ROOTING STRATEGIES OF SAVANNA SHRUBS IN THE KALAHARI BASIN: IMPLICATIONS FOR THE COEXISTENCE OF WOODY AND HERBACEOUS PLANTS AND SHRUB ENCROACHMENT IN THE AFRICAN SAVANNAS

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Abstract

The savanna biomes are characterised by a coexistence of two antagonist – woody plants and herbaceous plants in defiance of competition theories. Scientific efforts to understand this unique coexistence are still largely inconclusive; various theories have been proposed, but no unanimous theoretical framework exists to date.

Among these theories, the root niche-partitioning model offers the most popular, yet the most controversially debated viewpoint. It argues that this coexistence is a result of vertical root niche-partitioning, a natural mechanism by which woody plants develop deeper root systems to avoid competition with herbaceous plants. Despite its prominence and subsequent integration into models of species coexistence and arid eco-hydrology, several shortcomings of this model are evident. For example, it overlooks the critical issue of root plasticity. This study was thus designed to investigate the root systems of various savanna shrubs across a rainfall gradient in the Kalahari to test the aforementioned model. The overall aim was to investigate, compare, and contrast the root system architecture (RSA) of encroaching shrubs and those of non-encroaching shrubs within the proximate environmental setting.

Using a direct excavation method, 183 shrubs were sampled, had their roots exposed and were subjected to morphometric measurements. Shrub encroachers were randomly selected and four non-encroaching shrubs surrounding each of the sampled encroacher plant were systematically chosen, using the nearest-neighbour approach. Results indicated that shrubs in the Kalahari develop diverse root system architecture which exhibits significant inter- and intra-species plasticity. In particular, three bush encroaching shrubs, *Terminalia sericea, Senegalia mellifera,* and *Dichrostachys cinerea,* tend to develop root systems essentially composed significantly ($p < .001$) of lateral roots deployed within shallow soil sub-surfaces; and partly without taproots, more especially in the drier part of the Kalahari. Overall, the architecture of the savanna shrubs' root system can be classified into three major architecture groups: i) a fibrous or lateral root system, ii) a dual root system, and iii) a taproot system. These architecture groups are not necessarily unique to any species or environment, which suggests that plants develop their root systems plastically in response to prevailing environmental conditions. These findings are not consistent with the premise that the savanna shrubs are largely deep-rooted. This oversight has major implications for our current understanding of the savanna biomes. Whereas deeper-rooted shrubs may allow for root niche-partitioning with grasses, shallow-rooted shrubs are potentially in direct competition with grasses, suggesting that shrub encroachment is a probable manifestation of this competition. These findings may also explain why the phenomenon of shrub encroachment is largely attributed to shallow-rooted shrubs such as *T. sericea*.

Keywords: plasticity; rainfall gradient; root niche-partitioning; root system architecture; *Terminalia sericea*

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List of Acronyms

ANOVA	Analysis of Variance
CAB	Congo Air Boundary
CV	Coefficient of variation
DAAD	The Deutscher Akademischer Austauschdienst
GDP	Gross Domestic Product
ITCZ	Intertropical Convergence Zone
KT	Kalahari Transect
MAP	Mean Annual Precipitation
MAWF	Ministry of Agriculture Water and Forestry
NUST	Namibia University of Science and Technology
PET	Potential Evapotranspiration
RSA	Root System Architecture
S & T MODEL	State and Transition Model
SASSCAL	Southern Africa Science Service Centre for Climate Change and Adaptive Land Management
UNAM	University of Namibia
UNCCD	United Nations Convention to Combat Desertification

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Dedication

To the ‘Aakusinda clan’s children’, to serve as a source of inspiration for their efforts in education.

Declarations

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Publications and conference proceedings

1. **Nakanyala, J** & Hipondoka, M. (2018). Lateral roots of *Senegalia mellifera* and *Dichrostachys cinerea* shrubs in the Kalahari Basin: Implication on tree-grass coexistence in the African Savannas. *Paper presented at the 2018 International SASSCAL Science Symposium 16-20 April. Lusaka, Zambia.*

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3. **Nakanyala, J**., Kosmas, S., & Hipondoka, M. (2017). The Savannas: An integrated synthesis of three major competing paradigms. *International Science and Technology Journal of Namibia, 10, 119–132*.

1. CHAPTER ONE: GENERAL INTRODUCTION

1.1 Background

Approximately 20% of the Earth’s land surface, 40% of which is on the African continent, is occupied by terrestrial biomes called the savannas (Scholes & Walker, 1993). Located mostly in arid and semi-arid tropical regions (Mistry, 2000), the savanna biomes are distinguishable from other terrestrial biomes by the coexistence of two contrasting life forms (Higgins, Bond, & Trollope, 2000; Jeltsch, Milton, Dean, & Van Rooyen, 1996; Scholes & Archer, 1997; Scholes & Walker, 1993). The savannas are made up of a layer of trees and shrubs, collectively referred to as ‘woody plants’, and a layer of grasses and herbs collectively referred to as ‘herbaceous plants’ (Bond, 2008; Jeltsch, Milton, Dean & Van Rooyen, 1996; Jeltsch, Weber & Grimm, 2000; Sankaran et al., 2005; Sankaran, Ratnam & Hanan, 2004). Elsewhere, in forests or grasslands, for example, either woody or herbaceous plants dominate, respectively. It is this coexistence that makes the savannas unique biomes, particularly when observed from a scientific perspective.

Originally, derived from the Spanish word, ‘zavanna’ which means ‘treeless plain’ (Shorrocks & Bates, 2015), many definitions of the term ‘savannas’ have been proposed. According to Mistry (2000), ‘savannas’ can be defined as tropical biomes with a continuous layer of grasses/herbaceous plants and a discontinuous layer of woody plants of various height and density, whose growth patterns are closely associated with alternating wet and dry seasons. Similarly, Werner (2009) defines savannas as tropical grasslands with scattered trees and bushes, whose structure is influenced by both biotic and abiotic factors such as rainfall, soils, fire, and grazing.

The main distinguishing factor between woody and herbaceous plants of the savannas is their photosynthesis pathways, which, it is claimed, developed with the origin of the savannas during the Miocene, some eight million years ago (Beerling & Osborne, 2006). The savanna biomes are largely dominated by grass species that have evolved a C_4 photosynthesis pathway (Cerling, Wang & Quade, 1993; Pearcy & Ehleringer, 1984; Sage, Wedin & Li, 1999; Tipple & Pagani, 2007), whereas coexisting trees and shrubs, mostly use the ancestral C_3 photosynthesis pathway (Pearcy & Ehleringer, 1984; Sage & Monson, 1998).

Geographically, the savannas are widespread biomes and occur across all tropical regions of the world (Figure 1). The savannas are found in South America covering parts of northern Brazil, Colombia and Venezuela, as well as parts of North America, such as the southern parts of Mexico and the Caribbean (Cole, 1986). In Africa, savannas cover major parts of Southern Africa, as well as East Africa, extending to parts of Kenya, Sudan, Ethiopia, and most parts of North Africa below the Sahara Desert (Cole, 1986). The savannas extend further into Southeast Asia, covering parts of Burma, Laos, Thailand, Cambodia, and Vietnam, among others (Cole, 1986). The International Koppen Climate Classification System describes the savannas as biomes with a distinct short wet summer, a long dry winter, with a mean annual rainfall ranging between 250 mm and 2000 mm per annum, and with the potential evapotranspiration (PET) exceedingly higher than precipitation (Pidwirny, 2016).

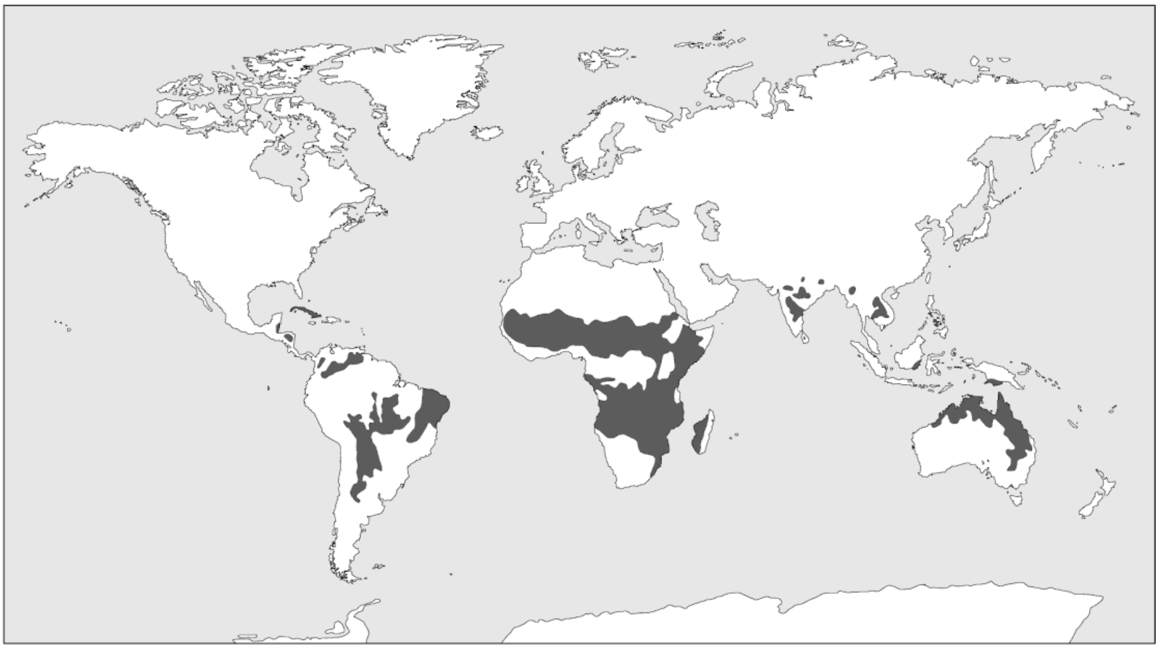

Figure 1: The global spread of savannas through tropical regions, covering parts of South America, Southern Africa, north-eastern Africa, Australia and parts of eastern Asia. (Source: Furley, 2016).

The savanna biomes can be distinguished into two types, based on the climatic conditions (Mistry, 2000). The dry savannas are found in a rainfall belt with less than 600 mm of rainfall per annum, and the wet savannas are in the rainfall belt of 600 mm and 2000 mm per annum (Abbadie, Gignoux, Roux & Lepage, 2006). Floristic differences are also evident in these two types of savannas. The dry savannas are often characterised by a discontinuous, loosely spaced layer of low trees and shrubs, and a continuous layer of grasses and herbs (Cole, 1986). The wet savannas, by contrast, are primarily made up of broad-leafed trees and shrubs, and an understory of grasses and herbs. The savanna biomes can also be classified into two groups based on soil nutrient: the nutrient-rich, and the nutrient-poor savannas, of which the dry savannas are mostly found on nutrient-poor substrates, while wet savannas are mostly found on nutrient-rich substrates (Scholes & Walker, 1993).

Water availability and soil nutrients are considered as the key determinants of the savannas' net primary production (Scholes & Walker, 1993), while fire and grazing are believed to be the main modifiers (Accatino, De Michele, Vezzoli, Donzelli & Scholes, 2010; Kambatuku, Cramer & Ward, 2011; Mistry, 2000). Water, in particular, is thought to control the duration of primary production and nutrient mineralisation, while nutrient availability regulates the growth rate of plants (Scholes & Walker, 1993). Fire is thought to influence the succession of woody plants, while grazing pressure reduces herbaceous cover. Whereas, water and soil nutrients are abiotic factors, grazing by domestic animals, and fire under contemporary frequencies and distribution are considered as anthropogenic activities, but still as an integral part of the savannas. These two anthropogenic factors arguably make it difficult to study the savanna biomes in their natural settings (Hipondoka & Versfeld, 2006).

Owing to their floristic characteristics and climate, the savanna biomes are some of the the most densely populated biomes in the world (Mistry, 2000), serving as good rangeland and supporting nearly one-fifth of the world's human population, whose livelihoods are directly dependent on extracting ecosystem services from the savannas (Mistry, 2000). Most of such communities are pastoralists, who are primarily dependent on livestock farming for their livelihood. An ever-increasing human population density in the savannas puts pressure on the ecosystem services, and so may compromise their sustainability (Ryan et al., 2016). Consequently, the savanna biomes are considered vulnerable to exploitation and degradation, a situation shared with many other drylands around the world (Mueller, Wainwright, Parsons & Turnbull, 2013).

The unique coexistence between woody plants and herbaceous plants of the savannas, which is the most distinctive feature of these biomes, is changing throughout many tropical regions due to a phenomenon called shrub encroachment (Buitenwerf, Bond, Stevens & Trollope, 2012; Eldridge et al., 2011; Gil-Romera, Lamb, Turton, Sevilla-Callejo & Umer, 2010). Shrub encroachment is loosely defined as an increase in cover and density of native shrubs on patches previously occupied by grasses (Smit, 2004; Van Auken, 2009; Ward, 2005). Although the term 'shrub encroachment' is used here, other terms such as 'thickening' or 'invasion' have been used to refer to this expansion of woody plants in the savannas, as discussed in detail in the subsequent sections. The United Nations' Convention to Combat Desertification (UNCCD) recognises shrub encroachment as a land degradation issue, because of its significant ecological and socio-economic consequences, particularly for livestock production in many arid and semi-arid environments (Angassa, 2005; De Klerk, 2004; Ward, 2005). The UNCCD defines land degradation as changes in ecosystem conditions toward a less productive state. In the case of shrub encroachment, such a manifestation occurs as rangeland forage productivity of palatable grass species decreases at the expense of increased bush thickets, thus making such rangeland less suitable for grazing (De Klerk, 2004). Although benefits such as fencing materials, fodder, firewood and charcoal can be derived from shrub encroached areas, these are largely adaptive measures implemented to reduce shrub cover.

The widespread distribution of the savanna biomes throughout many tropical regions also means that shrub encroachment is a widespread phenomenon. Shrub encroachment has been reported in several places, such as North America (Van Auken, 2009), north-eastern Africa (Angassa, 2005; Gil-Romera et al., 2012), Australia

(February, Higgins, Bond & Swemmer, 2013), but is most widespread in the savannas of Southern Africa (De Klerk, 2004; Moleele, Ringrose, Matheson & Vanderpost, 2002; Smit, 2004; Ward, 2005).

Land degradation in the form of shrub encroachment is considered as a major threat to the livelihood of the vast majority of the world's population, particularly those largely dependent on agriculture (Millennium Ecosystem Assessment, 2005). There is thus a great risk that shrub encroachment could emerge as one of the major threats to livelihoods, particularly in Africa in the 21st century (Kgosikoma & Mogotsi, 2013).

In Namibia, De Klerk (2004) estimated that approximately 25 million ha of land are shrub encroached. This is equivalent to approximately a third of the country's land mass, although shrub encroachment occurs predominantly on commercial farms which constitute some 43% of the total area surface. If no major human effort is made to reverse the extent of shrub encroachment in the country, this coverage is likely to increase over the years. Around the turn of the 20th century, it was estimated that shrub encroachment resulted in the reduction of beef production by up to 30%, or approximately 34 000 tonnes of beef per year for Namibia, translating into a loss of approximately US$ 7 million per year (Barnard, 1998). This loss has led to major de-bushing initiatives on many commercial farmlands in Namibia, costing millions of dollars. This alarming evidence highlights the importance of sustainable management of the savanna biomes based on sound, evidence-based scientific knowledge. The purpose of this study is to expand our understanding of the rooting strategies of savanna shrubs against the backdrop of and implications for tree-grass coexistence and shrub encroachment.

1.2 Problem statement

The coexistence of woody and herbaceous plants to form the savanna biomes and the embedded occurrence of shrub encroachment presents one of the longstanding and perplexing research problems in the history of vegetation ecology, a problem that remains unsolved to date (Holdo, 2013; Ratajczak, D'Odorico & Yu, 2017; Ward et al., 2013). This controversy, largely referred to as 'the savanna questions' or 'the savanna problem', is rooted in the premises of the competitive exclusion principle proposed by Gause early in the 20th century (Gause, 1934). This principle argues that two sympatric species or life forms that occupy the same ecological niche cannot coexist if the resources they depend on are limited. According to the competitive exclusion principle, this is because of interspecific competition for such limited resources, for which the two coexisting species or life forms will not compete equally, but one of the two will become a superior competitor, and therefore dominate the ecosystem. The domination by one species or life form would displace the other, driving such species or life form either into extinction, or into adapting a new mechanism through a process of natural selection. In contrast, a niche-partitioning mechanism will enable coexistence (Hastings & Gross, 2012; Miller, 2008; Putman, 2012).

'Niche' is used here to refer to the ecological requirements of a certain species necessary to thrive, while 'niche-partitioning' refers to a process whereby a certain species alters its pattern of resource use to avoid competition with its counterparts (Miller, 2008). Theoretically, this principle applies to all species of fauna and flora. Although some critics (e.g., Hardin, 1960; Heck, 1980) argue that this principle is not verifiable by means of scientific experiments, its contribution is very significant to the science of community ecology, species assemblage, and coexistence, particularly in the savanna.

As defined earlier, the savanna biomes are made up of two contrasting life forms, woody and herbaceous plants in coexistence. No other terrestrial biomes have such a character. In line with the competitive exclusion principle, this coexistence has triggered the following elusive ‘savanna questions’: (i) How can complete competitors coexist in the moisture-limited environment, defying the competitive exclusion principle? (ii) Why do woody plants not thicken up to form a forest that would exclude herbaceous plants? (iii) Why do herbaceous plants not grow and eliminate woody plants to form a grassland? (iv) Under which mechanisms do shrub encroachment occur? And does it imply that woody plants are superior competitors to herbaceous plants?

These savanna questions have attracted formidable research efforts for decades (e.g., Jeltsch et al., 1996; Jeltsch et al., 2000; Sankaran et al., 2004; Sankaran et al., 2005; Scholes & Archer, 1997; Scholes & Walker, 1993; Walker & Noy-Meir, 1982; Walker et al., 1981; Walter & Mueller-Dombois, 1971). However, such efforts and others that followed over the years have given rise to diverging, contradictory and competing theories, models and hypotheses, collectively hereafter referred to as ‘theories’, dedicated toward solving these elusive savanna questions. These theories can be classified within four major ecological paradigms, namely: equilibrium, non-equilibrium, disequilibrium, and climate change (Jeltsch et al., 1996; Jeltsch et al., 2000; Sankaran et al., 2005; Sankaran et al., 2004; Scholes & Archer, 1997; Scholes & Walker, 1993; Walker et al., 1981). The premises of these theories are not necessarily mutually exclusive, and remain inconclusive in addressing the savanna questions. Thus, our understanding of the savannas and its management is still flawed and incoherent, owing to a lack of consensus within and between the current theories. Despite the discrepancies between these theories, however, the major unifying factor is the role of water and how it influences the coexistence of woody and herbaceous plants. Of these theories, this study took a special interest in Walter's two-layer model (Walker & Noy-Meir, 1982; Walter & Mueller-Dombois, 1971; Ward, Wiegand & Getzin, 2013) which is the most popular and the most controversially debated model explaining tree-grass coexistence in the savannas.

According to Walter's two-layer model, in water-limited biomes such as the dry savannas, coexistence between woody and herbaceous plants is made possible by a natural regulating mechanism of vertical root niche-partitioning, whereby the deeper root systems of trees and shrubs help to avert competition with grasses and herbs, which are superior in the upper soil layer. By growing deeper roots, such woody plants would have exclusive access to water at greater soil depth, unreachable by the grasses and herbs. According to the model, this would allow trees and shrubs to survive during drought periods, in spite of reduced water availability, mostly because their roots are distributed across a greater portion of the soil profile, and infiltrated water at a greater depth may still be available for such plants during times of drought. Walter's two-layer-model does not make any quantifiable estimate of the depth at which trees may partition their roots in relation to grasses. Instead, the model focuses on the implicit differentiation in the root architecture of woody and herbaceous plants. The root architecture, such as the presence of a taproot or lateral roots, can thus be used as a proxy to infer the depth (deep vs shallow) from which such plants capture soil resources.

According to this model, shrub encroachment would result from overgrazing, an anthropogenic disturbance which reduces grass cover through overstocking, radically shifting the ecosystem off its equilibrium balance. This would result in inferior competitors, the woody plants out-competing herbaceous plants, because of an increased percolation of water in the subsoil, which would lead to enhanced recruitment of trees and shrubs. A review by Ward et al. (2013) provides a comprehensive analysis of this model. Because of its prominence, this model has subsequently been integrated into theories of species coexistence, arid eco-hydrology, and climate change, among others (Foley et al., 1996). However, several flaws are evident, despite its prominence.

Field experiments and theoretical models testing Walter's two-layer model have produced conflicting results over the years of its existence. The model puts the root systems of savanna plants at the centre of the savanna debate and effectively under continued scrutiny because the extent to which woody and herbaceous plants vertically partition their roots to enable a stable coexistence is still not well established. Nevertheless, a handful of studies have demonstrated the shallow and lateral extent of root systems among some savanna shrubs, such as *Terminalia sericea* (Hipondoka & Versfeld 2006; Hipondoka, Aranibar, Chirara, Lihavha & Macko, 2003), *Colophospermum mopane* (Smit & Rethman, 1998) and *Prosopis glandulosa* (Eggemeyer, 2011; Simmons, Archer, Teague & Ansley, 2008). However, given the limited spatial scales at which these studies were conducted, they conveyed limited information about how the root systems of the studied savanna plants grow under different environmental conditions, such as moisture and nutrient gradients. Therefore, this study was designed to investigate the root systems of selected savanna shrubs along the Kalahari rainfall gradient, encompassing three major sub-climatic zones: drier, mesic and wetter. The major objective was to determine how the availability and role of soil moisture, based on mean annual precipitation, may influence the patterns of plants root development among savanna shrubs. Understanding the root system architecture (RSA) of plants can generate an enhanced knowledge of below-ground interaction between shrubs and grasses in the savannas.

1.3 Aims and research questions of the study

Developing effective and predictive models of heterogeneous terrestrial biomes, such as the savannas, largely depends on our critical understanding of factors and mechanisms that govern the behaviour of such biomes. Some critical insights into obtaining such an understanding may be hidden in the RSA of plants. Through direct excavation, this study aimed to investigate the below-ground morphology of savanna plants, specifically their root systems, in order to test the savanna root niche-partitioning model. A study on RSA addresses major aspects, such as the shape and structure of the roots in soils (Hodge et al., 2009). Such efforts can generates knowledge about fundamental ecological processes, such as water and nutrient uptake, as well as competition for soil resources (Laio et al., 2006). In doing so, this study endeavours to contribute to unlocking the savanna paradox by providing answers to the following questions:

i. What are the rooting strategies employed by shrub-encroaching species, *D. cinerea, S. mellifera,* and *T. sericea* for foraging soil resources, such as moisture?

ii. At what soil depth do shrub-encroaching species mentioned in (i) deploy such roots?

iii. How do such rooting strategies respond to changes along the Kalahari rainfall gradient?

iv. How do the rooting patterns of such shrub-encroaching species compare to those of non-encroaching shrubs in close proximity and in similar environmental settings?

v. What implications may the rooting strategies of the Kalahari shrub have on the dynamic and functioning of the savannas?

1.4 Clarification of botanical names and concepts

A study involving woody species such as ‘*Acacia mellifera*’ presents a major botanical problem that needs to be addressed explicitly from the onset in this study. This problem is rooted in the controversy over the true ‘*Acacia'* species, considering the phylogenetic differences between the African ‘*Acacia'* species and the Australian ‘*Acacia*’ species (Moore et al., 2011; Robin & Carruthers, 2012). Despite objections by many African countries, including Namibia, in 2011 the International Botanical Congress voted in favour of changing the African ‘*Acacia*’ genus to ‘*Senegalia*’ and ‘*Vachellia*’ while retaining ‘*Acacia*’ as a genus for the Australian species. In order to keep up with this trend, this study has opted to use the internationally accepted species names as per the 2011 International Botanical Congress, while at the same time, acknowledging that this name change has not been unanimously accepted by all members of the scientific community, including Namibia, where this study was carried out.

This study deals with woody plants of the savannas. Woody plants can be broadly classified into two groups: trees and shrubs. It is important to understand the difference between these two groups of woody plants as interpreted in this study. However, the ecological differences between trees and shrubs are still poorly understood and clear ecological definitions of these two constructs do not exist (Dullinger, Dirnböck & Grabherr, 2003; Zizka, Govender & Higgin, 2014). Several morphological characteristics, such as plant height and the number of stems, have been used to distinguish shrubs from trees, but such classifications are highly ambiguous (Zizka et al., 2014). It is, for instance, not clear whether a shrub is simply a small tree if the criterion of plant size is considered, or whether shrubs belong to a distinct group of woody plants. The use of the term 'shrub' in this study was guided by a study of Zizka et al. (2014) which defines shrubs as small woody plants (up to 3 m tall) with many stems; a dense, relatively wide crown, and a relatively limited increase in height with stem diameter. It is also worth noting that most of the woody plants assessed in this study grow up to the level of a tree; however, using height as a guideline, all the woody plants excavated in terms of their height and per the definition of what constitutes a 'shrub' in this study, were shrubs because they were all less than 3 m in height. Lastly, the term 'tree-grass coexistence' is used interchangeably with 'woody-herbaceous coexistence' to include both trees and shrubs, as well as grasses and herbs.

1.5 Delimitations

As mentioned in Section 1.2, Walter's two-layer-model is implicit regarding the threshold depth at which trees and grasses may partition their roots. Within the Kalahari, Hipondoka et al. (2003) have demonstrated that grasses deploy the bulk of their roots within 40 cm and negligibly below 80 cm soil depth. Taking this result into account, this study resolved to focus exclusively on the root system and distribution of shrub roots up to a soil depth of 1 m for taproots, while the radial extent and depth of encountered laterals were determined by their length and terminal depth. In the same vein, knowing the average depth at which grasses, deploy their roots, this study found it redundant to sumple grasses, as it will not fill any knowledge gap.

1.6 Organisational structure of the dissertation

Chapter 1 provides an overview of the savannas, focusing on various aspects, such as the structure and classification of the savannas, their determinants, and global distribution. The chapter also frames the problem statement of the study and the key research questions.

Chapter 2 reviews the relevant literature and provides a detailed analysis, with a focus on three major aspects: first, an overview of the status of shrub encroachment in Namibia, followed by an outline of the socio-economic as well as ecological implications, and thirdly, a synthesis of various existing theories and models on the savanna. The chapter ends with a review of the literature on the RSA of terrestrial plants.

Chapter 3 investigates the root architecture of *S. mellifera* and *D. cinerea,* two common shrub encroachers in the Kalahari Basin, with the overall aim of understanding the rooting behaviour of these two species across a climatic gradient.

Chapter 4. In order to ascertain if the root behaviours exhibited by the two species studied in Chapter 3 are shared among other shrub encroachers found within the same environmental settings, this chapter investigates the root strategies of *T. sericea*, a shrub-encroaching species also found in the Kalahari Basin.

Chapter 5 examines the root architectural variations of various shrubs neighbouring the plants discussed in Chapters 3 and 4. The overall aim was to compare how the root strategies of such shrubs with their neighbouring shrub encroachers described in Chapters 3 and 4.

Chapter 6 synthesises the major findings of the study and interprets such findings within the context of the savanna questions, the coexistence of shrubs and grasses, and the occurrence of shrub encroachment in the African savannas. This chapter provides the conclusion and recommendations of the study.

2. CHAPTER TWO: LITERATURE REVIEW

2.1 Introduction

The objectives of this chapter are threefold. The first section provides an overview of the status of shrub encroachment in Namibia and seeks to emphasise the seriousness of shrub encroachment by highlighting its socio-economic and ecological implications for the Namibian savanna rangelands. The second section deals with 'the savanna debate', providing a synthesis of paradigms, theories and models that relate to the savannas and shrub encroachment, collectively referred to as 'the theoretical framework'. The aim is to put the savanna controversy into context and provide different perspectives proposed to address the savanna questions over the years. A critical aspect emerging from the theoretical framework is the importance of the root architecture of savanna plants and the mechanism of moisture uptake in influencing the functioning of the savanna biomes, as well as how such root systems governs the mechanism under which shrub encroachment occurs. The last section of this chapter focuses on aspects of root systema architecture (RSA), its developmental processes, and how such root systems respond to the different environmental conditions under which they grow.

2.2 Shrub encroachment in Namibia

The issue of shrub encroachment is a critical component of this study. Without the occurrence of shrub encroachment, perhaps the paradox of the savannas would have been easier to resolve. Shrub encroachment is not only part of the savannas mystery, but also a phenomenon that poses many socio-economic challenges to pastoralists and ranchers in Africa, and in many other semi-arid regions.

In order to put the issue of shrub encroachment into perspective, it is important first to clearly define this concept. A search for the definition of 'shrub encroachment' would yield varying and contrasting descriptions because this concept has been diversely defined in different contexts over the years. As a result, no unanimous definition of shrub encroachment as a concept exists to date. Perhaps the best approach to clarify this is to address the origin of the word 'encroachment' itself. According to the *Oxford Dictionary*, the use of the term 'encroachment' can be traced back from an Anglo-French word *encrochen* which means to 'intrude, infringe, impinge, entrench, or advance beyond the usual/desirable limit' (Stevenson, 2010). Based on that definition, the *Dictionary of Environment and Conservation* by Park (2007) defined shrub encroachment as 'an unplanned conversion of vegetation dominated by grassland to one dominated by woody species, often as a result of overgrazing' Although this definition puts a strong emphasis on overgrazing as the main cause of shrub encroachment, the argument is still largely contested (Ward, 2005).

The most relevant definition of shrub encroachment in the context of this study is the one which defines shrub encroachment as 'an invasion and increase in bush density, resulting in an imbalance of tree-grass ratio, a decrease in biodiversity, and a decrease in rangeland carrying capacity, accompanied by severe socio-economic consequences' (De Klerk, 2004). Unlike many others, this definition places its emphasis on rangeland degradation because of the socio-economic consequences of this phenomenon on pastoralism. The term 'shrub encroachment' is strictly used throughout in this study for the sake of consistency. Other terms, such as 'bush encroachment' (Kgosikoma & Mogotsi, 2013; Klerk, 2004; O'Connor, Puttick & Hoffman, 2014), 'shrub invasion' (Brown, 1950; Brown & Archer, 1999; Dullinger, Dirnböck & Grabherr, 2003; Grant, Madden & Berkley, 2004; McPherson, Wright & Wester, 1988), ‘bush thickening’ (Joubert, Rothauge & Smit, 2008; Joubert, Smit & Hoffman, 2012), and ‘shrub proliferation’ (Browning & Archer, 2011; Browning, Laliberte & Rango, 2011; Sharma, Vetaas, Chaudhary & Maaren, 2014; Sharma et al., 2014) have been used to refer to this expansion of shrubs on grasslands in semi-arid regions. According to Van Auken (2009) however, the use of the term ‘invasion’ to refer to shrub encroachment seems inappropriate in view of the fact that shrub encroachment is an ecological phenomenon that is usually caused by local native woody species, while invasion is popularly used to refer to invasive species from other geographical areas.

2.2.1 Geographical setting of shrub encroachment in Namibia

Namibia is situated on the south-western part of the African continent along the Atlantic Ocean, sharing borders with South Africa to the south, Angola to the north, Botswana to the east, as well as Zambia and Zimbabwe along the Zambezi River on the former Caprivi Strip, now the Zambezi Region. Namibia has a total land mass of approximately 825,418 km^2, and a population of approximately 2.5 million people (Namibia Statistical Agency, 2017). Namibia is an arid country with low and extremely variable precipitation. In terms of vegetation, approximately 64% of the country is classified as savanna, with a discontinuous layer of trees and shrubs of varying density (Klerk, 2004) which differ significantly along the northeast-southwest rainfall gradient. At a population density of nearly 2.6 people per km^2, Namibia is one of the least densely populated countries in the world (Udogu, 2011), leaving large parts of the land for agricultural purposes. It is therefore not surprising that, upon arrival in the early 19th century, the colonial settlers set aside large tracts of land for livestock farming (Werner, 1993). Since then, agriculture, particularly beef production, has become one of the country’s economic foundation stones, contributing significantly to gross domestic product (GDP) (World Bank, 2009). The national livestock census of 2015 puts the cattle population in Namibia at 2.7 million (MAWF, 2016). In essence, this means that there are marginally more cattle than people in Namibia. The sustainability of the beef sector in Namibia faces a major challenge, owing to the loss of palatable grasses as a result of shrub encroachment and the consequent deterioration of pasture.

The genesis of shrub encroachment in Namibia is not well documented. De Klerk (2004) provides a brief account of some earlier references to shrub encroachment made by German explorers in the late 19th century. He cites references to observations made by Anderson in 1856 and Chapman in 1863 who complained about dense thicket of thorny bushes between Omatako Mountains and Otjikoto Lake. According to these explorers, such thickets severely lacerated their livestock and made it difficult for their wagons to pass through. Earlier explorers saw those thickets as perfect safe havens for wildlife such as lions and impala. Although these accounts do not explicitly mention the term ‘shrub encroachment’, they describe habitats analogous to shrub-encroached areas.

At first, no major efforts were invested in quantifying the extent of shrub encroachment in the country; information that could have served as an important baseline for contemporary investigations of its geographical distribution in Namibia. Instead, scientific efforts were invested in understanding the factors that contribute to shrub encroachment. As early as the 1930s, Heinrich Walter, a German botanist, was already working on the savannas, in the then South West Africa, to understand mechanisms that allow for tree-grass coexistence and the occurrence of shrub encroachment. His research efforts would later culminate in a savanna theoretical model, Walter's two-layer model (Walker & Noy-Meir, 1982; Walter & Mueller-Dombois, 1971) which has been dealt with under Section 1.2 of this study.

To grasp the severity of shrub encroachment in Namibia, the importance of oral tradition cannot be ignored. According to De Klerk (2004), such evidence is found in anecdotal oral accounts of farmers around the Otjiwarongo and Outjo areas, which are, today, some of the most shrub-encroached parts of the country. These farmers assert that such areas were open in the early 1950s, but currently farms in the area are occupied by dense thickets. The farmers support their arguments by pointing out that, in the past, one could hunt for game in the bush in the area without risking laceration by thorny bushes such as *S. mellifera*. This does not necessarily mean that such species did not exist in the area at the time, but that their density and cover has significantly thickened over the years. Around the same time, Joubert et al. (1960) indicate that shrub encroachment was becoming a serious problem in the country, for which methods such as veld burning, and stem spraying with diesoline were applied in order to fight shrub encroachment.

Data on the extent of shrub encroachment in Namibia are sketchy; several estimates have been suggested (Bester, 1999). The first known estimate on the extent of shrub encroachment has been proposed by Van Niekerk and Bester (1979), who suggested that shrub encroachment in Namibia at the time covered some 8 million ha of land, of which nearly two-thirds were classified as seriously affected. This translates into approximately 10% of the total territory's landmass. However, these estimates fell short of the inferences of Adams, Werner and Vale (1990) whose findings suggested that approximately 15 million ha of land, equivalent to nearly half of all the commercial farms in Namibia, is affected. Later, Bester (1999) conducted a detailed vegetation survey in commercial farms of Namibia and suggested that the total area encroached by bushes amounts to some 17.5 million ha of all commercial farms. However, Bester's (1999) estimates have several weaknesses; an example that illustrates the vague nature of these estimates is the portrayal of the Etosha Pan, a barren depression in the Owambo sub-basin, as being shrub encroached.

In 2004, De Klerk conducted a national study on shrub encroachment and estimated that, on commercial farms, shrub encroachment occupies some 15 million ha, while on communal land, some 10 million ha are affected. Taken together, this translates into approximately 25 million ha of land, representing nearly one-third of the whole country's land mass. De Klerk (2004) has further estimated that the density of bushes varies from approximately 2500 bushes/ha to some 10 000 bushes/ha, depending on the mean annual rainfall range and encroaching species.

Not all shrubs are responsible for encroachment in Namibia; only a few shrub species have been classified as shrub encroachers.

Figure 2 shows the area encroached by different shrub encroachers in Namibia, while Figure 3 provides the geographical distribution of each encroaching species. The description and ecology of these shrubs are presented in Appendix D. According to Bester (1996), the extent of shrub encroachment per each encroaching species is as follows: *S. mellifera* is the dominant shrub encroacher and is estimated to have encroached some 9 million ha of commercial farms land and some 3 million ha of communal land. *S. mellifera* encroachment covers parts of the central highland, thorn bush shrubland and camelthorn savanna extending across Gobabis, Windhoek, Otjiwarongo and Otavi areas. Following *S. mellifera* is *D. cinerea,* occupying some 2.5 million ha of commercial farms and 1.2 million ha of communal land. Encroachment by *D. cinerea* dominates in the burkea woodlands, the dolomite karstveld and the tamboti woodlands covering parts of Tsumeb, eastern Etosha and Grootfontein. Meanwhile, *T. sericea* is most dominant in northern central Kalahari around Gobabis town, and *C. mopane* is mainly dominant on communal land west of Etosha Pan, covering parts of the Kaokoland and Omusati Region. Other species, such as *Senegalia reficiens* and *Terminalia prunioides,* are partly considered as bush encroachers, but their contribution to this phenomenon is negligible. Because of the vastness of the area affected by shrub encroachment in Namibia, the true extent of shrub encroachment may prove challenging to establish. Considering the uneven distribution of these shrub species across the landscape, this study will focus on species such as *T. sericea, S. mellifera* and *D. cinerea* whose geographical distribution is found across the Kalahari rainfall gradient.

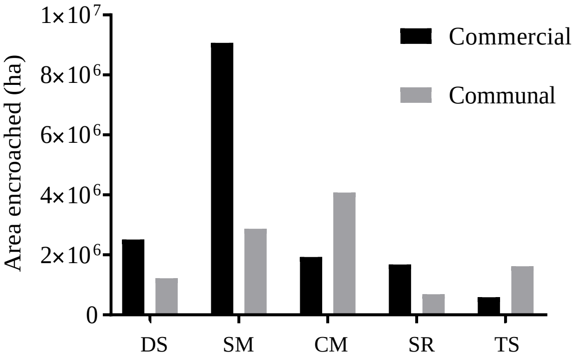

Figure 2: Area encroached by dominant shrub-encroaching species in Namibia. (Data source: De Klerk, 2004). Key: SD= *D. cinerea*, SM=*S. mellifera*, CM= *C. mopane*, SR= *S. reficiens*, TS= *T. sericea*.

In terms of climatic factors, Figure 3 indicates that shrub encroachment is predominant around the rainfall belt of 250 mm to approximately 500 mm per annum, an area with a rainfall coefficient of variation of approximately 30% to 40% (Engert, 1997). However, these sub-regional climatic conditions may change in the future. Existing climate change models predict significant changes in both rainfall and temperature patterns over the sub-region (Maúre et al., 2018). In terms of temperature, most parts of Namibia are expected to experience an increase in temperature larger than the mean global warming. Precipitation is expected to decrease by an amount ranging between at least 0.2 and 0.4 mm per day, an amount which translates into approximately 10%–20% of the climatological values over most of the central subcontinent and parts of the subcontinent (Maúre et al., 2018). The change in precipitation is expected to translate into an increase in the number of consecutive dry days and a decrease in consecutive wet days over the region (Maúre et al., 2018). It is not certain how this will influence the savanna and shrub encroachment in Namibia.

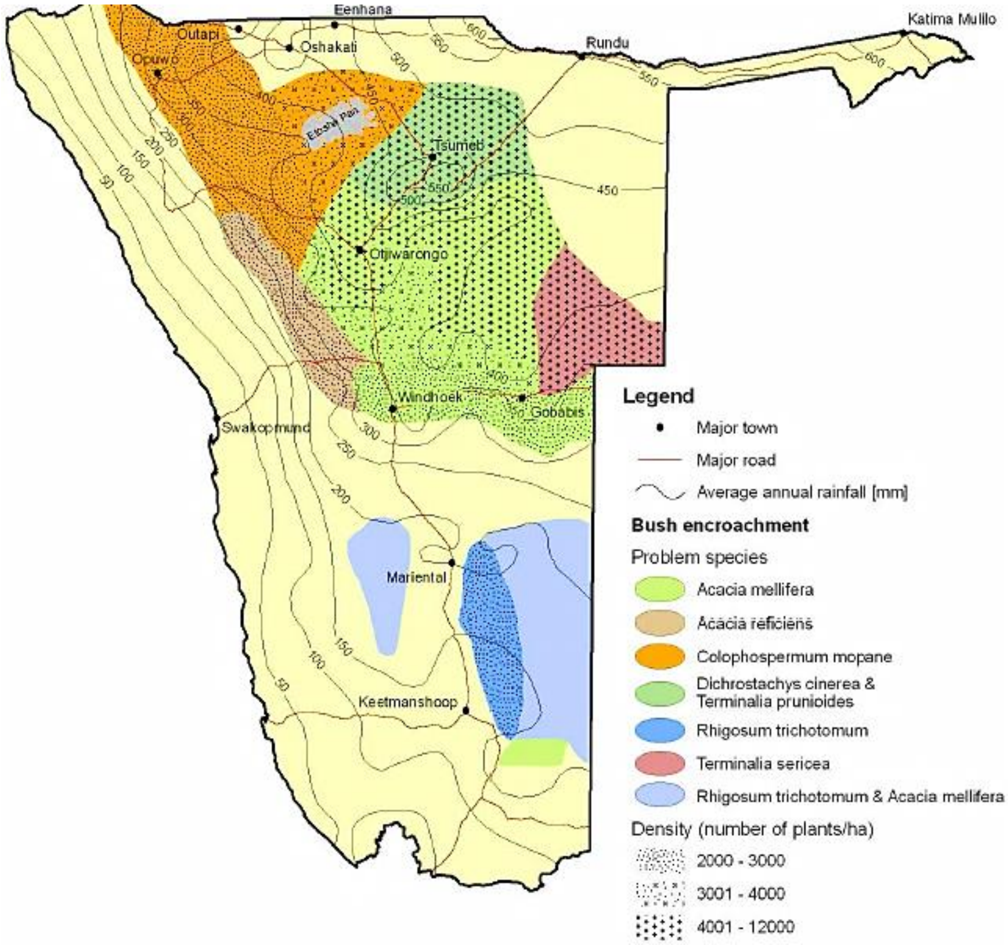

Figure 3: The geographical extent and density of shrub encroachment in Namibia. (Data source: Bester, 1996).

