

## Root system of *Terminalia sericea* shrubs across rainfall gradient in a semi-arid environment of Etosha National Park, Namibia

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### Abstract

Unlike any other biome, savannas consist of both trees and grasses in a persistent and equitable manner. This unique mixture of two different life forms attracted scientific scrutiny for decades. Embedded in this body of research studies is bush encroachment that affects many overgrazed savannas. Despite scientific efforts, however, the underlying factors that shape the functioning of this biome and govern bush encroachment remain largely elusive. *Terminalia sericea* is one such encroaching woody plant at the expense of herbaceous layers in overgrazed areas of southern Africa. Recent studies indicated a potential link between rainfall amount and opportunistic rooting systems of encroaching species for harvesting near-surface soil water. This study was thus carried out to specifically test this theory in Etosha National Park across a rainfall gradient. A total of 31 *T. sericea* shrubs were excavated to examine their rooting systems. Results show that although all plants surveyed showed a shallow root system, only two out of 15 shrubs in the drier section of the park exhibited a taproot. In contrast, half of the 16 shrubs studied in the wetter part displayed a taproot. This suggests that *T. sericea* shrubs employ a rooting strategy attuned to local climatic conditions. A differential competition between woody plants and the herbaceous layers for soil water is thus variably enhanced, which might act as one of the feeding mechanisms for bush encroachment. Future ecological models of the savanna ecosystems should therefore recognise variation in the rooting characteristics of this, and possibly other bush encroaching plants, in response to precipitation.

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### 1. Introduction

Terrestrial plants make use of their roots for foraging water and nutrients from the soil. In the savanna ecosystems, these two resources are regarded as the main limiting factors in plant developments

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(Walter, 1971; Sarmiento, 1984; Scholes and Walker, 1993; Belsky, 1994). Water in particular, is thought to control the duration of the growth period, whilst nutrients govern the growth rate during that period (Scholes and Walker, 1993). Savannas are uniquely different from all other biomes because they are characterized by a co-dominance of trees and grasses. As a result, formidable bodies of research studies have specifically investigated the interactions between these two contradictory plant life forms and the functioning of savannas (e.g. Walter, 1971; Walker and Noy-Meir, 1982; Sarmiento, 1984; Skarpe, 1992; Scholes and Walker, 1993; Belsky, 1994). These studies and others gave rise to diverse and competing ecological models of savannas, categorized into equilibrium, non-equilibrium and disequilibrium models, as reviewed by Scholes and Archer (1997) and more recently by Sankaran et al. (2004). Despite the differences, however, a unifying variable among plausible models is the role of soil water in the functioning of savannas.

Complicating the efforts in understanding the functioning of savannas is a superimposed utilization of these areas as grazing lands under varying management styles. In particular, a common feature in heavy grazed areas is a drastic decrease in herbaceous species, while woody plants increase in density and abundance (e.g. Skarpe, 1990; Smit and Rethman, 2000; Moolele et al., 2002), thus changing the perceived normative vegetation structure of savannas. Although this phenomenon, commonly known as bush or brush encroachment, is linked to overgrazing and the absence of fires (Skarpe, 1990; Scholes and Walker, 1993), the exact physical factors that govern its temporal and spatial nature are little understood. Notwithstanding, certain advances have been made and documented, for example, a typical shallow root system of selected encroaching species, such as *Acacia mellifera* (Cole and Brown, 1976), *Colospermum mopane* (Smit and Rethman, 1998) and *Terminalia sericea* (Cole and Brown, 1976; Rutherford, 1983; Hipondoka et al., 2003), in southern African savannas. Mutually, these findings implied a direct competition for soil water and nutrients between trees and grasses in the upper surface layers. However, most of these studies were carried out on field plots or micro-scale levels. This renders a liberal extrapolation of their results to even

the rest of the region, renowned for, among others, varying net water deficit (Scholes and Walker, 1993), as too premature. Acting on recent field evidence, which showed a shallow root system for *T. sericea* in the Kalahari of Botswana and a subsequent theory that this shrub deploys its roots opportunistically for harvesting soil water in both the surface and deep soil layers according to the prevailing climate condition (Hipondoka et al., 2003), this study was then initiated. It was specifically set out to rigorously test whether shrubs of *T. sericea* present different rooting system at a medium scale and across a rainfall gradient in Etosha National Park.

