VEGETATION-ENVIRONMENT RELATIONS ALONG AN ARIDITY GRADIENT ON KALAHARI SANDS IN CENTRAL NAMIBIA

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Declaration

I, Wilhelmina Ndapunikwa Hauwanga, hereby declare that the work contained in the thesis entitled: Vegetation-environment relations along an aridity gradient on Kalahari sands in central Namibia is my own original work and that I have not previously in its entirety or in part submitted it at any university or higher education institution for the award of a degree.

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Table of Contents

List of Figures

List of Tables

List of Acronyms

ANOVA-Analysis of Variance

BECVOL- The Biomass Estimates from Canopy VOLume

MAWF- Ministry of Agriculture, Water and Forestry

MBH- Maximum Browsing Heights

MDG’s- Millennium Development Goals

MET-Ministry of Environment and Tourism

NCCC-National Climate Change Committee

NCCP-National Climate Change Policy

NMS-Nonmetric Multidimensional Scaling

NPP-Net Primary Productivity

NUST -Namibia University of Science and Technology

OPTIMASS- Options for sustainable geo-biosphere feedback management in Savanna systems under regional and global change

PCQ- Point-Centered Quarter

PFA-Plant Functional Attributes

PFT-Plant Functional Types

SASSCAL-Southern African Science Service Center for Climate Change and Adaptive Land Management

Tukey’sHSD-Tukey’s honestly significant difference

UNFCCC-the United Nations Framework Convention on Climate Change

WIND-National Herbarium of Namibia.

“Nomenclature used in the thesis followed Klaassen and Kwembeya (2013).”

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Dedication

I dedicate my thesis work to my family and many friends. A special feeling of gratitude to my loving parents Magnaem and Petrus Hauwanga, and my grandmother Johanna Aron Namadhila yaLumbu, whose unconditional love, words of encouragement and push for tenacity ring in my ears. My best friend Billy McBenedict who has been a constant source of support and encouragement during the challenges of graduate school and life. I also dedicate this thesis to my aunts Rachel Lumbu, Hilaria Lumbu and Saara Lumbu, and uncle Simon Lumbu who have always loved me unconditionally and whose good examples have taught me to work hard for the things that I aspire to achieve.

Abstract

The distribution of the world's flora and fauna is shaped by different environmental factors. Such factors operate either locally, regionally or globally to influence species distribution. Studies of vegetation-environment relationship are very crucial especially under current and future changes in climate. The Kalahari basin also known as 'thurstland' offers an excellent basis for these studies at a sub-continental scale due to its variability and uncertainty of rainfall, high day temperatures and a uniform soil substrate that makes the Kalahari highly susceptible to climate change. This study was aimed at determining the main environmental factors influencing the distribution of vegetation, and investigate changes in the main plant functional and structural attributes in response to the detected main environmental factors along the Kalahari aridity gradient. Five study sites were selected along the Kalahari aridity gradient in central Namibia. Ten 50 m x 20 m plots were demarcated at each site in which grasses and phanerophytes were sampled using PCQ and BECVOL sampling methods respectively. For each site, grass sward density and for phanerophytes species richness, diversity, total basal area, total canopy volume, leaf volume production at 1.5 m, 2.0 m and 5.0 m, and density were calculated. Results revealed that mean annual rainfall was the main environmental factor influencing vegetation distribution on Kalahari sands. Phanerophytes in high rainfall areas were mainly evergreen with big leaves whereas phanerophytes in low rainfall areas were mostly decidious with small leaves. Phanerophytes species richness, diversity, total basal area, total canopy volume, leaf volume production at 1.5 m, 2.0 m and 5.0 m and density increased with rainfall while grass sward density decreased with increasing rainfall mainly due to competition from increasing phanerophyte density. It was concluded that overall phanerophyte productivity declines with decreasing rainfall and vice versa, and is anticipated to decrease further under projected change in climate.

Key words: Climate change, savanna, aridity gradient, environmental factors, Kalahari sands

Chapter 1: General Introduction

Background

Savannas are one of the world's most extensive and diverse biomes. Savanna vegetation covers about 60% of the global land surface, 65% of southern Africa and more than 80% of the Namibian landscape (Irish 1994, Scholes and Hall 1996, Scholes 1997, Okitsu 2005, Kaholongo and Mapaure 2014). These biomes are classified as the most diverse compared to forests and desert biomes due to their intermediate state between forest and desert. Savannas are generally defined as discontinuous tree stratums overlying continuous grassy ground layer that is occurring in regions subjected to wet-dry tropical climate, summer rainfall and an annual winter dry season (Walker and Menaut 1988, Belsky *et al.* 1989). There is a co-existence of trees and grasses in savannas as a result of a partitioning of soil moisture (Rossatto *et al.* 2014). Due to differences in root structure and levels of soil penetration, it has been hypothesized that grasses are superior competitors for water in the upper soil, while trees have exclusive access to water in deeper layers (Archer *et al.* 2017).