2.2.2 Socio-economic and ecological implications of shrub encroachment

Shrub encroachment has major socio-economic consequences on the livelihoods of farmers in Namibia. According to De Klerk (2004), some US$ 48 million to US$ 1.1 billion are lost annually in Namibia owing to poor veld production caused by shrub encroachment, a situation that particularly affects the beef sector, one of the major sources of revenue. Over the years, Namibia has exported beef meat products with a duty-free quota of 13 000 metric tonnes per annum to the European Union (Cabrera, Cochran, Dangelmayr & D'Aguilar, 2010; Chiriboga, Kilmer, Fan &

Gawande, 2008). However, Namibia has increasingly struggled to meet this demand, reaching merely some 70% of the quota, on average (Cabrera et al., 2010; Chiriboga et al., 2008). While it cannot be conclusively argued that the beef sector has failed to meet such a demand due to shrub encroachment on commercial farms, it is probable that the phenomenon has severely affected the productivity of commercial rangelands over the years, which in turn, affects livestock production and food security (Chiriboga et al., 2008). The situation is exacerbated during drought years when shrub encroachment aggravates drought impacts on the agricultural sector through increased animal mortality and poor animal health. In addition, the number of resources and the effort invested in the fight against shrub encroachment, such as bush clearing, worsen the socio-economic losses to livestock farmers as resources that could be invested in animal fodder are being used up to clear encroaching shrubs.

In addition to socio-economic losses that result from shrub encroachment, there are other associated, significant ecological losses. The thickening of bushes is known to influence the eco-hydrological systems by altering the flow of water (Archer, 2010). This chiefly happens when dense bushes interact both with above-ground and below-ground water using their broad leaves and roots. Naturally, a plant’s leaves intercept rainfall and their roots absorb water from the soils and release such water into the atmosphere through evapotranspiration. Therefore, the more shrubs there are, the higher the loss of rainfall amount and soil water to evapotranspiration. This premise has been tested in several studies. According to Scott, Huxman, Williams and Goodrich (2006), shrub encroachment has been responsible for a decline in stream-flow and an increase in evaporation from the soils, leading to a decline in soil water availability in a semi-arid environment of Arizona, western United States. Stream-flow is particularly affected as the dense above-ground canopy of encroaching shrubs intercept rainfall, leaving little water to recharge ground reservoirs. Scott et al. (2006) have further found that shrub encroachment has an effect on below-ground water in a similar environment, with water usage increasing more in shrub-encroached sites than in grasslands. Similarly, Grygoruk, Batelaan, Swiatek, Szatylowicz and Okruszko (2014) have established that there is a relationship between shrub encroachment and evapotranspiration, and concluded that uncontrolled encroachment of shrubs caused huge water loss due to evapotranspiration in the Middle Biebrza Basin of Poland. Admittedly, none of these studies have been conducted in a semi-arid savanna ecosystem; however, they demonstrate that there is a strong link between woody thickening and soil water loss, which can be applied to semi-arid arid environments such as the savanna of Namibia.

In Namibia, several estimates have been proposed on the effects of shrub encroachment on groundwater, but largely in grey literature. *S. mellifera*, one of the most notorious encroaching shrubs, has been estimated to extract some 32 500 litres of water from the soil per day for every 500 trees, while *T. sericea* consumes some 8 320 litres per day for the same number of shrubs (De Klerk 2004). Based on these estimates, De Klerk (2004) has extrapolated that some 31 trillion cubic metres of water are lost annually from the 25 million ha of land encroached by shrubs in Namibia. With Namibia being the driest country south of the Sahara, water scarcity is a major challenge and there are thus concerns that shrub encroachment contributes significantly to the depletion of its groundwater resources (De Klerk, 2004).

There is, however, some scepticism about these estimates. Firstly, evapotranspiration itself is considered to be a very challenging parameter to measure (Amatya et al., 2016), making it difficult to acquire reliable estimates. Secondly, the extent to which shrub-encroaching plants depend on groundwater aquifers for survival is still unclear, owing to the various root systems that they develop.

In addition to the impacts on groundwater resources, the effects of shrub encroachment on biodiversity and species behaviour have also been documented, although the results are somewhat uncertain (Eldridge et al., 2011). Some studies have predicted increased biodiversity with shrub encroachment (e.g., Kerley & Whitford, 2009; Ben-Shahar, 1992; Ayers et al., 2000), while others have envisaged a deterioration of biodiversity with shrub encroachment (Angassa, 2014). There are those who have predicted changes in animal behaviour in response to shrub encroachment (Blaum et al., 2007). These differences in opinion are largely attributed to the species involved in the experiments conducted. For example, shrub encroachment in Australia has been reportedly linked to an increase in avian biodiversity for some bird species. Kerley and Whitford (2009) have found an increase in wildlife species, such as ungulates and birds, as shrub encroached in New Mexico, USA. In Namibia, Karuaera (2011) has assessed the effects of shrub encroachment on the abundance, diversity and composition of small mammals, but found no significant influence of shrub encroachment on the said species diversity indicators, and has concluded that shrub encroachment did not affect the diversity and composition of small mammals. Further studies by Blaum, Rossmanith, Popp and Jeltsch (2007), focusing on large mammal carnivores in the Kalahari, have found that different mammals behaved differently in response to shrub encroachment, depending on the habitat preference of each species.

This confirmed earlier findings by Joubert (2003) who has investigated the relationship between shrub encroachment and mammal diversity, and found that certain mammals, such as endangered cheetah, are more adapted to open savanna than to thickets. As a result, such animals would be threatened if their habitats were shrub encroached. However, ungulates such as kudu, duiker, dik-dik and giraffe prefer dense bushes for browsing, although thick bushes may restrict the movement of such ungulates. In terms of reptiles, Meik, Jeo, Mendelson and Jenks (2002) have found a significant difference in the abundance and assemblage of lizards between open savanna and shrub-encroached sites, and have concluded that shrub encroachment has an effect on the population of reptiles. Mkandawire (2013) has investigated the effect of shrub encroachment on the ecology of invertebrates in the Kalahari, and concluded that shrub encroachment impacts their diversity, richness, composition, and abundance.

In terms of plants, shrub encroachment is seen as a threat to botanical diversity because of its ability to displace other species, resulting in species decline (Maggs, Craven & Kolberg, 1998; Uphoff et al., 2006). Such evidence suggests that shrub encroachment can potentially alter the integrity of ecological systems of both fauna and flora if not sufficiently controlled.

These findings indicate shrub encroachment is a serious problem in Namibia and beyond. Its effects range from socio-economic losses due to poor rangeland conditions, to alteration of eco-hydrological systems and its implication for biodiversity. Despite the magnitude of impacts on socio-economic and ecological systems, the mechanism under which shrub encroachment occurs is still poorly understood. As we will witness in the following sections, several theoretical frameworks have been proposed.

2.3 The theoretical framework of the study

According to Maxwell (1996), a theoretical framework is defined as a system of concepts, assumptions, expectations, beliefs, and theories that supports and informs research on a phenomenon being investigated. The theoretical framework provides the philosophical stance of the study in relation to the existing body of knowledge (Locke, Myers & Herr, 2001). A theoretical framework, therefore, informs the study with respect to the existing knowledge about the subject, by explicitly indicating what theories may guide the study, as well as other theories that are relevant to the study. The theoretical framework also serves as the foundation from which new knowledge can be constructed (Grant & Osanloo, 2015). In a study without a clear theoretical framework, the structure and vision would also be unclear (Osanloo, 2015).

Choosing a theoretical framework should not be an arbitrary decision Grant and Osanloo (2015) have argued, but should represent the investigator's beliefs and understanding about the nature of the existing knowledge on the subject. Choosing a theoretical framework is often, therefore, a major challenge in scientific investigations, owing to contrasting and competing theoretical perspectives that exist in various fields.

Savanna ecology, specifically tree-grass coexistence, is one such subject of inquiry with a troublesome theoretical framework. To date, there is no unanimous theoretical framework concerning the long-term functioning of the savannas and mechanism under which shrub encroachment occurs. Efforts are still being made to provide plausible theoretical explanations of the savannas.

Over the years, competing, diverging and conflicting theories, models, and hypotheses have been proposed to explain the nature and functioning of the savann biome. These theories can be classified within major ecological paradigms such as equilibrium, non-equilibrium, disequilibrium and climate change. The major disparities between these paradigms are the role of biotic and abiotic factors in driving the succession of vegetation in the savannas, as well as how such a biomes respond to disturbances, such as drought, grazing, and fire. These theories are discussed in turn below.

2.3.1 The savannas as equilibrium biomes

Our views on how ecological systems function has a significant influence on the approaches we advocate to manage or manipulate them (Ellis & Swift, 1988). For decades, our views on the savannas and many other terrestrial biomes have been profoundly dominated by the theoretical framework provided by the equilibrium theory (Archer, 1990; Eagleson, 1989; Noy-Meir, 1982; Walker, Ludwig, Holling & Peterman, 1981; Walker & Noy-Meir, 1982) and managed as such. Rooted in the ‘balance of nature metaphor’, this theory suggests that, in nature, organisms are homogeneously connected to one another so that a state of ‘equilibrium’ is sustained, creating balanced ecological systems over time (Cuddington, 2001; Egerton, 1973; Ehrlich & Birch, 1967; Pimm, 1991; Slobodkin, Smith & Hairston, 1967; Williams, 1964). Based on this metaphor, it was therefore assumed that terrestrial ecosystems are in states of equilibrium with their environments. A sustained equilibrium balance was considered a necessity for the survival of such ecosystems because, without it, organisms that make up such ecosystems would perish and the ecosystem collapse. Organisms would perish because various competing forces of nature would push them into extinction because of the lack of balance ‘equilibrium’ (Maiti & Maiti, 2011;

Russell, Hertz & McMillan, 2014). This theory gained popularity during the early to the middle part of the 20th century following the work of Clements (1916, 1936) which culminated in what would later become known as Clements' range succession model, popularly applied to rangeland and forest management (Pickett, Cadenasso & Meiners, 2009).

Proponents of the equilibrium theory see terrestrial ecosystems, such as the savannas, as stable ecosystems at a climax stage of vegetation growth. According to Clements, (1936), the climax is understood to be a stable, self-sustaining vegetation succession stage at which vegetation succession processes have reached endpoint growth maturity, a point at which an equilibrium balance with the local environmental conditions has been reached and sustained. Clements (1936) argues that climax is an important stage of vegetation growth because it represents a more permanent and final stage of the succession processes from which vegetation unit boundaries such as grassland, woodland, savanna or shrubland can be defined indefinitely. Such vegetation communities share almost the same characteristics for years. In turn, the ecosystem stability forms an important basis for a natural classification of plant communities as their indefinite static boundaries can be spatially defined.

The equilibrium theory also argues that the succession trajectory, a path through which the succession processes pass, and the end climax is believed to be a result of intrinsic factors, including the prevailing climatic condition and soils; the interspecific and intra-specific competition was thought to control the succession processes (Whittaker, 1953). To reach climax, a vegetation community's development processes typically progress steadily and predictably along a well-defined, deterministic succession trajectory, moving from pioneer species to climax species (Meeker & Merkel, 1984).

Vegetation development, therefore, follows a sequential replacement of herbaceous species by shrubs, and eventually trees, depending on the prevailing climate and soils (Pickett et al., 2009). However, there would be other places such as grasslands, where succession does not necessarily progress toward tree-form structure, owing to prevailing climatic conditions and soils that do not support such a life form. A typical example would be the Namib Desert environment that receives less than 150 mm of rainfall per annum (Mendelsohn et al., 2002). Such a precipitation amount is insufficient to support woodland-type of vegetation structure, but relatively sufficient to support a grass layer, making grassland the only possible climax for the Namib Desert environment.

This theory further argues that ecological disturbances, such as fire and grazing, are considered as episodic, with negligible impacts on vegetation (Hobbs & Suding, 2008). Such episodic events are regarded as not having significant effects on vegetation structure once at the climax (Meeker & Merkel, 1984). This stability, according to the equilibrium theory, exists because terrestrial ecosystems are resistant, an important factor which gives such ecosystems the ability to tolerate disturbances without suffering a significant change in ecosystem structure and function; or such ecosystems are resilient enough to return to their pre-disturbance states when disturbances cease. Overall, vegetation communities are seen as stable super-organisms for which available species are naturally interconnected and share a common evolutionary history (Clements, 1936). In the absence of climate variability and anthropogenic intervention, the ecosystems such as the savannas would remain in a stable equilibrium state, unchanged for years.

2.3.1.1 Walter’s two-layer model: an equilibrium model of the savannas

The theoretical perspective presented above has had an overwhelming influence on how savanna biomes are perceived and eventually managed as per Walter’s two-layer model (Figure 4) which has already been discussed under Section 1.2. In this framework, the savannas are perceived as stable biomes in an equilibrium balance with the local climatic conditions and soils, and are regulated by a natural mechanism such as tree-grass ratios and root niche-partitioning (Accatino et al., 2010; Mistry, 2000; Scheiter & Higgins, 2007; Scholes & Walker, 1993; Wiegand et al., 2006). According to Gil-Romera et al. (2010), tree-grass coexistence is seen as the only possible final climax life form allowed by the prevailing climate of the tropical regions where the savanna biomes are found because soil moisture is often in short supply. As a result, the tree-grass ratio would tend to hover around a fixed point where neither of the two contrasting life forms out-competes the other. This equilibrium, according to Gil-Romera et al. (2010), is made possible because the superior competitors, trees, become self-thinning at a level insufficient to exclude the inferior competitors, the grasses. As a result, grasses would grow to compete with the trees. In this context, shrub encroachment is seen as an unnatural phenomenon, the result of overgrazing (Walter, 1964). Overgrazing radically changes the ratio between trees and grasses and such radical changes eventually shift the savanna biomes out of equilibrium (Sankaran et al., 2004), creating a competitive advantage for trees, and forming woody-dominated biome. By implication, then, shrub encroachment is a result of inappropriate land use on the part of the farmers. Without overgrazing occurring on the land, shrub encroachment would be a non-existent phenomenon in the savanna (Walter, 1964; Walter & Mueller-Dombois, 1971). For decades, this understanding shaped how the savanna was perceived and managed.

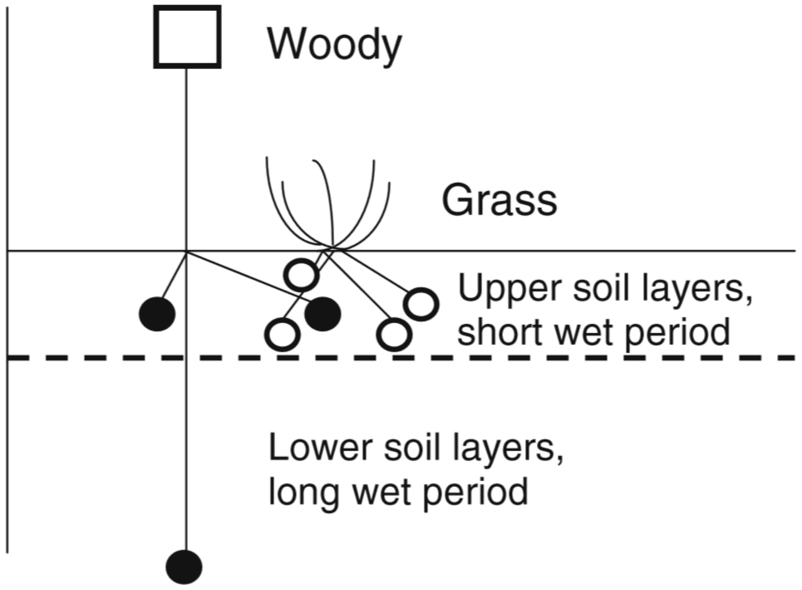

Figure 4: A conceptual model illustrating Walter’s two-layer model. (Source: Walker and Noy-Meir, 1982).

In the late 1980s and early 1990s, following the works of various scholars in arid and semi-arid parts of the world, the relevance of the equilibrium theory and Walter’s two-layer model started attracting some major scrutiny (Ellis & Swift, 1988; Westoby, Walker & Noy-Meir, 1989). Such scrutiny would later give rise to an alternative competing theoretical framework, a framework which questioned the relevance of the equilibrium theory, particularly in respect of arid and semi-arid environments where vegetation is mainly controlled by inter-annual climatic variation. Specifically, the following critical issues were highlighted.

Firstly, no universal definition of the term ‘equilibrium’ or ‘stability’ existed. It was not clear what it really means for an ecosystem to be in a stable state, or in equilibrium.

Such a shortcoming could create confusion about applying this concept to management of the savanna.

‘Equilibrium’ is defined by the *Oxford English Dictionary* to mean ‘a state in which opposing forces or processes are balanced’ (Stevenson, 2010). In ecology, the term ‘equilibrium’ may be used to refer to numerical stability, such as the average population size of either plants or animals over a considerable time, where fluctuation is at its minimum in a certain geographical area (Cuddington, 2001). It may also be used to refer to the ecosystem state where the rate of change in species population density is zero. Other concepts that have been used to refer to equilibrium are terms such as ‘resistant’, which refers to the capacity of a system to absorb any external shock without suffering significant change, or an ecosystem which is ‘consistent’, such that it stays essentially unchanged in time and space (Germino, Chambers & Brown, 2016). Such ecosystems can also be considered as resilient ecosystems if they have the ability to return to their pre-disturbance state after a temporary disturbance has ceased (Hobbs & Suding, 2008). Equilibrium ecosystems are also considered to be those that are persistent through time, and remain within a defined limit in time and space (Hobbs & Suding, 2008). Orderliness, stability and predictability are important factors in such ecological systems (López et al., 2013). For the purpose of preserving order in such an ecosystem, all organisms are interconnected, allowing nature to strike a balance between disparate forces. Small fluctuations are considered as being of negligible importance. As a result, the existence of such varying definitions may make it difficult to apply the equilibrium theory to the management of terrestrial ecosystems.

Secondly, the equilibrium theory downplays the role of ecological disturbances, such as fire and grazing, in influencing the structure and dynamics of terrestrial ecosystems

(Hobbs & Suding, 2008). The idea that ecological disturbances play a negligible role in ecosystems is ill-conceived. Disturbances such as fire and grazing are seen as unnatural forces, prohibiting ecosystems from reaching their natural climax (Clements, 1936). In terms of grazing systems such as the savannas, this framework argues that, in order to maintain the integrity of vegetation under grazing pressure, it is imperative that an equilibrium between grazing pressure and vegetation succession tendency is sustained (Dyksterhuis, 1949) because vegetation succession towards climax is considered as a steady and predictable process, while grazing is considered as a progressive process, which is in direct opposition to the vegetation succession tendency (Dyksterhuis, 1949). An equilibrium balance between grazing pressure and succession could thus be reached by determining the optimum carrying capacity of the ecosystem. Hixon (2008) has defined ‘carrying capacity’ as ‘the maximum population size that can be supported indefinitely by a given environment in a sustainable manner’. When this concept was first introduced to ecosystem management, its definition attracted several controversies, making its application somewhat complex, especially in environments which continuously change spatio-temporally (Caughley, 1979). Thus, under this theoretical framework, resource management puts a strong emphasis on ecosystem carrying capacity, although vegetation succession in response to grazing pressure is often not predictable.

Studies on ecosystem disturbance, more specifically in arid and semi-arid regions, demonstrate that vegetation response to disturbances is often not consistent, not continuous, and not reversible; nor is it predictable, contrary to the assumptions of the equilibrium theory (Westoby et al., 1989). Such disturbances are often characterised by varying frequency, intensity, extent and duration, which significantly influence how vegetation responds to such disturbances (Voller & Harrison, 2011).

Thirdly, the equilibrium theory overlooks the significant impact of climate variability, such as drought, on the stability of terrestrial ecosystems. It was observed that above-average rainfall increases vegetation succession toward a climax, while drought merely affects vegetation the same way as grazing does (Westoby et al., 1989). Thus, the impact of drought can equally be managed by reducing grazing pressure so to not degrade the ecosystems. However, Elto (1930) has indicated that terrestrial ecosystem dynamics vary consistently to a greater or lesser extent due to climatic factors, and those variations are usually irregular in duration, amplitude and space. As a result, species would adapt to such climatic variations and thereby change the equilibrium point (Looman, 1976). These dynamics make the behaviour of such ecosystems largely unpredictable. In addition, such ecosystems are characterised by spatial heterogeneity brought about by spatio-temporal variation in soils, rainfall, and disturbance frequency, duration and intensity which influence the distribution of vegetation across the landscape (Hobbs & Suding, 2008).

Similarly, despite its prominence in savanna ecology, Walter's two-layer model is subject to several shortcomings. Firstly, field evidence has demonstrated root systems overlap between some grass species and some savanna shrubs (Seghieri, 1995; Hipondoka et al., 2003; Hipondoka & Versfeld, 2006; Kambatuku et al., 2013). Secondly, studies using stable isotopes have revealed that trees and grasses might have the same water source (February & Higgins, 2010; Kulmatiski, Beard, Verweij & February, 2010), pointing to direct competition. Moreover, evidence of shrub encroachment has also been reported on ecosystems that were historically known to have received very little grazing pressure (Anderson, 1856; cited in Wiegand, Saltz and Ward, 2006) such as around Gobabis and Otjiwarongo, areas described by earlier explorers around the 18th century (see also De Klerk, 2004). Meanwhile, recruitment of some shrub-encroaching species, such as *Prosopis glandulosa* (Brown & Archer, 1989; Simmons et al., 2008), and *S. mellifera* (Kraaij & Ward, 2006) have been found to be not necessarily influenced by grass cover, as most seedlings also depend on shallow soil water during germination. Similarly, Wiegand et al. (2005) found evidence suggesting that tree-grass coexistence is possible on shallow soils, too shallow to allow root niche separation, which rules out the possibility that root niche-partitioning is the main factor responsible for tree-grass coexistence and shrub encroachment, when eventually one of the competitors is removed.

The equilibrium framework laid the foundation for understanding the behaviour of the savannas using Walter's two-layer model. Evidence has been claimed where the premises of this framework do not hold, especially in arid and semi-arid regions where the savanna biomes are most widespread. The recognition of this discrepancy has generated a search for alternative theories which better represent the vegetation dynamics that have been observed over the years in arid and semi-arid environments. Thus, the concept of ecosystems with a single equilibrium state has been rejected in several quarters of the scientific community (e.g., Ellis & Swift, 1988; Westoby et al., 1989). This rejection was done in favour of alternative theoretical perspectives, such as the non-equilibrium theory. The non-equilibrium theory emphasises alternative stable states, discontinuous, reversible, and irreversible thresholds. This paradigm shift significantly brought a new perspective to how terrestrial ecosystems function. However, Walter's two-layer model continues to influence the science of savanna ecology to date.

2.3.2 The savannas as non-equilibrium biomes: a paradigm shift?

According to Kuhn (1962), science does not progress as a linear accumulation of new knowledge, but undergoes periodic revolutions called paradigm shifts. A theoretical discussion on the savanna biomes without raising the issue of paradigms and paradigm shift would largely be deemed incomplete.

Our knowledge of the savannas has undergone through several paradigm shifts in recent years. In the late 1980s, pioneers of the non-equilibrium theory, such as Ellis and Swift (1988), as well as Westoby et al. (1989), working on the savannas in semi-arid regions were confronted with patterns of ‘anomalies’ inconsistent with the provisions of the equilibrium theory, the dominant paradigm in vegetation ecology at the time. Their works are particularly credited with fuelling the debate that brought about the momentum for a paradigm shift in vegetation ecology and gave rise to the non-equilibrium paradigm, although the issue of non-linear and complex ecosystems was already known in the early 1900s (Gleason, 1926, 1927). However, such ideas perhaps came too early at the time when the proponents of the equilibrium paradigm were dominating vegetation ecology, and thus could not prosper.

A non-equilibrium ecosystem is defined as an ecosystem that is continuously changing in time and space. According to DeAngelis and Waterhouse (1987), and Ellis and Swift (1988), non-equilibrium ecosystems are characterised by loosely coupled herbivore-plant interaction, density-independence, and where vegetation’s primary production is mainly controlled by inter-annual rainfall variation, as opposed to human disturbances. The effect of human disturbances, such as fire and grazing, in influencing vegetation patterns are acknowledged, but their impacts are considered secondary. Despite the fact that consumers such as grazers/browsers impact vegetation through grazing or browsing, their impacts are often insignificant when compared to the impact of climate variability, such as drought, on the long-term sustenance of vegetation primary production (Hobbs & Suding, 2008). Moist ecosystems where rainfall is predictable are different, so is vegetation production, and therefore, the variation in vegetation production will not be influenced by rainfall fluctuation as much as it will be influenced by grazing, for instance (Hobbs & Suding, 2008). Moreover, in non-equilibrium ecosystems, interspecific competition between coexisting species is considered to have a negligible influence on the long-term vegetation community structure.

The non-equilibrium theory suggests that the savannas are open and unstable biomes controlled by inter-annual rainfall variation (Westoby et al., 1989). Such biomes are found in regions where the inter-annual rainfall coefficient of variation is larger than 33% (Ellis & Swift, 1988). In such areas, the spatio-temporal rainfall variation is considered sufficiently large to influence the vegetation structure, rendering the impacts of grazing and fire negligible in the long run. As we will see in the subsequent sections, the issue of fire and grazing gives a new twist to the whole savanna controversy.

On disturbance, this theory acknowledges that while grazing clearly requires forage, the availability of that forage is mainly driven by overriding abiotic factors, primarily rainfall and substrate conditions (Sullivan & Rohde, 2002). Further, the non-equilibrium theory argues that, in arid and semi-arid ecosystems, plant composition and biomass production are primarily driven by rainfall variation and not necessarily by grazing pressure, because animal numbers are kept below equilibrium densities by frequent droughts, and that degradation of the vegetation as a result of overgrazing is thus unlikely (Vetter, 2005). This would, therefore, imply that degradation problems, such as shrub encroachment, cannot necessarily be a direct result of overgrazing alone as predicted by previously discussed models, but are a shift in an ecosystem state in response to rainfall variability, as predicted by the non-equilibrium framework.

Contrary to the equilibrium theory that predicts one steady state at the end of the vegetation succession pathway, the non-equilibrium theory predicts a web of non-linear, dynamic and complex behaviours, multiple steady states and thresholds (DeAngelis & Waterhouse, 1987; Hobbs & Suding, 2008; Illius & O'Connor, 1999; Tarlock, 1993; Wallington, Hobbs & Moore, 2005). Several models have been developed to advance the non-equilibrium theory and its application to arid and semi-arid ecosystems in particular. One such model is the state and transition model, to which we turn in the next section.

2.3.2.1 The state and transition model: a non-equilibrium model of the savannas

The state and transition model developed by Westoby et al. (1989) is the common non-equilibrium model at present, and has been applied to vegetation dynamics to demonstrate non-equilibrium behaviours (Figure 5). The state and transition model regards vegetation communities as represented by catalogues of discrete states, with numerous transitions taking place between these states. Vegetation states are defined as comprising a recognisable, resistant, and resilient complex of vegetation structure, soils, and climate that are connected through an array of integrated ecological processes and that interact to produce a sustained stable vegetation community. Transitions refer to the trajectories of change of such ecosystems that are precipitated by events/stressors such as drought, fire, and grazing (Westoby et al., 1989). It is these stressors that trigger transitions between the different states from time to time, and from one space to the other. Although it was earlier argued under the non-equilibrium framework that disturbances such as fire and grazing play a negligible part, the state and transition model acknowledges these events as possible environmental stressors that can trigger vegetation transition from one state to the other.

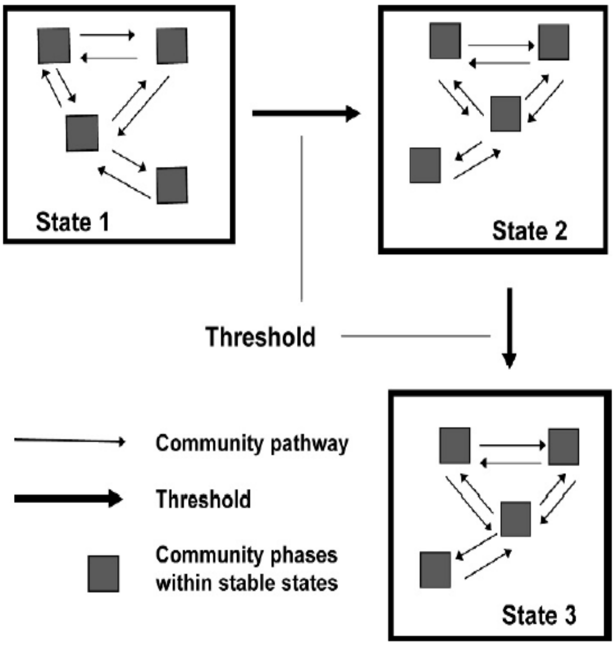

Figure 5: The state and transition model illustrating how non-equilibrium vegetation communities oscillate between states. (Source: Stringham, Krueger & Shaver, 2003).

In addition, vegetation communities will have transient states that are not persistent states, but change to any one of the persistent states, depending on the prevailing stressors. A transient state toward a shrub-dominated state can be reversed to a grassland state due to the occurrence of wildfire. In order to understand the vegetation dynamic using the state and transition model, one has to characterise catalogues of possible alternative states as well as catalogues of possible alternative transitions and factors/stressors that may drive the ecosystem from one state to the other. In advancing the state and transition model, Stringham, Krueger and Shaver (2003) have suggested that vegetation transition from one state to the other follows either reversible or irreversible pathways/transitions. The main difference between reversible and irreversible transitions is embedded in the ecosystems' ability to self-repair. These self-repair mechanisms are determined by the resistance and resilience of such ecosystems to prevailing stressors. In this context, resistance refers to the ability of the ecosystems to withstand impacts of the prevailing stressors and to be able to perform the necessary ecological processes and provide ecosystem services. Resilience refers to the ecosystems' ability to return to their pre-disturbance states when the stressors cease to exist, either naturally, or as a result of management interventions. Resistance and resilience are considered as inherent properties found in ecosystems, based on their physical components and the functional capacity of the associated ecological processes (Stringham et al., 2003). The transition from one state to the other does not necessarily mean moving across a threshold into a completely new type of community. Even an oscillation of species composition within a community is considered as a phase shift (Stringham et al., 2003). However, when such a transition occurs, an ecosystem moves into a completely new irreversible state: the ecosystems have passed a critical point or threshold; a point where one or more of the primary ecological processes responsible for maintaining the stability of a certain state has been degraded beyond the point of self-repair, even when stressors are removed (Stringham et al., 2003). At this point, it is not possible for such an ecosystem to revert to its previous state on a practical timescale without a substantial amount of human input into restoring such an ecosystem. A typical example is the encroachment of trees on grasslands, which cannot be reversed unless a substantial and a costly de-bushing exercise or fire has taken place. The management objectives under this framework are thus to ensure that, when the transition trajectories are moving the ecosystem states to new thresholds, it is important that stressors triggering such transitions are eliminated in order to avoid irreversible and undesirable states, such as an ecosystem changing from a desirable, grassy state to an undesirable, woody state (Joubert et al., 2008).

Within this framework, the savannas are seen as unstable biomes comprising different heterogeneous states, with vegetation structure continuously moving from one state to the other in a spatio-temporal manner (Westoby et al., 1989). Transitions from one state to the other follow various non-linear, unpredictable, reversible, and irreversible thresholds, driven by stochastic factors, including rainfall variation, and anthropogenic practices such as grazing, fire, deforestation, and other human land uses. Rainfall fluctuation over the years may cause temporal variation in the species recruitment rate, where, during droughts, grass recruitment and growth takes place at the expense of trees, while trees' growth and dominance would be common during the rainy periods (Vazquez, López, Calabrese & Munoz, 2010). According to Meyer et al. (2009), this dynamic change from grass-dominated to tree-dominated savannas is what we call shrub encroachment, although it is merely one extreme threshold towards a woody-dominated savanna into which an ecosystem has shifted from time to time. Since an encroachment of shrubs on grasslands hardly flips back to a grass-dominated ecosystem without a substantial input, this transition represents one of the irreversible thresholds of this dynamical behaviour in the savanna. In Namibia, Joubert et al. (2008) have applied the state and transition model to the dynamical behaviours of *S. mellifera*, one of the common encroaching shrubs in the highland savanna of central Namibia, and have discovered nearly five (5) states and numerous trajectories of transition (Figure 6). The states described are (1) 'climax-grassy state' (2) 'pioneer grass state’, (3) ‘unstable state with woody seedlings’, (4) ‘vigorous bush-thickened state’, and (5) ‘senescent bush-thickened state’.

In terms of transitions from one state to the other, as indicated by black arrows, this model argues that transition (1) is a typical retrogressive succession in a grass-dominated sward, promoted by excessive and continuous grazing, and by periods of drought. Transition (2) is a typical succession towards a climax state from a pioneer state in a grass-dominated sward, promoted by high rainfall years and lenient grazing. In elaborating these transitions, Joubert et al. (2008) have further argued that transition (3) can be viewed as vegetation movement from the state (1) to state (2) following several years of higher rainfall, seed production, the survival of seedlings, and eventually, an establishment of *S. mellifera* shrubs. Transition (4) indicates the movement from state (3) to state (1) as a result of fire killing seedlings, and consequently, turning the ecosystem back to a grass-dominated setting. For details on all the different transitions indicated in this model, refer to Joubert et al. (2008).

The transitions from one state to the other are particularly attributed to drivers such as drought, grazing, and fire. Similar ecosystem behaviours have been demonstrated in the Ethiopian savannas (Angassa & Oba, 2009).

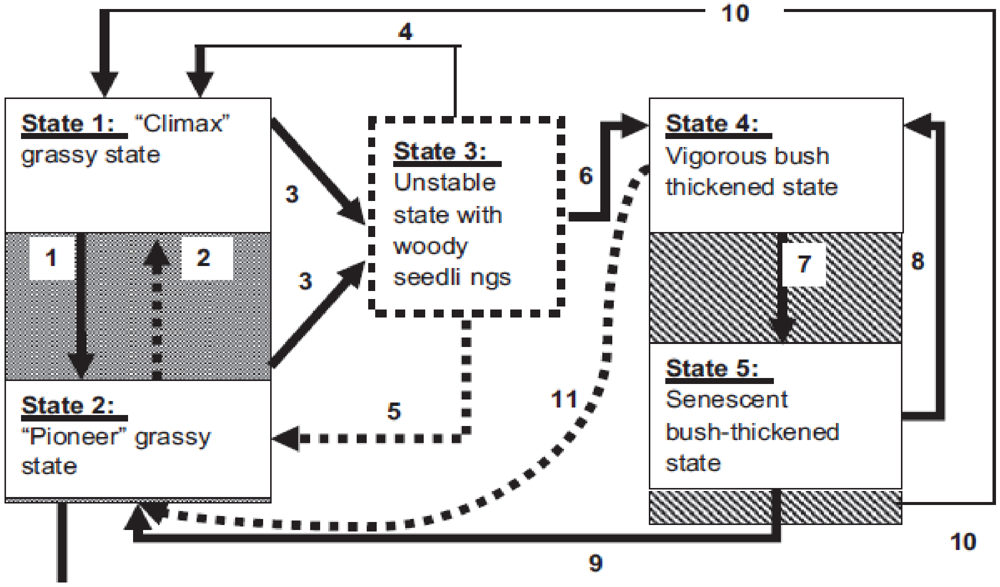

Figure 6: Schematic state and transition model for vegetation in the highland savanna of Namibia. Solid lines represent likely transitions, dotted lines represent less likely transitions (Source: Joubert et al., 2008).

The state and transition model is by far the most popular explanation of the savannas and mechanisms under which shrub encroachment occurs, following Walter's two-layer model. The main difference between these two models is that the latter is guided by the principles of the equilibrium paradigm, whereas the former belongs to the non-equilibrium paradigm camp. In principle, they disagree on issues such as factors that regulate vegetation behaviours, including rainfall, grazing, and fire.

2.3.3 The savannas as disequilibrium biomes

The search for plausible answers to the savanna questions has gone as far as generating ideas that can be classified within the disequilibrium theory. Although this framework has received relatively little consideration in vegetation ecology compared to the two previously presented theoretical frameworks, the rise of the disequilibrium theory has brought new perspectives to how we view the savannas. According to Luo and Weng

(2011), a disequilibrium system occurs when opposing internal and external forces prevent the system from achieving an equilibrium point, resulting in an unstable system. Applied to the savannas, this framework argues that pure grasslands or forests are the only equilibrium states possible, but the occurrence of ecosystem disturbances allows the savannas to persist in a disequilibrium state by buffering the natural succession processes, preventing such biomes from transition to either one of the two extreme states: grassland or forest (Jeltsch et al., 2000).

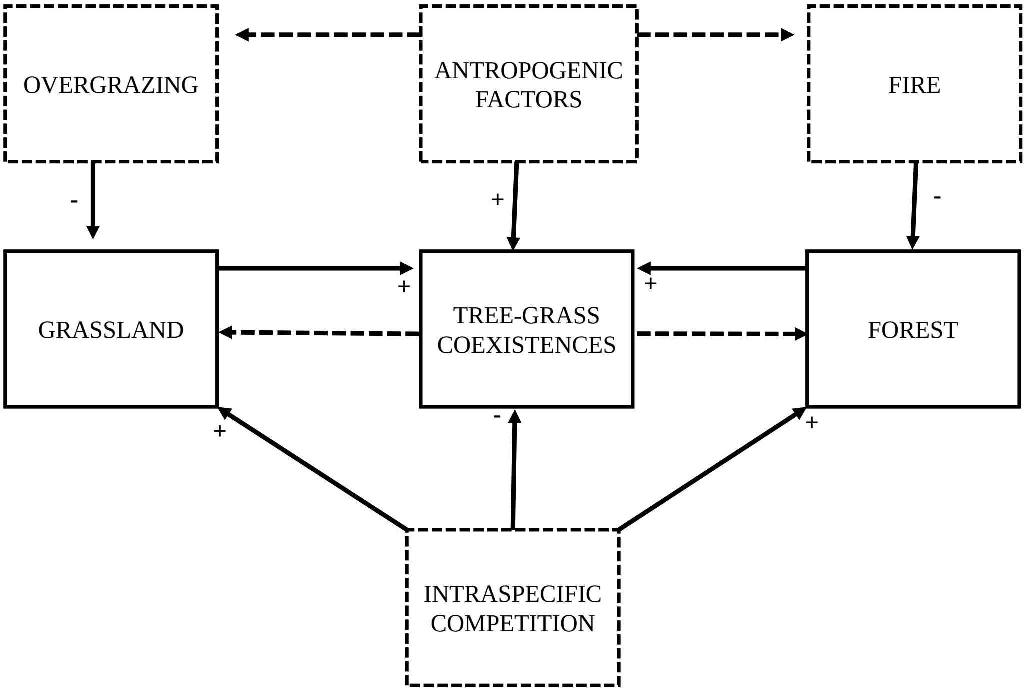

Figure 7: Conceptual model illustrating how fire and grazing may promote tree-grass coexistence. Note: unlike grass, trees take longer to regenerate after being destroyed by fire; overgrazing affects only grasses. Key: + Sign represents positive feedback, while - represents negative feedback. Diagram based on Sankaran et al. (2004) and Van Auken (2009).

As demonstrated in Figure 7, the disequilibrium theory argues that, under natural circumstances, long-term coexistence between trees and grasses to form the savanna biomes is not possible because of interspecific competition between the two coexisting life forms, as predicted by the competitive exclusion principle. Instead, because of competition, trees and grasses will segregate, leading to two distinct and extreme vegetation communities, grassland and forest woodland, where each one is a superior competitor (Sankaran et al., 2004). However, this segregation and exclusion process is never completed due to the bottleneck effects of the persistent occurrence of ecological disturbances in the ecosystems, such as fire and grazing, shifting the ecosystem processes off their segregation course (Sankaran et al., 2004). In terms of this premise, trees can invade grassland if the grass cover is reduced by grazers, leading to shrub encroachment, which will turn the ecosystem into either shrubland or woodland. Conversely, increasing tree cover could be reduced by fire, allowing grasses to grow in the open areas, turning the ecosystem into a grassland (Van Auken, 2009; Wiegand et al., 2006). It is these bottleneck effects that sustain tree-grass coexistence. In the absence of such disturbances, one superior competitor would dominate the vegetation community structure, turning the ecosystem into either grassland or forest. Several studies have since claimed that trees are superior competitors over grasses, using shrub encroachment as an example (e.g., Belay & Moe, 2012), while others support grasses as superior competitors (Cramer, Wakeling & Bond, 2012; Morrison, Holdo, Rugemalila, Nzunda & Anderson, 2018). It is likely that this superior competition between trees and grasses also varies at different spatial and temporal scales. Because of these distrtubances it is thus precieved that the savannas are manmade biomes and therefore have no primary determinants.

The disequilibrium theory emphasises the relation between grazers and browsers in influencing the coexistence of trees and grasses, where grazers and browsers keep the savanna biomes in a state of disequilibrium. Grazers control the quantity of grasses. In turn, the grass fuel load controls the spread and intensity of fires, which influence the recruitment of trees seedlings and saplings (Jeltsch et al., 2000). Without fire, trees would thrive. Browsers, on the other hand, particularly mega-browsers such as elephants, control the abundance and distribution of trees by influencing their survival, growth and reproduction (Anderson & Walker, 1974; Barnes, 1982; Ben-Shahar, 1993, 1996; De Beer, Kilian, Versfeld & Van Aarde, 2006). Therefore, it is largely believed that mega-browsers such as the African elephant can potentially transform the savanna landscape, especially if their movements are restricted to small areas (Cowling & Kerley, 2002; Guldemond & Van Aarde, 2008; Holdo, 2003), because such browsers exert dramatic effects on plant communities, converting the ecosystem between various alternate stable states via consumption of plants, and so earning themselves the nickname, ‘ecosystem engineers’ (Ben-Shahar, 1998; Beuechner & Dawkins, 1961; Haynes, 2012; Holdo, 2003). Arguably, maintaining a balanced population of both browsers and grazers is important in sustaining a stable ratio between trees and grasses in the savanna. According to Blanc et al. (2005), Douglas-Hamilton (1987) and Georgiadis et al. (1994), the number of large herbivores has declined significantly over the last decades as a result either of poaching, translocation into National Parks and Game Reserves, or culling in most parts of Southern Africa. The result has been a reduction in the population of browsers in their natural habitats below a point at which they could control the spread of trees, while grazers, such as livestock, have significantly increased beyond the ecosystems' carrying capacity (O’Connor et al., 2014). This shift has arguably created an unbalanced competition between trees and grasses in such a manner that trees have become strong competitors against grasses. It has thus been postulated that the occurrence of shrub encroachment in the savanna biomes are due to the absence of mega-herbivores, such as elephant that control the growth of trees (e.g., Holdo, 2003; Laws, 1970; Valeix et al., 2011). However, sceptics argue that the response of vegetation to large herbivores is often challenging to interpret as it may be influenced by drought, fire, diseases, and inter-annual rainfall variation (Guldemond & Van Aarde, 2008; Valeix et al., 2011).

Overall, the disequilibrium perspective maintains that disturbances from fire and herbivores not only modify tree-grass coexistence, but also maintain their long-term coexistence. This theory has created a strong link between the persistence of savanna and human settlements. This study thus contributes to a better understanding and improvement of this model, by testing theories of competition between shrubs/trees and grasses.

2.3.4 The savannas and the dynamics of atmospheric CO_2

The existence of the savanna biomes and the occurrence of shrub encroachment has, to a certain extent, also been attributed to global environmental change, particularly the fluctuation in atmospheric CO_2 concentration (Cerling et al., 1993; Ehleringer et al., 1997). This link is based on the foundation that plants naturally absorb CO_2 from the atmosphere for photosynthesis, the availability of which influences the growth of plants by altering their water-use efficiency, photosynthetic rates, light and nutrient use efficiency, and eventually, the relative performance of plants based on their photosynthesis pathways (Beerling & Osborne, 2006; Campbell et al., 2008; Taiz & Zeiger, 2006).