## 2. Methods

Etosha National Park is a large wildlife sanctuary situated in north-central Namibia and comprises a surface area of 22,270 km<sup>2</sup>. The park receives summer rains with an average annual rainfall increasing from around 250 mm in the southwest to 500 mm in the east (Mendelsohn et al., 2002). A major portion of the park falls within the western extremity of the Kalahari basin (Thomas and Shaw, 1991) and is mantled with Kalahari sands. Etosha Pan, a large ephemeral basin, occupies a major portion of the park.

The distribution and abundance of *T. sericea* in the park is portrayed in Fig. 1, which was compiled using Le Roux (1980) description of the vegetation units of the area. *T. sericea* are typically found on deep Kalahari sands. Beugler-Bell and Buch (1997) mapped the soils of the park and classified those of the study area as Cambic or Ferralic Arenosols with very low nutrient content and very high infiltration rate. Dominant grasses in the areas occupied by *T. sericea* include *Stipagrostis* species, *Schmidtia pappophoroides*, *Schmidtia kalahariensis*, *Digitaria polevansii* and *Eragrostis* species. The common herbs were *Erhetia rigida*, *Fimbristylis exilis*, *Sesamun triphyllum* and *Acatosicyos naudiniana*. *Lonchocarpus nelsii*, *Terminalia prunioides*, *Commiphora angolensis*, *Dichrostachys cinerea*, *Grewia* species, *Colospermum mopane* and *Acacia erioloba* were the other common woody plants associated with sampling sites. The vegetation structure was usually low tree savanna, and there was no sign of overgrazing or bush encroachment. Mendelsohn et al. (2000)

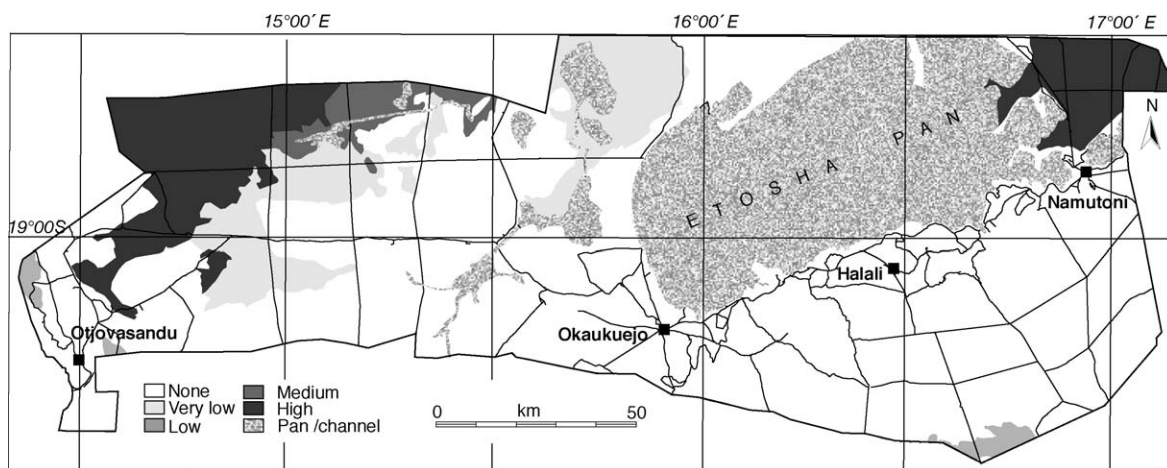


Fig. 1. Distribution and abundance of *Terminalia sericea* in Etosha National Park. (Data source: Le Roux, 1980.)

mapped the groundwater resources in the study area to lie between 10 and 30 m range below the surface.

For the purpose of this study, shrubs were taken to be any plant up to 3.5 m high. All *T. sericea* shrubs were eligible for inclusions in the study and sample plants were randomly selected. For ease of accessibility, however, plants sampled were located within a reasonable walking distance from existing roads. Fieldwork was undertaken between April 2003 and February 2004. Employing a dry excavation technique (Böhn, 1979), a total of 28 plants were excavated across a rainfall gradient and their root systems were studied. Additional three plants located immediately outside the perimeter of the park were also included in the study. This was due to ease of accessibility of these shrubs outside the park in that specific locality. The physical characteristics of that area outside the park mirror those of the vegetation community immediately inside the park, except that the outer unit is subject to a moderate and seasonal free-ranging domestic livestock. The two units are separated by a cattle fence.

