zone, larger lateral roots of up to 30 mm were deployed at a deeper terminal depth of approximately 40 cm than smaller lateral roots with a diameter of less than 10 mm, whose terminal depth was within an average of 20 cm. The wetter zone demonstrated a similar relationship exhibited by the mesic sites where larger lateral roots had deeper terminal depth, but there were also extremely smaller lateral roots in terms of diameter whose terminal depth was

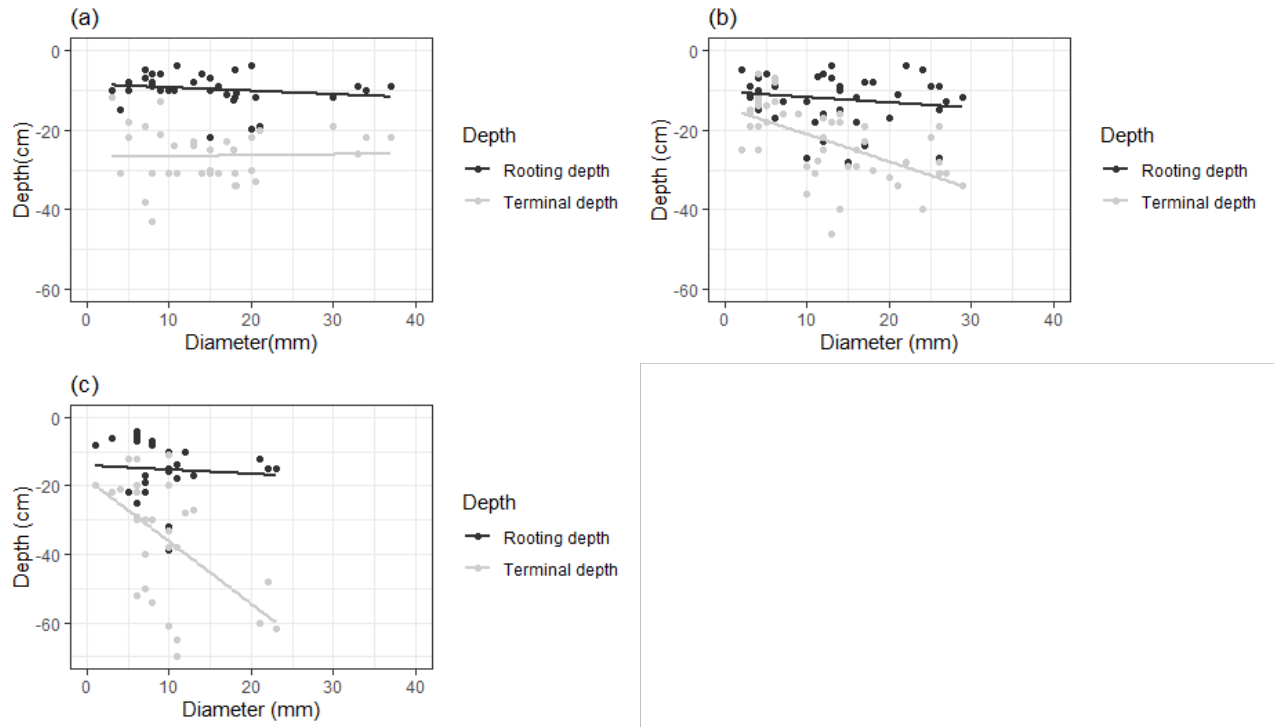


Figure 6: Scatter plots with best-fit line plots illustrating how *T. sericea* shrub’s lateral rooting depth and terminal depth changes with lateral root diameter. Plot (a) presents data from drier zone, while plot (b) and (c) provide data from mesic and wetter zone, respectively.

below 50 cm. Overall, while lateral root depth does not necessarily change with diameter, lateral root terminal depth changes according to the diameter and also along the rainfall gradient, particularly with an increase in terminal depth toward the mesic and wetter sites.

DISCUSSION

The main objective of this study was to investigate how *T. sericea*, one of the common encroaching shrubs in Namibia, develops its root system along the rainfall gradient in the Kalahari Basin. This study was done to effectively test the hypothesis that savanna shrubs are essentially tap-rooted, a niche-partitioning mechanism used by shrubs to evade competition with grasses in the shallow soil layer. Findings of this study did not support Walter’s two-layer hypothesis (Scholes and Walker 1993; Walker et al. 1981; Walker and Noy-Meir 1982; Ward et al. 2013). The study revealed that *T. sericea* is not essentially deeper rooted. For example, this study found that *T. sericea* shrubs along drier areas such as Omutambomawe and Utsathima tend to develop lateral roots at shallower depths than *T. sericea* found in wetter areas, such as Divundu and Katima Mulilo. Considering that the

depth at which *T. sericea* shrubs develop their lateral roots significantly changed along the rainfall gradient, suggests this plant develop its root system is response to the prevailing climatic conditions, which in turns influences soil moisture regimes. In addition, the diameter of such lateral roots did not significantly differ in terms of root depth, because all lateral roots were largely concentrated within a 20-cm soil layer, irrespective of their diameter. The presence of lateral roots of various diameters within the same depth suggests that resources at that depth are critical, right from the onset of the plant’s growth to maturity. The number of lateral roots developing from the tap root decreased significantly with depth up to 40 cm. Beyond that point, no lateral rooting was recorded. Equally, the absence of a taproot in some *T. sericea* shrubs, especially along the drier parts of the study areas, implies that a deep taproot is not a feature central to the survival of *T. sericea* shrubs.

These findings supports the views of Hipondoka et al. (2003) and Hipondoka and Versfeld (2006) that savanna plants’ root systems are not species specific but respond opportunistically to various prevailing environmental conditions, such as soil moisture. The findings also support the argument that the devel-

opment process of root systems is characterised by great plasticity because it is an evolutionary product of spatio-temporal variation in environmental resource supply, genetic drivers, and associated environmental constraints to growth for each individual plant (Grossman and Rice, 2012, Mou et al 2013; Zanetti 2015). The development of shallow lateral roots may contribute to competitive exclusion (Armstrong and McGehee 1980; Gause 1934; Hardin 1960) between shrubs species such as *T. sericea* and grasses, resulting in shrub encroachment. Eco-hydrological studies in the Kalahari (Hipondoka et al 2003) and elsewhere in similar environments (February and Higgins 2010; Kambatuku et al 2013) suggest that grasses deploy their roots beyond 4 cm depth, which in turn result in vertical niche competition between the lateral roots of *T. sericea* and those of grasses. The findings of this study are consistent with those of neotropical savannas of South America where savanna plants exhibit plastic behaviours with respect to water use strategies across environmental gradients (Rossatto et al. 2014)

CONCLUSION

Understanding the below-ground life of savanna plants may reveal new insights to understand the mechanisms under which shrub encroachment occurs. This study reveals that *T. sericea*, an encroaching shrub in Namibia, develops a substantial number of lateral roots within the shallower soil layers, particularly in the drier part of the Kalahari, creating a niche overlap with grasses. This create a likelihood of competitive interaction between trees and grasses, as predicted by the competitive exclusion principle. These findings suggest that Walter's two-layer hypothesis may be an oversimplification of rooting patterns among savanna plants because the hypothesis overlooks the issue of plasticity in plant root development in response to prevailing environmental conditions. Modifications to include such dynamics may be necessary to enhance its application to the savanna.

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