The concentration of CO_2 in the atmosphere has changed over time (Kürschner et al., 2008; Pagani et al., 1999; Pearson & Palmer, 2000). According to the IPCC (2014), atmospheric CO_2 concentration has increased significantly from 240 ppm in the 1850s to as much as 400 ppm in 2013 due to industrialisation, which contributes considerably to the burning of fossil fuel and subsequently to CO_2 emission. Such changes are believed to have significantly influenced changes in vegetation patterns in several parts of the world (Beerling & Osborne, 2006). The relationship between vegetation structure and atmospheric CO_2 is not a new phenomenon. It is believed that during the Cenozoic era, atmospheric CO_2 rose to as much as 1000 ppm, and the result was a spread in forest cover around the world, because the higher CO_2 concentration favoured the growth of trees over grasses (Bond & Midgley, 2000; Ehleringer et al., 1997).

The changes in vegetation structure in relation to changes in CO_2 depend on their photosynthesis pathways (Pearcy & Ehleringer, 1984; Sage & Monson, 1998). Such a photosynthesis pathway would thus dictate the direction of competition between trees and grasses. The savanna biomes are largely dominated by grasses that use a C_4 photosynthesis pathway (Cerling et al., 1993; Pearcy & Ehleringer, 1984; Sage et al., 1999; Tipple & Pagani, 2007). A C_4 photosynthesis pathway involves biochemical and anatomical modification to the photosynthesis mechanisms of terrestrial plants, particularly grasses; a modification that helps such grasses to thrive in hot, high-light, dry and carbon-scarce environments, whereas, most trees use the ancestral C_3 photosynthesis pathway (Pearcy & Ehleringer, 1984; Sage & Monson, 1998). It is hypothesised that during the Miocene, some eight million years ago, atmospheric CO_2

fell below a critical threshold where the photosynthesis efficiency of C_3 trees dropped below that of their C_4 grass counterparts, resulting in the expansion of grasslands in tropical regions at the expense of tropical forests (Cerling et al., 1993; Keeley & Rundel, 2005; Osborne, 2008). The result was a biome consisting of both woody and herbaceous plants we call the savannas today. An increase in CO_2 concentration is expected to favour trees at the expense of grasses, and reverse the expansion of grasslands. With atmospheric CO_2 now on the increase due to human activities, it is predicted that C_3 trees will regain their competitive advantage against grasses and reclaim their space in the environment (Bond & Midgley, 2000).

This hypothesis has attracted several criticisms, however. Of these criticisms, the following issues are important: firstly, some parts of the savannas around the world are occupied by C_3 grasses sharing the same photosynthesis pathway with trees (Archer et al., 1995; Auken, 2007). This hypothesis does not explain why C_3 trees invade C_3 grass habitats if both use the same photosynthesis pathway (Auken, 2007), and their photosynthesis efficiencies are both supposedly enhanced. Equally, this hypothesis does not explain why C_3 grasses do not replace C_4 grasses if C_3 plants are indeed competitive in a CO_2 amplified environment (Archer et al., 1995; Auken, 2007; Young & Young, 1983). Thus, a differentiation in the photosynthesis pathway between species may not necessarily trigger the competitive advantage of C_3 against C_4 plants. In Namibia, 95% of the listed grasses are classified as C_4, and found across most of the country, whereas C_3 grasses constitute some 5% and their distribution is limited to the area of Lüderitz (Ellis et al., 1980). Although C_3 grasses are also found in the African savannas, most of the C_3 grasses are found in temperate climatic regions, unlike the C_4 grasses that are dominant in tropical regions (Steffen, 2009).

Secondly, CO_2 is a global phenomenon, but shrub encroachment is most predominant in some parts of the savannas, particularly the African savannas. This hypothesis does not explain why some savannas do not experience shrub encroachment, unlike those savannas where shrub encroachment occurs, if all trees are subjected to the same increase in atmospheric CO_2 (Archer et al., 1995). Larger parts of Namibia, where shrub encroachment is taking place, are largely dominated by C_4 grasses. However, C_3 grasses are also found in the Namibian savannas. It remains to be seen whether shrub encroachment is a manifestation of this process.

2.4 Root system architecture of plants

The previous section dealt with the theoretical framework of the study. A critical aspect that emerged is the role of biotic and abiotic factors in influencing the coexistence between trees and grasses, and the mechanisms under which shrub encroachment occurs. The importance of moisture and its availability is the overall unifying factor among these role players in influencing how savanna plants respond to such biotic or abiotic factors. An understanding of RSA for savanna plants may, therefore, provide insights into how the below-ground morphology of the savanna plants and their interactions with soil moisture shape the structure of savanna biomes.

Plants with vascular systems, such as trees and grasses, are made up of two important components: shoot and root (Beck, 2010; Holbrook & Zwieniecki, 2011). ‘Shoot’ refers to the above-ground constituents of the plant such as the stem, branches, and leaves, whose main role is CO_2 and sunlight acquisition, photosynthesis and reproduction (Campbell et al., 2008). Roots are the below-ground parts of the plants consisting of various complex root systems (Eshel & Beeckman, 2013; Kroon & Visser, 2003). Although the shoot and root components of the plants have long been looked at in isolation, mainly due to their morphological, physiological and functional differences, Gregory (2008) has asserted that these two components of plants are coupled together and their functions form an integrated plant system. On this basis, Gregory (2008) has argued that the total above-ground growth of plants is strongly dependent on the developmental stage of the roots, and that the shoot of any plant can only reach its full above-ground potential after having developed a substantial root system. The main functions of plant roots are water and nutrient acquisition (Eshel & Beeckman, 2013; Kroon & Visser, 2003). These water and nutrient resources are then transported to the plant's shoot through the xylem (Barclay, 2007; Starr, Taggart, Evers & Starr, 2015). Roots also play an important role in anchoring the plants in the soils to ensure stability against forces of nature such as wind (Gregory, 2008).

The root is the first structure that emerges after seed germination, enabling the seedling to become anchored in the soil, as well as to absorb water and nutrients needed for survival (Raven, Evert & Eichhorn, 2005). According to Fitter (1987), roots account for approximately 40% to 85% of the net primary production of most terrestrial ecosystems. In arid and semi-arid ecosystems, where the growth of plants is limited mainly by soil-based resources such as moisture, understanding the functioning of terrestrial plants within their natural ecosystems requires knowledge of their RSA (Maeght, Rewald & Pierret, 2013). According to Bodner et al. (2013), an understanding of the RSA of such plants can thus provide insights into predictive changes in species distribution under global change. In the savannas, where both trees and grasses coexist, the RSA of plants and the way such plants forage for water and nutrients has been a contentious issue since the publication of Walter’s two-layer model, which has already been addressed in previous sections of this study.

Several studies have investigated RSA over the years in various terrestrial biomes (Canadell et al., 1996; Fitter, 1986; Holdo & Timberlake, 2008; Gregory, 2008; Jackson, Moore, Hoffmann, Pockman & Linder, 1999; Linder, 1999; Maeght et al., 2013; Schulze et al., 1998; Smit & Rethman, 1998; Visser, 2003). However, given the methodological challenges faced with exposing plants’ root systems for empirical measurements, knowledge of their architecture is still very limited (Bodner et al., 2013). The traditional method of root excavation used frequently in the study of roots has been described as laborious, time consuming and tedious (Böhm, 1979); a challenge that was confirmed in this study. This inherent difficulty has led to the plants’ root systems being referred to as the ‘hidden half’ (Eshel & Beeckman, 2013). Despite these challenges, certain advances have been made in understanding RSA.

2.4.1 Root system architecture of plants and the developmental processes

Root system architecture refers to the spatial configuration of plant roots in the soil (Gregory, 2008). In essence, RSA addresses major aspects such as morphology, topology, root distribution and root architecture itself (Hodge, Berta, Doussan, Merchan & Crespi, 2009). Morphology refers to the surface features of a root axis, including the root hairs, root diameter, the root cap, as well as the patterns of second-order and third-order root growth (Lynch, 1995). Root topology refers to how individual root axes are connected to each other through branching (Fitter, 1986). The distribution of roots refers to the presence of roots in a positional gradient, focusing on aspects of root biomass or root length, as well as the depth in the soil at which they are deployed, distance from the stem, lateral root expansion, and position between neighbouring plants (Lynch, 1995). Root length and distribution provide information about the exploration of the topsoil, while fine root ramifications and their ramification patterns provide insights into the exploration of resources in the soils (Gregory, 2008).

Studies of RSA are usually not concerned much with micro-aspects, such as root hairs as such, but focus mainly on the entire RSA, or a large subset of the root system of an individual plant (Gregory, 2008). According to Lynch (1995), root architecture plays an important role, more especially in drylands, where soil resources are patchily distributed. The spatial deployment of such roots determines the ability of plants to exploit soil resources and survive.

In order to understand and characterise plants' RSA, a classification scheme for plant roots is necessary (Bodner et al., 2013). Root characterisation is important because it helps to generate the information necessary to understand root system behaviour change in response to the environmental stimuli (Bodner et al., 2013). However, at present, no universal root classification scheme exists; a major challenge that has faced root system studies for decades. Over the years, several attempts have been made to produce a root system architectural classification framework for many terrestrial plants (Cannon, 1949; Zobel & Waisel, 2010), but none has been particularly successful, mainly because of the great plasticity of RSA (Grossman & Rice, 2012). Such efforts point to the fact that RSA is a complex phenomenon which varies significantly between and even within the same species (Eshel & Beeckman, 2013). The complexity of root systems among plants is arguably shaped by the dynamic developmental processes which are governed by genetically driven developmental rules interacting with environmental stimuli (Hodge et al., 2009). The plasticity of RSA among plants within and between species can thus be interpreted as an evolutionary product of spatio-temporal variation in environmental resource supply, genetic drivers, and associated environmental constraints at growth.

The complexities of RSA have given rise to various classification systems, based on aspects such as topology, root activities, and the developmental origin of roots (Hodge et al., 2009). Of these groupings, the development classification approach is the most frequently used for root classification, mainly because it is able to provide a distinctive view of plant roots in relation to their environment. In this classification, plant roots are classified according to their ontogenesis into three major classes, namely: primary, lateral, and adventitious roots (Hodge et al., 2009). Primary root are the roots that originate at the lower end of a seedling's embryo (Raven et al., 2005). The primary root is what is referred to as a taproot (Figure 8) once it continues to elongate downward. It has limited second-order roots branching out, making it the most central feature of the root system. Primary roots provide very strong anchorage for terrestrial plants as they are able to reach deeper into the soil than the lateral roots (Esau, 1960). Lateral roots, also referred to as secondary roots, develop as side roots from the primary root (Figure 8). Older lateral roots, which are usually thicker in diameter, are often shallower and mainly concentrated around the base of the root system, whereas younger lateral roots are often thinner in diameter, and are concentrated toward the root tip (Raven et al., 2005), suggesting that shallow soil moisture plays an important role in a plant’s life right from the start of the development stage of the plant root. As the primary root ceases to elongate, it is replaced by numerous lateral roots branching out, creating a network of roots called a fibrous root system (Figure 8). Fibrous roots are often shallow and spread horizontally, hence they do not provide a strong anchorage for plants, but provide an opportunity for plants to harvest water and nutrients from shallow soil layers (Esau, 1960).

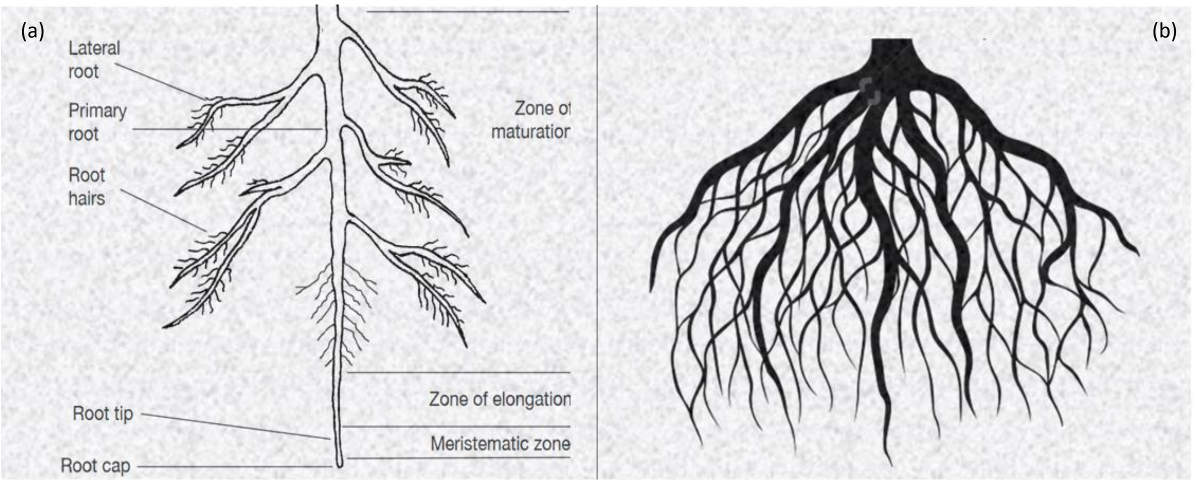

Figure 8: Root system structure of vascular plants (a) Vertical taproot elongation and lateral roots expansion, (b) a fibrous root system with no distinctive taproot. (Source: Kent, 2000).

The RSA of plants can also be classified from the developmental perspective of adventitious roots, also referred to as aerial roots. Adventitious roots develop above-ground on plant shoot (Davis & Haissig, 1994). According to Geiss, Gutierrez and Bellini (2009), adventitious roots can arise naturally from stem tissue because of stressful environmental conditions, or they may be induced by mechanical damage, or follow tissue culture regeneration of shoots.

Collectively, these root types can be grouped according to two distinct vesicular plant classes, namely the dicotyledonous and monocotyledonous plants (Hodge et al., 2009). In dicotyledonous plants, the primary root usually persists, and later, becomes a taproot, anchoring the plant in the soil to absorb water and nutrients from a lower soil depth. Lateral roots of dicotyledon plants branch out from the root base and follow a radial pattern of growth, with older lateral roots located at the upper soil layer, and younger lateral roots located toward the primary root tip (Hodge et al., 2009). Depending on the orientation of lateral roots to the primary root, the morphology of such a root system would either develop into a taproot, or a diffuse, fasciculate rooting system. Monocotyledon plants develop mainly from adventitious roots and lateral roots, forming a fibrous root system in which no one of the roots is more prominent than the others (Hodge et al., 2009). In monocotyledon plants, the taproot that emerges at the early stage of the plants' development is usually short-lived, and such plants are supported by a network of fibrous roots. Monocotyledon rooting patterns are most common among non-woody vesicular plants, whereas trees are dominated by dicotyledon rooting patterns.

The root developmental classification approach also acknowledges the existence of tertiary roots, also known as fine roots. Fine roots play a significant role in absorbing soil water and nutrients. It is the fine roots that transfer such resources to the coarse root that transports them further to the plant's shoot via the xylem. Fine roots are distinguished from coarse roots by their diameter. Any root part which is less than 2.0 mm in diameter is regarded as a fine root (Bohn, 1979). However, Bohn (1979), warned that this classification should only be used as a guide for collecting information as the diameter's upper limit of such a root was arbitrarily chosen to aid that purpose. The amount of fine root biomass, or root length per unit soil volume indicates the intensity of soil exploitation, and the ability of a species to compete for soil nutrients (Muthukumar et al., 2003).

The development of RSA follows some basic processes that give it its shape and structure (Hodge et al. 2009). Firstly, roots result from the emission of a new main axis after germination to create either a primary, or an adventitious root. Thereafter, branching and elongation of lateral roots follows. When developing lateral roots, coordination between root elongation and branching is a critical process needed to maintain an equilibrium between root number and length (Hodge et al., 2009). Lateral root branching is significantly affected by soil heterogeneity as roots are often very sensitive to environmental stimuli such as soil nutrients. Another crucial aspect of the plant's root system is an understanding of plant root axial growth which refers to the development of roots at the root tip. Root axial growth defines root elongation and the trajectory of such elongation. Both elongation and trajectory play an important role in the architecture of plant root systems. Root elongation provides the necessary information on soil colonisation, while root trajectory gives the root system its shape (Hodge et al., 2009). Most dicotyledonous plants develop root systems that follow a radial growth pattern needed to perform a range of functions, such as water harvesting, anchoring, resource storage capacity, as well as protection against predation and drought, among other environmental stimuli or threats (Hodge et al., 2009). As plants develop different types of root architecture for foraging water and nutrients with high plasticity, such plants deploy their roots in relation to the availability of necessary resources. When resources decrease below a certain sustainable threshold, such plants give up on these root segments, and develop new root segments in soil zones where necessary resources are more abundant, thereby increasing resource acquisition efficiency (Hodge et al., 2009).

Lastly, plants develop their roots in various heterogeneous environments where they are subjected to several stimuli, known as tropisms that strongly influence their architecture (Gilroy & Masson, 2008). Tropism is a growth response that involves bending and curving plant parts toward or away from an external stimulus that determines the direction of movement (Gilroy & Masson, 2008; Hart, 1990). According to Kumpf and Nowack (2015), the development of plant roots is chiefly affected by tropisms such as geotropism (also known as gravitropism), hydrotropism, and chemotropism. Geotropism or gravitropism refers to plants' directional movement in relation to gravity (Abas et al., 2006; Rashotte, Brady, Reed, Ante & Muday, 2000; Swarup et al., 2005), while hydrotropism is the response of root growth to the soil moisture gradient (Eapen et al., 2005; Gregory, 2008; Takahashi, 1997). Chemotropism is the response of root growth to soil chemical stimulus such as nutrients (Forde & Lorenzo, 2001). Since plants are stationary, they respond to such environmental stimulus by adjusting their individual pattern of growth and development (Campbell et al., 2008). For this reason, root systems between, and even within, species are a highly plastic phenomenon, owing to the prevailing variation in the environmental stimuli which influence how such plants develop their RSA. According to Guevara and Giordano (2015), hydrotropism is particularly important because the water in the soil is heterogeneously distributed both horizontally and vertically, and roots are able to respond to and exploit the water patches they encounter in the soil with increased local root proliferation and absorption. This allows plants to shift water uptake from drier to wetter soil areas at the same time as roots in the drier zone send signals to the shoots, inducing a conservative use of water. Roots can also grow towards an increasing moisture gradient, which could contribute to more precise exploitation of water patches and drought avoidance. Iwata, Miyazawa, Fujii, and

Takahashi (2013) also found that the species *Arabidopsis thaliana* adapts its root architecture by growing its lateral roots so that the roots follow a soil moisture gradient in order to enhance drought tolerance.

A study along the east-west rainfall gradient of Etosha National Park in Namibia (Hipondoka & Versfeld, 2006) revealed two different rooting systems from the same shrub species, *T. sericea* and postulated that such a shrub species adapts its rooting strategy in response to environmental stimuli such as soil moisture (Figure 9). This finding was confirmed in similar studies by Bhattachan et al. (2012); Verweij, Higgins, Bond and February (2011), as well as Zanetti, Vennetier, Mériaux and Provansal (2015). In a simulated environment, Guevara and Giordano (2015) found that three desert species, *Bulnesia retama, Prosopis flexuosa* and *Prosopis alpataco,* responded to hydrotropism in their lateral roots, but not in their pivotal roots. Compared to the behaviour exhibited by *T. sericea*, this reaction suggests that plants may respond to hydrotropism in different ways.

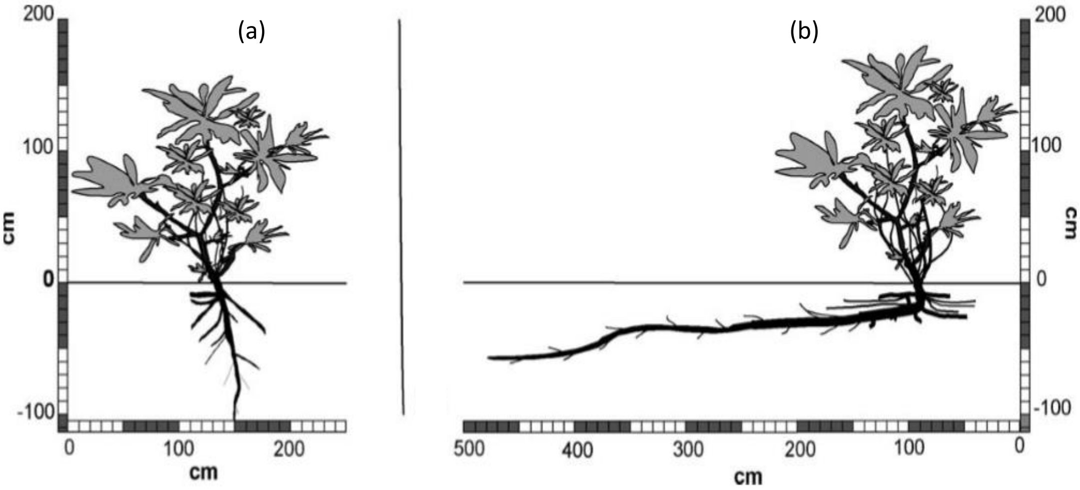

Figure 9*:* A conceptual model illustrating how *T. sericea*, a shrub-encroaching species opportunistically develops its root system: (a) represents the root system toward the moist part of the study area, while (b) shows how the root system

has adapted toward the drier part of the study area (Source: Hipondoka & Versfeld, 2006).

Plants' root architecture can also be affected by various mechanical impediments which not only affect plant root growth and morphology, but also the direction of growth, the growth trajectory, and subsequently, the soil that will be colonised by such roots. Soil bulk density or compaction, where heavily compacted soils prevent root penetration, for example, has a significant impact on plant root development, (Bengough, McKenzie, Hallett & Valentine, 2011).

The processes discussed above suggest that the development of RSA involves complex processes influenced by various environmental factors. Given the complexity and heterogeneity of factors contributing to plant root systems, it is not surprising that most plant root systems develop plastically.

2.4.2 Root depth and lateral spread in semi-arid environments

At what depth do terrestrial plants harvest water and nutrients? This intriguing ecological question has attracted scientific attention over the years. Particular attention has been paid to the relationship between rooting depth, mean annual precipitation (MAP), and potential evapotranspiration (PE). Findings from such studies have given rise to three major hypotheses. The oldest and most popular hypothesis argues that maximum rooting depth increases with aridity (Figure 10), thus, in areas where the MAP is extremely low, and PE is higher, plants tend to develop deeper roots than those found in moist regions (Schenk & Jackson, 2002). The second hypothesis predicts that terrestrial plants will have the deepest roots in moist regions rather than in drier regions

(Figure 11). The third hypothesis argues that plant roots and rooting depth are highly plastic phenomena because root development responds to various environmental stimuli and thus cannot be predicted directly from MAP and PE alone (Nippert & Holdo, 2015).

The hypothesis that plants’ maximum rooting depth increases when MAP decreases, because the water table is lower, has dominated eco-hydrology studies since the 1990s (see a comprehensive review in Canadell et al., 1996, and Jackson et al., 1996). Since then, the structure and dynamic of terrestrial vegetation have been largely inferred from the maximum rooting depth, because biogeographically, maximum rooting depth was assumed to increase with aridity. Many of these inferences were supported by evidence from species such as *Boscia albitrunca* and *Vachellia erioloba* whose roots have been observed at a surprising depth of more than 60 m in the Kalahari (Canadell et al., 1996), an arid environment; whereas in Brazil’s Pantanal wetlands, the depth of most tree roots was very shallow at approximately 8 cm (Salis, Lehn, Mattos, Bergier & Crispim, 2014). This apparent contradiction resulted in a conclusion that such shallow rooting was due to a high water table level that did not require a deeper taproot. This premise was the basis of Walter’s two-layer model, which stimulated the underlying research questions of this study.

Despite its prominence in savanna ecology, Walter’s two-layer model has several shortcomings, as discussed in Section 2.1.2.3 of this study. Of particular interest is the deployment of shallow lateral roots by some savanna shrubs which may facilitate competitive exclusion between trees and grasses and eventually, shrub encroachment (Hipondoka & Versfeld, 2006; Hipondoka et al., 2003; Seghieri, 2008). Therefore, the premise that vertical root niche-partitioning is an important determinant of woody grass coexistence, and that trees' rooting depth increases with aridity, does not adequately address the savanna questions.

The second hypothesis is directly opposed to the first hypothesis. It argues that plants found in moist regions develop deeper rooting systems than those found in drier areas. Schenk and Jackson (2002) developed a statistical model to predict the relationship between rooting depth and MAP, and found that a decrease in MAP significantly explains a decline in rooting depth. Similar studies demonstrated shallow roots among several trees in the Kalahari, a semi-arid environment, as well as the absence of a taproot among a shrub-encroaching *T. sericea* shrub towards the arid part of western Kalahari (Hipondoka & Versfeld, 2006). These findings contradict the first hypothesis that plants' rooting depths tend to increase and reach their maximum in the driest environments.

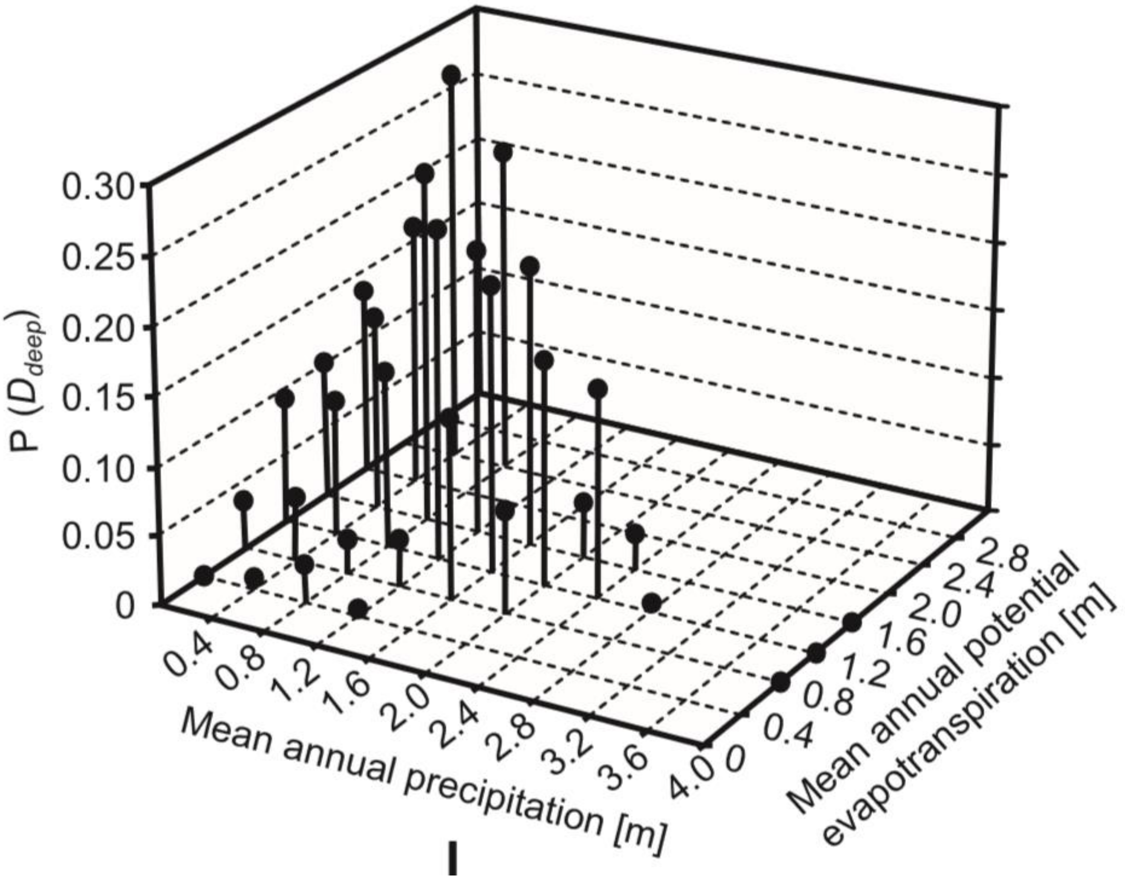

Figure 10: Model predicting the relationship between MAP and the rooting depth of terrestrial plants (Source: Schenk & Jackson, 2005).

The third hypothesis argues that the development of plant roots is a plastic phenomenon. Variations in the rooting systems have been observed between species and within individuals of the same species (Grossman & Rice, 2012; Hodge, 2004; Taiz & Zeiger, 2006; Zanetti et al., 2015). Such studies postulate that plant rooting patterns, including depth, are significantly shaped by several environmental stimuli (Zanetti et al., 2015) as opposed to rainfall and evapotranspiration only. Other factors which may influence plants' roots are soils and competition.

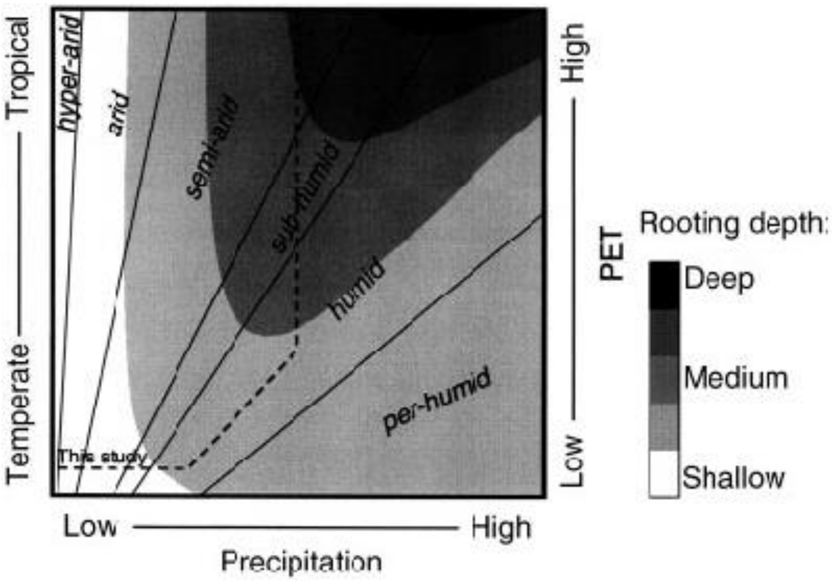

Figure 11*:* Model of the hypothesised relationship between precipitation and the rooting depth of terrestrial plants (Source: Schenk & Jackson, 2002).

2.4.3 Water and nutrient uptake by roots

Plant physiologists investigating how plants acquire water from the soil have demonstrated that roots absorb water from the soils through the process called osmosis (Figure 12), in which water moves from areas of high water potential to an area of low water potential through diffusion (Raven et al., 2005). Because of soil infiltration, there is often more water in the soils than water content in the root and shoot of the plants. This differentiation in water concentration creates an osmotic pressure that allows water to move from the soils into the plant roots.

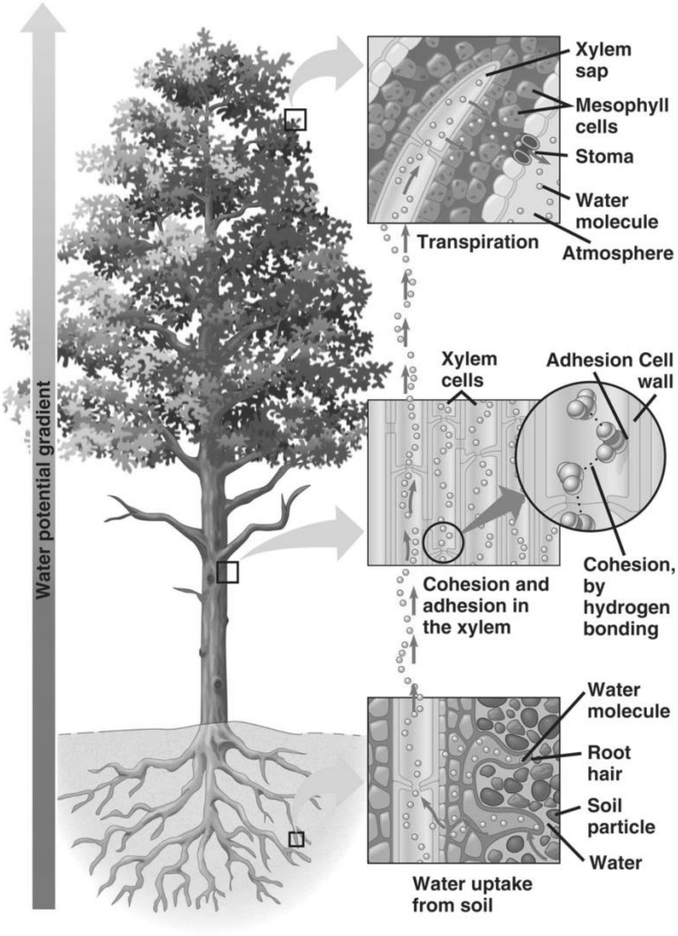

Figure 12: Conceptual model illustrating how vascular plants absorb water and nutrients from the soils through the process of osmosis. (Source: Raven et al., 2005).

Once water enters the root system, it must be transported to the shoot part of the plant against the force of gravity and in the absence of a pumping mechanism. That movement is well explained by the cohesion-tension theory (Angeles et al., 2004; Steudle, 2001; Tyree, 1997; Wei et al., 1999) which argues that water forms a continuous hydraulic system from the soil, via plant roots, to shoots, then to the atmosphere through evapotranspiration. It further argues that evapotranspiration from leaves reduces the leaves' water potential, causing water to move from the xylem to the leaves, and eventually to the atmosphere. This, in turn, lowers the water potential of the xylem, creating a gradient, an osmotic pressure that causes water inflow as a cohesive chain of molecules connected by hydrogen bonds, moving from the soil into the roots and thence to the leaves (Starr et al., 2015).

Overall, in order for plants to survive, water absorption to the roots and evapotranspiration through the leaves must be in balance. It is for this reason that many savannas are occupied by deciduous plant species which shed their leaves when undergoing water stress, more especially during the dry season (Box & Fujiwara, 2014).

Soil is the reservoir of nutrients. In addition to water uptake, plant roots also play an important role in nutrient uptake from the soils. As with water availability, nutrient availability significantly affects the survival of terrestrial plants. Roots acquire macronutrients such as nitrogen, phosphorus, potassium, calcium, magnesium, and sulphur, as well as micronutrients such as iron, manganese, copper, zinc, boron, molybdenum and chlorine (Campbell et al., 2008). The uptake of soil nutrients by plant roots is directly related to the concentration of such nutrients in the soils. Unlike water that follows a water potential gradient to the plant shoot, nutrients are absorbed into the shoot metabolically (Campbell et al., 2008). The supply and quantity of nutrients to the plant shoot is controlled by the metabolic demand of that plant (Campbell et al., 2008; Karamanos, 2013; Peel, 2013). There are three mechanisms of nutrient uptake by the plant, namely, root interception, mass flow, and diffusion (Karamanos, 2013). Root interception is the process by which roots grow through the soil profile to come in contact with the soil and absorb nutrients from it. The process depends on the roots foraging for nutrients in the soils and requires a good soil structure for interception.

Soil compaction can greatly limit root growth and interception with nutrients in the soils (Karamanos, 2013). On the other hand, mass flow refers to the movement of dissolved nutrients in the soil solution towards the plant root as the plant root takes in water (Campbell et al., 2008; Kent, 2000). The nutrients are swept towards the plant root together with the water. During diffusion, roots grow throughout the profile and use up nutrients directly around the root system and the root hairs. As the concentration of nutrients around the root system drops, nutrients from areas with a higher concentration diffuse toward areas of low concentration, and the roots (Karamanos, 2013). In order to fully understand the dynamic of root water and nutrient uptake across the root, transport within the plant xylem requires a detailed knowledge of physical, biological and chemical concepts which are beyond the scope of this study.

2.5 Summary

To conclude this chapter, available evidence suggests that shrub encroachment has severe socio-economic and ecological impacts in Namibia and many other semi-arid environments. Efforts to understand the savanna and shrub encroachment has attracted diverse theoretical explanations over the years and continues to attract contentious debates. All the major theories and models synthesised here are still inconclusive in addressing the savanna questions. Conflicting and contradictory ideas have been proposed. These ideas have not only broadened our knowledge on how the savannas possibly functions, but have also, paradoxically, amplified our uncertainties on the ecology of the savanna. There is a need to develop a unifying theoretical framework which includes the different perspectives presented.

While acknowledging the merit of both equilibrium and disequilibrium in understanding the behaviours of terrestrial ecosystems, this study recognises that tropical and sub-tropical savannas are very heterogeneous ecosystems, and that spatio-temporal climatic factors, such as rainfall and drought, are the major underlying drivers of such heterogeneity. This study also recognises that disturbances such as grazing and fire indeed affect the savanna vegetation structure, but the magnitude and severity of such impacts are regulated by inter-annual climatic variability. The impacts of fire on vegetation would be expected to be severe after a rainy year because of abundant fuel biomass, as opposed to a drought year. Similarly, the impact of overgrazing is expected to be severe during a drought year because animals would compete for every palatable blade of grass available, while insufficient moisture would lead to poor regeneration. In terms of the timeline of these scenarios, vegetation succession occurs at different timescales, depending on the intensity, duration, frequency, and magnitude of the disturbances, as well as on the resilience and resistance of such ecosystems. It is therefore not possible to allocate different timelines to changes in vegetation structure. For that reason, this study subscribes to the non-equilibrium theory as the underlying framework because it provides the most realistic views of the savanna, and thus forms the basis upon which the findings of this study are interpreted.

This chapter examined the issues of terrestrial plants' root systems, a fundamental concept in understanding the behaviour of terrestrial plants, more especially in water-limited environments such as the savanna. It addressed issues of RSA, factors that influence plants' root system development as well as the functional role of roots. Based on studies reviewed here, our understanding of factors that influence plants' rooting system architecture is still fragmented. Efforts to thoroughly understand the underlying factors that influence plant rooting patterns is complicated to some extent by the methodological challenges involved in root studies.

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3. CHAPTER THREE: MANUSCRIPT (I)

The root system architecture of encroaching shrubs, *Senegalia mellifera* subsp. *Detinens* (Burch.) Brenan and *Dichrostachys cinerea* (L.) Wight and Arn in the Kalahari Basin: Implications for tree-grass coexistence in the African savannas

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Abstract

The mechanisms proposed to explain the coexistence between trees and grasses in the savannas and the occurrence of shrub encroachment are a contentious issue in savanna ecology. To date, no unanimous theoretical framework has been proposed to explain this unique coexistence; a coexistence that has been popularly interpreted in the context of a vertical root niche-partitioning hypothesis. This hypothesis states that savanna trees and shrubs develop deeper root systems to avoid competition with grasses and herbs for moisture in the shallow soil layer, leading to an equilibrium coexistence of the two contrasting life forms. Elsewhere, these two life forms are antagonists. Using a direct excavation method, this study investigated the root system architecture (RSA) of two shrub encroachers, *Senegalia mellifera* subsp. *Detinens* (n=37) and *Dichrostachys cinerea* (n=35). The excavation was carried out along the Kalahari rainfall gradient in Namibia to test the vertical root niche-partitioning hypothesis. Results suggest that these two shrub encroachers develop a web of complex root systems in response to varying environmental conditions, such as rainfall gradient. Of particular interest is that both shrub species invest the significant ($p < .001$) bulk of their lateral roots within shallower sub-surfaces of about 25 cm depth. This average depth is within reach of roots from many grass species in the Kalahari. Equally, the absence of taproot systems among a larger proportion of shrubs excavated along the drier part of the transect suggests that the survival of trees in water-limited ecosystems such as the savanna does not necessarily depend on tapping water from the water table. The study concluded that shallow-rooted trees and shrubs in the savanna are potentially in competition with grasses, contrary to the premise of the vertical root niche hypothesis.

Keywords: Kalahari; lateral root; root niche-partitioning; shrub encroachment; taproot

3.1 Introduction

Vascular plants are made of two important components, roots and shoots. Unlike shoots, plant roots are rarely studied owing to the inherent difficulties involved in exposing them (Böhm, 1979; Hodge, Berta, Doussan, Merchan & Crespi, 2009; Lynch, 1995). Because of this challenge, several studies (e.g., Eshel & Beeckman, 2013; Montgomery & Biklé, 2015), refer to plant roots as the ‘hidden half’. Notwithstanding, plant roots are known to play an important role in the functioning of terrestrial ecosystems. They acquire soil moisture and nutrients (Starr, Taggart, Evers & Starr, 2015), anchor plants in the soil for stability (Gregory, 2008), and interact with other plants below ground. It is therefore important to study plant roots because some of the critical insights into understanding the functioning of terrestrial ecosystems may be hidden in the roots below the soil surface.

In the savannas, with a unique coexistence of woody plants, including trees and shrubs (hereafter referred to as ‘trees’), as well as herbaceous plants, which include both grasses and herbs (hereafter referred to as ‘grasses’), plant roots and the way they acquire water and nutrients is a topic of contentious scientific debate. This debate is based on the competitive exclusion principle suggested by Gause (1934) during the early 20th century which argues that complete competitors cannot coexist if they occupy the same ecological niche, where essential resources are in limited supply. This principle has significantly influenced the science of community and population ecology of both fauna and flora because of its implications for species assemblage, coexistence, and competition (Cushing, Levarge, Chitnis & Henson, 2004; Levin, 1970; Mayfield & Levine, 2010; Morin, 2009).

The savannas are not an exception to this debate, because of their unique coexistence of both trees and grasses. In other biomes, such as forests or grasslands, these two contrasting life forms, trees and grasses, are antagonists. This coexistence has largely been interrogated in the context of the so-called 'savanna questions' (Higgins, Bond & Trollope, 2000; Mills & Fey, 2005; Riginos, 2009; Vazquez, López, Calabrese & Munoz, 2010). To date, no unanimous theoretical framework has been achieved to solve these elusive savanna questions. Notwithstanding, certain advances have been made (e.g., Scholes & Walker, 1993; Walker, Ludwig, Holling & Peterman, 1981; Walker & Noy-Meir, 1982; Walter & Mueller-Dombois, 1971). The efforts of these researchers culminated in a popular savanna model called 'Walter's two-layer model', or alternatively, the 'root niche-partitioning hypothesis'. This hypothesis argues that trees in the savannas develop deeper root systems to extract water from the lower soil depth, unreachable by grasses; a niche-partitioning mechanism which, in turn, allows a stable coexistence between these two contrasting life forms. Studies (e.g., February & Higgins, 2010; Sankaran, Ratnam & Hanan, 2004; Smit & Rethman, 1999; Verweij, Higgins, Bond & February, 2011; Ward, Wiegand & Getzin, 2013) which have tested this hypothesis have produced conflicting findings, leaving it largely inconclusive. This study aims to establish how the two savanna shrub species, *Dichrostachys cinerea* and *Senegalia mellifera* subsp. *detinens*, develop their root systems in the Kalahari, which is a semi-arid structural basin made up of deep Kalahari sand sheet in Southern Africa. These two shrub species are among the most common encroaching woody plants in Namibia, and are responsible for the thickening up of millions of hectares of productive agricultural land, accompanied by significant socio-economic impacts on pastoralism, one of the major sectors of the economy (De Klerk, 2004). Overall, this study tested the hypothesis that savanna shrubs develop contrasting root strategies deployed at different soil depths under different environmental settings in the Kalahari savanna. This study predicts that plants from drier environments will exhibit more adaptive strategies than those in wetter climatic regions because of limited soil moisture.