Given the discontinuous spatial distribution of the vegetation communities of interest across the park, this study was designed to excavate no less than 15 plants from each of the area east and west of Etosha Pan. Each site where sampled plant is located was described in terms of ground cover, vegetation structure and density, dominant plants of all forms and the level of range utilizations. Classifications for

the vegetation structure and density was based on Bougey's (1957, cited by Sannier et al., 1995) scheme, which was adapted to the semi-arid conditions of Etosha by Sannier et al. (1995). For each specimen, data were collected from both the above- and below-ground. The above-ground data included the plant height, canopy diameter and number of stems. Because of laborious efforts required, root excavation targeted taproots and followed each one to no less than 100 cm depth or its maximum length, depending on its architecture. Where the taproot tilted from its initial downward vertical orientation and adapted a horizontal extension, a taproot was recorded to be absent. In few cases where a taproot was missing entirely, the thickest lateral root was excavated.

Morphometric data obtained for laterals included the dip angle of what originally was a taproot, its diameter at base, root length and depth at the root's tip end. Measurements for taproots involved the taproot's diameter at base and at the terminal depth of excavation, pre-set to 100–120 cm. This depth was determined on the basis of empirical findings of this species' taproot in Botswana, where its rooting system distinguished itself at a depth of less than 30 cm below the surface and from the crown (Hipondoka et al., 2003) and to render the method being destructiveless to the subject plant. The total number of lateral roots was also recorded, but these were not excavated beyond the crown.

Table 1  
Description of sites where sampled plants are located

Site no.	Ground cover	Vegetation structure	Vegetation density	Range utilization	Type of dominant grass
E1	Grass and litter	LTS medium	Low–medium	Moderate	Annual
E2	Grass and litter	LTS medium	Very low	Moderate	Annual
E3	Grass and litter	LTS medium	Low–medium	Moderate	Annual
E4	Grass and litter	LTS medium	Low–medium	High	Annual
E5	Grass and litter	LTS medium	Low–medium	High	Annual
E6	Grass and litter	LTS	Medium	High	Annual
E7	Grass and litter	LTS	Low	Very high	Perennial
E8	Grass and litter	LTS	Low	Very high	Annual
E9	Grass and litter	LTS	Low	High	Annual
E10	Grass and litter	LTS	Low–medium	High	Annual
E11	Grass and litter	LTS	Low–medium	High	Annual
E12	Grass and litter	LTS	Low–medium	Moderate	Annual
E13	Grass and litter	LTS	Low–medium	High	Annual
E14	Grass and litter	LTS	Low–medium	Moderate	Annual
E15	Grass and litter	LTS	Low–medium	Moderate	Annual
E16	Grass and litter	LTS	Low–medium	Moderate	Annual
R18	Litter	LTS medium	Medium	Low	Annual
R19	Bare	LTS medium	Medium–high	Low	Perennial
R20	Litter	LTS medium	Low–medium	Low	Annual
R21	Grass tufts	SS medium	Medium	Low	Perennial
R22	Grass	LTS medium	Medium	Low	Annual
R23	Leaves and tufts	SS medium–high	Medium	Low	Annual
R24	Grass	SS low	Low	Low	Annual
R25	Bare ground	STS medium	Low	Low	Annual
R26	Litter and grass	LTS very low	Medium	Low	Annual
R27	Grass	LTS very low	Low	Low	Annual
R28	Grass	SS medium	Medium	Low	Annual
R29	Grass	SS low	Low	Low	Annual
R30	Grass	SS low	Low	Low	Annual
R31	Grass	LTS medium	Medium–high	Low	Annual
Dominant class	Grass and litter	LTS medium	Low–medium	Low	Annual

Key: LTS, low tree savanna; SS, shrub savanna. See Fig. 3 for the location of the plants.

### 3. Results

Table 1 presents the description of sites where sampled plants were located, whereas the above-ground data recorded are shown in Table 2. Two main types of rooting systems were identified as plants with taproots (Table 4) and those without (Table 3). Their respective average morphological characteristics are presented in Fig. 2. Locations of plants studied in relation to long-term annual average rainfall and the individual rooting system of each shrub examined, are shown in Fig. 3.

Of the 15 plants located west of Etosha Pan or below or near the 400 mm isohyet, all but two exhibit no taproot. In contrast, the two forms of root architecture occur in the eastern part at equal

proportions. For plants, which lack taproots, generally what initially starts out as a taproot, takes a near right-angle turn some few centimetres below the surface and becomes a regular lateral root. No apparent mechanical or edaphic impedance was encountered when a root changed its course from vertical penetration. There were also few cases when such a taproot was missing altogether. Both occurrences are distinguished from plants, which displayed a well-developed, conventional taproot structure. Taproots have an average diameter of 6.2 cm at base and tapers to a mean of 1.7 cm at an average depth of 98 cm (Table 4).