Isaacson (1995) disclosed that savannas support the highest population of plants and animals and sustain about half of the Namibian human population through agriculture. This highlights the need to understand the grass-woody interaction for managing purposes given their immense contribution to the economy and ecological maintenance. Nevertheless, the relationship between grasses and woody plants is generally poorly understood thereby inhibiting the development of strategies to improve and preserve savannas especially that this relationship is shaped by various environmental factors (Priyadarshini *et al.* 2016). According to Cowling *et al.* (2004), environmental factors are all external conditions that influence and affect the life and development of an organism thereby shaping biomes.

The two main factors determining the distribution of life on Earth including savanna coverage are temperature and moisture (Cowling *et al.* 2004). However, Scholes and Walker (1993) indicated that moisture and nutrients are the key factors affecting the patterns of primary production and plant palatability to herbivores in savannas. Nonetheless, there are other environmental factors that influence plants distribution including; radiant energy, composition of the atmosphere, soil structure, biotic factors, supply of mineral nutrients and growth-restricting substances (Barbour *et al.* 1980). According to Cowling *et al.* (2004) and Archer (2017), savannas occur under a wide range of soil conditions and atmospheric moisture conditions coupled with unpredictable rainy and dry seasons. This makes savannas rather unstable and susceptible to change in climate.

The term thirstland has been used variously to describe the extensive flat sand covered plain that occupies a substantial part (2.5 million ha) of interior southern Africa (Thomas 2002). This area is widely known as the Kalahari. Kalahari is a sandy, largely semi-arid region that lies within the southern Africa summer rainfall zone (Thomas and Shaw 1991, Scholes *et al*. 2002, Thomas 2002). According to Thomas and Shaw (1991), the Kalahari area gains its distinctiveness from dominant surface sediment of aeolian origin. Thomas (2002) further argued that some of the main important environmental factors shaping the Kalahari vegetation are its variability and uncertainty of rainfall, high evaporation due to daytime temperature exceeding 35°C, and relative infertility of the sandy arenosols. Despite its aridity, the Kalahari supports a variety of flora and fauna that are unexplored research wise. Scholes and Parsons (1997) stated that the relative vertical and horizontal uniformity of the sandy substrate makes the Kalahari gradient an ideal environment for studying large-scale trends in vegetation structure and function.

The Kalahari forms a clear south to north gradient of increasing mean annual precipitation of 150 mm per annum to over 1200 mm per annum (Scholes *et al.* 2002). This gradient extends from the vineyards on the margins of the Orange River at Upington, South Africa to the north of the Congo River into the south-east corner of Equatorial Gabon (Thomas 2002). As indicated in **Table 1,** this study represented the aforesaid gradient by collecting data from Mile 46 (with an average annual rainfall of 540 mm per annum), Sonop (with an average annual rainfall of 500 mm), Waterberg (with an average annual rainfall of 440 mm), Sandveld (with an average annual rainfall of 400 mm) and Ebenhaezer (with an average annual rainfall of 280 mm). Study sites were selected based on the evidence that they lie along the Kalahari aridity gradient (Pitman 1980, Mendelson *et al.* 2009, Jürgens *et al.* 2010).

It is predicted that Namibia's climate will undergo an increase in temperature of between 1°C to 4°C (Dirkx *et al.* 2008). The projected warming in temperature is proposed to lead to an increase in evaporation, evapotranspiration and a reduction in rainfall (Dirkx *et al.* 2008). This will presumably negatively impact the country in ways not limited to, a reduction in runoff and drainage in river systems (Midgley *et al.* 2005, Dirkx *et al.* 2008). Studies have shown that the aridity gradient creates steep climatic and ecological changes over relatively short distances (Aronson *et al.* 1992, Kadmon and Danin 1997, Volis 2007). Therefore, this study was aimed at investigating the ecological effects of changes in climatic factors and soil variables on vegetation along an aridity gradient in Namibia.

1.2 Statement of the problem

Overstocking on southern African savannas and poor rangeland management have brought about a serious problem of bush encroachment (Roques *et al.* 2001). Similar trends have been recorded in several areas of Namibia (De Klerk 2004, Wagenseil and Samimi 2007). Bush encroachment has a negative impact on the country's progress in terms of conservation efforts, economic stability and livelihood. This corroborate with De Klerk (2004) and Joubert *et al.* (2008) who stated that Namibian livestock ranchers forego an estimated N$700 million loss annually linked to bush encroachment. Extreme variation and instability of Namibian climate coupled with poor rangeland management may lead to a high intensity of bush encroachment in the country. This may have many ecological implications such as extirpation or extinction of plant species and a colonization by encroacher species (e.g. *Acacia mellifera)* leading to unwanted changes in plant species composition, structure, and loss of species diversity. Lack of diversity can cause the ecosystem to become vulnerable to perturbation and can lead to irreversible changes such as desertification. Nonetheless, there is a lack of knowledge on the condition of Namibia's vegetation and this creates a barrier in detecting early changes in vegetation conditions and implementing measures against bush encroachment and desertification.