3.2 Materials and methods

3.2.1 Description of the study area

3.2.1.1 The Kalahari Basin

This study was conducted in the Kalahari Basin located in the interior of Southern Africa. It was designed to form part of the popular Kalahari Transect (KT) which is a mega-transect recognised as part of the International Geosphere-Biosphere Programme (IGBP), designed to explore continental-scale links between climate, biogeochemistry, ecosystem structure, and functions (Porporato, Laio, Ridolfi, Caylor & Rodriguez-Iturbe, 2003; Ringrose, Matheson & Vanderpost, 1998; Shugart et al., 2004). Along the KT, this exploration has particularly investigated natural parameter gradients such as the link between vegetation variables and rainfall gradient (Caylor, Shugart, Dowty & Smith, 2003; Privette et al., 2004; Scholes et al., 2002; Scholes & Parsons, 1997). Although the transect for this study followed an east-west direction, as opposed to the original IGBP north-south direction, the transects share two important factors: the climate gradient, and homogenous soil along which the data collection took place.

The Kalahari is a structural basin composed of thick sand sheet which covers some 2.5 million km^2, stretching across the south, as well as the north-western parts of Namibia and Botswana, then extending across Zambia and the Democratic Republic of Congo (DRC) (Thomas & Shaw, 1991). The basin is located at an average altitude of some 1000 m, and its size makes the Kalahari Basin one of the largest sand seas in the world (Thomas & Shaw, 1991). The thickness of the Kalahari sediment is estimated to reach up to 50 m along the basin peripheries and around 400 m in the Owambo sub-basin (Miller et al., 2016). Its origin and age are not precisely known, but it is supposed to be the result of tectonic activities that precipitated the breakup of the Gondwana supercontinent between the Triassic and Cretaceous periods, and to a mixture of fluvial and aeolian processes that followed during the Mid- to Late Tertiary Period (Lawson & Thomas, 2002; Thomas & Shaw, 1991).

The vast size of the Kalahari Basin meant that this study concentrated on the Namibian part of the Kalahari Basin, along the east-west rainfall gradient extending a distance of 1200 km across from Omutambomawe, through to Uutsathima, northern Etosha, Onyuulaye, Okongo, Nkurenkure, Divundu, as far as Katima Mulilo (Figure 13). It is important to note that all these sites are located along a flat landscape of the Kalahari, which is a prerequisite for Walter's two-layer hypothesis, the main theory underpinning this study.

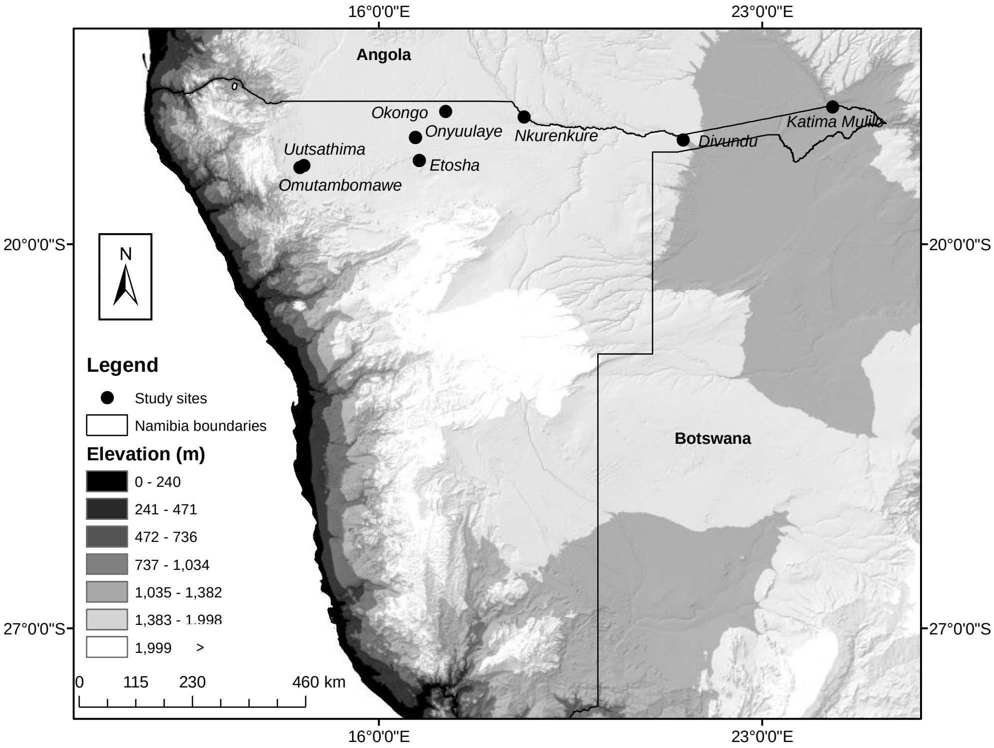

Figure 13: Elevation of the study area. All study sites are located on a largely featureless landscape of the Kalahari Basin.

3.2.1.2 Climate, soil and groundwater recharge in the Kalahari

Climate is one of the key determinants of terrestrial ecosystems. It affects the availability of moisture as well as the distribution of soil, and effectively, the abundance and diversity of plants on land. The climate of the KT is described by Tyson and Crimp (1998) who have pointed out that, due to the vast latitudinal extent of the Kalahari Basin, this basin is characterised by a significant north-south climate gradient ranging from arid, semi-arid, and sub-humid to humid. As illustrated in Figure 14, the most arid part of the Kalahari Basin mainly covers parts of south-western Botswana and north-western Namibia, while the sub-humid and humid conditions are found along the eastern parts of Namibia, northern Botswana, Zambia, and southern parts of the DRC (Tyson & Crimp, 1998). The climate, like many parts of Southern Africa, is largely influenced by the regional atmospheric circulations and the seasonal migration of the Inter-Tropical Convergence Zone (ITCZ) towards the Southern Hemisphere during the austral summer, and how the ITCZ interacts with other regional atmospheric circulations, such as the Congo Air Boundary (CAB) (Tyson & Crimp, 1998). The southerly migration of the ITCZ divides the ridge of high pressure responsible for the stable winter conditions during April-October, and paves the way for the Indian easterly low-pressure system which brings summer convective rainfall. The Atlantic Ocean also plays an important role, bringing in moisture via the tropical westerly trade wind (Burrough, Thomas & Bailey, 2009; Tyson & Lindesay, 1992). It is the interaction of these air masses that shapes the climate of the Kalahari Basin. The interior of the Kalahari Basin is therefore mostly characterised by a wet, hot summer from October to March, and a cool, dry winter from April to September.

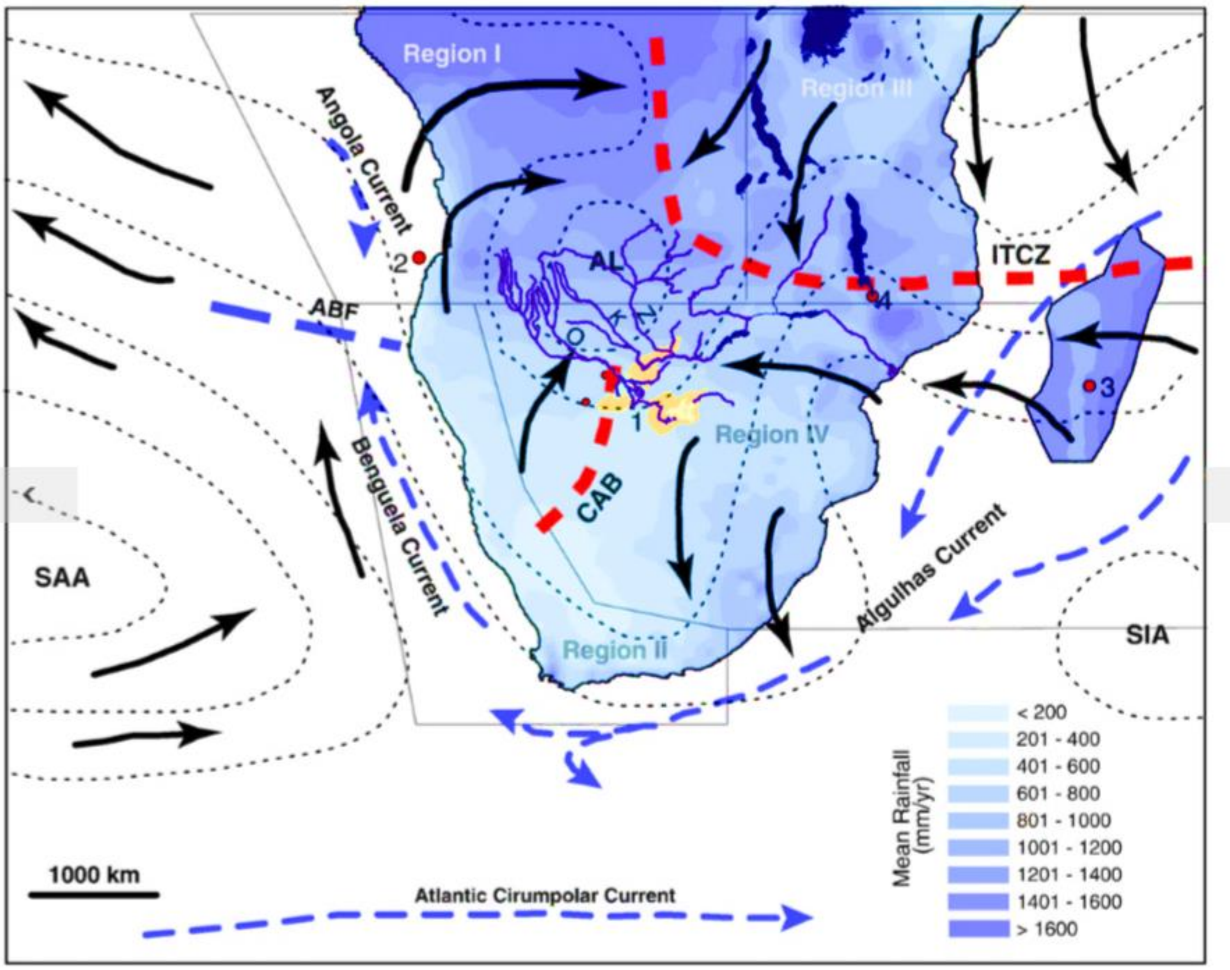

Figure 14: Different atmospheric and oceanic circulations that affect the Kalahari Basin climate. This circulation changes between summer and winter, creating varying atmospheric conditions throughout the year. Note the Kalahari Basin's rainfall gradient along the east-west direction and the inflow of the (O) Okavango River, (K) Kwando River, and (Z) Zambezi River as well as the Makgadikgadi Pans in the interior of the Kalahari Basin. (Source: Burrough et al., 2009).

Rainfall pattern is one of the most important features of the Kalahari Basin's climate gradient. The arid parts of the Kalahari Basin along the south-western parts of Botswana and south-western parts of Namibia receive the lowest mean annual precipitation of some 150 to 250 mm per annum (Tyson & Crimp, 1998). Precipitation increases progressively to nearly 300 to 400 mm around the north-central parts of Namibia and north-western parts of Botswana. The wetter parts of the Kalahari Basin, such as the Zambezi Region and northern Botswana, receive mean annual precipitation of more than 600 mm per annum. Mean annual rainfall continues to increase to some 900 mm in northern Zambia, and eventually, to the moistest parts of the Kalahari Basin, reaching nearly 1500 mm in southern DRC. Accompanied by strong spatio-temporal variations, the Kalahari Basin's rainfall occurs mainly between October and April. The length of the wet season and rainfall amount decrease toward the south-western parts of the basin, making parts of Botswana and Namibia some of the driest places, where the rainfall coefficient of variation can reach up to 45% (Tyson & Crimp, 1998).

Compared to rainfall, temperature follows a reversed south to north gradient in the Kalahari Basin. During summer, the most arid parts of the Kalahari, such as along the south-western edge of the basin, have the highest mean temperature of approximately 30 °C; while maximum summer temperature oscillates around 20 °C along the wetter parts of the north-eastern Kalahari Basin, such as in the Zambezi Region and central Zambia (Tyson & Crimp, 1998). During winter, however, the temperature gradient reverses, such that the driest places have the lowest temperature of around 12 °C, while the moist parts of the Kalahari Basin are slightly warmer, at 16 to 18 °C. Potential evapotranspiration has been measured at several places around the Kalahari Basin and ranges from 4000 mm per annum over the south-western part of the Kalahari Basin to about 2000 mm per annum on the north-eastern part of the basin (Tyson & Crimp, 1998). The largest potential evapotranspiration occurs during December and January, while the lowest evapotranspiration occurs during the months of June and July. Low rainfall, high temperature and high evapotranspiration mean that little water recharges the water table in the Kalahari Basin. Studies on aquifer recharge in the Kalahari Basin suggest that the groundwater is located somewhere between 20 m and 100 m below the soil surface (Obakeng, 2007). Groundwater recharge is estimated to be 8 mm per annum, representing merely 2% of mean annual precipitation (Wanke, Dünkeloh & Udluft, 2008). Despite high infiltration made possible by deep, permeable sandy soil, the water table is kept at such a substantial depth because water is mostly used up by vegetation and lost through evapotranspiration owing to hostile environmental conditions (Obakeng, 2007). With the water table located at such a substantial depth, there is pressure on deeper-rooted plants, such as *Vachellia erioloba* and *Boscia albitrunca*, whose roots are known to reach as deep as 60 m (Canadell et al., 1996), and are therefore heavily dependent on the water table for survival.

The Kalahari Basin sand is relatively homogenous in both physical and chemical properties (Ringrose, Matheson & Vanderpost, 1998; Wang, Okin, Caylor & Macko., 2009; Wang, D'Odorico, Ries & Macko, 2010). The basin is mantled with deep sand which belongs to the arenosol soil group (Thomas & Shaw, 1991). In terms of particle distribution, 95% of the soil in the Kalahari Basin is made of fine sand grains (Dougill & Thomas, 2004). The rest of the soil is made of particles of silt and clay. The dominant sand texture of the Kalahari Basin soil means that water drains through such soil quickly, leaving little moisture at shallow soil depth for plants to harness. Furthermore, the Kalahari Basin sand soil is low on organic matter, ranging from 0.20% in the upper soil layer, to 0.08% at sub-surface layers (Ringrose et al., 1998). The dominant soil mineral concentrations are iron and oxide, giving such soil a reddish colour, poor in nutrients. These estimates are expected to slightly change along the north-south climate gradient because of variation in rainfall and nutrient cycling.

The conditions highlighted above are testimony to the harsh and extreme environmental circumstances of nutrients and the water deficit under which the Kalahari Basin plants grow, more especially in the most arid parts of the basin where low rainfall reduces the available soil moisture, and high temperature increases plant stress because of high evapotranspiration. For these reasons, the Kalahari Basin is considered a perfect natural laboratory for eco-hydrological investigations because of its climatic characteristics and soil, such that the effects of changing hydrologic conditions on ecological systems can be investigated without the confounding effects of soil types (Bhattachan et al., 2012).

In terms of site-specific climatic conditions, several sources (e.g., Fick & Hijmans, 2017; Mendelsohn et al., 2002) and unpublished data from the meteorological stations of the Southern Africa Science Service Centre for Climate Change and Adaptive Land use (SASSCAL) Weather observatory as summarised in Table 1 can be used to estimate the climatic conditions of the specific study sites. The first three sites, Omutambomawe, Uutsathima and Etosha, are located along the western edge of the Kalahari Basin, within a rainfall isohyet of approximately 300–450 mm per annum. Because of their low mean annual precipitation, these two sites were collectively classified as ‘drier sites’. Sites such as Onyuulaye, Okongo and Nkurenkure receive a moderate mean annual rainfall of 450 mm to 550 mm per annum and were thus classified as mesic. The last two sites, Divundu and Katima Mulilo, receive the highest rainfall of approximately 600 mm per annum, and were thus classified as ‘wetter sites’.

Table 1. Climate indicators of the study sites across the Kalahari Transect.

Study sites	Omutambomawe	Uutsathima	Etosha	Onyuulaye	Okongo	Nkurenkure	Divundu	Katima Mulilo
Sub-climatic zone	Drier	Drier	Drier	Mesic	Mesic	Mesic	Wetter	Wetter
MAP (mm/year)	300	300	450	470	550	550	600	660
Average summer temperature (°C)	23	23	34	26	27	34	35	35
Average winter temperature (°C)	19	19	19	18	18	18	19	19
PE range (mm/year)*	1960 – 210	1960 – 2100	1960 – 2100	1960 – 2100	1820 – 1960	1820 – 1960	1820 – 1960	< 1680
Rainfall coefficient of variation (%)	45	45	35	35	35	35	35	35

*PE refers to potential evapotranspiration, the quantity of water which could evaporate from a surface per unit area and unit time under existing atmospheric conditions.

In terms of water availability, which largely depends on the prevailing climate, these sites are located in different aquifers. For example, Omutambomawe and Uutsathima are located in the Omusati Multi-zoned Aquifer (KOM) with a water depth of 10 to 60 m, 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/dolocrete, but also 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 lie on top of the major Kalahari aquifer with an estimated average depth of about 20 m (Christelis & Struckmeier, 2001).

3.2.1.3 Vegetation types

Vegetation is probably the most studied ecological parameter of the Kalahari Basin, partly due to its intriguing relation with the prevailing climate and soil (Caylor et al., 2003; Privette et al., 2004; Ringrose et al., 2003; Scholes et al., 2002). However, an important limitation associated with vegetation studies in the Kalahari Basin is that the geographical scope of most such studies was limited by the geographical boundaries of the countries in which they were conducted, with most studies focusing on vegetation description for the Kalahari part of Botswana only, although such studies referred to the entire Kalahari Basin. This challenge had already been noted decades ago by Thomas and Shaw (1991), but to date, no major efforts have been made to provide an inclusive vegetation description of the entire Kalahari Basin at finer spatial scale.

At a coarse scale, the vegetation of the Kalahari Basin can be classified as savannas, whose diversity and biomass of vegetation production increase linearly in the north-eastern direction in line with the rainfall gradient (Thomas & Shaw, 1991). According to Ringrose et al. (1998), the vegetation of the Kalahari Basin can be classified into six major classes, based on climate. The arid south-western edge of the Kalahari Basin is mainly dominated by savanna shrubs and is therefore frequently classified as shrubland, and dominated by woody species such as *S. mellifera, Terminalia sericea, B. albitrunca* and *Rhigozum trichotonum*. Eastward, vegetation shifts toward bush savannas, also termed thornveld, which is characterised by dense thickets of *V. erioloba, S. mellifera, B. albitrunca, Grewia flava, Grewia retinervis, D. cinerea* and *Ziziphus mucronata* mixed with grassy plains (Ringrose et al., 1998). Further toward the north-eastern parts of the Kalahari Basin, where rainfall is higher, the vegetation structure changes to a continuous layer of woodland, called ‘moist savannas’ and dominated mainly by species such as *Baikiae plurijuga, Bauhinia spp., R. rautanenii, Pterocarpus angolensis, Burkea africana, Erythrophleu africanum, Lonchocarpus capassa* and *T. sericea.* They cover parts of the eastern Zambezi region, northern Botswana, Zambia and further north (Ringrose et al., 1998).

There were some notable site-specific differences between the study sites in terms of vegetation coverage and structure. The Omutambomawe and Uutsathima sites are located in the western Kalahari woodland along the north-western edge of Etosha National Park. These two sites share some common features in terms of vegetation and land use. Dominant woody species are *T. sericea, S. mellifera, Senegalia nebrownii*, *V. erioloba, Elephantorrhiza suffruticosa, Bauhinia petersiana, Albizia anthelmintica, Catophractes alexandri, Croton gratissimus, Grewia flavescens, Searsia marlothii* and *Vachellia reficiens*. These sites are characterised by sparsely distributed woody plants, more than 3 m in height, as well as multi-stemmed shrubs growing on a flat sandveld. Verbal interactions with the locals suggest that this area is used as rangelands for pastoralists mostly from the Omusati Region, and as a result, grass cover was significantly low. A higher density of encroaching species, such as *T. sericea* and *S. mellifera*, than other species seems to confirm that this area is bush encroached as Bester (1996) had suggested earlier. Because of human activities in the area, care was taken to sample at sites of minimal disturbance in order to ensure the integrity of the data.

The Etosha site is located in the Kalahari sandveld along the north-eastern edge of the Etosha National Park boundaries. This area is dominated by deep Kalahari sand. Dominant woody species found at the study sites are *Commiphora glandulosa, Commiphora angolensis, G. flavescens, T. sericea, Ximenia americana* and *C. gratissimus*. The density of woody species was higher at the Etosha site than at Omutambomawe and Uutsathima. The structure of the vegetation is a mixture of both trees and shrubs. Like the Omutambomawe and Uutsathima sites, this site is also on communal land used for livestock grazing, and exhibits signs of moderate grazing pressure.

Onyuulaye and Okongo have similar vegetation types, partly because they belong to the same vegetation community, the north-eastern Kalahari woodland, which consists of dense, tall savanna trees. Compared to the previous three sites, Onyuulaye and Okongo carry predominantly more trees than shrubs, partly because the sites receive higher rainfall. Dominant woody species are *T. sericea, B. africana, V. erioloba,* *C. gratissimus, B. albitrunca, D. cinerea, B. petersiana* and *Mundulea sericea.* Similarly, Onyuulaye and Okongo are used as grazing areas on a communal basis. Such practice has had an evident impact on grass cover around those study sites.

Nkurenkure is located some 200 km away from Okongo along the C45 road. Compared with the previous sites, Nkurenkure demonstrates a progressive change in vegetation structure from the dominance of shrubs to dense deciduous trees and shrubs such as *B. albitrunca, B. africana, B. petersiana, Baphia massaiensis, P. angolensis, Philenottera nelsii, C. angolensis, C. gratissimus, Ochna pulchra* and *Combretum imberbe*. Divundu and Katima Mulilo sites, being within the same precipitation belt, share common dominant woody species, with species such *Schinziophyton rautanenii, T. sericea, P. angolensis, B. plurijuga, Combretum collinum,*, and *B. massaiensis*.

With regard to the herbaceous layer, with a particular focus on grass species, the Kalahari Basin is dominated by both perennial and annual grasses, with changes in species composition along the rainfall gradient (Klaassen & Craven, 2003; Müller, 2007). For example, the eastern parts of the transect covering the Zambezi Region and eastern Kavango, where Katima Mulilo and Divundu sites are situated, are largely dominated by species such as *Andropogon spp, Heteropogon contortus*, and *Perotis patens.* Other common grass species found are *Chloris virgata*, *Cynodon dactylon, Dactyloctenium, giganteum*, *Panicum kalaharense*, and *Schmidtia pappophoroides* (Klaassen & Craven, 2003; Müller, 2007). The central parts of the study area, covering study sites such as Nkurenkure, are largely dominated by species such as *Anthephora pubescens, Heteropogon melanocarpus, Microchloa caffra, P. patens, Chloris virgata, C. dactylon*, *Dactyloctenium aegyptium,* and *Digitaria erianth*a. There are also grass species such as *Triraphis schinzii, C. virgata, Pogonarthria fleckiii, Aristida congesta, S. pappophoroides,* and *Eragrostis dinteri* which occur around the study area

(Klaassen & Craven, 2003; Müller, 2007). The western part of the study area where rainfall is less than at other sites, is largely dominated by species like *Anthephora schinzii, H. contortus, Tragus racemosus, C. virgata, C. dactylon, D. aegyptium, Sporobolus ioclados, and Stipagrostis uniplumis*. Other dominant species known to occur around the area are *Eragrostic rotifer, P. fleckiii, Aristida adscensionis, Schmidtia kalahariensis*, and *E. dinteri* (Klaassen & Craven, 2003; Müller, 2007). Large parts of Namibia, including the Kalahari Basin, are occupied by C_4 grasses as opposed to C3 grasses. According to Ellis and Furs (1980), approximately 95% of the grass species in Namibia use the C_4 photosynthesis pathway. The majority of such grass species are highly palatable; thus, the Kalahari serves as good rangeland for the northern and north-eastern communal pastoralists. Principally, grass cover around major parts of the Kalahari is kept low due to overgrazing, frequent fire, and drought.

All the sites are on a homogenous flat landscape, and are used as grazing areas for domestic livestock, such as goats and cattle. Efforts were made to ensure that all sites that were noticeably disturbed by soil erosion, human settlement, fire and severe animal trampling were not included in the study as those can affect both the below-ground and above-ground morphological characters of the studied woody plants.

3.2.1.4 Anthropogenic disturbances in the Kalahari savannas

Arguably, the savannas are anthropogenic biomes, resulting from diverse human activities such as grazing pressure and fire (Beerling & Osborne, 2006; Bond & Zaloumis, 2016; Laris & Dembele, 2012). The savannas of the Kalahari Basin found around northern and north-eastern Namibia, where this study was conducted, are also modified by human activities such as fire, grazing, and human settlement. The

Kalahari Basin is among the most densely populated parts of the country with a population density of approximately 10 people per square kilometre, whose livelihoods depend largely on agriculture such as cattle farming (Mendelsohn, 2006). It is estimated that 58% of the total cattle population in Namibia are found on the northern and north-eastern communal areas, with a density of approximately 10 to 20 cattle per square km (Mendelsohn, 2006). The recommended stocking rate in that area is 5 to 10 cattle per square km (Mendelsohn, 2006). This level of overstocking (Schneiderat, Siegmund-Schultze & Steinbach, 2005; Siegmund-Schultze, Lange, Schneiderat & Steinbach, 2012; Watts, 2012) means that the northern and north-eastern Kalahari Basin savannas are subjected to intense grazing pressure, which results in a loss of the natural integrity of such savanna ecosystems. The impact of grazing pressure in the Kalahari Basin savannas is most clearly evident around water points (Burke, 2004; Katjiua & Ward, 2007; Klintenberg & Verlinden, 2008; Nangula & Oba, 2004; Van Rooyen, Bredenkamp, Theron, Bothma & Le Riche, 1994).

Anthropogenic disturbances in the Kalahari Basin can also be understood in the context of fire regimes. Figure 15 shows areas affected by fire between 2003 and 2010. Fire affects plants through direct burning, and the magnitude of the impact of such burning can be understood in terms of fire intensity, fire duration and severity, as well as the timing of burns, which in turn, is related to the physical characteristics of the fuel load (Graz, 2005; Sheuyange, Oba & Weladji, 2005). The Kalahari savannas burns nearly every year during the dry season. While natural phenomena, particularly lightning, can cause a wildfire, most fires are the result of deliberate human activities such as clearing land for crop cultivation, or local farmers burning the veld to clear away old grass shortly before the next rainy season. This is part of the reason why the African savanna biomes are strongly linked to the occurrence of fire. The eastern savannas covering parts of Kavango and the Zambezi Region burn more frequently than those in the western Kalahari. Such recurrent anthropogenic disturbances make it difficult to study the savannas in their natural settings.

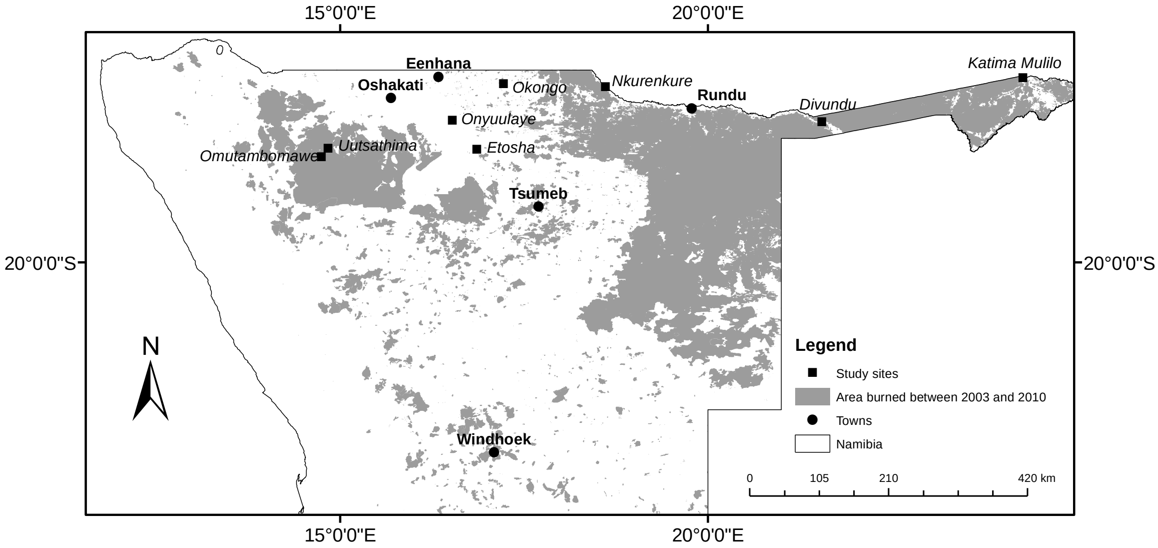

Figure 15: Areas burned by wildfire in Namibia between 2003 and 2010. Most of the vegetation communities along the Kalahari Transect of this study are frequently subjected to burning. (Data source: Namibian Ministry of Agriculture, Water and Forestry).

3.2.2 Data collection and analysis

Data collection was conducted from eight (8) sites (Figure 17) in Namibia, along the east-west rainfall gradient of approximately 1200 km in the Kalahari. This study randomly selected 37 individuals of *S. mellifera* and 35 individuals of *D. cinerea* shrubs from an area of 10 m x 10 m measured using a flexible tape. Each excavated shrub was selected using a random number table. Thereafter, the root system of each selected shrub was exposed using the following excavation technique (Böhm, 1979): the soil surrounding each selected plant was carefully removed, starting at the stem, to establish the number of lateral roots growing from the plant. Thereafter, identified lateral roots were excavated laterally, using a trowel or spade, depending on its depth, to determine and measure their full horizontal extent. A spade was also used to dig downwards to determine the vertical depth of the taproots. For taproots, excavation was abandoned at a depth of 1 m. After excavation, the morphological features of each excavated root system were measured using a flexible tape and Vernier callipers. Because of the uneven distribution of vegetation across the landscape, it was not possible to excavate both shrub species at exactly the same study site. In order to overcome this challenge, efforts were made to ensure that within each sub-climatic zone (drier, mesic and wetter) roots from both shrub species were at least sampled, although not necessarily from exactly the same site. Empirical data collected include above-ground variables, such as plant height, canopy diameter measured from the longest y-axis and x-axis of the shrub canopy using a flexible measuring tape, and stem diameter measured from the base of each shrub's shoot using Vernier callipers. When the selected shrub was multi-stemmed, the diameter was measured for all the stems to determine an average stem diameter. The above-ground size of both *S. mellifera* and *D. cinerea* were quantified using standing height, canopy diameter, and stem diameter.

Below-ground variables measured include lateral rooting depth, measured as the vertical depth at which the lateral root develops from the taproot; root diameter, measured as the thickness of the lateral root at the base, and lateral root abundance defined as the number of lateral roots growing per plant. Other variables measured were lateral root terminal depth, measured as the vertical depth at the terminal end of lateral root with respect to the soil surface, as well as lateral root angle of elongation, which is the acute angle that a plant's roots make in relation to the soil horizontal plane as they elongate in the soil. The angle of elongation was calculated using lateral rooting depth, terminal depth, and root length. Lastly, lateral root horizontal extent was determined, based on lateral root length (Figure 16).

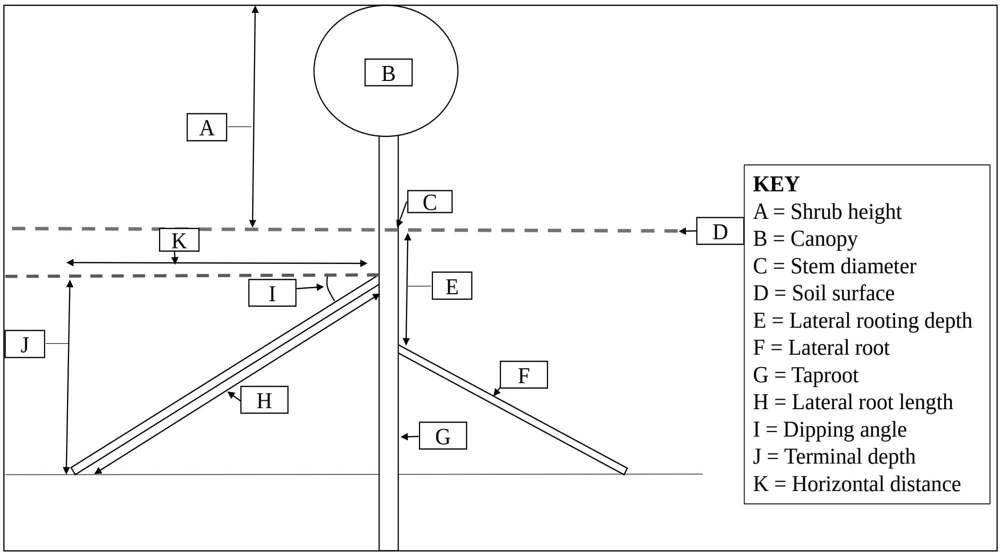

Figure 16: Schematic diagram representing various components of the plant measured.

Data analysis was done in R 3.3.1 (R core team, 2017. A two-way factorial analysis of variance (ANOVA) was conducted on the effects of independent variables, such as sub-climatic zone and shrub species, on the dependent variables of shrub height, canopy diameter and stem diameter. Prior to data analysis, normality of the data distribution was confirmed using the Shapiro-Wilk test. All post hoc analyses were done using Tukey’s honest significant difference test. Results were interpreted as significant at alpha level.05 or less.

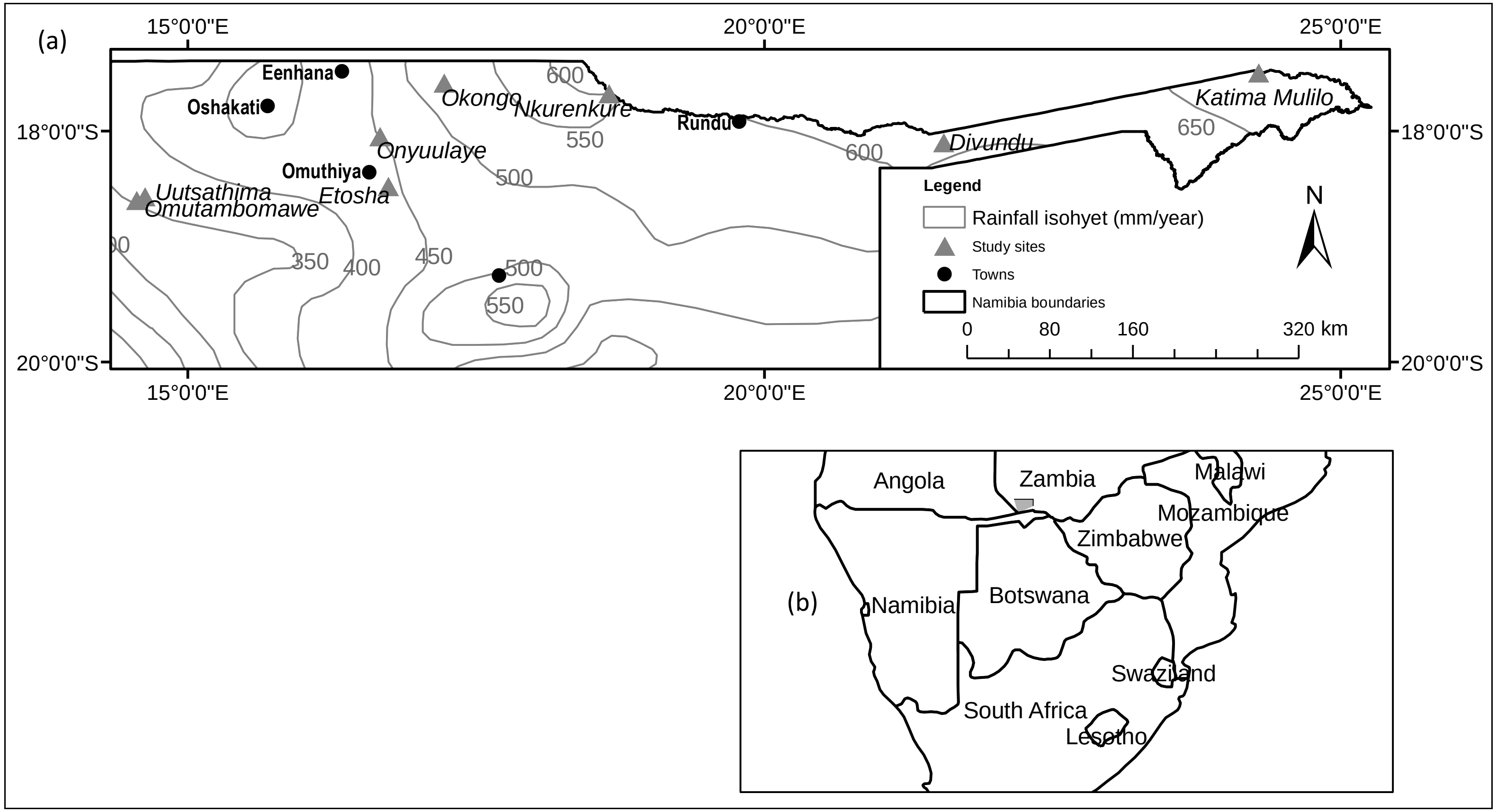

Figure 17: The distribution of study sites along the Kalahari rainfall gradient of northern Namibia. Map (a) shows the geographical extent of the study areas, while map (b) shows the location of the study area in Southern Africa. (Data source: Mendelsohn et al., 2002).

3.3 Results

3.3.1 Above-ground morphometric properties of *S. mellifera* and *D. cinerea* shrubs

Table 2 provides descriptive statistics on above-ground variables of the excavated plants. A two-way factorial ANOVA conducted on the effects of independent variables, such as sub-climatic zone and shrub species, on the dependent variables, shrub height, canopy diameter and stem diameter, revealed that shrub height was not significantly different between drier, mesic and wetter sub-climatic sites, ($F_{(2, 91)} = 1.47$, $p = 0.235$). The same is true for variation in shrub height between *S. mellifera* and *D. cinerea* shrubs, ($F_{(1, 91)} = 0.161$, $p = 0.689$). Table 2 shows that the standing height of *S. mellifera* ranged from 184.3 ± 26.1 cm at drier sites to 167.9 ± 22.4 cm at mesic and 220.0 ± 15.1 cm at wetter sites. Meanwhile, *D. cinerea* had the shortest mean standing height of 144.8 ± 31.3 cm for mesic sites, followed by drier sites with a mean standing height of 187.0 ± 36.6 cm, then wetter sites with a mean standing height of 213.3 ± 6.3 cm. These are pooled statistics from various sub-sites which were located within each of the three sub-climatic sites classified based on their MAP. The shrub height was not significantly different between drier, mesic and wetter sub-climatic sites ($F_{(2, 91)} = 1.47$, $p = 0.235$).

Further two-way factorial ANOVA revealed that canopy diameter was significantly different between the three sub-climatic sites, ($F_{(2, 91)} = 35.92$, $p < 0.001$) as well as between the two shrub species ($F_{(1, 91)} = 25.34$, $p < .001$). Tukey’s honest significant difference post hoc test showed a significant difference ($p < .001$) between mesic and drier sites, as well as between mesic and wetter areas. No significant difference ($p = 0.405$) was observed between drier and wetter sites. Drier sites had a large pooled mean canopy diameter of 237.9 ± 26.7 cm, while mesic and wetter sites were almost equal with a canopy diameter of 175.9 ± 31.0 cm and 173.1 ± 17.3 cm, respectively. Meanwhile, *D. cinerea* canopy diameter was largest at mesic sites, with a thickness of 190.3 ± 27.0 cm, followed by drier sites with a canopy diameter of 150.3 ± 21.6 cm, then wetter sites with a canopy diameter of 145.5 ± 18.0 cm. When these two shrub species are compared against each other, *S. mellifera* had a larger canopy diameter than *D. cinerea* at drier and wetter sites. Stem diameter was significantly different between drier, mesic, and wetter areas ($F\ (_{2,\ 91}) = 10.22$, $p < .001$), and was also significantly different between the two shrubs, *S. mellifera* and *D. cinerea* ($F\ (_{1,\ 91}) = 8.22$, $p < .001$). Stem diameter ranged from 24.0 ± 6.0 mm to 17.0 ± 11.0 mm for both species. Following the pattern exhibited by canopy diameter for stem diameter, it was also the mesic sites which differed significantly ($p < .001$) from both the drier and wetter sites, as confirmed by a post hoc test.

Table 2. Descriptive statistic (mean ± standard deviation) of the above-ground morphometric properties of *S. mellifera* and *D. cinerea*.

Shrubs	*S. mellifera*			*D. cinerea*		
Variables	Drier	Mesic	Wetter	Drier	Mesic	Wetter
Shrub height (cm)	184.3 ± 26.1	167.9± 22.4	220.0 ± 15.1	187.0 ± 36.	144.8 ± 31.36	213.3 ± 6.3
Canopy diameter (cm)	237.9 ± 26.7	175.9 ± 31.0	173.1 ± 17.3	150.3 ± 21.6	190.3 ± 27.0	145.5 ± 18.0
Stem diameter (mm)	23.0 ± 07.0	19.0 ± 6.0	24.0 ± 6.0	18.0 ± 06.0	25.0 ± 2.0	17.0 ± 11.0

3.3.2 The root system architecture of *S. mellifera* and *D. cinerea* shrubs

The exposed roots for both *S. mellifera* and *D. cinerea* yielded two distinct rooting patterns. The first rooting pattern is a dual root system made up of both lateral roots and taproot components. The second rooting pattern comprises lateral roots only. The taproots typically grow vertically from the radicle into the subsoil, while lateral roots grow horizontally from the taproot, or otherwise from the radicle when a taproot is absent. Of the 37 individuals of *S. mellifera* excavated, all but seven (19%) had both taproot and lateral roots. Those with no taproot were excavated at Uutsathima (3), Okongo (2) and Nkurenkure (2). Only five (14%) of the 35 *D. cinerea* individuals excavated exhibited no taproot. These plants were excavated at Omutambomawe (2), Uutsathima (2) and Divundu (1). For both species, the presence of a taproot was always accompanied by lateral roots; however, when the taproot was absent, the lateral roots were the central feature of the root systems. Overall, drier sites had a higher proportion of shrubs with no taproot than other sub-climatic sites. A visual illustration of these architecture types is presented in Figure 18.