Generally, there was no diagnostic characteristic between plants with taproots and those without. However, plants with taproots were on average, shorter (152 cm) than those that displayed no taproot,

Table 2  
Above-ground characteristics of sampled plants

Site no.	Plant height	Estimated no. of leaves	No. of stem	Canopy diameter
E1	163	700	5	187
E2	122	800	8	110
E3	250	15000	5	220
E4	79	450	1	110
E5	350	50000	9	450
E6	163	1000	1	520
E7	120	100	2	122
E8	155	50	2	105
E9	87	320	1	68
E10	110	80	3	122
E11	250	1500	4	250
E12	350	8000	5	400
E13	200	40	1	145
E14	350	2500	5	300
E15	350	1200	7	270
E16	80	10	3	76
R17	177	29200	8	311
R18	132	2560	6	133
R19	82	8640	10	231
R20	85	4200	7	205
R21	91	3500	8	133
R22	109	1850	16	238
R23	105	5400	6	192
R24	62	75	10	95
R25	155	11800	9	210
R26	290	21600	4	403
R27	172	12940	29	242
R28	91	9800	27	255
R29	150	5500	4	280
R30	120	7280	14	210
R31	91	2800	10	202
Average	164.2	6738.5	7.4	219.2

Table 3  
Below-ground characteristics of plants with taproot

Site no.	Taproot diameter at base	Taproot diameter at end	Depth from surface to beginning of taproot	Max depth reached	No. of lateral roots	Remarks
E1	12.50	3.3	32	100	10	Split in two at 72 cm
E2	7	1	17	80	12	
E4	3	1	0	50	10	Taproot bends and split in two at 35 cm, then going vertical again
E6	3.5	1	0	107	15	
E9	2.1	0.7	12	131	28	
E11	6.5	3.8	8	100	21	
E12	7.7	1.5	14	100	46	
E13	5	1.1	6	110	24	
R17	9	3.2	8	100	10	
R31	6	1.9	4	102	14	
Average	6.2	1.7	10.1	98	19.0	

which averaged 181 cm height. The ratio between the numbers of stems and laterals was also lower for plants with taproots (1:3 versus 1:6). The highest number of stems and laterals recorded was 28 and 46, respectively, the latter read from a plant with a taproot. Laterals had an average depth of 53 cm.

The incidence of encountering shrubs with no taproot in the western part of the park was four times higher than those in the east. However, plants in the wetter eastern part that had no taproots were found to dispense their roots at marginally shallower depths, averaging 48 cm as oppose to 58 cm for the western plants. The average laterals extent was in excess of 432 cm (range 100–875 cm). This average length is two times the average canopy diameter.

#### 4. Discussions

The results presented above highlight two crucial ecological aspects. Firstly, they demonstrated that rooting system is not species specific. Secondly, a lack of plants with taproots in the drier part of Etosha and a co-dominance of the two types of rooting system in the wetter east, suggest that this plant species respond to local climatic stimuli and strategies its rooting system accordingly.

These findings generally support the premise set forward by Hipondoka et al. (2003), which was fundamentally tested in this study. That premise is essentially that *T. sericea* shrubs adapt their rooting system in accordance to the prevailing climatic