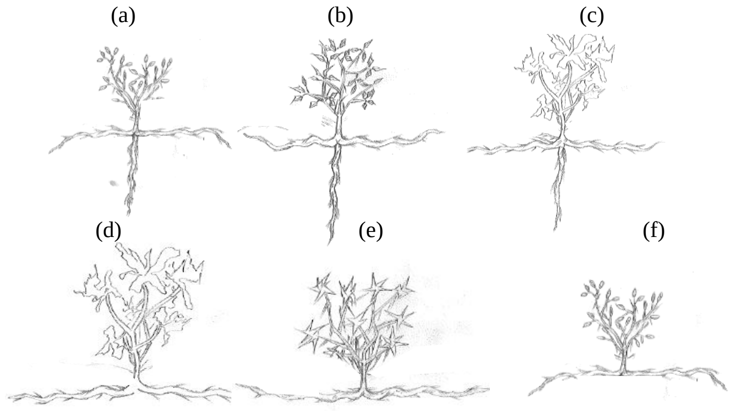

Figure 18: Illustrations of the two distinct and the minor variations within rooting patterns of both *S. mellifera* and *D. cinerea* shrubs.

Several rooting patterns can be observed, such as those with a dual root system consisting of both taproot and lateral root, as well as those whose root system consists entirely of lateral roots. Within these two root systems, variations in terms of rooting depth are evident. For example, shrubs (a), (b) and (c) show root systems consisting of both lateral roots and taproot. However, for plant (a), the lateral roots deepen as they elongate away from the taproot, while for shrub (b), such lateral roots grow and elongate towards a shallower subsoil surface, resulting in a shallower terminal depth than the lateral rooting depth. Shrub (c) maintains the same lateral rooting depth as the root starts elongating away from the taproot. These behaviours were also observed among shrubs that had no taproot component, as illustrated in (d), (e) and (f).

3.3.3 Variation in below-ground morphometric properties of *S. mellifera* and *D. cinerea* roots

Morphologically, the root systems of these two shrubs are characterised by attributes such as the depth of lateral root growth, lateral length, terminal depth, and root diameter. The two-way factorial ANOVA results (Table 3) revealed that lateral root depth was not significantly different (p = 0.127) between the three sub-climatic regions (drier, mesic and wetter) or between *S. mellifera* and *D. cinerea* (p = 0.374). However, there was a significant interaction (p =.01) between the sub-climatic zones and encroaching species where *D. cinerea's* lateral rooting depth in a mesic sub-climatic zone differed significantly (p =.02) from the drier and wetter sub-climatic zones, as revealed by the post hoc analysis. Terminal depth was not significantly different (p = 0.274) between the three sub-climatic zones, but was significantly different between *S. mellifera* and *D. cinerea* shrub species. There was also a significant interaction (p = 0.03) between sub-climatic zone and shrub species, which shows that the terminal depth of lateral roots for the two species behaves differently, depending on the sub-climatic zone. The lateral rooting depth of *S. mellifera*, the depth at which lateral roots branched away, was marginally highest (19.2 ± 2.0 cm) at drier sites, followed by wetter sites with a mean lateral rooting depth 18.4 ± 3 cm, then mesic sites with 17.9 ± 3.0 cm. The shallowest lateral root was found at a depth of 7 cm at Nkurenkure, a mesic site, while the deepest (37.4 cm) was excavated at Etosha, a drier site. In terms of terminal depth, measured at the end of each lateral root tip, the drier sites had a mean terminal depth of 19.5 ± 3.0 cm, while mesic and wetter sites had a terminal depth of 16.6 ± 5.0 cm, and 22.5 ± 1.0 cm, respectively. The shallowest terminal depth of 4 cm was excavated at Omutambomawe, a drier site, while the deepest terminal depth was found at Okongo, a mesic site, at a depth of 36 cm. Wetter sites, however, exhibited a different pattern. For example, while mean lateral rooting depth did not change compared to other sites, the terminal depth increased significantly (p <.001), reaching a mean depth of some 22.5 ± 6.0 cm. In contrast, *D. cinerea* followed a different rooting pattern. Drier and wetter sites had the highest mean depth of approximately 20.4 ± 1.0 cm and 19.4 ± 1.0 cm, respectively, while the lateral rooting depth at mesic sites was 16.3 ± 1.0 cm. Such variations are not necessarily linearly associated with the rainfall gradient. Of all excavated plants, the shallowest lateral root was excavated at a depth of 3 cm at Okongo, a mesic site, and the deepest lateral rooting depth was excavated at a depth of 39 cm at Divundu, a wetter site. What appears to distinguish *D. cinerea* from *S. mellifera* is that, for drier and mesic sites, the average terminal depth was significantly ($p < .001$) shallower than the growth depth, decreasing downwards from approximately 20 cm deep to some 16.4 ± 4.0 cm for drier sites, and from 16.31 ± 8 cm deep to a terminal depth of 13.6 ± 3.0 cm (Figure 19).

These results indicate that, instead of such roots deepening, they rise toward the surface as they spread and elongate away. This pattern was, however, not found in the wetter sites, where both the starting and ending depth sustained nearly the same depth range of 19 cm each, with no statistically significant difference (*p* > .05). The shallowest terminal depth was recorded at 5 cm (Uutsathima), while the deepest terminal depth was recorded for Divundu at 75 cm.

Table 3. Summary of factorial ANOVA on the effects of the sub-climatic zone and shrub species type on morphometric properties of roots.

Dependant variables	Independent variables	*DF*	*MS*	*F*	*p*
(a) Lateral root depth	Sub-climatic zone	2	121.74	2.1	0.127
	Species	1	46.07	0.79	0.374
	Sub-climatic zone x species	2	273.5	4.734	0.01
	Residual	88	57.77		
(b) Terminal depth	Sub-climatic zone	2	269.6	1.31	0.274
	Species	1	2165	10.52	0.001
	Sub-climatic zone x species	2	328.4	9.59	0.03
	Residual	89	205.8		
(c) Lateral root extent/length	Sub-climatic zone	2	25802	6.28	0.002
	Species	1	8434	2.05	0.151
	Sub-climatic zone x species	2	35538	8.65	0.0003
	Residual	89	4104		
(d) Lateral root diameter	Sub-climatic zone	2	278.26	10.73	0.000
	Species	1	224.35	8.65	0.000
	Sub-climatic zone x species	2	85.04	3.28	0.042
	Residual	89	25.91		

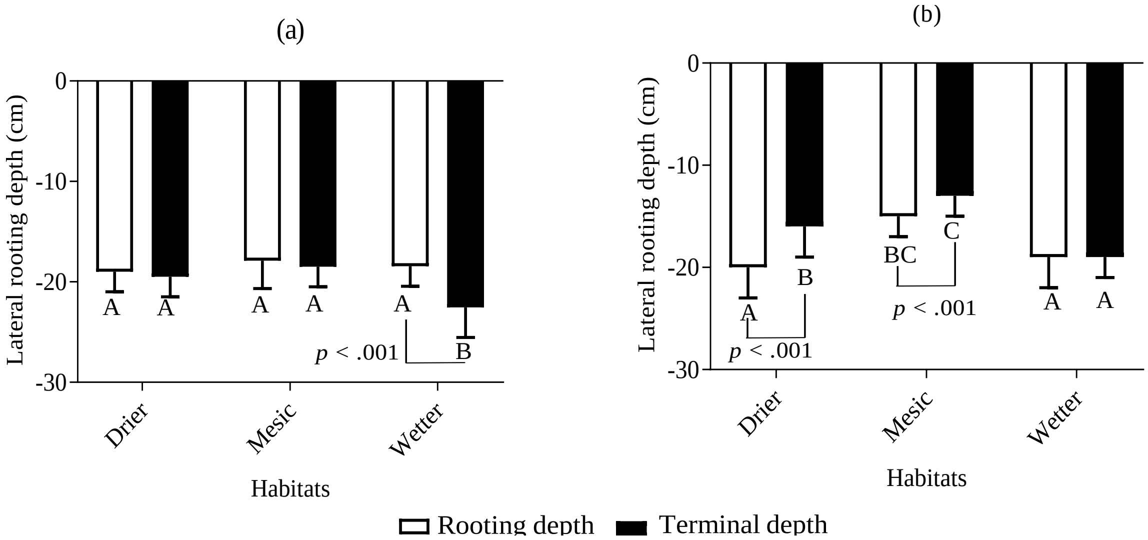

Figure 19: Lateral starting and terminal/end depth of a) *S. mellifera* and b) *D. cinerea* shrubs in relation to the three sub-climatic zones along the Kalahari Transect. Different letters over the bars indicate significant differences between the sites. Sites not connected by the same letters are significantly different.

3.3.4 Lateral root length, diameter and dipping angle

In addition to rooting depth and terminal depth, another important root morphological attribute is the horizontal extent of such lateral roots, their thickness based on both diameter and dipping angle, and how such attributes vary between the two encroacher species as well as across the sub-climatic zones. Results (Table 3) indicate a significant difference (p =.002) in rooting length between the three sub-climatic zones, but the same was not significantly different (p = 0.151) between *S. mellifera* and *D. cinerea* shrubs. There were also significant (p < .001) interaction effects of sub-climatic zone and species types on lateral root length of the two shrub species, where the two shrub species shared the same root length in one sub-climatic zone, but exhibited contrasting rooting extents in another sub-climatic zone. For example, the mean lateral root length for *D. cinerea* was significantly different (p < .001) from that of *S. mellifera* in a drier sub-climatic zone, as is between *D. cinerea* in a wetter sub-climatic zone and *S.*

mellifera in a drier sub-climatic zone. Other significant interaction effects were between *D. cinerea* shrubs in a drier sub-climatic zone and shrubs of the same species in a mesic sub-climatic zone.

The lateral roots of *S. mellifera* were longest (181.6 ± 40 cm) at drier sites, followed by mesic sites with 133.2 ± 50 cm mean length, then wetter sites with a mean length of 128.5 ± 77 cm. None of the mean lateral root extents was longer than the average canopy diameter. However, in a few instances, the longest recorded lateral root length extended beyond the average canopy diameter. For instance, the drier sites had a canopy diameter of 237.9 ± 26.7 cm, but the longest recorded lateral root extension reached as far as 240 cm. These statistics are summarised in Table 4.

Using the rooting depth, terminal depth, and lateral root extension for all three sites, such roots maintain, on average, a dipping angle of between 6° and 10° as they traverse the soil. Such a shallow trajectory shows the shallowness of *S. mellifera* lateral roots. What appears to distinguish *S. mellifera* in terms of the rainfall gradient is its higher abundance of lateral roots. In the drier sites *S. mellifera* had, on average, twice as many lateral roots as those in the mesic and wetter sites. At the Divundu site, for example, an individual *S. mellifera* shrub exhibited only two lateral roots, as compared to those in the drier sites where the minimum number of laterals was five for an individual excavated at Uutsathima.

Table 4. Mean ± standard deviation of morphological features of roots.

Morphometric properties of roots	*S. mellifera*			*D. cinerea*		
Variables	Drier	Mesic	Wetter	Drier	Mesic	Wetter
Lateral rooting depth (cm)	19.2 ± 2.0	17.9 ± 2.8	18.5 ± 3.1	20.4 ± 6.2	16.3 ± 7.8	19.4 ± 8.7
Lateral root terminal depth (cm)	19.5 ± 3.4	18.6±4.5	22.5 ± 6.4	16.4 ± 3.5	13.6 ± 2.7	19.2 ± 3.8
Lateral root horizontal extent (cm)	181.6 ± 39.9	133.2 ± 58.6	128.5 ± 77.3	107.8 ± 61.3	190.6 ± 83.0	104.3 ± 61.4
The angle of elongation (◦)	8.0 ± 00	10.1 ± 2.0	8.8 ± 1.0	4.1 ± 1.0	10.6 ± 3.0	6.2 ± 1.0
Lateral root diameter (mm)	11.6±4	13.1± 7.0	6.0 ± 2.0	8.4 ± 2.0	12.0 ± 8.0	9.9 ± 4.0
Relative root abundance	7.0	5.5	5.0	6.0	5.0	5.5

In terms of root elongation, the longest mean lateral root length for *D. cinerea* was recorded from a mesic site, and reached approximately 190.6 ± 82.9 cm. This was followed by a sample from a drier site of some 107.8 ± 61.3 cm, then samples from the wetter sites with a mean length of 104.34 ± 61.4 cm. At all sites, the mean length of lateral roots significantly ($p < 0.05$) fell short of the mean canopy diameter. The elongation of lateral roots from drier sites followed a much shallower trajectory of elongation of approximately 4° relative to the base point at which they developed from the taproot as well as the soil surface, than those from mesic and wetter sites. In terms of lateral root abundance, the average number of lateral roots per plant excavated did not vary much with the rainfall gradient, although drier sites had the highest mean of six lateral roots per plant.

Figure 20 illustrates the relationship between lateral rooting depth and diameter, while Figure 21 shows the relationship between lateral root diameter and taproot diameter. These morphometric variables showed distinctive patterns in the two shrub species. *S. mellifera* had a mean lateral root diameter ranging from 11.0 ± 4.0 mm at drier sites, to 13.0 ± 7.0 mm and 6.0 ± 2.0 mm at wetter sites. Its lateral root diameter was directly related to lateral rooting depth. For example, thinner lateral roots of just above 5 mm mostly dominated a depth shallower than 15 cm. When rooting depth increased, say to 20 cm, root thickness increased dramatically to over 10 mm in diameter. This shows a pattern between rooting depth and lateral root diameter where younger lateral roots rather than older, larger roots are found within a shallower sub-surface. The mean diameter of *D. cinerea* lateral roots was 8.0 ± 2.0 mm at drier sites, 12.0 ± 4.0 mm at mesic sites, and 10.0 ± 4.0 mm at wetter sites. Compared to *S. mellifera*, *D. cinerea* exhibited contrasting patterns in terms of its morphometric variables. Its lateral rooting depth was not necessarily associated with root diameter; nor did smaller lateral roots necessarily occupy the upper segment of the taproot. Instead, lateral roots of different sizes were deployed opportunistically at various depths. For example, while the upper, shallower depth of approximately 5 cm was occupied by lateral roots of 5 mm on average, such root diameter was also dominant at a depth of over 15 cm. Likewise, lateral roots of a diameter range of close to 10 mm were also found within a shallow depth of approximately 5 cm. An exception is a single case where a lateral root with a diameter more than 10 mm was located at a depth below 30 cm. In addition to depth, the diameter of lateral roots for *S. mellifera* was also influenced by the diameter of the taproot, when it was present. For example, shrubs with a taproot diameter of less than 10 mm had larger lateral roots of more than 15 mm in diameter; but when the taproot diameter increased to approximately 30 mm, lateral root diameter decreased to less than 10 mm on average. This was not the case with *D. cinerea*. The thickness of lateral roots was independent of the thickness of the taproot in all three sub-climatic environments, oscillating between approximately 8 mm and 12 mm on average, irrespective of the rainfall gradient or the taproot diameter.

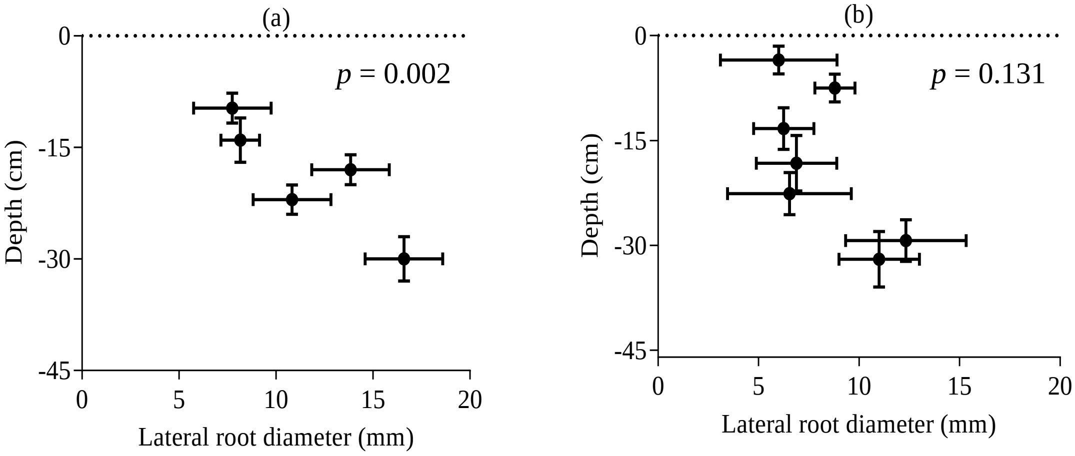

Figure 20: Variation in lateral rooting depth by variation in lateral root diameter. (a) *S. mellifera*, (b) *D. cinerea*. Each point represents the mean and standard deviation of lateral rooting depth, as well as the mean and standard deviation for the diameter of such roots.

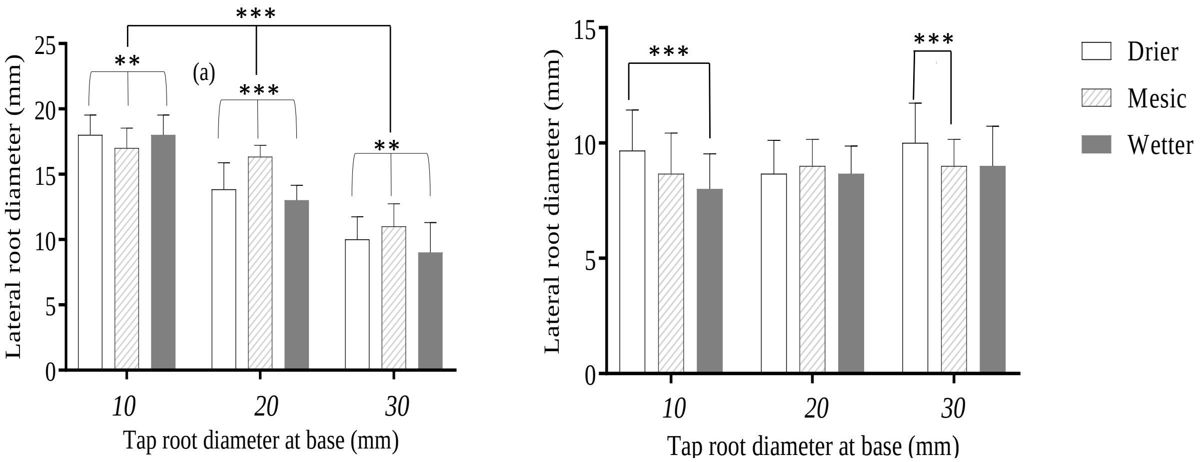

Figure 21: Relationship between taproot diameter and lateral roots average diameter of (a) *S. mellifera*, (b) *D. cinerea* shrubs. Groups that a statistically significant are indicated with asterisks, where ***$p < .001$, **$p < .01$, * $p < .05$.

3.4 Discussion

The savannas have been interpreted in the context of the tree-grass root niche-partitioning hypothesis, a premise advocated by Walter's two-layer model (Walker & Noy-Meir, 1982; Walker et al., 1981; Scholes & Walker, 1993; Ward et al., 2013; Walter & Mueller-Dombois, 1971). This model postulates that deeper root systems are the central feature for the survival of trees in water-limited environments such as the sub-tropical savannas. This study investigated how two shrub-encroaching shrubs, *D. cinerea* and *S. mellifera,* develop their roots for foraging water and nutrients in the Kalahari, a semi-arid environment in Southern Africa. The overall aim of the study was to test the relevance of the root niche-partitioning hypothesis to these two shrub species.

The major insight emerging from this study is that both *D. cinerea* and *S. mellifera* develop two distinctive rooting patterns. The first rooting pattern comprises both lateral roots and taproot, while the second pattern is characterised exclusively by lateral roots. While the taproot, when it was present, was always deeper than the undertaken excavation efforts of up to 1 m deep, the bulk of lateral roots were deployed within a shallower depth of 20 cm below the surface.

Although marginal compared to those with a taproot, the higher proportion of shrubs with no taproot in and towards the drier parts of the study transect seems to suggest that this rooting pattern is influenced by rainfall. The terminal depth, angle of elongation, as well as lateral spread may also reveal insights into the catchment area in which roots are deployed to acquire soil resources. For example, within the wetter sub-climatic sites, *S.*

mellifera had the lowest (128 ± 77 cm) mean lateral root extent, which increased up to 181 ± 39.9 cm towards the drier sites. This could be attributed to the decline in soil resources, such as moisture, for which plants in a drier area may need to expand their rooting ranges as a survival mechanism in order to cope with a moisture-deficient environment.

Of particular interest, is that lateral roots of *D. cinerea* grow towards shallower depths as the roots spread out from the primary root. According to Kobayashi et al. (2007), the direction of plant root elongation is affected by three major environmental stimuli: phototropism, gravitropism and hydrotropism. The horizontal pattern of lateral root growth for both *D. cinerea* and *S. mellifera* cannot be in response to gravitropism stimulus, otherwise gravity would force the root tip into a near-vertical pattern as it grew. Phototropism is an unlikely factor because of soil opacity. Rather, it is likely that hydrotropism is a major driver, whereby roots grow in the direction of the moisture gradient. If this is the case, this implies that soil moisture may be an important factor in regulating the deployment of plants' lateral roots. No evidence of disturbances, such as soil erosion or any mechanical impediment, was apparent at these sites. With a high abundance of lateral roots within the shallow sub-surface as opposed to a greater depth, it can also be argued that the deployment of such lateral roots is not entirely a random process, but responds to certain environmental factors, of which moisture is the most probable.

In terms of the root size of *S. mellifera*, younger, smaller lateral roots rather than bigger, older lateral roots were found at shallower depths. For example, lateral roots of 7 mm diameter were mainly found within depths of less than 15 cm, while those that were more than 15 mm in diameter were mainly located at depths of more than 30 cm. This may mean that, during its life span, *S. mellifera* shrubs first grow their lateral roots at an intermediate depth. However, realising the abundance of resources at a shallower depth, younger, smaller roots begin to grow in order to tap such resources. This is different from *D. cinerea* whose roots were abundantly deployed at various depths. For example, *D. cinerea* lateral roots of 7 mm in diameter were opportunistically deployed anywhere within a depth range of less than 5 cm to approximately 25 cm.

Finally, the absence of a taproot among some *S. mellifera* and *D. cinerea* shrubs, predominantly along the drier and mesic parts of the Kalahari, suggests that the taproot is not an essential feature to the survival of such plants and that lateral roots are more significant for their sustenance. Evidently, such shrubs can still thrive with lateral roots only, contrary to the view that a taproot is the main root component because it can tap water from deeper soil layers.

These findings contradict the premises of Walter’s two-layer root niche-partitioning hypothesis, and, in fact, demonstrate the importance of lateral roots to the survival of trees in resource-limited environments, such as the Kalahari Basin. With its highly variable rainfall and deeper water table made possible by the thicker permeable sediments of the Kalahari, it is improbable that many shrubs would extract water from the water table using their taproot all year round. However, sporadic rainfall events may be sufficient to saturate shallow soil from time to time after a prolonged period, which may serve as an opportunity for plants with lateral roots to harvest such moisture and thrive. According to Hipondoka, Aranibar, Chirara, Lihavha, and Macko (2003), as well as February and Higgins (2010), grasses in the Kalahari develop their roots about or even beyond a depth of 30 cm. Considering the average depth at which most lateral roots of these two shrubs are deployed, such revelations suggest that *D. cinerea* and *S. mellifera* may be sharing the same vertical niche with grasses in terms of extracting soil resources. Although this study did not sample grassroots, the presence of lateral roots within 30 cm depth, more especially at drier sites, seems to confirm the hypothesis that some trees may be in direct competition with grasses for soil resources. The findings from this study are also consistent with Bhattachan et al. (2012) who argue that savanna plants may be employing different strategies to acquire soil resources in different environments.

3.5 Conclusion

The coexistence of trees and grasses in the savannas has largely been interpreted in the context of vertical root niche-partitioning between trees and grasses, as predicted by Walter's two-layer model. Findings of this study demonstrate that, contrary to the vertical root niche differentiation hypothesis, some savanna shrubs, such as *S. mellifera* and *D. cinerea*, may be in partial competition with grasses for resources within the shallow soil layer. This competition arises because these two shrubs deploy the bulk of their lateral roots within the soil sub-surface, a depth within reach of the roots of some grass species. While sustaining a deeper taproot is important for anchoring plants in the soil, and indeed for extracting water from greater depths, such plants seem to be cognisant of the importance of resources at a shallower depth, more especially when the water table is too deep or inaccessible for tapping. Furthermore, some individuals of both *S. mellifera* and

D. cinerea had no taproot, yet these individuals were able to survive, especially towards the drier parts of the western Kalahari where the discontinuous, multi-layer aquifers have limited yield, and where the water table is deeper than 20 m, partly due to increasing aridity. Two factors that may, therefore, affect moisture available to plants from such an environment are the substantial depth at which the water table is located, and the volume of water, which is significantly low. These plant species, then, depend largely on lateral roots to supply resources such as moisture from the soil. On this basis, it can be argued that taproots are not the central feature of the root system architecture of this species. The presence of shallow lateral roots at depths reachable by grasses is critical. Looked at in the context of species competition theories, it is expected that trees and grasses would compete for soil resources at that depth, triggering the competitive exclusion. When grass cover is reduced by grazing for example, trees with such a rooting pattern will gain a competitive advantage and exclude the grasses. Perhaps this is why the phenomenon of shrub encroachment is limited to only a few shrub species, such as *S. mellifera* and *D. cinerea,* which exhibit such rooting patterns.

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4. CHAPTER FOUR: MANUSCRIPT (III)

The root structure of *Terminalia sericea Burch. ex DC*, an encroaching shrub in the Kalahari Basin

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Abstract

Shrub encroachment is one of the common manifestations of land degradation in Namibia, and has significant socio-economic and ecological impacts on rangeland resources. The mechanisms by which shrubs out-compete grasses, resulting in shrub encroachment, are still not well understood. Popular savanna models, such as root niche-partitioning, predict deeper rooting systems among savanna shrubs as a natural regulatory mechanism by which woody plants avoid competition with grasses within shallower soil layers. However, their relevance to several savanna shrubs has been questioned. Probing into the below-ground structure of savanna shrubs, particularly those responsible for encroachment of semi-arid and arid savanna, may reveal insights into the drivers of shrub encroachment. This study investigated how *Terminalia sericea*, one of the common encroaching species in the Namibian savanna, deploys its roots in the soils of the Kalahari Basin. Using direct excavation methods, 39 shrubs were randomly selected and excavated along the Kalahari Basin rainfall gradient. The study revealed contrasting rooting strategies by *T. sericea* under different environmental conditions. For example, *T. sericea* displayed dominantly lateral rooting habits in the drier part of the transect, but in the wetter part the shrubs mostly exhibited a dual root system of both taproots and lateral roots. Statistical significance occurred between the drier, mesic and wetter study sites for below-ground root system variables such as lateral rooting depth ($F(_{7,\,110}) = 3.75$, $p < .001$), terminal depth ($F(_{7,\,110}) = 9.22$, $p < .001$), lateral root diameter ($F(_{7,\,110}) = 3.37$, $p < .001$), and dipping angle ($F(_{7,110}) = 2.61$, $p = .01$). The study demonstrated that *T. sericea* invests the bulk of its roots in the shallower sub-surface soils, more especially in the drier areas of the Kalahari.

These findings are consistent with the hypothesis that certain savanna shrubs opportunistically develop root systems in response to the prevailing environmental stimuli. Some tree species may subsequently exploit this behaviour and manifest into shrub encroachment in distinct settings. This study concluded that the occurrence of shrub encroachment is linked to savanna shrubs whose shallow roots occupy the same niche as grasses.

Keywords: Kalahari, root structure, savanna, shrub encroachment, tree-grass coexistence.

4.1 Introduction

Shrub encroachment, defined as a conversion from open grassland savanna to shrub-dominated thickets, is a major socio-economic and ecological problem in savannas all over the world (Angassa, 2014; Eldridge et al., 2011; Kgosikoma & Mogotsi, 2013; Kulmatiski & Beard, 2013; Van Auken, 2009). In Namibia, one of the driest countries in sub-Saharan Africa, it is estimated that some 26 million ha of productive agricultural land, are severely affected by this phenomenon (De Klerk, 2004). This land degradation has serious consequences for the socio-economic livelihoods of many pastoralists in the country as open savannas covered with palatable grasses is turned into impenetrable thickets of unpalatable shrubs (Jacobs, 2000), rendering such rangelands unsustainable for livestock production. Scientific efforts to understand the mechanisms under which shrub encroachment occurs have led to various contrasting and inconclusive savanna theories and models (Accatino, De Michele, Vezzoli, Donzelli & Scholes, 2010; Gil-Romera, Lamb, Turton, Sevilla-Callejo & Umer, 2010; Jeltsch, Milton, Dean & Van Rooyen, 1996; Jeltsch, Weber & Grimm, 2000; Sankaran, Ratnam & Hanan, 2004; Scholes & Archer, 1997). Thus, no unanimous theoretical framework exists to address the savanna controversy.

Probing into the below-ground ecology of savanna plants, particularly those responsible for shrub encroachment, such as *Terminalia sericea*, may reveal necessary insights into solving the savanna puzzle. Some earlier notable works on this subject are such as those of Walker, Ludwig, Holling and Peterman (1981), Walker and Noy-Meir (1982), as well as Walter and Mueller-Dombois (1971).

These studies argue that the below-ground life of the savanna plants is critical to the functioning of the savanna biomes, and that the occurrence of shrub encroachment, because of vertical root niche-partitioning, is a natural regulating mechanism between shrubs and grasses. Vertical root niche-partitioning allows a stable coexistence between the two contrasting plant forms by deterring them from interspecific competition. These studies further argue that overgrazing, a human-induced activity, increases the competitive advantage of shrubs by reducing grass cover, a radical change that leads to shrub encroachment. Although necessary efforts, such as those of Hipondoka, Aranibar, Chirara, Lihavha and Macko (2003), Hipondoka and Versfeld (2006), Kulmatiski and Beard (2013), and Le Roux, Bariac and Mariotti (1995) followed to interrogate the root niche-partitioning model, scant attention has been devoted to the role of the lateral roots of savanna shrubs, particularly those responsible for shrub encroachment. The attempts of Schenk and Jackson (2002) were exceptional, but their focus was limited to the allometric relationship between the above-ground and below-ground variables of savanna plants.

Lateral roots are defined in this study to mean roots that extend horizontally from the plant’s radicle or, alternatively, from the taproot, often deployed within the shallow sub-surface (Eshel & Beeckman, 2013; Schenk & Jackson, 2002). Such roots come in different sizes and grow at different depths. According to Raven, Evert and Eichhorn (2005), older lateral roots are usually shallower and located toward the base of the plants’ root system, unlike young lateral roots which are often found toward the root tip. Plants that develop shallow lateral roots are highly dependent on soil moisture from shallow soil surface right from the onset of plant growth (Raven et al., 2005).

Understanding the distribution of these roots may, therefore, provide clues to the below-ground interactions between shrubs and grasses that may influence the long-term behaviours of the savanna. This paper assessed how *T. sericea,* one of the common encroaching shrubs in Namibia, develops its root system architecture (RSA) along the rainfall gradient of the Kalahari Basin in Southern Africa. The study is contextually designed to test two opposing hypotheses related to plant root development. The popular root niche-partitioning model, also referred to as Walter's two-layer model, generally argues that savanna shrubs develop deeper root systems to avoid competition with grasses in the shallow soil layer. The opposing view postulates that savanna plants are opportunistic and thus develop their root system architecture (RSA) in response to prevailing environmental stimuli (Bhattachan et al., 2012; Hipondoka et al, 2003; Hipondoka & Versfeld, 2006). One such stimulus is moisture availability.

4.2 Materials and methods

4.2.1 Study area

4.2.1.1 Geology, soils, climate and groundwater aquifers

Fieldwork was carried out within the Kalahari Basin (KB), a semi-arid to sub-humid environment covering approximately 2.5 million km^2 (Thomas & Shaw, 1991). The Kalahari Basin is found in Southern Africa, stretching across parts of seven countries, namely South Africa, Namibia, Botswana, Angola, Zambia, Zimbabwe and the DRC. Its latitudinal extent is estimated to range from 14° S to 28° S, while its longitudinal extent ranges from 21° E to 28° E (Thomas & Shaw, 1991). The main distinctive features of the Kalahari Basin are the homogeneity of soils covering the entire basin and the climatic gradient along which plants grow. The basin was formed from tectonic events associated with the breakup of Gondwanaland some 140 million years ago, followed by successive deposition of sand, resulting in a sand sheet up to 400 m deep (Miller et al, 2016). The landforms of the Kalahari Basin, such as the network of fossil dry valleys, paleolakes and linear dunes dating to the late Quaternary indicate that both fluvial and aeolian processes contributed to the formation of the basin (Burrough, Thomas, & Bailey, 2009; Thomas & Shaw, 1991). Located at an altitude of approximately 1000 m above sea level, the basin shares similar physical and chemical properties, despite its vastness. Approximately 95% of the basin is covered under a sheet of fine, well-drained sand grains, poor in organic matter. The Kalahari Basin sand belongs to the arenosol soil group, a soil group known for its coarse texture, low water-holding capacity, rapid permeability, and low nutrient content. Dougill and Thomas (2004) provide a detailed analysis of the physical and chemical properties of the Kalahari Basin soils.

The climate of the Kalahari Basin is described by Frssaf and Crimp (1998) as well as Thomas and Shaw (1991) who indicate that the basin's climate can be classified as arid along the south-eastern edge, to semi-arid along the central part of the basin. Sub-humid and humid climatic conditions are found in the northern parts of the basin covering parts of northern Zambia and the so uthern 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 Intertropical 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. Rainfall variation is the most conspicuous indicator of the Kalahari Basin's climate gradient. For example, the northern edge of the basin, south of the DRC, receives mean annual precipitation of approximately 1500 mm per annum, whereas the southernmost edge of the basin along the Orange River receives less than 200 mm per annum. The eastern edge of the basin located in Zimbabwe receives mean precipitation of 700 mm per annum, while the western edge of the basin in Namibia, located just before Kaokoveld, receives precipitation of approximately 250 mm per annum. This study is part of the Kalahari Transect (KT), and thus contributes to the international Geosphere-Biosphere Programme (IGBP), which explores the link between climate and vegetation. The present work is restricted to northern Namibia (Figure 1) along the west-east rainfall gradient. According to Fick and Hijmans (2017) and Mendelsohn et al, (2002), the climatic indicators of the study sites show that Omutambomawe and Uutsathima are the driest study sites, receiving a mean annual precipitation of about 300 mm per annum and with an average temperature of some 23 °C during the summer, a temperature that decreases to approximately 19 °C in winter. The rainfall coefficient of variation (CV) for these two sites is estimated to be within a range of 40% to 50%. Evapotranspiration rates for the areas around Uutsathima and Omutambomawe are in a range of 2100 mm to 2240 mm per annum. For Etosha, the nearest weather station at Okashana indicates that the temperature ranges from around 34 °C during the hot summer to approximately 19 °C in winter months. Mean annual precipitation is just below 450 mm per annum, whereas the evapotranspiration rate is estimated to be in the range of 1960 mm to 2100 mm per annum. Collectively, these three sites are considered as ‘drier’, based on the indicated climatic figures. Onyuulaye and Okongo receive a mean annual precipitation of nearly 470 mm and 550 mm per annum, respectively. Onyuulaye has an estimated mean temperature of about 26 °C during the summer months, which decreases to some 18 °C during winter. Similarly, Okongo has an average temperature of 27 °C during summer, which decreases to approximately 18 °C during winter. While Onyuulaye falls within evapotranspiration belt of 1960 mm to 2100 mm per annum, Okongo is found within a relatively drier range with potential evapotranspiration in a range of 1820 mm to 1960 mm per annum. Nkurenkure receives a mean annual precipitation of 55 mm per annum and an average maximum temperature of 35 °C, and the lowest temperature can reach an average of 18 °C during winter. Nkurenkure shares the same evapotranspiration belt. Divundu and Katima are the moistest study sites, each receiving marginally over 600 mm per annum. Divundu shares the same potential evapotranspiration with Nkurenkure of 1820 mm to 1960 mm per annum. However, Katima Mulilo is located in an evapotranspiration belt of less than 1680 mm per annum, making it the wettest study site along this KT. Most of the sites discussed above are located within a climatic zone where the rainfall CV is in a range of 30% to 40%.

Such harsh climatic conditions indicate that the Kalahari Basin is a dry environment in which plants grow. Groundwater aquifers 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/dolocrete, 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 & Struckmeier, 2001).

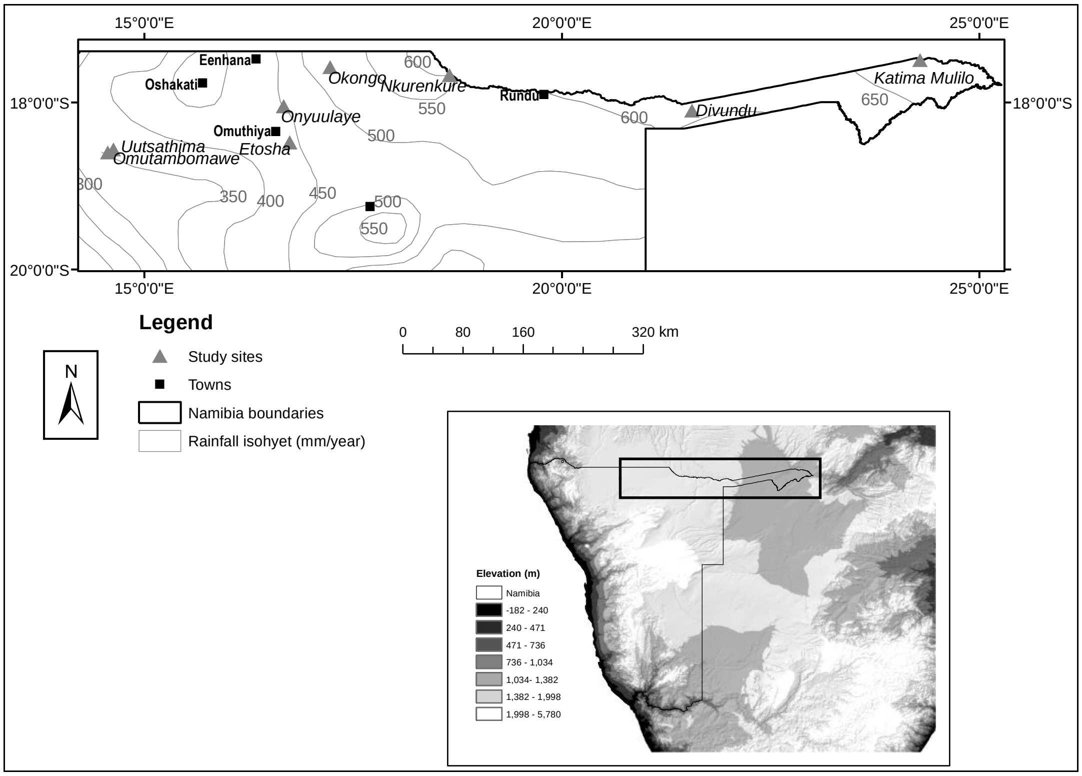

Figure 22: Map showing the study sites along the east-west Kalahari rainfall gradient.

4.2.1.2 Vegetation and land use

Vegetation in the Kalahari can be broadly classified as savanna, the diversity, structure and biomass of which change across the rainfall gradient. Its arid western edge, where Omutambomawe and Uutsathima are located, is dominated by shrubs such as *T. sericea.*, *S. mellifera, Senegalia nebrownii, V. 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 *Anthephora schinzii, Heteropogon contortus, Tragus racemosus, Cynodon dactylon, Dactyloctenium aegyptium, Sporobolus ioclados,* and *Stipagrostis uniplumis*. Other dominant species known to occur in the area are *Eragrostic rotifer, Aristida adscensionis*, *Schmidtia kalahariensis,* and *Eragrostis dinteri* (Klaassen & 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 Uutsathima, 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, Philenottera nelsii, C. angolensis, C. gratissimus, Ochna 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 virgata, Cynodon dactylon, Dactyloctenium giganteum, Panicum kalaharense, and Schmidtia 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, as described in Walter and Mueller-Dombois (1971), and further summarised in Ward, Wiegand and Getzin (2013).

4.2.2 Data collection

4.2.2.1 Sampling and data analysis

A total of 39 *T. sericea* shrubs, translating into at least five shrubs per site, were randomly selected, and their roots were excavated using a spade, a method described by Böhm (1979). 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, defined as the average vertical depth at which lateral roots started developing; lateral root diameter, defined as the thickness of lateral roots at base; and lateral root length, measured as the horizontal extent of the lateral roots. Other morphological attributes recorded include the terminal depth of lateral roots, measured as the vertical depth at the tip of lateral roots, and the dipping angle, which was computed as an acute angle that lateral roots make in relation to the soil's horizontal plane as the roots elongate in the soil. Dipping angle was subsequently calculated using trigonometric methods, whereby slope of a lateral root is vd‘/hd‘, where vd‘ is the vertical distance of lateral root growth from base to end, and hd‘ is horizontal distance of the lateral root from starting point of growth to the end. Although the excavation method has been described as laborious, destructive and time consuming, it was employed in this study because of its potential to yield a great deal of quantitative data pertaining to plant RSA.

4.2.2.2 Data analysis

Data analysis was done in R 3.3.1 (R Development Core Team, 2017), using a one-way ANOVA. Location and sub-climatic zone were used as the predictors, and the morphometric attributes measured were used as response variables. Although there are two main factors in this model, location and sub-climatic zone, these two factors are not necessarily independent of each other, thus cannot be analysed in a factorial design. For example, Omutambomawe, Uutsathima and Etosha sites all belong to the drier sub-climatic zone, while Onyuulaye, Okongo and Nkurenkure sites belong to the mesic sub-climatic zone. Prior to data analysis, and as a prerequisite for parametric tests, a normality test was done using the Shapiro-Wilk test. In addition, chi-square was used to test the distribution of root type between the three major sub-climatic zones. Results were considered significant at $p < 0.05$ alpha level. All post hoc pairwise comparisons were done using Tukey’s honest significant difference test.

4.3 Results

4.3.1 Shrub height, canopy diameter and stem diameter

The above-ground morphometric properties of the excavated shrubs varied between the study sites, as well as between the three sub-climatic zones. For example, shrub height was significantly different between the study sites ($F(_{7,\ 110}) = 18.56$, $p <.001$) as well as between the drier, mesic and wetter sub-climatic zones ($F(_{2,\ 115}) = 5.16$, $p < .001$). Similarly, canopy diameter was significantly different between the study sites ($F(_{7,\ 110}) = 85.44$, $p < .001$) and between drier, mesic and wetter sub-climatic zones ($F(_{2,115}) = 16.87$, $p < .001$). In addition, stem diameter was significantly different between the study sites ($F(_{7,\ 110}) = 19.33$, $p < .001$) as well as between the sub-climatic zones ($F(_{2,\ 115}) = 5.96$, $p <.001$). Pairwise post hoc comparisons using Tukey's honest significant difference test revealed that virtually all the above-ground morphometric indicators – height, canopy diameter, and stem diameter – followed the same pattern in terms of which sites or sub-climatic zones were different from the others. The significant difference ($p < .001$) was mostly found between study sites such as Okongo and Divundu, Omutambomawe and Divundu, Nkurenkure and Etosha as well as Okongo and Etosha. A significant difference ($p < .001$) in above-ground morphometric indicators was also found between study sites such as Omutambomawe and Uutsathima, Etosha, Okongo, Nkurenkure or Katima Mulilo, as well as Onyuulaye and Etosha, Okongo or Katima Mulilo. Figure 2 illustrates how these variables change between the study sites and the three sub-climatic zones. Standing height (Figure 23(a)), canopy diameter (Figure 23(b)) and base stem diameter (Figure 23(c)) were larger at Omutambomawe, followed by Okongo and Onyuulaye sites than they were at Uutsathima, Etosha, Nkurenkure, Divundu and Katima Mulilo. Post hoc results (Figure 23) indicate that virtually every study site had distinctive shrubs in terms of their above-ground indicators. This distinctiveness was also evident at sub-climatic zones, where each of the three zones, drier, mesic and wetter, was significantly different (p <.001) from the others.

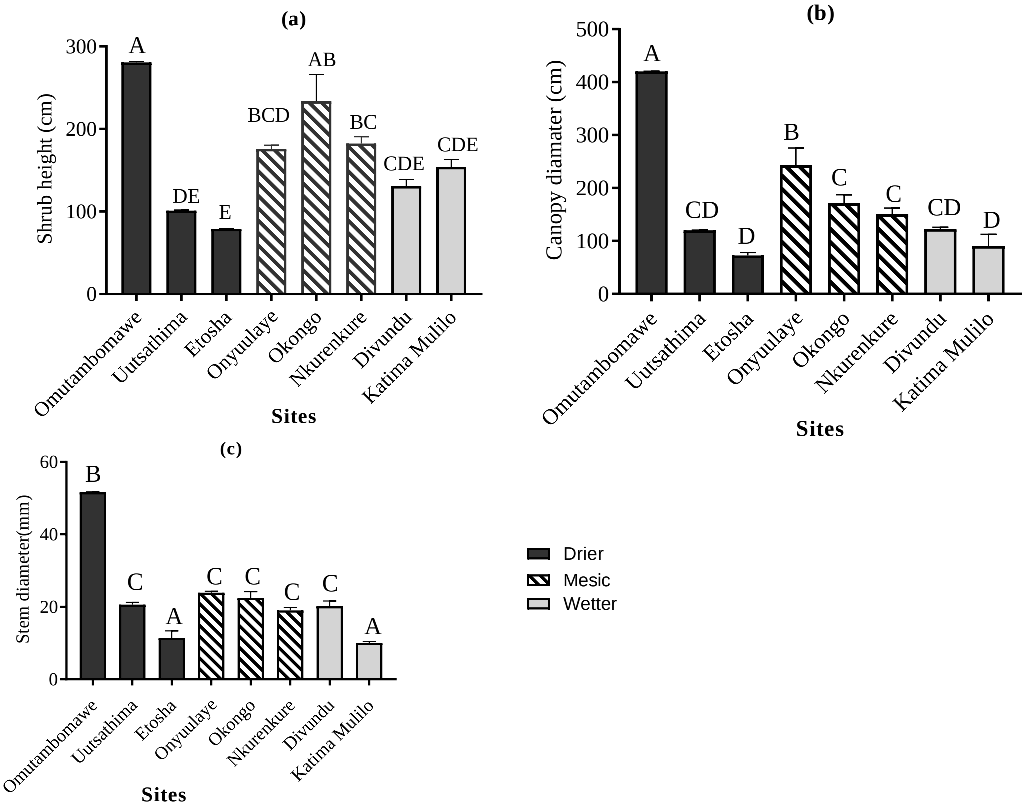

Figure 23: Mean ± Standard Error of *T. sericea* above-ground variables at various studies sites: (a) standing height, (b) canopy diameter, and (c) stem diameter at the base. Capital letters over the bars indicate significant differences between the sites. Sites not labelled with the same letter are significantly different; refer to text for more details.

4.3.2 Below-ground structure of *T. sericea* shrub across the Kalahari rainfall gradient

Table 5, details the proportion of *T. sericea* shrubs with taproot and lateral roots (dual) against those with no taproot and lateral roots only, per study site. Of the 39 *T. sericea* shrubs excavated, 67% (n= 26) had a root system consisting of both taproot and lateral roots, while the remainder 33% (n = 13) had a root system consisting of lateral roots only. Where a taproot was present, its component penetrated deeper into the soil beyond the excavation effort of 1 m depth. The majority (9) of *T. sericea* shrubs with no taproot were excavated mainly toward the drier parts of the KT at sites such as Omutambomawe and Uutsathima than on the wetter side of the KT, where only a marginal number (four) of shrubs exhibited an exclusive lateral root system. For example, only one of the six shrubs excavated at Omutambomawe exhibited a root system with a taproot, translating to a ratio of 5:1. For Uutsathima, of the four shrubs excavated, all but one exhibited no taproot, resulting in a ratio of 3:1. However, that proportion continued to decline with increasing rainfall along the transect to such a point that plants with a taproot were more dominant than those without a taproot. For instance, at Nkurenkure, only two of the six shrubs excavated at each of the two study sites had no taproot, a ratio of 1:2. Chi-square test results revealed that the distribution of the observed shrubs with a taproot against those without a taproot was significantly ($p < .001$) dependent on the sub-climatic zone. Overall, however, plants with a taproot system outnumbered by half those having lateral roots only. Figure 24 provides an example of how *T. sericea*'s lateral roots are deployed within a shallow soil sub-surface.

Table 5. The proportion of *T. sericea* shrubs with taproot and lateral roots (dual) against those with no taproot (lateral roots only) per study site.

Sub-climatic zone	Sites	No taproot	Taproot and laterals (dual)	Total	No taproot: Taproot ratio
Drier	Omutambomawe	5	1	6	5:1
	Uutsathima	3	1	4	3:1
	Etosha	0	3	3	0:3
Mesic	Onyuulaye	1	1	2	1:1
	Okongo	0	5	5	0:5
	Nkurenkure	2	4	6	1:2
Wetter	Divundu	2	4	6	1.2
	Katima Mulilo	0	7	7	0:7
Total		13	26	39	1:2

Figure 24: Exposed *T. sericea* shrub's lateral roots growing within shallow soil profile at Omutambomawe.

Figure 25 illustrates the variation in lateral rooting depth and terminal depth across the study sites in the three sub-climatic zones. ANOVA results revealed a significant difference in lateral rooting depth between the study sites ($F(_{7,\,110}) = 3.75$, $p <.001$) as well as between the three sub-climatic zones ($F(_{2,\,115})= 6.97$, $p <.001$). Further pairwise comparison using Tukey's honest significant difference test showed that, for the study sites, the significant difference ($p < 0.001$) was between sites such as Omutambomawe and Katima Mulilo, Onyuulaye and Katima Mulilo, as well as between Uutsathima and Katima Mulilo. However, for sub-climatic zones, the significant difference ($p < 0.001$) was 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, while the deepest individual lateral root developed at a depth of 39 cm at Katima Mulilo. Similarly, the shallowest mean (7.4 ± 1.0 cm) lateral root depths were recorded at Uutsathima and Onyuulaye (8.7 ± 2.0 cm), followed by Omutambomawe (9.6 ± 1.0 cm), then the depth increased progressively at Okongo and Divundu, reaching a maximum mean depth of 17.8 ± 3.0 cm at Katima Mulilo (Figure 25). Terminal depth exhibited a pattern similar to lateral rooting depth. Results showed a significant difference between the study sites ($F(_{7,\,110}) = 9.22$, $p < .001$), where the Katima Mulilo site differed significantly from all the other study sites ($p <.001$). There was also a significant difference ($F(_{2,\,115}) = 10.79$, $p < .001$) between the drier, mesic and wetter sub-climatic zones for terminal depth, with a significant difference between the wetter and drier zones, as well as the wetter and mesic zones. No significant difference ($p = 0.21$) was found between mesic and drier zones. The shallowest lateral root terminal depth was found at 6 cm at Okongo, while the deepest lateral root terminal depth was found at 70 cm at Divundu, followed by Katima Mulilo with the deepest lateral root terminal depth of 62 cm. On average, lateral root terminal depth was 19.84 ± 1.94 cm at Okongo, 21.2 ± 2.0 cm at Nkurenkure, and 21.9 ± 2.5 cm at Uutsathima. Katima Mulilo had the deepest mean lateral root terminal depth of 45.0 ± 5.7 cm, followed by Omutambomawe with 31.1 ± 2.1 cm and Onyuulaye with 30.5 ± 2.2 cm. Etosha and Divundu had mean lateral root terminal depths of 23.2 ± 1.72 cm and 28.9 ± 3.3 cm, respectively.

Unlike lateral rooting depth, which seems to increase linearly along the rainfall gradient, there was no clear distinct pattern in terms of the terminal depth. For example, while shrubs at sites such as Divundu and Katima exhibited deeper terminal depth consistent with the lateral rooting depth, there were also cases where shrubs at certain sites such as Onyuulaye and Omutambomawe showed, at the same time, shallower lateral root depth and deeper terminal depth than their counterparts at Okongo and Nkurenkure. Given that the main distinctive factor for these study sites is rainfall range, the rainfall gradient appears to be the main determinant of variation in lateral rooting depth. Taking the ratio between the lateral rooting depth and terminal depth into consideration, both drier sites exhibited the highest ratio of 3:1, decreasing to an average of 2:1 for both mesic and wetter sites. Okongo is exceptional in that the lateral rooting depth and terminal depth of shrubs was generally even, with a ratio of 1:1. Lateral roots across the entire climatic gradient were, on average, deployed within a 10 cm to 45 cm soil profile. This extended soil profile in which laterals are deployed is more pronounced in the drier and wetter sites, while a narrower zone (within 5 cm depth variation) dominates the mesic zone.

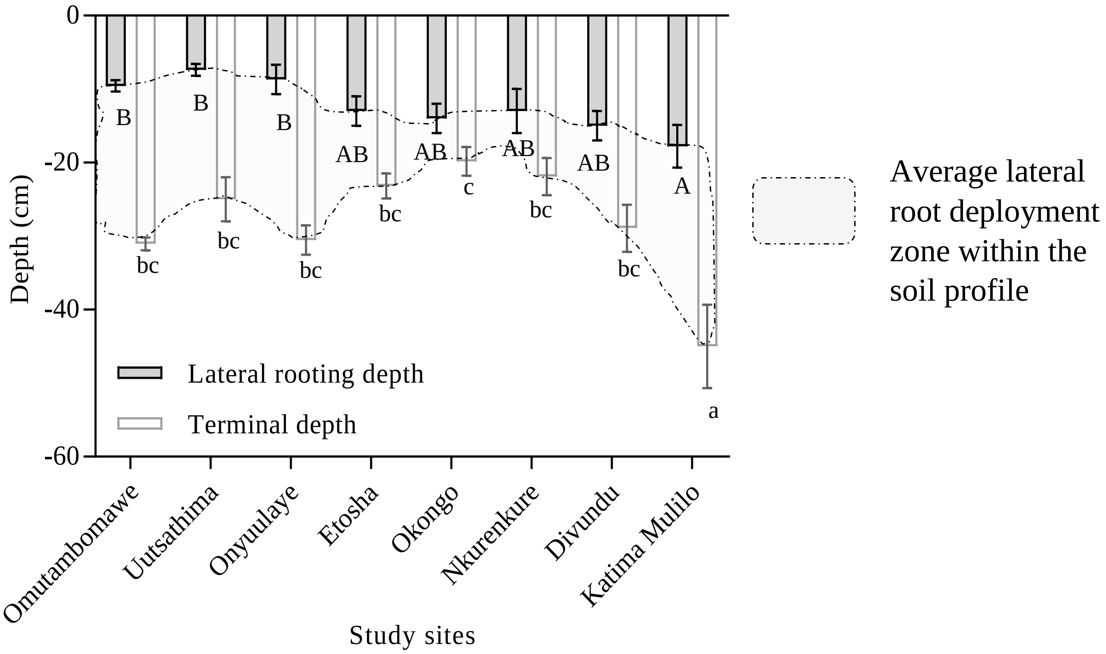

Figure 25: Lateral rooting depth at the base and an elongated terminal depth of *T. sericea* shrubs. Different letters over the bars indicate significant differences between the sites. Sites not connected by the same letters are significantly different.

The morphometric structure of the *T. sericea* shrub's lateral roots can also be described in terms of its lateral root diameter, lateral root length and the dipping angle of elongation. ANOVA results showed that the excavated lateral roots varied significantly ($F(_{7,\ 110}) = 3.37, p <.001$) in diameter across the study sites. The diameter was also significantly ($F_{(2,\ 115)} = 5.42, p < .001$) different between the drier, mesic and wetter sub-climatic zones. Tukey's honest significant difference test showed that, for study sites, the significant difference ($p<.\ 001$) was largely between Divundu and Omutambomawe as well as between Divundu and Onyuulaye; whereas, for sub-climatic zones, the significant difference was found between the wetter and drier zones. The variation in lateral root diameter per study site is illustrated in Figure 26, which shows that the largest mean lateral root diameter of 17.0 ± 2.0 mm was recorded at Onyuulaye, a mesic sub-climatic zone, followed by Uutsathima, a drier sub-climatic zone with 16.0 ± 5.0 mm, then it decreased marginally to 15.0 ± 2.0 mm at Omutambomawe. Divundu, a wetter sub-climatic zone had the smallest mean lateral root diameter of 7.0 ± 1.0 mm followed by Nkurenkure where the mean diameter was 10.39 ± 2.01 mm. At Etosha, the mean lateral root diameter was 14.0 ± 2.0 mm, while shrubs at Okongo and Katima Mulilo had a lateral root diameter of 11.0 ± 1.0 mm and 12.0 ± 2.0 mm, respectively. Overall, plants at drier sites had larger lateral roots, which decreased linearly along mesic and wetter parts of the KT. A noteworthy exception to this pattern is Onyuulaye where lateral root diameter was larger than at Omutambomawe and Uutsathima, as is root diameter at Katima Mulilo in comparison to Okongo.

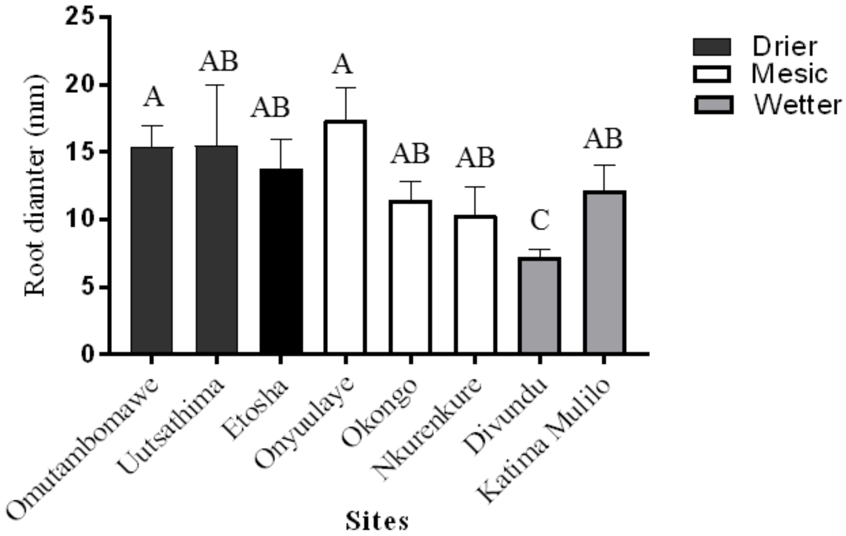

Figure 26: Mean ± standard error of diameter for lateral roots measured at the base. Different letters over the bars indicate significant differences between the sites. Sites not connected by the same letters are significantly different.

The thickness of lateral roots, using diameter as an indicator, was significantly influenced by the interaction (*p* <. 001) of the sub-climatic zone and terminal depth. Figure 27 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) sites. For all sites, such as that of drier, mesic and wetter, nearly all lateral roots, irrespective of diameter, developed within a depth range 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 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.

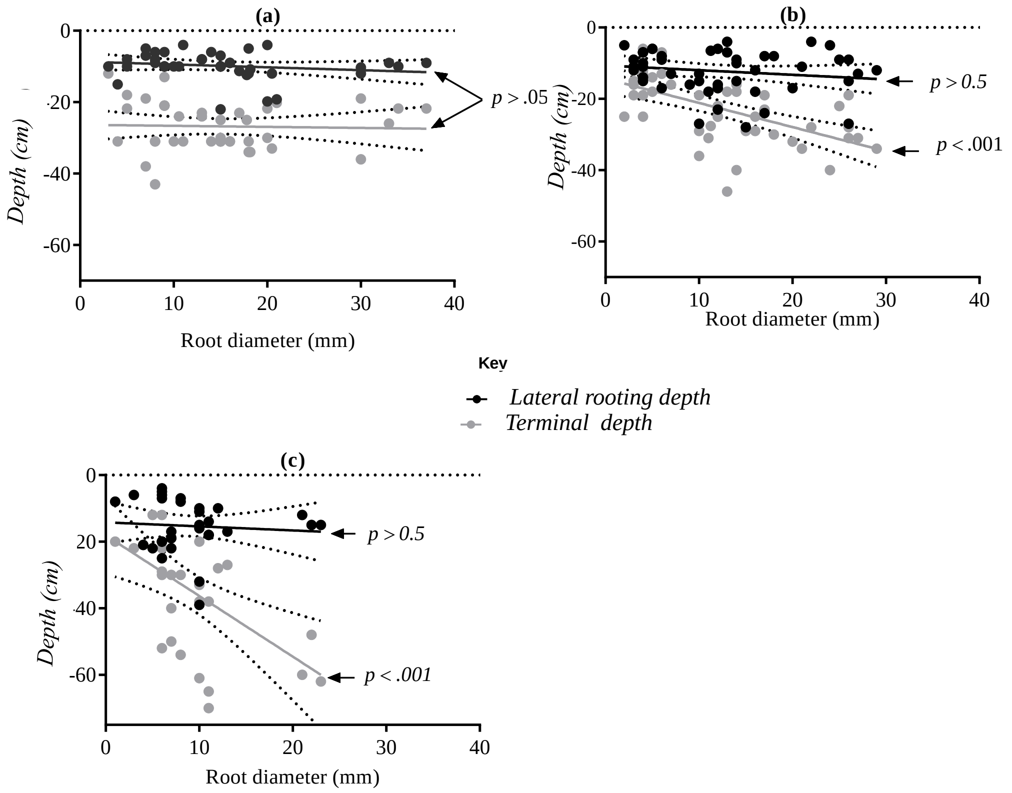

Figure 27: Scatter plots with best-fit line plots illustrating how *T. sericea* shrub's lateral rooting depth and terminal depth changes with lateral root diameter. Plot (a)

presents data from drier savannas, while plot (b) and (c) provide data from mesic and wetter savannas, respectively.

In addition to diameter and depth at which *T. sericea* develops lateral roots, other noteworthy morphological indicators are the horizontal extent of lateral roots and their dipping angles as they elongate across the soil profile. Figure 28 presents an illustration of lateral root lengths which vary significantly ($F(_{7,\,110})$= 5.48, $p < .001$), at various study sites. A significant difference was found between Omutambomawe and Divundu, Etosha and Omutambomawe or Okongo. On average, shrubs at Omutambomawe had the longest mean lateral roots, followed by plants at Onyuulaye, then Katima Mulilo. Plants at Etosha had the shortest lateral roots, followed by those at Divundu. However, these results were not significantly different ($F(_{2,\,115})$ = 3.00, p = .053) between the three sub-climatic zones.

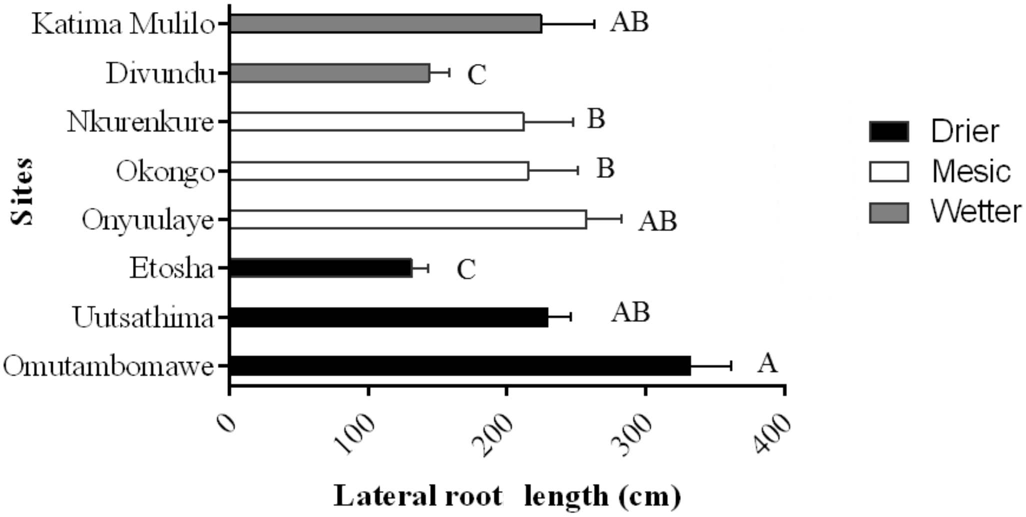

Figure 28: Lateral root length of *T. sericea* shrub at various study sites. Different letters over the bars indicate significant differences between the sites. Sites not connected by the same letters are significantly different.

As lateral roots elongate across the soil profile, they are deployed at various angles. There are those that follow a steeper gradient, whereas others retain a gentle gradient with respect to the soil surface horizontal plane. Table 6 provides information on lateral roots' dipping angle, a measure of lateral roots steepness, expressed as degree (º) relative to the soil horizontal plane, while Figure 29 shows the relationship between lateral root length and dipping angle. Dipping angle was significantly different between the study sites ($F(_{7,110})$ = 2.61, $p < .01$), as well as between the climatic zones ($F(_{2,115})$ = 7.86, $p <. 001$). Results on post hoc pairwise comparison and the average dipping angle per study site are presented in Table *6*. The dipping angle of lateral roots was also significantly related to lateral root length, as illustrated in Figure 29. Lateral roots with a steeper dipping angle were shorter in length than those with a gentle slope, which were often longer.

Table 6. Descriptive statistics (mean ± standard error) and post hoc pairwise comparison results on variation in dipping angle of lateral root development of *T. sericea.*

Study sites	Sub-climatic zone	Dipping angle/ gradient (°)	Tukey's post hoc pairwise comparison
Uutsathima	Drier	5.6 ± 0.7	C
Omutambomawe	Drier	7.6 ± 1.9	C
Etosha	Drier	10.3 ± 0.9	ABC
Onyuulaye	Mesic	7.4 ± 1.0	BC
Okongo	Mesic	8.2 ± 2.2	C
Nkurenkure	Mesic	7.6 ± 1.0	C
Divundu	Wetter	13.3 ± 1.6	AB
Katima Mulilo	Wetter	15.7 ± 3.7	A

Note. Under Tukey's post hoc pairwise comparison, sites not connected by the same letters are significantly different.

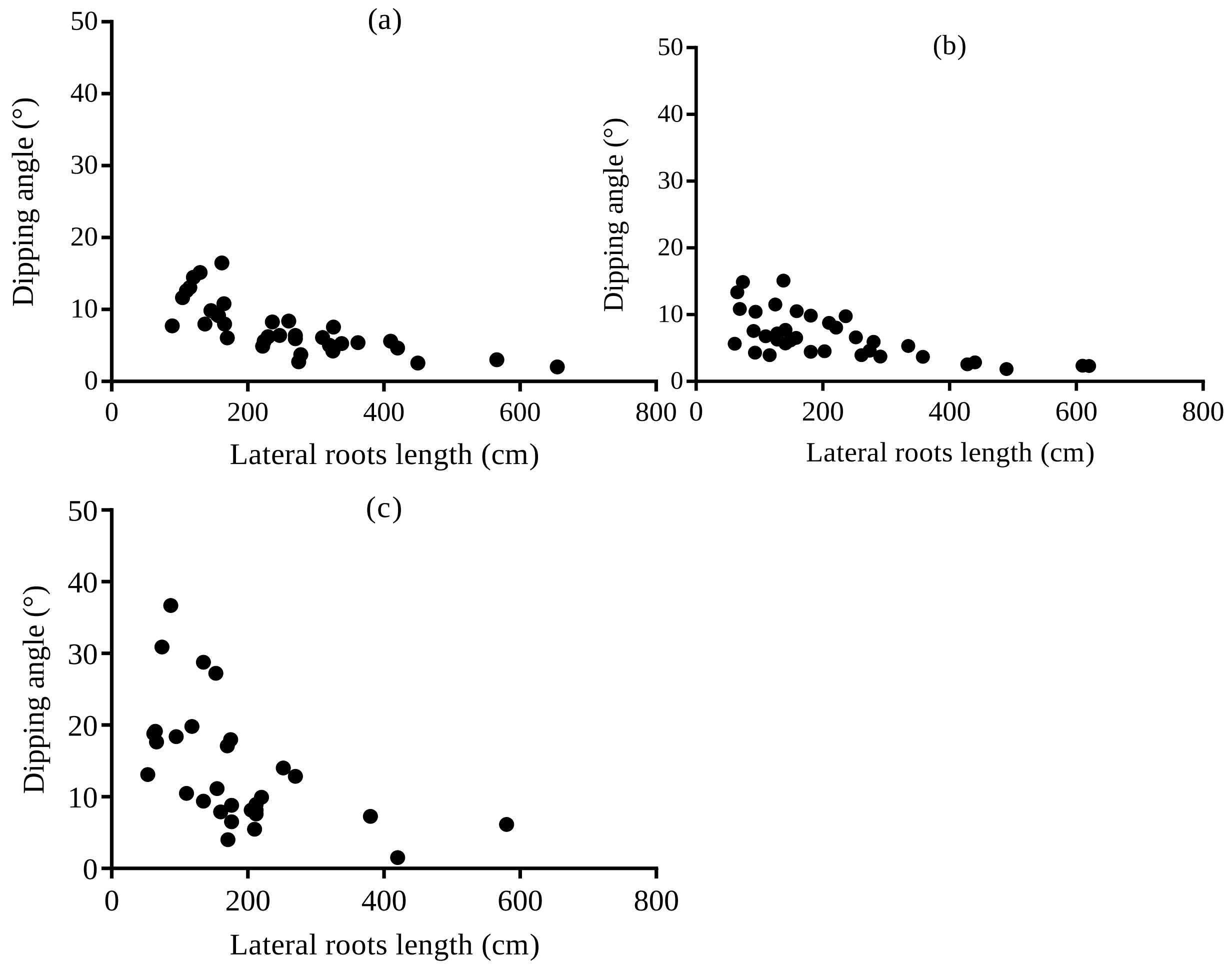

Figure 29: Relationship between root dipping angle and lateral root length of *T. sericea* shrubs in the Kalahari, from the drier (a), mesic (b) and wetter (c) sub-climatic regions.

The RSA of *T. sericea* can be grouped into several architecture patterns, based on the topological arrangement of their root systems (Figure 30). The major distinguishing factor is the presence or absence of the taproot component, as well as the depth at which lateral roots are deployed. For example, the first architecture pattern (a) is distinguishable by its network of lateral roots which follow a near-horizontal trajectory. The second architecture pattern (b) also exhibits shallow deployed lateral roots, accompanied by a vertical taproot. These two architecture patterns are found predominantly along the drier parts of the KT. Although the architecture pattern illustrated in (c) is similar to that of (a), the major distinguishing factor is the terminal depth. Lateral roots tend to deepen as they elongate away from the radicle, a configuration also shared with root architecture (d), which possesses a vertical taproot in addition to lateral roots.

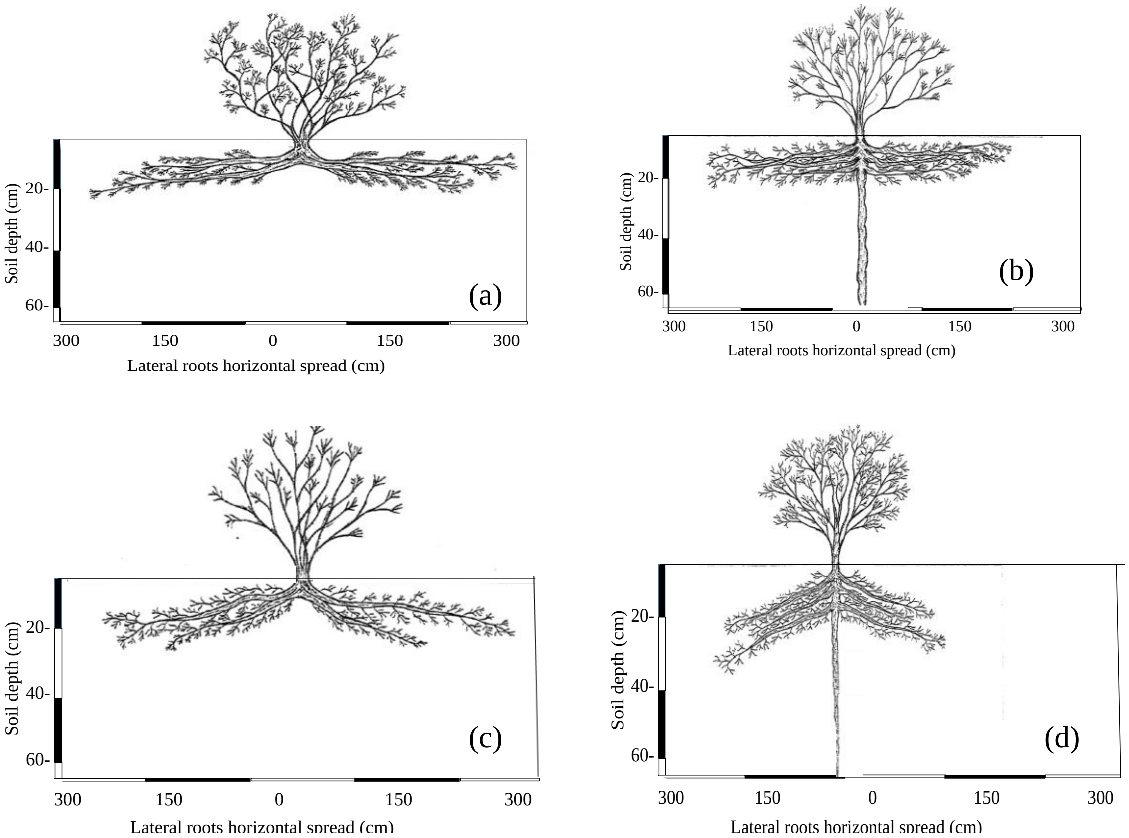

Figure 30: Various root system architecture exhibited by *T. sericea* shrubs. Note: Above-ground part not to scale.

4.3.3 Relation between above-ground and below-ground morphometric structures of *T. sericea* shrub

While this study has demonstrated the dynamic behaviour of *T. sericea*'s root structure along the Kalahari climate gradient, it is also important to acknowledge the interactions that were found between different root components and their above-ground plant components, which may serve as confounding factors in shaping the root architecture of *T. sericea* shrubs. Table 7 illustrates the correlation between various components of the *T. sericea* root system as well as their relation to the plant structure above-ground. Lateral root length and lateral root diameter were significantly ($p < .001$) related to shrub height and canopy diameter, and lateral root diameter was significantly ($p <. 001$) related to lateral root length. Furthermore, terminal depth was significantly ($p < .001$) correlated to stem diameter and lateral root depth. Lastly, there was an inverse significant ($p < .001$) correlation between lateral root length and dipping angle.

Table 7. Correlation coefficient between various components of *T. sericea* above-ground and below-ground morphometric properties.

Correlation coefficient	H	CD	SD	LRD	LRL	RD	TD	DA
H	1							
CD	0.68***	1						
SD	0.16	0.32	1					
LRD	0.06	-0.14	0.00	1				
LRL	0.40**	0.45***	0.14	0.07	1			
RD	0.21*	0.33***	0.07	0.02	0.41***	1.00		
TD	0.05	0.13	0.48***	0.13	0.19	0.24**	1.00	
DA	-0.15	-0.18	0.14	0.14	-0.55***	-0.10	0.39***	1.00

Note. *H=height, CD=Canopy diameter, SD=Stem diameter, LRD=lateral rooting depth, LRT=Lateral root length, RD=Root diameter, TD= Terminal depth, & DA= Dipping angle.*
**** $p < .001$, **$p < .01$, *$p < .05$.*

4.4 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. The overall aim was to study the root system of this encroaching species in order to understand its mechanism for foraging below-ground resources, such as soil moisture and nutrients, in the Kalahari savanna where interspecific competition between trees and grasses is claimed to be the major factor governing the coexistence between trees and grasses. This study was done effectively to test two contrasting hypotheses on the rooting behaviour of savanna plants. The first hypothesis, popularly known as ‘Walter's two-layer hypothesis’, argues that trees develop deeper roots in the subsoil to avoid competition with grasses in the shallow soil layer. The hypothesis thus predicts that *T. sericea*, a dominant woody species in the Kalahari savanna, would invest the bulk of its root system at a substantial depth as an adaptation to avoid competition with grasses. The second hypothesis suggests that savanna trees opportunistically develop their root systems in response to local environmental stimulus, and therefore the development of such roots is not species specific, but rather, shaped by environmental factors such that different environmental conditions yield contrasting root systems of the same plant species. This hypothesis predicts that *T. sericea*, as a woody species, will exhibit distinctive patterns of root growth under different environmental conditions. These two hypotheses are therefore central to the interpretation of the findings of this study.

Findings of this study did not support the first hypothesis. On the contrary, the study revealed that the rooting patterns of *T. sericea* are consistent with the second hypothesis. For example, this study found that *T. sericea* shrubs along drier areas such as Omutambomawe and Uutsathima 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 was independent of above-ground variables such as stem diameter, canopy cover and standing height, but significantly changed along the rainfall gradient, suggests the importance of below-ground resources in influencing the development of plant roots, more especially in arid and semi-arid environments where such resources are scarce. 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. This suggests that even younger lateral roots tend to develop within the shallow soil layer. 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. 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.

This study also demonstrated that, in the drier part of the Kalahari, *T. sericea* shrubs dip their lateral roots at a lower angle in relation to the growth depth at base and the soil surface; that is, such shrubs keep their lateral roots at a constant shallow depth as they elongate away from the primary root. An exception are shrubs at Katima Mulilo, a wetter sub-climatic zone, where the dipping angle nearly doubled to an average angle of 15°.

These findings are consistent with those of Hipondoka et al. (2003) and Hipondoka and Versfeld (2006) that 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 development process of root systems is characterised by great plasticity (Grossman & Rice, 2012, Mou, Jones, Tan, Bao & Chen, 2013; and Zanetti, Vennetier, Mériaux & Provansal, 2015), and that the rooting pattern is an evolutionary product of spatio-temporal variation in environmental resource supply, genetic drivers, and associated environmental constraints to growth. The presence of lateral roots at shallower depth may contribute to competitive exclusion (Armstrong & McGehee, 1980; Gause, 1934; Hardin, 1960) between woody species such as *T. sericea* and savanna grasses. Eco-hydrological studies in the Kalahari (Hipondoka et al, 2003) and elsewhere in similar environments (February & Higgins, 2010; Kambatuku, Cramer & Ward, 2013) suggest that grasses deploy their roots at about the same vertical depth those of *T. sericea* lateral roots.

4.5 Conclusion

Understanding the below-ground life of savanna plants may reveal new insights to unlock the savanna paradox. 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. Grasses deploying their roots within the same shallow soil layer may increase the probability of competition 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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5. CHAPTER FIVE: MANUSCRIPT (III)

Root system architecture of savanna shrubs neighbouring encroaching shrubs along the Kalahari Transect

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Abstract

Root system architecture (RSA) is an important aspect of the life of terrestrial plants. In the savanna biomes, where both trees and grasses coexist, RSA of these two contrasting life forms is considered to be the major determinant of this unique coexistence. In particular, trees are thought to develop deeper root systems to avoid competition for limited resources with grasses, more especially in drier environments such as the Kalahari. This study hypothesises that having a deeper root system is not necessarily the central feature of savanna shrub's RSA, because such shrubs develop their root system in accordance with the prevailing environmental stimuli, which vary across space. A total of 73 shrubs comprising 16 species from 10 families were selected from three major sub-climatic zones using a nearest-neighbour approach, and had their root systems excavated for morphometric measurement. Results indicate that, contrary to the belief that such shrubs develop deeper root systems, three major RSA groups are dominant: i) a fibrous/lateral root system, ii) a dual root system, and iii) a tap root system. Of these, the fibrous root system is the most dominant with 49%, followed by dual root system which comprises 24%. A tap root system was the least dominant by 24%. These RSA groups are not necessarily unique to any species, family, or sub-climatic zone. The depth at which these savanna shrubs deployed their root systems depended largely on the architecture type used. These results suggest that the popular belief that the root zone of savanna shrubs is a homogenous layer of deeper root systems is a poor representation of the below-ground morphology of the savanna plants. While acknowledging that there are indeed some savanna shrubs, such as *Commiphora africana*, *Commiphora angolensis* and *Vachellia erioloba*, that develop deeper taproots, consistent with the premises of the root niche-partitioning hypothesis, there also exist shrubs such as

Asparagus nelsii, Baphia massaiensis, Catophractes alexandri, Diplorhynchus condylocarpon, *Elephantorrhiza suffruticosa*, and *Grewia flavescens* which grow shallow fibrous roots exclusively. This calls for existing savanna models to incorporate the aspect of root architecture diversity and plasticity to better understand the below-ground structure of the savanna shrubs.

Keywords: excavation, lateral root, nearest neighbour, savanna

5.1 Introduction

5.1.1 Background

Root system architecture (RSA), a spatial configuration of plants' roots in the soils (Bodner et al., 2013; Hodge, Berta, Doussan, Merchan & Crespi, 2009) is an important part of the life of terrestrial plants. RSA includes major aspects of plant root systems, such as root morphology, topology, and the spatial distribution of roots in the soils (Hodge et al., 2009). These features give each plant's RSA its shape and structure. Shape is the three-dimensional arrangement of the roots in the soils, which is mostly described using root morphological indicators such as root length, depth, density, and diameter. In contrast, root structure refers to the diversity of root components that make up the root systems and their topological relationships (Ritz & Young, 2011).

Studies of RSA (e.g., Eshel & Beeckman, 2013; Kroon & Visser, 2003; Schmidt, 2014) suggest that it is a complex and dynamic phenomenon, which varies within and between species, and across environmental gradients. According to Ritz and Young (2011), plants are dynamic organisms that grow in heterogeneous environments where they interact symbiotically or competitively with other organisms across environmental gradients, and their RSAs systematically respond to such interactions. Variations in plants' RSA are largely attributed to a suite of small-effect loci, which interact with the environment (De Dorlodot et al., 2007). In support, Hodge (2009) argues that in-situ morphology of plants' root systems follows complex patterns, a reflection of the interplay between root developmental processes and environmental constraints.

A well-developed RSA of a plant is important because of its role in acquiring moisture and nutrients (Lynch, 1995; Danjon, Caplan, Fortin & Meredieu, 2013). These two functions make the RSAs of plants a central feature in the functioning of terrestrial ecosystems (Danjon et al., 2013). The efficient acquisition of water and nutrients by plants depends largely on their RSA (Gregory, 2008).

Studying the RSA of plants, particularly in arid and semi-arid ecosystems, such as the savanna, where plant growth is limited by water and nutrient availability, is therefore fundamental in understanding the mechanisms by which plants cope in such extreme environmental conditions (Bodner et al., 2013). For example, it has been hypothesised that, in the Kalahari savanna, where trees and grasses coexist, vertical differentiation in the RSA between these two contrasting plants (‘woody plants’ and ‘herbaceous plants’) is the main determinant of their unique coexistence (Scholes & Walker, 1993; Walker, Ludwig, Holling & Peterman, 1981; Walker & Noy-Meir, 1982; Walter & Mueller-Dombois, 1971; Ward, Wiegand & Getzin, 2013).

This premise, known as ‘Walter's two-layer model’ or the ‘vertical root niche-partitioning model’, has been hotly debated in savanna literature (Germino & Reinhardt, 2014; Hipondoka, Aranibar, Chirara, Lihavha & Macko, 2003; Kulmatiski & Beard, 2013; (Le Roux, Bariac & Mariotti, 1995; Sankaran, Ratnam & Hanan, 2004; Scholes & Walker, 1993), but remains inconclusive, partly because of conflicting evidence presented over the years. By postulating deeper taproot systems as the central feature of savanna woody plants, critics of this model argue that this is overly simplistic, and represents an oversimplification of the RSA of savanna plants. This model does not take into account issues of plasticity traits in rooting patterns which occur within and between plant species, as well as across environmental gradients, as predicted by the adaptive phenotypic plasticity theory (Callaway, Pennings & Richards, 2003; Ghalambor, McKay, Carroll & Reznick, 2007; Pigliucci, 2005; Sultan, 2000; Van Kleunen & Fischer, 2005). This oversight calls for more complex, dynamic, spatially explicit as well as individual-based models that take into account such plasticity. However, little has been done to fill this gap, particularly in the drier Kalahari savannas where vegetation growth is suppressed by water stress caused by high temperature and evapotranspiration (Ringrose, Matheson, Wolski & Huntsman-Mapila, 2003; Scholes et al., 2002; Thomas & Shaw, 1991). The work of Holdo and Timberlake (2008), O'Donnell et al. (2015) is acknowledged, but given that their efforts were limited to the moist savanna of Zambia and Zimbabwe, such studies say little about the RSA of woody plants in the drier savannas of the western Kalahari. Besides, such studies overlooked the aspect of plasticity, a critical trait in heterogeneous environments such as the savannas.

The main objective of this study was therefore to characterise the RSA of shrubs found in close proximity to encroaching shrubs in the Kalahari Basin. Information on the RSA of shrubs neighbouring encroaching shrubs in the Kalahari is pivotal in understanding the competitive interactions between these savanna shrubs. Competition among plants, which occurs when one plant reduces the availability of soil resources required by another plant, is an important determinant of plant performance and community structure (BassiriRad, 2005). RSA is considered an important indicator of this competition because it shows the extent to which plants within proximate areas partition their soil niche for resource acquisition. According to Oppelt (2003), species with complementary and dissimilar

RSAs compete less, and thus become preferred neighbours. Results from this study may reveal new insights into the hidden below-ground morphology of the savanna plants. The study hypothesises that individual shrubs develop contrasting root systems, independent of species or environmental settings.

5.1.2 Root system architectural classification framework

The ability of scientific investigations to achieve valid generalisations about nature rests in classification (Warburton, 1967). Classification is the arrangement of organisms into a series of groups, particularly based on their morphological characteristics (Lebeda, Spencer-Phillips & Cooke, 2008) and is thus the basis for plant and animal systematics (Crowson, 1970; Richards, 2016; Spilsbury & Spilsbury, 2008).