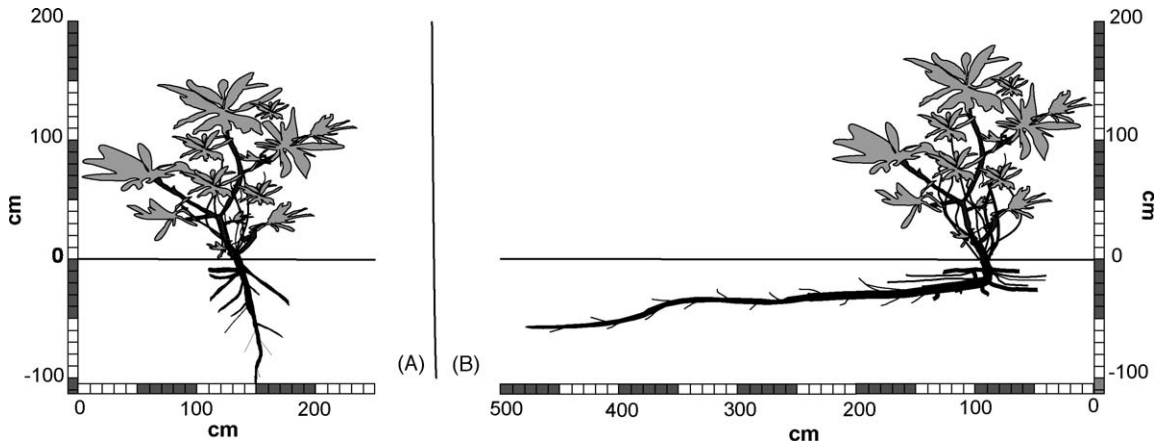


Fig. 2. Patterns and main average characteristics of the two types of rooting systems of *Terminalia sericea* shrubs encountered in Etosha National Park: (A) plant with taproot and (B) plant without taproot.

regime. Comparatively, their study sites, located in west-central and south-western Botswana, were in a climatic zone similar to that of western Etosha, and all 10 of their excavated *T. sericea* shrubs exhibited no taproot. It is not surprising, therefore, that our results of the western part were in accordance with theirs in terms of widespread occurrence of plants having no taproots. It must be acknowledged,

however, that in western Etosha our study encountered two out of 15 of these shrubs with taproots. Spatially, there are no immediate logical interpretations for the specific locations where these two plants with taproots were found. Nevertheless, their sheer presence served to rule out a potential assumption that in drier savannas these shrubs are exclusively without taproots.

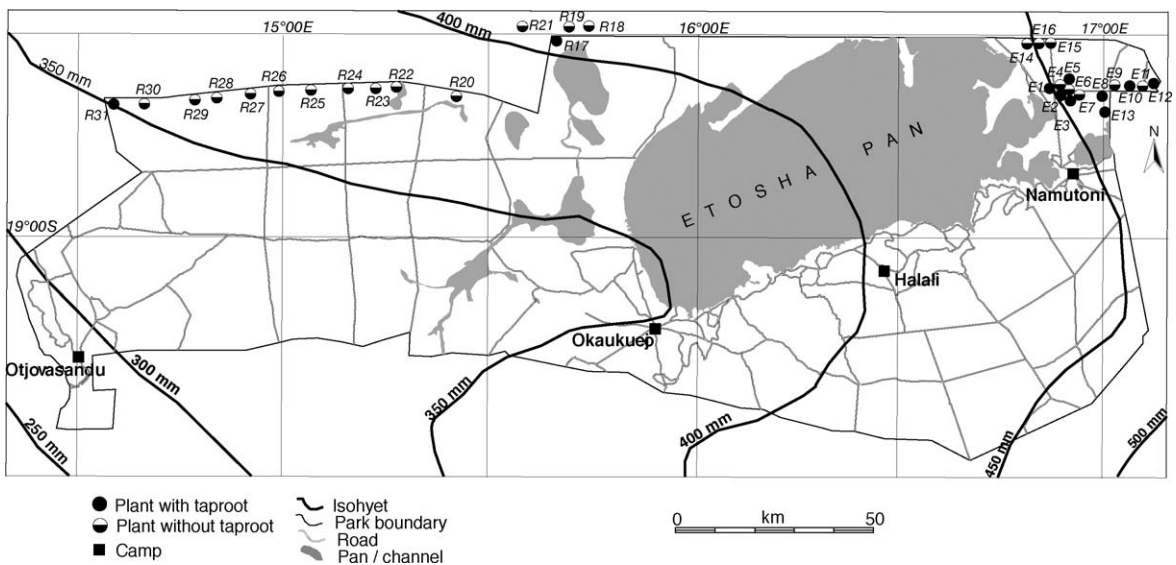


Fig. 3. Location of studied *Terminalia sericea* and their respective type of rooting system and overlay of long-term annual average rainfall of the area. Numbering, such as E1 or R20, refers to site number (Tables 1 and 2). (Isohyet modified from Mendelsohn et al., 2002.)