To characterise and differentiate types of plant RSA, a root system classification framework is essential. However, over the years, plants have been classified exclusively based on their above-ground morphological features as opposed to their below-ground features. As a result, no universal root classification framework exists at present, partly due to soil opacity and the difficulties involved in exposing plant roots, a major challenge facing RSA studies.

Nevertheless, several attempts have been made to produce RSA classification frameworks based on topology, root activity and the developmental origin of roots (Cannon, 1949; Zobel & Waisel, 2010; Hodge et al., 2009; Ritz & Young, 2011). This study favoured and employed the development classification approach, mainly because it is able to classify plant roots based on their morphological features. In accordance with this classification, plant roots are characterised by their ontogenesis into major root systems, such as the taproot system and the fibrous root system (Hodge et al., 2009). Other terms used to refer to this classification are: primary root, secondary root and adventitious roots. This classification is consistent with the recommendations of the International Society for Root Research (ISRR) on RSA classification and nomenclature (Zobel & Waisel, 2010).

5.2 Methods and materials

5.2.1 Study area

This study was carried out on a nearly 1200 km long east-west transect across the Kalahari rainfall gradient in Namibia. The Kalahari is a mega-structural basin located in Southern Africa which covers some 2.5 million km^2 (Thomas & Shaw, 1991). It extends from the Orange River in South Africa to the Congo River in the DRC, and its longitudinal extent ranges from north-western Namibia to western Zimbabwe. In Namibia, the Kalahari covers parts of north-western Namibia, the Kavango Region and the former Caprivi Strip, now the Zambezi Region, as well as the Omaheke Region.

The Kalahari Basin is made up of an arenosol sand sheet up to approximately 400 m deep (Miller et al, 2016), making it one of the deepest and largest sand seas in the world (Thomas & Shaw, 1991). The climate of the Kalahari Basin is largely controlled by the seasonal changes in circulation systems such as the Inter-Tropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB). As a result, the climate of the Kalahari Basin ranges from an arid environment along the south-western edge of the Kalahari Basin to a humid environment along the north-eastern edge of the Basin in northern Zambia and parts of southern DRC (Burrough, Thomas & Bailey, 2009; Frssaf & Crimp, 1998), with a rainfall gradient from approximately 300 mm per annum to 1500 mm per annum. Because of the rainfall gradient and homogenous soils, the Kalahari Basin is considered to be a perfect environment for exploring links between climate, biochemistry, and ecosystem functions and structure, such that the effects of changing climatic conditions on vegetation structure and functions can be investigated without the confounding effects of soil type. It is therefore not surprising that the International Geosphere-Biosphere Programme (IGBP) has introduced the popular Kalahari Transect (KT) to study the links between vegetation parameters and the rainfall gradient (Bhattachan et al., 2012; Porporato, Laio, Ridolfi, Caylor & Rodriguez-Iturbe, 2003; Ringrose, Matheson, Wolski & Huntsman-Mapila, 2003; Shugart et al., 2004). It is within that context that this study was designed to follow the Kalahari rainfall gradient and contribute to the IGBP.

This study was conducted along the Kalahari rainfall gradient traversing three major sub-climatic zones: ‘wetter’, ‘mesic’ and ‘drier’, classifications based on MAP. Sites such as Omutambomawe, Uutsathima and Etosha are located along the western edge of the Kalahari Basin, along a rainfall isohyet of approximately 300-450 mm per annum. Because of their low mean annual precipitation, these three sites were collectively classified as ‘drier sites’. Onyuulaye, Okongo and Nkurenkure receive a moderate mean annual rainfall of 450 mm to 550 mm per annum and are thus classified as ‘mesic’. The last two sites, Divundu and Katima Mulilo, receive the highest rainfall of over 550 mm per annum, and were thus classified as ‘wetter sites’. The variations in climatic conditions along the KT translate into contrasting vegetation in terms of structure and biomass. The drier sub-climatic zone is largely dominated by sparsely distributed shrubs of various types. However, moving eastward, vegetation starts to change toward a tree-dominated structure with an increase in density and cover. Groundwater depth in the Kalahari Basin varies according to the local geology. For example, Omutambomawe and Uutsathima have the shallowest groundwater (10–60 m) and are located in the Omusati Multi-zoned Aquifer (KOM), which is made up of consolidated and semi-consolidated sediments of sand, clay and calcrete, while Onyuulaye and Okongo are located in the Kalahari aquifer with a water depth between 30 m to 160 m. Table 8, provide information on climatic indicators of the study sites, while dominant vegetation species are listed in Table 9.

Table 8. Climate, soil and groundwater indicators of the study sites along the Kalahari Transect.

Study sites	Location	Climate indicator	values	Soil group	Aquifer	Aquifer depth (m)
Omutambomawe	X [14.722]	Rainfall (mm/annum):	300	Arenosols	Omusati Multi-zoned aquifer (KOM)	10 – 60
	Y [-18.478]	Temperature (°C):	19 - 23			
		Rainfall coefficent of variation (%):	45			
Uutsathima	X [14.836]	Rainfall (mm/annum):	300	Arenosols	Omusati Multi-zoned aquifer (KOM)	10 – 60
	Y [-18.449]	Temp range (°C):	19 - 23			
		Rainfall coefficient of variation (%):	45			
Etosha	X [16.814]	Rainfall (mm/annum):	450	Arenosols	Oshivelo multi-layered aquifer	30 – 150
	Y [-18.489]	Temperature (°C):	19 - 34			
		Rainfall coefficient of variation (%):	35			
Onyuulaye	X [16.528]	Rainfall (mm/annum):	470	Arenosols	Ohangwena multi-layered aquifer	60 – 160
	Y [-18.195]	Temperature (°C):	18 - 26			
		Rainfall coefficient of variation (%):	35			

Okongo	X [17.221]	Rainfall (mm/annum):	550	Arenosols	Ohangwena multi-layered aquifer	60 – 160
	Y [-17.579]	Temperature (°C):	18 - 27			
		Rainfall coefficient variation (%):	35			
Nkurenkure	X [18.607]	Rainfall (mm/annum):	550	Arenosols	Kalahari aquifer	20
	Y [-17.619]	Temperature (°C):	18 - 34			
		Rainfall coefficient of variation (%):	35			
Divundu	X [21.561]	Rainfall (mm/annum):	600	Arenosols	Kalahari aquifer	20
	Y [-18.115]	Temperature (°C):	19 - 35			
		Rainfall coefficient of variation (%):	35			
Katima Mulilo	X [24.283]	Rainfall (mm/annum):	660	Arenosols	Kalahari aquifer	20
	Y [-17.492]	Temperature (°C):	19 - 35			
		Rainfall coefficient of variation (%):	35			

Sources: Bittner, 2006; Christelis & Struckmeier, 2001; Fick & Hijmans, 2017; Mendelsohn et al., 2002.

Table 9. Dominant woody species and grasses along the study transect.

Study sites	Dominant woody species		Dominant grass species	
Drier sub-climatic zone i. Omutambo mawe ii. Uutsathima iii. Etosha	*Abizia anthelmintica* *Bauhinia petersiana* *Croton gratissimus* *Catophractes alexandri* *Colophospermum mopane* *Commiphora angolensis* *Commiphora glandulosa* *Elephantorrhiza suffruticosa*	*Grewia. flavescens* *Senegalia mellifera* *Senegalia. nebrownii* *Searsia marlothii* *Terminalia sericea* *Vachellia erioloba* *Vachellia reficien* *Ximenia americana*	*Anthephora schinzii* *Aristida adscensionis* *Cynodon dactylon* *Dactyloctenium aegyptium* *Eragrostic rotifer* *Eragrostis dinteri*	*Heteropogon contortus* *Schmidtia Kalahariensis* *Sporobolus ioclados* *Stipagrostis uniplumis* *Tragus Racemosus*
Mesic sub-climatic zone i. Onyuulaye ii. Okongo iii. Nkurenkure	*Burkea. africana* *Boscia. albitrunca* *Bauhinia petersiana*	*Dichrostachys cinerea* *Terminalia sericea.* *Ochna pulchra*	*Anthephora schinzii* *Anthephora pubescens* *Cynodon dactylon*	*Digitaria eriantha* *Heteropogon contortus* *Heteropogon melanocarpus*

	Bauhinia petersiana	*Pterocarpus angolensis*	*Chloris virgata*	*Microchloa caffra*
	Baphia massaiensis	*Philenottera . nelsii*	*Dactyloctenium. aegyptium*	*Perotis patens*
	Commiphora angolensis	*Terminalia sericea*		*Sporobolus ioclados*
	Croton. gratissimus	*Vachellia erioloba*		*Stipagrostis uniplumis*
	Combretum imberbe			*Tragus racemosus*
Wetter sub-climatic zone i. Divundu ii. Katima Mulilo	*Baphia massaiensis,* *Baikiae plurijuga* *Combretum collinum*	*Pterocarpus angolensis* *Schinziophyton rautanenii* *Terminalia sericea*	*Heteropogon contortus* *Perotis patens* *Chloris virgata* *Cynodon dactylon*	*Dactyloctenium giganteum* *Panicum. kalaharense* *Schmidtia pappophoroides*

Source: Klaassen & Craven, 2003; Müller, 1983; Roux, Müller & Mannheimer, 2009.

5.2.2 Data collection

This study employed the nearest-neighbour sampling method to identify the non-encroaching shrubs to be excavated. To implement the nearest-neighbour method, the first individual, an encroaching species, was randomly identified using a random number table. Thereafter, the four nearest neighbouring shrubs were identified based on their proximity to the reference encroaching shrub by selecting those within the shortest distance (Figure 31). Such shrubs were located within a distance of 2 to 3 m of the encroaching shrubs. All the selected shrubs were identified to species level. Thereafter morphometric indicators such as shrub height, stem diameter, and canopy diameter were recorded. Stem diameter was measured using a Vernier callipers at the base of the shrub stem, while canopy diameter was measured along the widest sides of the shrub canopy. In total, 73 non-encroaching shrubs were excavated across the three sub-climatic zones.

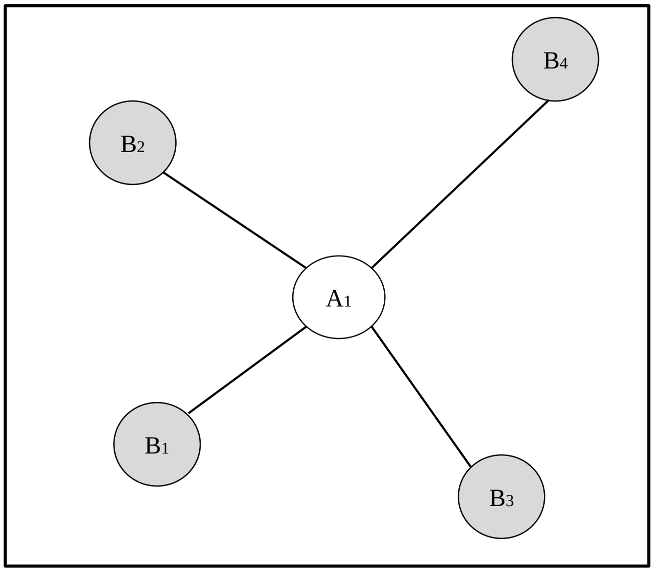

Figure 31: Schematic illustration of how the nearest-neighbour method was employed in the field to select shrubs for excavation. A1 represents an encroaching shrub randomly identified. B_{1-4} represent non-encroaching shrubs identified based on their proximity to the encroaching shrub.

To generate information on the root architectures of the selected shrubs, the following excavation technique was used to expose them (Bohn, 1979): using a shovel, the soil layer surrounding the upper part of each shrub's root system was removed to uncover the root system. Excavation started at the base of the root system for establishing the number of lateral roots present. Thereafter, excavation continued to expose the full horizontal extent of lateral roots. A flexible measuring tape was used to measure the depth of lateral roots, as well as their length. Meanwhile, the Vernier calliper was used to measure the diameter of the lateral roots excavated. A trench was dug to determine the depth of the tap root if one was present. Because of the effort required during excavation, digging was abandoned at 100 cm. Lastly, the excavated roots were classified into three major groups: tap root system, dual root system and lateral root system, based on their architecture. This method is highly laborious, destructive, and time consuming, so labourers were hired from local farmers to assist with excavation.

5.3 Results

Table 10 presents the results of the 73 individual shrubs studied belonging to 16 species from 10 families. Of these shrubs, 38.6% are from the Fabaceae family, followed by Burseraceae and Euphorbiaceae, each constituting 9.3%. Shrub species from other families such as Apocynaceae, Combretaceae, Malvaceae, Ochnaceae, and Olacaceae were also represented, which collectively constituted 42.8% of the shrubs excavated.

Table 10. Above-ground indicators of shrubs excavated from the three sub-climatic zones along the Kalahari Transect

Species name	Family	n (73)	Sub-climatic zone	Standing height (cm)	Canopy diameter (cm)	Stem diameter (mm)
Asparagus nelsii Schinz.	Asparagaceae	4	Drier + Mesic	40.6 ± 13.0	52.7 ± 18.4	4.2 ± 1
Baikiaea plurijuga Harms.	Fabaceae	4	Mesic + Wetter	139.1 ± 60.5	134.0 ± 42.2	80.50 ± 40

Baphia massaiensis Taub.	Fabaceae	5	Mesic + Wetter	97.0 ± 14.6	143.0 ± 31.1	12.00 ± 8
Bauhinia petersiana Bolle.	Fabaceae	4	Mesic + Wetter	70.0 ± 21.4	35.5 ± 17.2	10. ± 9
Catophractes alexandri D. Don.	Bignoniaceae	5	Drier + Mesic	153 ± 34.0	190.0 ± 25.3	33.9 ± 12
Combretum collinum Fresen.	Combretaceae	6	Drier + Mesic + Wetter	71.0± 17.3	50.0 ± 05.4	15 ± 6
Commiphora africana (A. Rich.) Endl.	Burseraceae	4	Drier + Mesic	35.0 ± 08.17	101.00 ± 17.2	17 ± 5
Commiphora angolensis Eng l.	Burseraceae	3	Drier + Wetter	104.2 ± 1	157.0 ± 2.0	45 ± 2
Croton gratissimus Burch.	Euphorbiaceae	7	Drier + Mesic+ Wetter	240.6 ± 98	256.1 ± 98.0	42 ± 3
Diplorhynchus condylocarpon (Müll.Arg.) Pichon.	Apocynaceae	5	Mesic + Wetter	207.0 ± 21.24	136.0 ± 24.1	28 ± 6.0

Elephantorrhiza suffruticosa Schinz.	Fabaceae	6	Drier + Mesic +Wetter	101.0 ± 24.4	98.0 ± 26.4	9.0 ± 06
Ochna pulchra Hook.	Ochnaceae	3	Mesic + Wetter	102.7 ± 31.4	57.10 ± 07.2	13 ± 07
Grewia flavescens Juss.	Malvaceae	4	Drier + Mesic Wetter	145.7 ± 26.4	180.4 ± 24	12 ± 5
Searsia marlothii (Engl.) Moffett.	Anacardiaceous	4	Drier	107.0 ± 21.3	174.0 ± 13.5	12 ± 05
Vachellia luederitzii (Engl.) Kyal. & Boatwr. var. luederitzii.	Fabaceae	4	Drier + Mesic	139.0 ± 51.3	101.00 ± 37.29	36 ± 11
Vachellia erioloba (E. Mey.) P.J.H. Hurter.	Fabaceae	5	Drier + Mesic + Wetter	145.0 ± 38.7	188.0 ± 14.2	46 ± 13

On average, four individual shrubs were excavated per each species, of which *C. gratissimus* had the largest representation with seven individual shrubs excavated, followed by C. *collinum* and E. *suffruticosa* with six individuals each. Approximately 29% of the shrubs were excavated from a drier sub-climatic zone, and 41% and 30% were excavated from mesic and wetter zones, respectively. Only five species, *V. erioloba, C. collinum*, *E. suffruticosa*, *C. gratissimus* and *G. flavescens* were recorded from all three sub-climatic zones. The rest of the excavated shrubs were shared between the two sub-climatic zones. In terms of their morphometric indicators, these shrubs varied in size from larger shrubs, such as *C. gratissimus* with an average standing height of approximately 240 cm, a canopy diameter of 256 cm and stem diameter of 42 mm, to as little as *A. nelsii* with an average standing height of 41 cm, canopy diameter of 52.7 cm and average stem diameter of 4.0 mm.

Table 11. Variations in root system architecture within and between shrub species across the rainfall gradient.

Species name	Drier	Mesic	Wetter
Asparagus nelsii	≠ ≠	≠ ≠	-
Baikiaea plurijuga	-	† *	**
Baphia massaiensis	-	≠ ≠	≠ ≠ ≠
Bauhinia petersiana	-	**	**
Catophractes alexandri	≠ ≠ ≠	≠ ≠	-
Combretum collinum	†	† †	* * †
Commiphora africana	††	††	-
Commphora angolensis	- ≠ ≠	-	†
Croton gratissimus	≠ ≠ *	≠ *	* *
Diplorhynchus condylocarpon	-	≠ ≠ †	≠ ≠
Elephantorrhiza suffruticosa	≠	≠ ≠	≠ ≠ ≠

Grewia flavescens	≠ ≠	≠	≠
Ochna pulchra	-	† †	†
Searsia marlothii	**	* *	-
Vachellia erioloba	† †	† †	†
Vachellia luederitzii	**	* *	-

Note. ≠Fibrous/lateral, *Dual root system architecture, †Taproot system architecture; - means no sample excavated for this species under the indicated sub-climatic zone. Each symbol represents an individual plant.

Three groups of root architecture can be identified, based on the topological arrangement of the plant root segments and structure, as presented in Table 11, and further illustrated in Figure 32. The first architecture group (I) comprises individual shrubs whose root systems consist entirely of fibrous/lateral roots growing directly from the stem into the soil, and which are deployed at various depths, with varying trajectories. All roots from individual shrubs of the same species in this group shared nearly the same morphometric characteristics such as diameter, rooting depth, length and angle of elongation. As a result, none of the root components could be identified as the primary root. Variations in terms of these morphometric variables were nonetheless noticeable between species, although they largely follow one common rooting pattern. In a few cases, such fibrous roots were made of first-order, second-order, and third-order roots. Those root segments branch off from other roots.

The second RSA group (II) is associated with shrubs whose root systems consist of two main conspicuous components. The first component is the taproot, or alternatively, a primary root, vertically deployed at nearly 90° in the soil. The second component are the lateral roots, which grow obliquely as secondary roots from the taproot or radicle. This root architecture is referred to as a dual root system. Although there were notable variations in the morphometric variables such as depth, diameter and dipping angle between species, the architectural arrangement of such roots follows one common pattern.

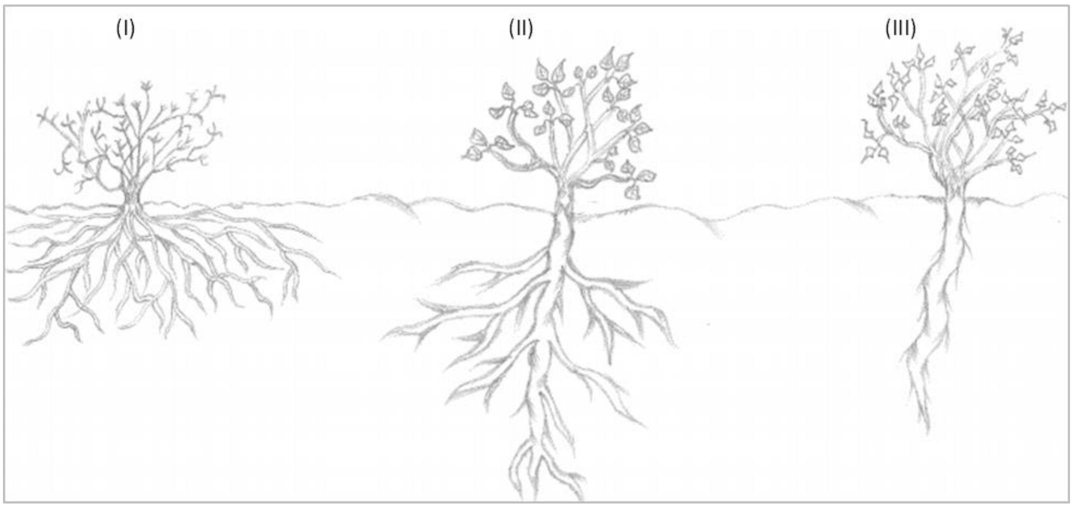

Figure 32: Generalised illustration of the three major root system architectural groups of savanna shrubs in the Kalahari Basin. [Not to scale].

The third RSA group (III) features individual shrubs whose root systems were entirely made up of a taproot component. The taproot was the only part of the plants' root system, growing vertically in the soils. For purposes of consistency, the names of the RSA group (I), (II) and (III) will be used hereafter to refer to these different rooting patterns.

Although the root architecture groups identified appeared to be unique to most plants studied, results also showed that this pattern is not necessarily shared by all the shrub species, neither in their families nor the sub-climatic zones from which they were excavated. Shrub species that developed their roots strictly consistently with architecture group (I) were *A. nelsii*, *B. massaiensis*, *C. alexandri*, *D. condylocarpon*, *E. suffruticosa* and *G. flavescens.* Collectively, these species made up approximately 46% of sampled plants. In terms of their individual morphometric variables, *A. nelsii* had its roots abundantly deployed within an average depth of 07.6 cm. Its shallowest root segment was recorded at a depth of 3 cm from the soil surface at Uutsathima, while its deepest root segment was recorded at 13 cm at Okongo. Such roots extended obliquely for nearly 2.5 m on average. The average terminal depth of *A. nelsii* was approximately 4.4 cm. At both Etosha, a drier site, and Okongo, a mesic site where this species was excavated, its root architecture exhibited a similar pattern. Species *B. massaiensis* was only excavated at Nkurenkure and Divundu and the fibrous roots were deployed at a vertical depth of 08.5 ± 2 cm, with a near-horizontal extent of 44.1 ± 2 cm, a thickness in diameter of approximately 22 mm, and a terminal depth of 30 ± 03.4 cm. All individuals of *C. alexandri* excavated had a complex network of thin (11 mm) fibrous roots developing at a vertical depth of approximately 09.8 ± 1 cm. Such roots were often longer, reaching an average length of 162 ± 10 cm and a terminal depth of 15 ± 1 cm. Meanwhile, *D. condylocarpon* deployed its fibrous roots within an average vertical depth of 15 ± 1 cm, with a horizontal extent reaching an average length of 132 ± 13 cm and a diameter of 16 mm. Such roots had a terminal depth of approximately 7 cm. These patterns were also shared with species such as *E. suffruticosa* and *G. flavescens*. The proportion of these three major root architecture groups between the three major sub-climatic zones is presented in Figure 33 Approximately 40% of all the shrubs in architectural group I were from the drier sub-climatic zone, while mesic and wetter sub-climatic zones shared the remaining 37% and 23%, respectively.

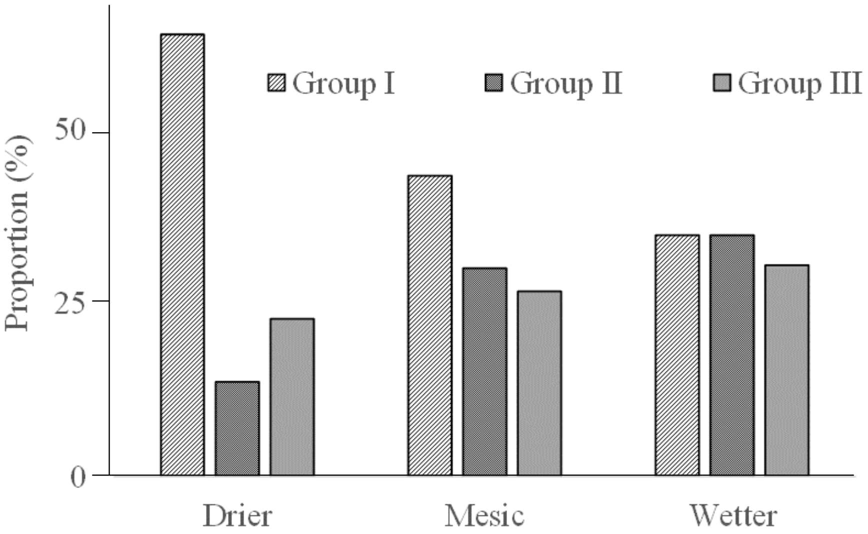

Figure 33: Proportion of the three major root system architecture groups in the three climatic zones along the Kalahari Transect.

Shrub species such as *B. petersiana*, *S. marlothii* and *V. luederitzii* exhibited a RSA entirely consistent with architecture group (II). In all cases, the taproot of these shrubs exceeded the excavation depth of 1 metre. However, the morphometric variables, such as length, abundance, diameter and rooting depth of their lateral roots varied extensively between shrub species in this architecture group. For example, *B. petersiana*, on average, had only four lateral roots growing at an average depth of 25.7 ± 13.4 cm. Such lateral roots grow as long as 198.2 ± 34.7 cm, reaching a terminal depth of approximately 45.6 ± 11.6 cm. The lateral roots of *S. marlothii* grow to a depth of 05.01 ± 0.6 cm, and, despite their shallow depth, such roots were, on average, 88.7 ± 12.05 cm long. With a thickness of about 11 mm, they reached a terminal depth of approximately 24.01 ± 2.5 cm. This architectural group comprised approximately 26% of the total shrubs excavated. In terms of their distribution per sub-climatic zone, 15% were in a drier sub-climatic zone, 45% were from a mesic zone, and 40% from a wetter sub-climatic zone of the study area.

Shrubs such as *C. africana*, *C. angolensis*, *V. erioloba* had one common root system consistent with architecture Group III. Their root system comprised a vertical taproot only, deployed at nearly 90° downwards, irrespective of the sub-climatic zone where the shrubs were excavated. The taproot was the only feature that made up the root system. All such shrubs had taproots penetrating deeper than 1 m. Approximately 40% of this architectural group was excavated from a mesic sub-climatic zone, while the drier and wetter zones had shares of 25% and 35%, respectively.

There were also individual species such as *B. plurijuga, C. collinum, C. gratissimus* and *D. condylocarpon*, which exhibited mixed types of rooting patterns. For example, one individual shrub belonging to *B. plurijuga* species excavated at Nkurenkure had only a taproot system (Group III), while the second individual shrub of that same species excavated from the same climatic zone (mesic) as well as those excavated closer to a more moist environment at Divundu had a dual root system. Its lateral roots developed at a vertical depth of 24.9 ± 5 cm, with a mean length of 127 ± 12.1 cm and a diameter of 21.0 ± 3.0 mm. These lateral roots can penetrate to a depth of up to approximately 85 cm. Similarly, *C. collinum* shrubs exhibited two types of rooting patterns. The first two individual shrubs excavated from a mesic zone exhibited a Group III RSA, while another two individuals excavated at Divundu yielded two contrasting rooting patterns, one consistent with architecture Group III, while the second individual was consistent with architecture Group II. The pattern of *C. collinum* shrubs lateral root deployment was similar to that of *B. plurijuga*, although slightly shallower. Shrub species *C. gratissimus* behaved in a similar fashion, with its individuals exhibiting mixed types of root architecture, even in the same sub-climatic zone.

5.4 Discussion

This study demonstrated that the savanna houses shrubs of different root architecture types: those with exclusively shallow fibrous root systems (I), others with root architecture consisting of a dual system with both taproot and fibrous/lateral roots (II), while others have a RSA exclusively made up of a deeper taproot (III). The study further revealed that RSA is not necessarily unique to any certain species, or family, or environment. While the majority of shrubs of the same species covered in this study exhibited one specific RSA, irrespective of the sub-climatic zone where they were found, there were also cases where others of the same species developed different RSAs within the same environment; or alternatively, changed their RSA types between the three sub-climate zones. For example, *C. gratissimus* exhibited two types of root architecture at the drier and mesic sites (Group I and II), but changed its root system to a different architecture group in the wetter zone (Group II). This is also true for other species, such as *C. collinum* and *B. plurijuga*.

Shrubs of different RSA, both shallow and deep-rooted, were found coexisting, a possible root niche-partitioning within the woody plants themselves. This also indicates that not all woody plants in the study area depend on the water table for moisture supply. According to Cooper and Burton (2002), plants that have a taproot system have the ability to survive in moisture-limited environments because they grow deeper in the soils, extracting water from the water table, while plants with fibrous roots do not tolerate drought conditions, but are well adapted at harvesting water from shallow soils (Gibson, 2012).

These results suggest that the popular belief that posits the root zone of savanna shrubs as a homogenous layer of deeper root systems is a poor representation of the below-ground morphology of the savanna plants. While acknowledging that there are indeed some savanna shrubs, such as *C. africana, C. angolensis* and *V. erioloba*, that develop deeper taproots, consistent with the premises of the root niche-partitioning hypothesis, there also exist shrubs such as *A. nelsii, B. massaiensis, C. alexandri, D. condylocarpon, E. suffruticosa*, and *G. flavescens* which exclusively grow shallow fibrous roots. Thus, theories of root niche-partitioning may aid in understanding the coexistence between deeper-rooted shrub and shallow-rooted shrubs, but may not necessarily be useful in understanding the coexistence between woody shrubs and grasses because shallow-rooted shrubs such as *C. alexandri, D. condylocarpon* and *G. flavescens* mostly share the same soil depth with grasses. Since this study focused on adult shrubs, and not seedlings, perhaps grasses are superior competitors to shrub seedlings, and reduce shrub seedling establishment, as suggested by Morrison, Holdo, Rugemalila, Nzunda & Anderson (2018).

The variations in RSA within and between species suggests that savanna shrubs behave differently under contrasting environmental conditions, resulting in inter- and intra-species variation in RSA. This is explained by the adaptive phenotypic plasticity theory (Chevin, Lande & Mace, 2010; Gedroc, McConnaughay & Coleman, 1996; Rewald, Falik, Godbold & Rachmilevitch, 2014; Sultan, 1995; Via et al., 1995) which argues that individual organisms, either plants or animals, can change their morphological characteristics in response to the prevailing environmental conditions. The findings of this study are also consistent with those of O'Donnell et al. (2015) and Holdo and Timberlake (2008) on the diversity of root structure in the Kalahari. The study also confirms the view of Zanetti, Vennetier, Mériaux and Provansal (2015) that species type does not have much influence on root architecture; rather, root architecture is shaped by genetic drivers and environmental conditions. This is likely to be more evident in heterogeneous ecosystems, such as the savannas (Augustine, 2003; du Toit, 2003; Jeltsch, Milton, Dean, Rooyen & Moloney, 1998). Architectural plasticity is thus an important trait because it may allow savanna plants to adapt to such heterogeneity. Those findings are also consistent with those of Schenk and Jackson (2002) who found that differences in the shapes and sizes of root systems may also be caused by physiological, anatomical, or morphological traits that are specific to a species or plant family.

5.5 Conclusion

The root system of the Kalahari savanna shrubs can be classified into three major architecture groups based on their ontogenies. Those with i) a shallow-rooted fibrous root system, ii) a root system consisting of the primary root, the taproot accompanied by secondary lateral roots, and iii) those exhibiting deeper taproots as the sole feature that makes up the root system. This implies that savanna plants employ several strategies for harnessing water and nutrients, whereas shrubs with the shallow-rooted fibrous structure are largely dependent on water from shallow sub-surface sources, while deeper-rooted shrubs have exclusive access to water at a deeper level. This seems to suggest a root niche-partitioning mechanism between various savanna shrubs. This study further revealed that species type is not necessarily an important determinant of RSA as plants seem to modify their root architecture under contrasting environmental conditions. Excavated shrubs demonstrated inter- and intra-species plasticity in their RSA. Future savanna models thus need to be cognizant of the diversity of root structure exhibited by various woody plants and how they change across environmental gradients.

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6. CHAPTER SIX: GENERAL DISCUSSION AND CONCLUSION

6.1 Introduction

Savanna biomes, where both trees and grasses coexist in defiance of competition theories (Sankaran, Ratnam & Hanan, 2004; Scholes & Archer, 1997), are undergoing a major ecological transformation of shrub encroachment (De Klerk, 2004; Van Auken, 2009). As covered in Chapters 1 and 2, this shift in savanna tree-grass ratio is accompanied by significant socio-economic as well as ecological consequences. Yet these biomes present one of the longstanding and perplexing research problems in vegetation ecology, termed ‘the savanna questions’ or ‘the savanna problem’ (Gil-Romera, Lamb, Turton, Sevilla-Callejo & Umer, 2010; Holdo, 2013). These savanna questions can be defined as four sub-questions, as follows: (i) How can complete competitors, woody plants and herbaceous plants, coexist in a resource-limited environment, defying competition theories? (ii) Why do trees and shrubs not thicken up to form a forest that would exclude grasses and herbs? (iii) Why do grasses and herbs not grow and eliminate trees to form a grassland? (iv) What mechanisms cause shrub encroachment? And does it imply that shrubs are superior competitors to grasses?

Scientific efforts to answer these questions have culminated in diverging, competing, conflicting, and inconclusive models and theories with regard to mechanisms that regulate the coexistence of these two contrasting life forms, and effectively the functioning of the savannas. Of these, Walter’s two-layer model, also known as the root niche-partitioning model (Scholes & Walker, 1993; Walker et al., 1981; Ward, Wiegand & Getzin, 2013) provides the most popular, yet the most controversially debated viewpoint. It argues that the coexistence between trees and grasses is a result of vertical root niche-partitioning, a natural regulating mechanism whereby trees grow deeper root systems to avoid competition with grasses. By postulating deeper root systems among trees, this model puts the root system architecture (RSA) of the savanna plants at the centre of the savanna debate and effectively under continued scrutiny because the extent to which trees and grasses vertically partition their roots to enable stable coexistence is still not well established. Following a critique of this model, this study in its endeavour to unlock the savannas' paradox, aimed at providing answers to the following questions:

i. What are the rooting strategies employed by shrub-encroaching species for foraging soil resources such as moisture?
ii. At what soil depth do shrub-encroaching species deploy such roots?
iii. How do such rooting strategies respond to changes along the Kalahari rainfall gradient?
iv. How do the rooting patterns of shrub-encroaching species compare to those of non-encroaching shrubs in close proximity, and in a similar environmental setting?
v. What implications do the rooting strategies of the Kalahari shrubs have for the dynamic and functioning of the savannas?

To that end, Chapters 3 and 4 investigated relevant variables of three shrub species, *Dichrostachys cinerea,* S*enegalia mellifera subsp. detinens* and *Terminalia sericea,* known as encroacher species in Namibia; Chapter 5 explored rooting patterns of immediate neighbouring plants with respect to the three target plants mentioned earlier. The present chapter consolidates results obtained from this study as a springboard for addressing the fifth research question above.

6.2 Root architecture of shrub-encroaching species, *S. mellifera*, *D. cinerea* and *T. sericea*

Shrub species such as *S. mellifera*, *D. cinerea* and *T. sericea* are among the most common encroachers in Namibia, responsible for woody encroachment of vast tracts of agricultural land. De Klerk (2004) reported that *S. mellifera* has encroached approximately 12 million ha, while *D. cinerea* is responsible for encroaching some 3.7 million ha of agricultural land. Encroachment by *T. sericea* occurs in central Kalahari, north of Gobabis, in the Omaheke Region, on a deep, dry Kalahari sand, covering some 2.2 million ha. Other undocumented areas may also be encroached by these species. It is still not certain what contributes to the competitive advantage these species have that enables them to encroach and displace grasses, which many other woody species do not do. Popular models on terrestrial plant root systems predict deeper root systems in drier environments, such as the Kalahari (Canadell et al., 1996; Jackson et al., 1996). Much of this premise was based on evidence from species such as *Boscia albitrunca* and *Vachellia erioloba,* whose taproots have been intercepted in boreholes at approximately 68 m and 45 m depth, respectively, in the Kalahari (Jackson et al., 1996). These findings sustain the idea that woody plants are essentially deeper-rooted in drier environments.

In Chapter 3, this study found that the two shrub species, *S. mellifera* and *D. cinerea,* develop a web of contrasting root systems in response to variation in climatic conditions. Of particular interest is how the two species adapt their RSA in response to the Kalahari rainfall gradient. In drier areas, for example, the two species develop root systems of predominantly lateral roots (Figure 34), and partly without taproots, which are deployed within a shallower depth of approximately 18 cm. In addition, *D.*

cinerea exhibited an interesting phenomenon where its lateral roots grow toward shallower soil sub-surface as they spread away from the stem, a behaviour probably in response to hydrotropism, an environmental tropism.

In Chapter 4, this study demonstrated that *T. sericea* shares environmental traits exhibited by *S. mellifera* and *D. cinerea.* Approximately 33% of shrub studies exhibited a RSA consisting exclusively of lateral roots, predominantly found along the drier western Kalahari areas; yet these shrubs are able to survive in such a harsh water-limited environment. The shrubs that possessed a taproot system were always accompanied by the presence of lateral roots, creating a dual root system. Shrub *T. sericea* restricted its growth of lateral roots within 40 cm from the soil's surface. None of the excavated shrubs had lateral roots below that depth. The absence of a taproot among several shrubs of the three species presented in Chapters 3 and 4, especially along the drier areas of the Kalahari, seems to suggest that a taproot is not a central feature of these encroaching shrubs because they could still survive without the taproot component.

Figure *34:* Lateral roots of *D. cinerea*. A higher abundance of lateral roots along the upper segment of the taproot than the lower segment is clearly visible.

Table 12 presents the results of different root architecture groups for the three bush encroachers, *D. cinerea*, *S. mellifera* and *T. sericea*, while Table 13 provides results of a generalised linear model on shrub counts. Of the 111 individuals of the shrub encroachers studied, 77% exhibited a dual root system, whereas 23% exhibited a lateral root system. Surprisingly, none of these shrubs exhibited a root system consisting of a taproot alone. Of the root architecture type, the sub-climatic zone used in the general linear model, only root architecture and climatic zone were significantly associated with variations in shrub counts ($p < .001$), meaning that the variation in the counts of different root architecture groups can largely be attributed to climatic zones where the study took place.

Table 12. Variation in root system architecture across the climatic gradient. Three shrub encroachers, *D. cinerea*, *S. mellifera* and *T. sericea* are represented.

Encroaching plant species	Climatic condition	Lateral roots only/fibrous (%)	Taproot only (%)	Taproot + lateral (%)
D. cinerea (n=35)	Drier	40.0	0.0	60.0
	Mesic	0.0	0.0	100.0
	Wetter	9.0	0.0	91.0
	Subtotal	14.3	0.0	85.7
S. mellifera (n=37)	Drier	33.0	0.0	67.0
	Mesic	26.0	0.0	74.0
	Wetter	0.0	0.0	100.0
	Subtotal	19.3	0	80.7
T. sericea (n=37)	Drier	61.5	0.0	38.5
	Mesic	23.1	0.0	76.9
	Wetter	15.4	0.0	84.6
	Subtotal	33.3	0	66.7
Grand Total (n=111)		22.6	0.0	77.4

Table 13. Generalised linear model illustrating the factors responsible for variation in individual shrub counts.

Factors	Coefficient	Standard error	Z-score	*p*
Shrub species	0.52	0.36	1.44	0.154
Sub-climatic zone	-0.63	0.36	-.75	0.016
Root architecture group	0.25	0.04	6.48	0.001

As mentioned in Chapters 3 and 4, these findings are not consistent with the premises of Walter's two-layer model (Scholes & Walker, 1993; Walker et al., 1981; Walter & Mueller-Dombois, 1971; Ward et al., 2013). On the contrary, they support an emerging theory that savanna plants opportunistically adapt their root systems in accordance with the prevailing environmental conditions in order to optimise soil resource acquisition. This study thus agrees with the premise that having lateral roots deployed within shallower soil sub-surface may potentially contribute to direct niche competition between certain woody species and grasses in the savannas (Bhattachan et al., 2012; February & Higgins, 2010; Hipondoka, Aranibar, Chirara, Lihavha & Macko, 2003; Smit & Rethman, 1998; Verweij, Higgins, Bond & February, 2011) because such lateral roots are deployed at depths within reach of grassroots. According to Weltzin and McPherson (2003), plants deploy their roots partly in response to resource abundance. The presence of lateral roots of the aforementioned species within shallower soil layers suggests that these plants are highly dependent on soil moisture from that soil sub-surface. Savanna biomes are characterised by frequent drought periods, and the occurrence of rapid, sporadic rainfall events may saturate the vadose zone where such lateral roots are deployed, but may not necessarily recharge the water table, which would have been significantly lowered following a prolonged period with no rain. Having their lateral roots deployed within such a vadose zone may enable these shrubs to still harness such moisture and survive, as well as harvest moisture coming from below through hydraulic lift/redistribution (Caldwell, Dawson & Richards, 1998; Caldwell & Richards, 1989; Ludwig, Dawson, de Kroon, Berendse & Prins, 2003; Querejeta, Egerton-Warburton & Allen, 2007). Hydraulic lift or redistribution is the process whereby water from the moist or wet layer of soils, usually at deeper levels in the soil profile, is moved up to the drier upper soil layer closer to the surface through the roots of plants (Eamus, Hatton & Cook, 2006). This movement occurs because of differences in water potential between the wet soils and the dry soils, and it occurs particularly at night, when evapotranspiration is low. This may, therefore, benefit shallow-rooted plants.

The competitive capacity of these shrubs may be enhanced by factors such as the ability to adapt their root systems to the prevailing moisture conditions, to grow longer lateral roots to increase catchment area, to grow larger lateral roots for temporary storage or rapid transportation of resources whose availability is limited in space and time in drier environment, and to maintain a shallow lateral root dipping angle. Lastly, those shrubs with a dual root system are likely to benefit from both shallow and deeper moisture sources, where lateral roots acquire moisture from the upper soil layer, and the taproot acquires moisture from a relatively deeper layer.

6.3 Root system architecture of non-encroaching shrub species as compared to 'encroaching shrubs'

Chapter 5 of this study outlines the investigation of the RSA of non-encroaching, nearest-neighbour plants of the encroaching shrubs presented in Chapters 3 and 4. Several studies in Namibia and Botswana (e.g., Bester, 1999; Christian, 2010; De Klerk, 2004; Moleele, Ringrose, Matheson & Vanderpost, 2002), where environmental conditions, such as climate and soils, are similar to those described in this study have recognised various shrub-encroaching species, common on either side of the border. Clearly, the occurrence of shrub encroachment can be attributed to certain specific savanna shrubs. One of the objectives of this study was to test how the rooting strategies of bush encroaching species compare to the shrub species with no record of shrub encroachment, hereafter referred to as 'non-encroaching shrubs'. As evidenced in Chapters 3 and 4, shrub-encroaching species are predominantly shallow rooted, and partly with no taproot. By comparison, non-encroaching shrubs such as *Vachellia erioloba, Commiphora africana, Commiphora. angolensis*, *Ochna pulchra,* exhibit root systems consisting exclusively of a taproot, a root system which was not exhibited by any of the shrub encroachers. There were also individuals of species such as *Baikiaea plugrijuga* and *Combretum collinum* which exhibited a root system which switched between a taproot, a dual, and a fibrous root structure. Admittedly, there are also non-encroacher species, such as *Aspragus nelsii, Baphia massaiensis, Diplorhynchus condylocarpon*, *Elephantorrhiza suffruticosa* and *Grewia flavescens,* which also grow shallow fibrous roots. The confounding factors which inhibit their competitiveness are not immediately apparent, but could be related to aspects such as water-use efficiency, flowering cycle, seed dispersal, seedling recruitment, soil nutrients, and fire. For example, the seed of the encroacher species, *D. cinerea,* can remain viable for approximately five years in the deep soil (Garner & Witkowski, 1997). Such longevity means that seeds may germinate whenever ideal conditions for recruitment emerge. However, the same extended viability has not been demonstrated for many other savanna plants.