Table 4  
Below-ground characteristics of plants without taproot

Site no.	No. of lateral roots	Depth from surface to beginning of main root (cm)	Dip angle	Main root's diameter at base (cm)	Length of main lateral root	Depth at end of main lateral root	Main root's diameter at end (cm)	Remarks
E3	10	28	90	9	>450	31	2	
E5	8	15	90	8	875	30	0	
E7	4	14	30	4.2	300	53	1.2	Rooting status
E8	12	10	50	3	365	76	1.2	vague–hermaphrodite
E10	11	7	35	2	391	44	0.2	
E14	23	13	45	3.2	200	49	2.2	
E15	24	14	2	6	610	41	0.9	
E16	14	12.5	90	1.8	394	58	0.2	
R18	7	21	90	2.2	100	100	2.4	
R19	6	13	10	3.5	526	44	0	
R20	9	15	10	4.2	470	72	2.3	
R21	15	8	8	2	>228	35	0.5	
R22	20	10	3	2.5	>400	44	0.6	
R23	11	11	90	3.5	180	45	2.5	Dead at end
R24	18	8	5	3.1	411	85	1	Dead at end
R25	18	5	10	3.2	520	51	0.7	
R26	15	13	6	6	600	46	2.9	
R27	20	18	3	3	667	55	1.6	
R28	21	11	2	1.8	460	90	1	
R29	24	13	20	1.9	390	34	1.5	(Dead at that terminal
R30	18	12	5	2.9	530	58	0.7	length, but continued)
Average	14.7	12.9	33.0	3.7	>431.8	54.3	1.2	

Admittedly, moist or humid savannas were not represented in our study. Although a division of savannas along the degree of aridity is implicit (Scholes and Walker, 1993), a 500 mm isohyet is generally regarded as the precipitation divide between semi-arid and moist or humid zones (e.g. Hulme et al., 1992). This would effectively place the study of Rutherford (1983), which excavated a *T. sericea* shrub in a South African savanna, receiving an annual average rainfall of 630 mm, in a moist zone. The rooting system of that shrub was categorized as bimorphic, which was similar to two trees of the same species in the same area. Essentially, a bimorphic rooting system refers to plants having a superficial root system in addition to a deep ranging root structure. Should this bimorphic system be representative of *T. sericea* shrubs in moist savannas, then an intuitive hypothesis is that with increasing precipitation, the rooting system of this plant is predominantly with taproot, penetrating even to greater depths. In this context, it can then be assumed that in drier savannas the rooting structure of *T. sericea* is predominantly

without taproots, as the western part of our study area and central-western Botswana (Hipondoka et al., 2003) testified. In the same vein, by using the spatial distribution of this shrub's rooting system as a criteria, the eastern part of our study area is evidently a transition zone from dry to moist savannas, based on the empirical results of the two types of rooting systems at, strikingly, equal proportions.

Mutually, the results have intrinsically showed that although *T. sericea* shrubs displayed two main rooting systems, the plant is undoubtedly shallow rooted in both the drier and transition zones. Taproots tapering from a mean diameter of 6.2–1.7 cm at an average depth of 98 cm, imply a shallow depth, which was approximately twice as deep as the average depth of lateral roots. This translates into apparent implications in terms of trees–grasses interactions with respect to vadose water held in the sands after rains. In our study area, there was no sign of overgrazing or bush encroachment, which suggests that the current rangeland utilization is within the local threshold of functional savannas. It is, therefore, likely that in

the event of an aggressive removal of herbaceous layer in this area through overgrazing, for example, the existing dynamic balance between shallow rooted woody plants and grasses, in particular would inevitably be altered. Such an alteration and subsequent symptoms could well be what is collectively referred to as bush encroachment.

## 5. Conclusions

*T. sericea* shrubs presented two types of shallow rooting system. Plants in the drier part of the Park are predominantly characterized by a rooting system lacking a taproot. The horizontal extent of the laterals that these plants exhibited was more than twice the canopy diameter. In the wetter part of the Etosha National Park, plants with and those without a taproot were encountered at equal proportions.

Diagnostically, *T. sericea* shrub demonstrated and indicated its ability to adapt itself to the prevailing local climatic regime. Its tendency for deploying its roots near the surface effectively enables it to compete for available soil water and nutrients with all other shallow rooted plants, such as grasses. This in turn, could be one of the axioms as to why encroaching bushes continue to persist at the expense of herbaceous layers even after the removal of livestock (e.g. Skarpe, 1990). Thus, the below-ground structure of the *T. sericea* has far-reaching repercussions to the incidence and proliferation of bush encroachment. Future models for the tree–grass interactions of the savannas should therefore be cognizant of the variable rooting system of this plant species across a rainfall gradient. Ultimately, the root architecture of this shrub, and possibly other bush encroaching species, can be used as an ecological indicator for determining locally appropriate management practices of this biome and enhance its utilization as a continuously productive rangeland.

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