Table 14 presents frequencies of the proportion of three major root architectures for shrub encroachers compared to non-shrub encroachers across the three major sub-climatic zones. Unlike shrub encroachers, of which approximately 77.4% have roots made up of both taproot and lateral root, that is, a dual system, non-encroaching shrubs are spread across all the three root architecture groups, including those whose root system is made of a taproot only. Table 15 indicates that variation in the frequency of the 185 shrubs excavated can be significantly predicted by RSA as opposed to other factors, such as climatic zone or species.

Table 14. Variation in root architecture between shrub-encroaching species and non-encroaching shrubs across three sub-climatic environments.

Encroacher species (n=111)	Lateral roots only/fibrous (%)	Taproot + lateral roots (%)	Taproot only (%)
Drier	46.8	53.2	0.0
Mesic	16.7	83.3	0.0
Wetter	8.3	91.7	0.0
Subtotal	22.6	77.4	0.0
Non-encroacher species (n=73)	**Lateral roots only/fibrous**	**Taproot + lateral roots (dual)**	**Taproot only**
Drier	63.6	13.6	22.7
Mesic	41.9	29.0	29.0
Wetter	42.9	38.1	19.0
Subtotal	48.6	27.0	24.3

Table 15. Generalised linear model illustrating variation in individual shrubs counts.

Predictors	Coefficient	Standard error	Z-score	*p*
Encroacher vs non-encroacher	2.41	1.63	1.47	0.478
Sub-climatic zone	0.05	0.09	0.56	0.09
Root architecture group	-0.05	0.01	-4.27	0.003

6.4 Shrub encroachers and below-ground interaction with their nearest neighbours

Below-ground competition among plants occurs when one plant reduces the availability of soil resources required by another plant, and is an important determinant of plant performance and community structure (BassiriRad, 2005). Root architecture is an important indicator of this competition because it reveals the extent to which plants within proximate areas partition their soil niche for resource acquisition. Plants with complementary and dissimilar root architectures compete less and thus become preferred neighbours (Oppelt, 2004). This adaptation can be interpreted as a coexistence strategy in which only plants with differentiated root systems tend to share the same neighbourhood. This study tested the premise by investigating the rooting behaviours of shrub encroachers in relation to their nearest neighbours.

Table 16 provides results of the root architectural behaviour of shrub encroachers and their nearest neighbours. The main pattern illustrated therein is that savanna shrubs do not necessarily share the same RSA with their neighbours. For example, most (40.7%) of the excavated shrubs near encroaching dual-rooted *D. cinerea* species had root systems of a lateral root architecture nature. Of all the shrubs excavated, only 3.7% of the neighbouring shrubs had either a lateral or a dual root system when the individuals of *D. cinerea* exhibited a lateral root system. Significant variations between the sub-climatic sites are also evident. For example, in mesic and wetter sites, no *D. cinerea* exhibited a lateral RSA, so are the nearest non-encroaching shrubs. This trend is shared with *S. mellifera:* approximately 32% of its nearest neighbours exhibited a lateral root system when *S. mellifera* had a dual root system, while a dual root system was shared by 16% of the shrubs, both encroaching and non-encroaching. In terms of *T. sericea*, a major differentiation in root architecture with its nearest neighbours was observed between dual-rooted *T. sericea* shrubs: approximately 31% of the neighbours had a lateral root system. Approximately 20% of the tap-rooted nearest neighbours were found where the shrub-encroaching species, *T. sericea,* had a dual root system. Overall, the aggregated results indicate that, when encroaching species are dual rooted, approximately 35% of their nearest neighbours often have lateral root systems, whereas, approximately 21% share a dual root system. It is very rare (10%) to find a lateral-rooted shrub encroacher surrounded by the nearest non-encroaching shrubs with lateral root systems. The same applies to a lateral-rooted shrub encroacher and its nearest non-encroaching shrubs with a dual root system. Figure 35 provides a visual illustration of the dominant below-ground neighbourhood root architecture differentiation in the study area. At Uutsathima for example, an excavated *T. sericea* with a lateral root system had four of its neighbours each with distinct root architecture.

The first two nearest neighbours, *V. erioloba,* had a tap root system, while the second nearest neighbour, *C. alexandri,* had a fibrous root system. The last two nearest-neighbour shrubs, *C. gratissimus* and *S. marlothii,* had dual root systems. The same cannot be said for the wetter sites. This differentiation is important because it allows plants in close proximity to access soil resources differently, thereby avoiding inter-specific competition.

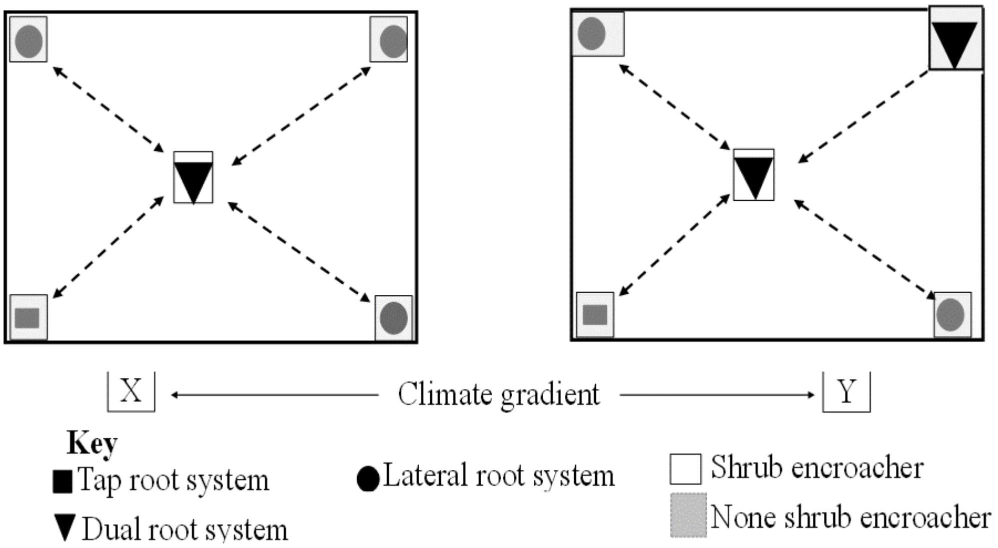

Figure 35: Schematic diagram showing average below-ground ground interaction between shrub encroachers and their nearest neighbours in two extreme environments: drier (X) and wetter (Y). Edaphic factors are assumed to be homogenous.

Table 16. Below-ground root architectural behaviour between shrub encroachers (n=*19*) and their nearest neighbours (n=*73*).

Bush encroaching species	Root structure combination	Bush encroaching vs undifferentiated non-bush encroaching plants (%)			Total (%)
		Drier	Mesic	Wetter	
D. cinerea	L: L	3.70	0.00	0.00	3.70
	L: D	3.70	0.00	0.00	3.70
	L: T	7.41	0.00	0.00	7.41
	D: L	14.81	14.81	11.11	40.74
	D: D	0.00	18.52	11.11	29.63
	D: T	0.00	11.11	3.70	14.81
Total					100
S. mellifera	L: L	15.79	10.53	0.00	26.32
	L: D	0.00	5.26	0.00	5.26
	L: T	5.26	5.26	0.00	10.53
	D: L	15.79	10.53	5.26	31.58
	D: D	0.00	5.26	10.53	15.79
	D: T	0.00	5.26	5.26	10.53
Total					100
T. sericea	L: L	3.45	3.45	0.00	6.90
	L: D	10.34	3.45	0.00	13.79
	L: T	3.45	6.90	0.00	10.34
	D: L	0.00	13.79	17.24	31.03
	D: D	0.00	3.45	13.79	17.24
	D: T	6.90	6.90	6.90	20.69
Total					100
All shrub encroachers (aggregated)	L: L	6.67	4.00	0.00	10.67
	L: D	5.33	2.67	0.00	8.00
	L: T	5.33	4.00	0.00	9.33
	D: L	9.33	13.33	12.00	34.67
	D: D	0.00	9.33	12.00	21.33
	D: T	2.67	8.00	5.33	16.00
Total					100

Note. One-to-many relationship between shrub encroachers and their nearest neighbours in terms of root architecture group. *L= Lateral root. D= Dual root. T=Tap root.*

6.5 Root system architectural plasticity among savanna shrubs - a missing piece of the puzzle in solving the savanna controversy?

The main issue emerging from Chapters 3, 4 and 5 is the root system architecture plasticity of savanna shrubs because of their intra- and inter-species variations in RSA, which was observed across the study area. In order to put this concept into perspective, a clear definition of the term plasticity is essential. Plasticity is broadly defined as the capacity of an individual organism to alter its behaviour in direct response to changing environmental conditions (Palmer, Bush, & Maloof, 2012; Palmer et al., 2012; West-Eberhard, 2003). Other definitions of plasticity have also been suggested. For example, Schlichting (1986) and Sultan (1995) defined plasticity as the ability of an organism to express different phenotypes in response to distinct environmental conditions. According to DeWitt and Scheiner (2004) and Sultan (2000) plasticity can also be defined as any change in an organism's characteristics in response to an environmental signal. Other terms used to refer to plasticity are: deformability, responsiveness, and flexibility (West-Eberhard, 2003). The plastic alterations include changes in physiology, morphology, growth, life history and demography (Miner et al., 2005). A typical example (Figure 36) of plasticity was demonstrated by Callaway et al. (2003) on *Quercus douglasii* (blue oak) along the mesic fringes of grasslands in the Central Valley, California, USA. Plasticity is important because it allows organisms to survive in otherwise hostile environments by producing novel and complex traits to adjust to environmental stress. According to Palmer, Bush and Maloof (2012) and to Schlichting (1986), plasticity is particularly important in plants whose sessile life cycle subjects them to ambient environmental conditions. The ability of organisms to respond to their immediate environments can thus be considered a critical factor to the success of such organisms, particularly in heterogeneous regions, such as arid and semi-arid environments, where both biotic and abiotic constraints are patchily distributed (Dougill & Thomas, 2004; du Toit, 2003; Grossman & Rice, 2012; Mou, Jones, Tan, Bao & Chen, 2013). Plant roots can show considerable plasticity in terms of total surface area, mass-to-surface area ratios, rooting density, the timing of growth and placement, and architecture (Callaway et al., 2003).

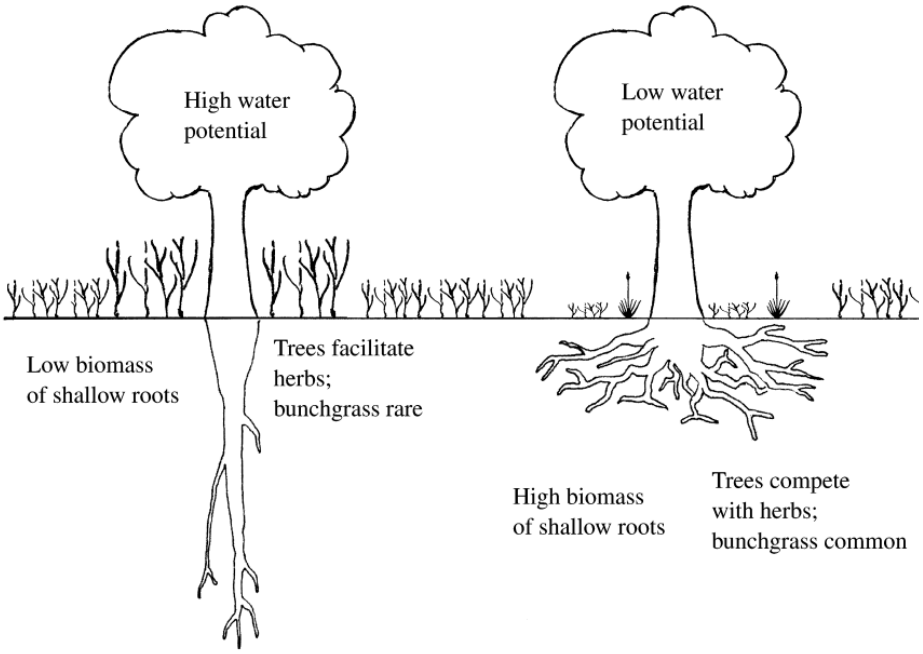

Figure 36**:** Plasticity of oak tree root system in response to understory herb layer in California, USA. Where herb layer is dense, the oak has a deeper root system; when the herb layer is reduced, the oak has a shallow root system. (Source: Callaway et al., 2003).

The plasticity framework best explains the rooting strategies of savanna shrubs for the following reasons: firstly, this study found that RSA is not a species-specific phenomenon, which means individuals of the same species can develop contrasting RSA within similar environmental settings, or individuals of two different species can develop analogous RSA within similar environmental settings. Secondly, the study found that RSA is not environment specific, which means that individuals of the same species can develop contrasting RSA under different environmental settings. Thirdly, there was a higher differentiation of RSA among shrubs within close proximity in drier areas than in wetter areas. Callaway et al. (2003) found that the presence and identity of plants can induce a plastic response to neighbours in root allocation and architecture. Plants influence the plastic behaviour of their neighbours as they compete for resources. Variation in root architecture can thus reduce root niche overlap, and therefore, competition between coexisting species (Callaway et al., 2003). If resource availability is the primary determinant of plasticity, Callaway et al. (2003) have further argued that the superior competitor is expected to be more plastic because plasticity would allow for the rapid deployment of roots where resources are abundant.

In order to demonstrate this plasticity, Figure 37 provides a hypothetical model illustrating the individual behaviour of three different plants from two environments, X and Y. The X environment represents the drier sites such as Omutambomawe and Uutsathima, whereas the Y environment represents the wetter environment such as Katima Mulilo. The mesic sites are left out in order to restrict the comparison to two extreme environments. This model also provides three different scenarios (a, b & c) on the complexity and plasticity of savanna shrubs RSA. The model recognises that the RSA of individual shrubs, irrespective of species, behave differently, in a non-linear pattern, in response to changes in the environmental settings. Figure 37(a) models a situation where three plants, A, B and C, excavated from two extreme environments, may develop a common root architecture in environment Y, but when the same species are excavated in environment X, they can yield contrasting root systems. For example, in environment X, plant species (A) had a dual root system, plant species (B) had a tap root system, while plant (C) had a lateral root system, whereas in environment Y, all the three plants species exhibited the same RSA.

Figure 37(b) illustrates a more complex situation in terms of the rooting behaviour of individual plants. For example, certain individuals of plant A can exhibit a shared root system, such as a dual root system, in two contrasting environments, but other individuals of the same species can alter their root systems to either a lateral or fibrous system. On the other hand, individuals of plant B can develop a common root system in environment Y, but develop differentiated root systems in environment X. In Figure 37(c) an individual plant can develop a dual root system in environment X, but can change its architecture to a taproot system in environment Y. Alternatively, a plant can develop a lateral root system in environment X, while in environment Y it develops a dual root system.

These behaviours may dictate the mechanisms of resource acquisition and below-ground interaction between the savanna shrubs, particularly among non-encroaching shrub species, as the shift in their architecture is non-linear. These dynamics can be interpreted in the context of the adaptive phenotypic plasticity theory which argues that the RSA of plants is a product of spatio-temporal variation in environmental resource supply, genetic drivers, and associated environmental constraints at the growth of each individual plant. Therefore, the RSA will vary significantly between and within species, as well as across environmental gradients. As a result, one factor alone, such as climate gradient, may not be adequate to explain the plasticity of the RSA of savanna shrubs.

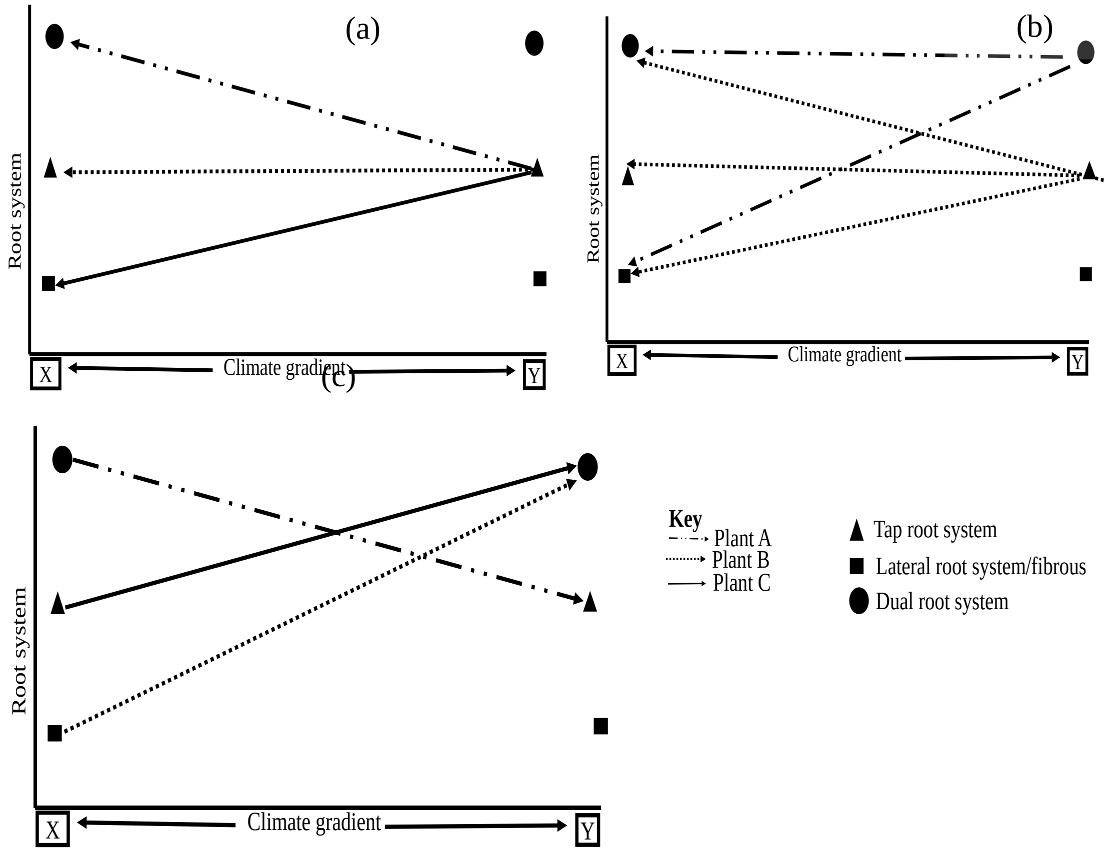

Figure 37: Schematic model illustrating the individual behaviour of three savanna shrubs in two extreme environments, drier (X) and wetter (Y). Each of the three figures (a, b & c) represents different sets of individuals.

6.6 Modified version of Walter’s two-layer model

Figure 38 provides a modified version of the root niche-partitioning model to include such plasticity. This improved model argues that savanna shrubs follow diverse rooting patterns, for example, such as those with an exclusive taproot (A), and those whose root system consists of dual components (B). In terms of dual components, the model recognises the distinction between shrubs whose lateral roots are deployed within the shallow soil layer (L1) as well as those whose lateral roots are deployed at a deeper layer (C) penetrating into the L2 soil depth. Note that the original Walter’s two-layer-model is implicit regarding the threshold depth at which trees and grasses may partition their roots. Instead, the model focuses on the implicit differentiation in the root architecture of woody and herbaceous plants. The root architecture, such as the presence of a taproot or lateral roots, can thus be used as a proxy to infer the depth (deep vs shallow) from which such plants capture soil resources.

This modified version of Walter’s two-layer model also recognises the presence of shrubs whose root system consists solely of lateral roots, without a taproot (D). Lastly, this model contends that these different types of RSA are not necessarily unique to any species or environment, with a few exceptions. On that basis, this study postulates that shrub encroachment is largely caused by shallow-rooted shrubs whose lateral roots are deployed within the upper soil layer, resulting in direct niche competition with grasses. When the grass layer is removed, possibly because of overgrazing, this direct competition amplifies the competitive advantage of trees, leading to shrub encroachment. This view is in contrast to the current premise which argues that it is the infiltration of water to the deeper soil layer which increases the recruitment rate of trees, following replenishment of the water table (Walker et al., 1981; Walker & Noy-Meir, 1982; Walter, 1964; Walter & Mueller-Dombois, 1971; Ward et al., 2013). The empirical evidence presented above suggests that lateral roots are not attuned to foraging moisture from the deeper soil layer or the water table. This equally means that only areas where such shrubs plastically adapt their root system to either lateral or dual root systems are likely to experience shrub encroachment.

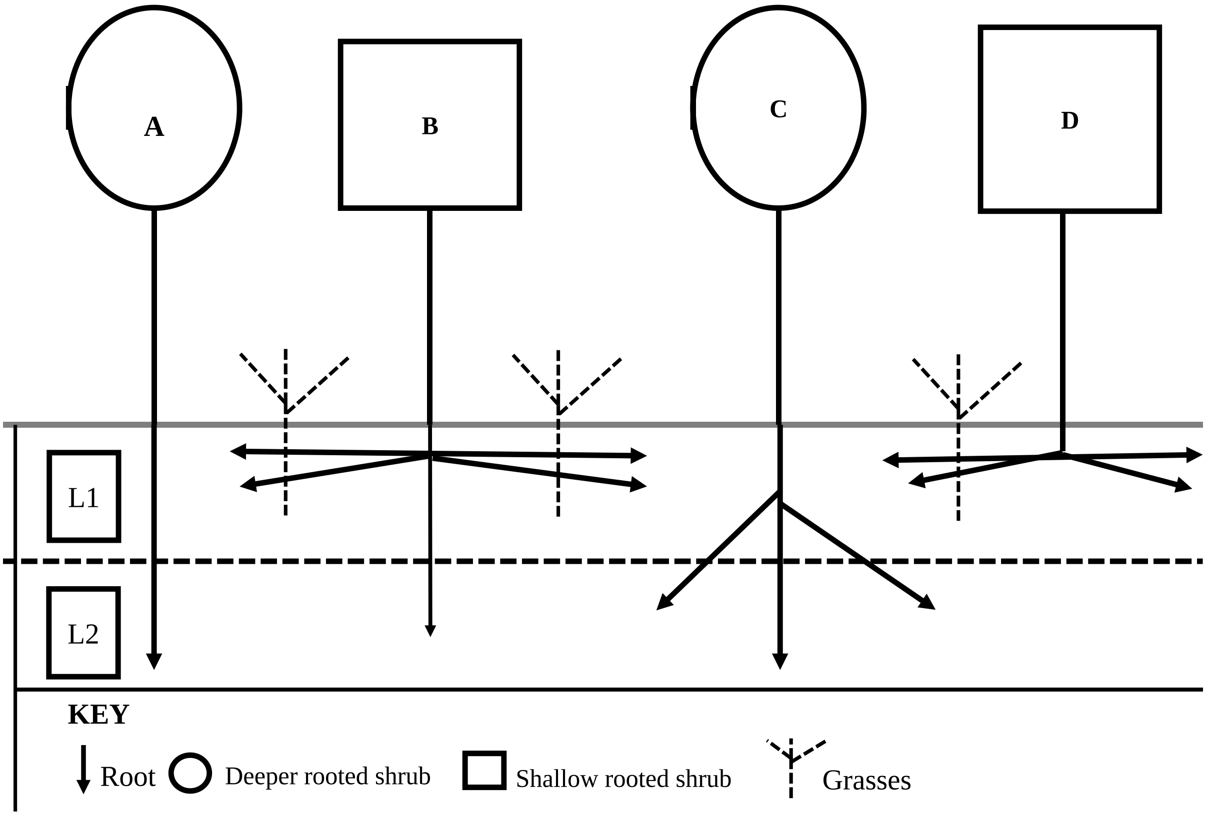

Figure 38: Modified version of Walter's two-layer model. Modifications of this model include the distinctions between deeper-rooted and shallow-rooted shrubs as well as the deployment of lateral roots within the upper soil layer. L1= upper soil layer, L2= lower soil layer.

6.7 Conclusion

This study shows that the ontogenesis of root systems among shrubs of the Kalahari Basin follows diverse architectural patterns which, to some extent, vary between plant species and families, and across the Kalahari climate gradient. The common architectural patterns are: i) a lateral root system/fibrous, ii) a dual root system of both lateral roots and a taproot component, iii) a taproot system made up of the taproot component alone. The soil depth at which individual shrubs deploy their roots is partly dependent on their architecture type. For example, lateral roots are often deployed within a shallow soil layer, while a taproot system is largely deployed at relatively deeper soil sub-surfaces, presumably to extract water from a deeper soil layer.

This study thus established two fundamental issues: firstly, evidence gathered seems to suggest that the root niche-partitioning model is an oversimplification of the RSA of savanna shrubs. The diversity of rooting patterns found among savanna shrubs cannot be accommodated within one simplistic root architecture model. Secondly, root architecture is not species-specific or environment specific. It is possible for individuals of the same shrub species to develop different root architecture within the same environment, or between different environments. In particular, encroaching shrubs such as *T. sericea*, *S. mellifera* and *D. cinerea* tend to develop root systems which respond to the rainfall gradient. In the drier sub-climatic zone of the Kalahari, the root systems developed by such shrubs essentially consist of lateral roots deployed in a shallow soil layer and mostly without a taproot component, unlike the root systems developed in mesic and wetter sub-climatic environments where shrubs exhibit deeper root systems, consisting of a taproot. These results have implications for our understanding of tree-grass coexistence and the long-term functioning of the savanna. For example, while the presence of a deep taproot may contribute to resource partitioning with grasses, the development of solely lateral roots in shallow soils by some savanna shrubs points to direct niche competition with grasses, with shrub encroachment a probable manifestation of this competition. This view may also explain why the phenomenon of shrub encroachment is particularly attributed to shallow-rooted savanna shrubs. The utilisation of the savannas as grazing land where such shallow-rooted shrubs occur may thus suffer from shrub encroachment following the removal of grasses by herbivores. It is therefore critical for the management of such rangelands resources to be cognizant of the belowground architecture of dominant plants and how it relate to rangeland utilisation.

6.8 Avenues for future research

The findings of this study lead to the following recommendations:

- The design and scope of the study did not aim to investigate the root architecture of shrub encroachers within the habitats where encroachment is taking place, with an exception of Omutambomawe. It would be interesting to study the root structure of such encroacher species within the environmental setting where they are encroaching to determine the most dominant root architecture type. In addition, it would be interesting to determine the below-ground and above-ground ratio of shrub-encroaching species across climatic gradients.
- This study found that rainfall gradient alone is not sufficient to explain the plasticity of the RSA of savanna shrubs. Future work could include other aspects, such as soil nutrients, tropisms, land use, competition, and ecological disturbances as possible predictors for root plasticity.

- Further studies should investigate shrub encroacher species at different life stages to understand the mechanisms under which such plants grow or abandon their taproot component.

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7. APPENDICS

Appendix A: Field Data collection sheet

<table>
<tr><td>Date:</td><td colspan="3">Site name:</td><td></td><td colspan="2">Lat(DD)</td></tr>
<tr><td>Recorder:</td><td colspan="3">Sub-site No:</td><td></td><td colspan="2">Long(DD)</td></tr>
<tr><td></td><td></td><td></td><td colspan="2"></td><td></td><td></td></tr>
<tr><td colspan="4">General site description
Savanna type
Grassland savanna
Shrubland savanna
Thick tree savanna
Savanna dominated by both tall grass and trees
Grazing pressure
Very high
High
Medium
Low
Very low</td><td colspan="2">List of dominant woody species
…………………………………
……………
…………………………………
…………….
…………………………………
…………….
………………………………….
……………..
…………………………………
……………..
Woody density
Very high
High
Medium
Low
Very low</td><td>Grass percentage cover (%)
0-5%
5-25%
25-50%
50-75%
75-100%
Landscape
Topography
Flat
Rise and Fall</td></tr>
</table>

DATA COLLECTION SHEET FOR WOODY PLANT ROOT SYSTEMS IN THE KALAHARI				
Location information				
Observer………… ….				Dates………………
Site name………	Sample number……………	Sample sub-number…………	GPS Location	Lat…………………… ……
				Long……………….
Above ground data				
Species Latin name………………………………		Bush encroacher Yes No	shrub height(cm)	. Stem type Single stem Multiple stems Number of stems ………………….
. Species local name……………………………….		.	. Diameter at base (cm)	. Canopy Diameter Cover(cm)
. Distance to nearest neighbor#1		. Distance to nearest neighbor#2………	. Distance to nearest neighbor#2…………..	Distance to nearest neighbor#4
Below ground data				

<table>
<tr>
<td rowspan="2">. Upper depth of lateral roots (cm)</td>
<td rowspan="2">. Lower depth of lateral roots development (cm)</td>
<td>. Number of lateral roots (cm)
……………………………….</td>
<td rowspan="3">. Length of lateral roots
(1)…………………
(2)…………………
(3)…………………
(4)…………………
(5)…………………</td>
<td rowspan="3">. Ending depth(cm)
(1)……………
(2)……………
(3)……………
(4)……………
.
(5)……………</td>
</tr>
<tr>
<td rowspan="3">. <u>Diameter</u> of first order lateral roots at base.
(1)………………………
(2)………………………
(3)………………………
(4)………………………
(5)…………………………</td>
</tr>
<tr>
<td rowspan="3">. Soil erosion intensity.
Very high
High
Medium
Low
Very low</td>
<td rowspan="3">. Ending depth of lateral roots
1
2
3
.</td>
</tr>
<tr>
<td rowspan="2">. Dipping angle of taproot.
…………</td>
<td rowspan="2">. Dipping angle of lateral roots
(1)………
(2)……….
(3)……….
(4)……….
(5)……….</td>
</tr>
<tr>
<td></td>
</tr>
</table>

Comments

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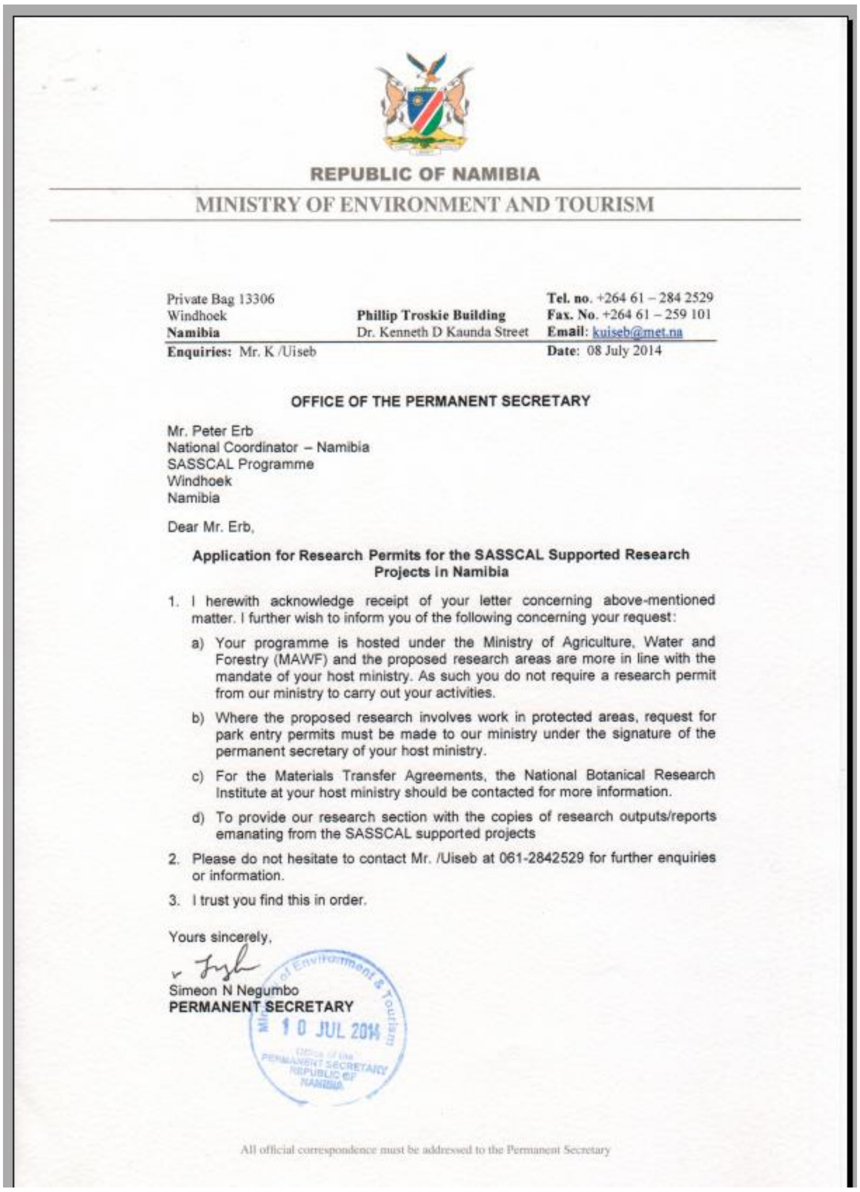
Appendix B: Research permit from the Ministry of Environment and Tourism.



REPUBLIC OF NAMIBIA
MINISTRY OF ENVIRONMENT AND TOURISM

Private Bag 13306
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Namibia

Phillip Troskie Building
Dr. Kenneth D Kaunda Street

Tel. no. +264 61 – 284 2529
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Email: kuiseb@met.na

Enquiries: Mr. K /Uiseb

Date: 08 July 2014

OFFICE OF THE PERMANENT SECRETARY

Mr. Peter Erb
National Coordinator – Namibia
SASSCAL Programme
Windhoek
Namibia

Dear Mr. Erb,

Application for Research Permits for the SASSCAL Supported Research Projects in Namibia

1. I herewith acknowledge receipt of your letter concerning above-mentioned matter. I further wish to inform you of the following concerning your request:
   a) Your programme is hosted under the Ministry of Agriculture, Water and Forestry (MAWF) and the proposed research areas are more in line with the mandate of your host ministry. As such you do not require a research permit from our ministry to carry out your activities.
   b) Where the proposed research involves work in protected areas, request for park entry permits must be made to our ministry under the signature of the permanent secretary of your host ministry.
   c) For the Materials Transfer Agreements, the National Botanical Research Institute at your host ministry should be contacted for more information.
   d) To provide our research section with the copies of research outputs/reports emanating from the SASSCAL supported projects
2. Please do not hesitate to contact Mr. /Uiseb at 061-2842529 for further enquiries or information.
3. I trust you find this in order.

Yours sincerely,

Simeon N Negumbo
PERMANENT SECRETARY

10 JUL 2014

All official correspondence must be addressed to the Permanent Secretary

Appendix C: UNAM UREC decision on the study's ethical clearance.

MINUTES 2/2018 OF THE UNIVERSITY RESEARCH AND PUBLICATIONS COMMITTEE

DATE: 15 March, 2018

1. FACULTY OF HUMANITIES AND SOCIAL SCIENCE

EXTRACT FROM THE UNIVERSITY OF NAMIBIA RESEARCH AND PUBLICATIONS COMMITTEE MINUTES ON ETHICAL CLEARANCE

"1.6 Savanna Woody Plants Root System Architecture and Bush Encroachment in the Kalahari Water Deficient Ecosystems, Namibia - JESAYA NAKANYALA (no student number)

The Committee discussed and APPROVED the research."

Appendix D: Ecology of the shrub encroaching species that were assessed in this study.

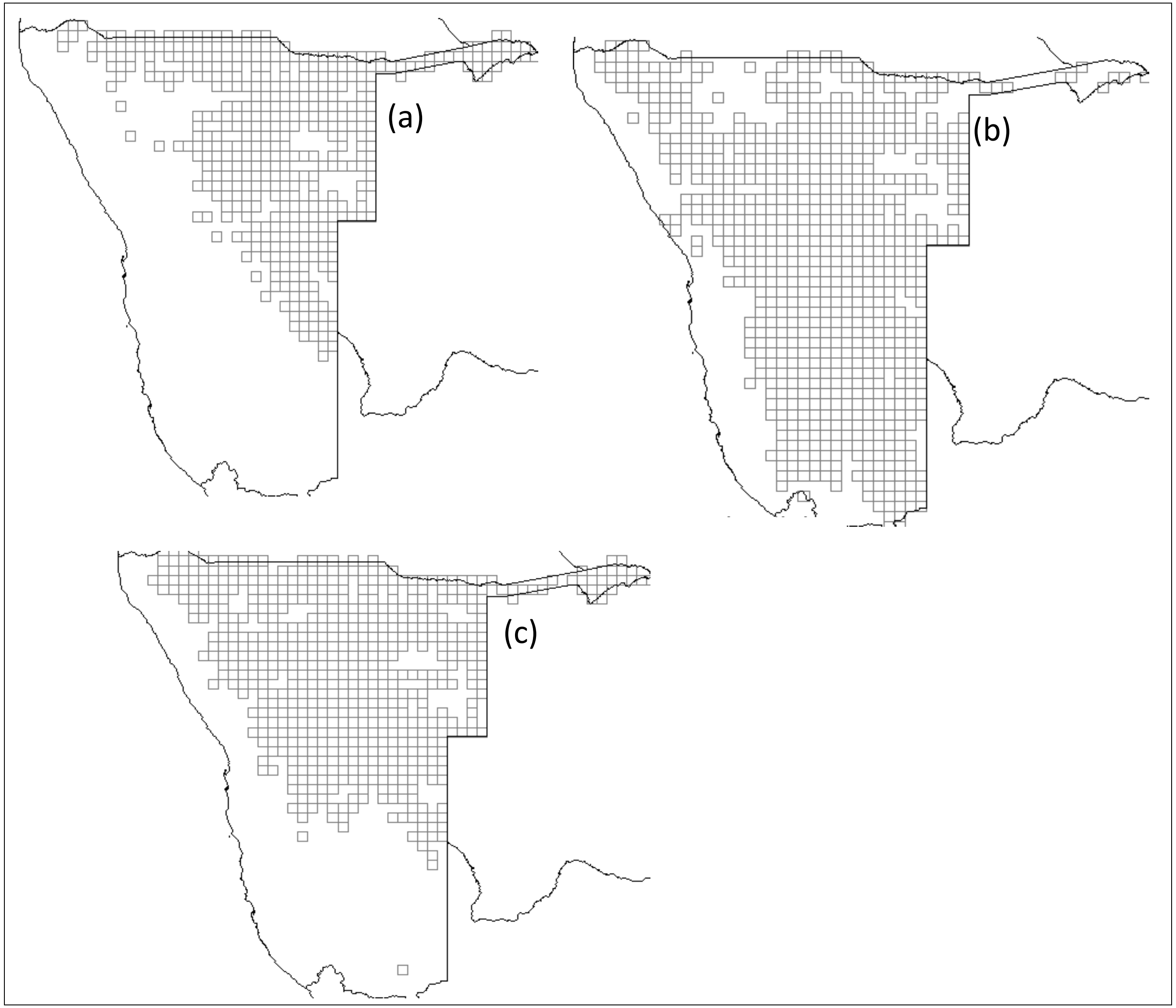
Ecological Description	*Terminalia sericea*	*Senegalia mellifera*	*Dichrostachys cinerea*
Local name	Omugolo/mugaro/ vaalboom	Okankono/omusaona/swarthaak	Sickle-bush/omutjete, sekelbos
Family	*Combretaceae*	*Fabaceae*	*Fabaceae*
Species growth form	Can grow as a shrub or as a tree.	Can grow as a shrub or a single stemmed tree.	Can grow as a shrub or small tree.
Shoot structure	It can grow as single stem or a multi-stemmed plant up to approximately 8 m with horizontally layered branches.	It can grow as singled stemmed or multiple stemmed plant of up to 8 m, with a V-shaped shoot canopy structure.	Often multiple stemmed with lateral branches and spinous long sturdy with sharp tips.

Habitat description	*Terminalia sericea* occurs in a variety of types of open woodlands particularly on sandy soils. It may grow as a dominant or co-dominant species in mixed deciduous forests such as *Brachystegia*, mopane, *Combretum* or *Senegalia* (Acacia) forest. It occurs from Tanzania and the DRC southwards to Angola and Namibia, Zimbabwe, Botswana and South Africa	It is found in larger parts of southern Africa, from South Africa to Tanzania. In Namibia it is found in the Caprivi Strip, Kaokoveld, Otjiwarongo, Outjo, Okahandja and Gobabis districts and further south. It prefers deep sandy or gravelly soils found in arid savanna, dry woodland and bush. A drought-resistant species, it is considered as a pioneer on shallow soils and is an invader in many disturbed areas, often forming an impenetrable thicket. It is distributed through Namibia, with the exception of the Namib desert.	*Dichrostachys cinerea* is widespread throughout Africa. It also occurs in Madagascar, India, Indonesia and Australia. It occurs in a diverse range of habitats and is a conspicuous component of many plant communities. In southern Africa it is very common in the warm, dry savannas.

Ecology and use	Silver cluster-leaf is a deciduous tree of the Combretaceae family that occurs in tropical and sub-tropical zones and on the plateau. They grow almost invariably on sandy soil and may be dominant in open woodlands. In the areas where they occur they often colonize open areas such as cutlines and fire breaks or areas opened by timber harvesting. Silver cluster-leaf has a tendency to form thickets and to produce a very large biomass *Terminalia sericea* is important in traditional medicine. The leaves and roots are boiled in water and the infusion is taken orally for the treatment of coughs, diarrhoea and stomach ache. The leaves can be used as an antibiotic for wounds. In the case of bleeding, a paste can be made by cooking the leaves in water and placing them on the wounds.	Its twigs and pods are very nutritious to livestock and game; in the wild it is browsed by animals such as black rhino, kudu, eland and giraffe. This species spreads rapidly, both from seed and vegetatively, to the extent that it can become a menace, forming impenetrable, tangled thickets. The leaves and pods are browsed by game as well as livestock. The trunk is used for curving pick and axe handle, while thicker stems are used for fencing. The heartwood is termite-resistant and used as fencing posts. The pods, young twigs, leaves and flowers are all highly nutritious and are eagerly eaten by stock and game. The dark heartwood becomes almost black when oiled and highly	*Dichrostachys cinerea* is a nitrogen-fixing legume and therefore has a positive effect on the nitrogen content of the soil. It has the ability to colonize disturbed veld quickly and curbs erosion. The pods are very nutritious to animals and are eaten by stock and game, including monkeys, rhinoceros and bushpigs. The stem is strong and thus used for pick handle, and firewood. It is also used for making bow.

	The wood is used as a source of energy for cooking and boiling water, for constructing huts, for fencing material and for solid structures.	polished. The wood is attractive, hard, and used as fuel.	

Species distribution in Namibia	Map (a)	Map (b)	Map (c)


(a)
(b)
(c)