Namibia is currently experiencing a decrease in rainfall due to climate change. Significant changes in vegetation structure and function are predicted to occur in several parts of Namibia due to climate change. The predictions are that the dominant vegetation type termed grassy savanna is anticipated to lose its spatial dominance to desert and arid shrub land vegetation with expected increases in bush encroachment in the north-eastern parts of Namibia (Midgley *et al.* 2005, Dirkx *et al.* 2008), species are projected to become locally extinct due to their areas becoming climatically unfavorable, and are required to migrate or be translocated to occupy new areas that are suitable (Midgley *et al.* 2005), and alien invasive species are anticipated to predominate. Hence, all these changes are predicted to culminate into a downfall in the country's economy at large. A lack of studies and reports on how climate change is impacting Namibia's vegetation creates a gap in implementing appropriate interventions towards conservation and restoration of Namibian savannas. Furthermore, information regarding species response to environmental factors along an aridity gradient is limited and this impedes the development and implementation of strategies to conserve and preserve species negatively affected by the aforesaid environmental factors.

1.3 Research objectives and hypothesis

The overall objective of this study was to determine the main environmental (climatic and soil) factors influencing the distribution of vegetation at the five study sites along an aridity gradient on Kalahari sands in central Namibia.

The following were the specific objectives of the study:

a) To determine the relationship between phanerophyte functional attributes and environmental factors along an aridity gradient.
b) To investigate how phanerophyte species richness, Shannon-Wiener and Simpsons diversity indices respond to main environmental factors along an aridity gradient.
c) To Investigate the relationship between total phanerophyte canopy volume, leaf volume production at maximum browsing heights (MBH) of 1.5 m, 2.0 m and 5.0 m, and main environmental factors along an aridity gradient.
d) To compare phanerophyte species diversity and richness among the selected study sites along an aridity gradient.
e) To compare phanerophyte total canopy volume and leaf volume production at maximum browsing heights (MBH) of 1.5 m, 2.0 m and 5.0 m among the selected study sites along an aridity gradient.

f) To determine and compare phanerophyte density and grass sward density among the selected study sites along the aridity gradient.

g) To investigate phanerophyte total basal area and height distribution among the selected study sites along an aridity gradient.

The hypothesis of the study were:

a) There is no relationship between phanerophyte functional attributes and environmental factors along an aridity gradient.

b) There is no relationship between environmental factors and phanerophyte species richness, Shannon-Wiener and Simpsons Diversity indices along an aridity gradient.

c) There is no relationship between phanerophyte total canopy volume and leaf volume production at maximum browsing heights (MBH) of 1.5 m, 2.0 m and 5.0 m, and main environmental factors along an aridity gradient.

d) There is no significant difference in species diversity and richness of phanerophyte among the selected study sites along an aridity gradient.

e) There is no significant difference in phanerophyte total canopy volume and leaf volume production at maximum browsing heights of 1.5 m, 2.0 m and 5.0 m among the selected study sites along an aridity gradient.

f) There is no significant difference in phanerophyte density and grass sward density among the selected study sites along the aridity gradient.

g) There is no significant difference in phanerophyte total basal area and height distributions among the selected study sites along an aridity gradient.

1.4 Significance of the study

The results of this study provided information useful in vegetation conservation and ecological restoration by identifying main environmental factors influencing vegetation and areas that are adversely affected by bush encroachment. The Ministry of Environment and Tourism (MET) can use the findings of this research to coordinate environmental management projects, promote public awareness and assist the public in efforts to reduce bush encroachment while simultaneously avoiding desertification. Furthermore, it provided evidence that can be used to improve biodiversity management and conservation which in turn advances the tourism and agriculture sector which are one of the pillars of Namibia's economy. Moreover, studies along environmental gradients are needed to generalize findings across ecosystems and to predict patterns of plant traits and plant performance under changing environmental conditions (Holzapfel *et al.* 1993). This highlights the significance of studying the spatial distribution of vegetation and its influencing factors in order to protect the ecological environment.

1.5 Limitation of the study

The study was limited to the aridity gradient along Mile 46, Sonop, Waterberg, Sandveld and Ebenhaezer and used respective sites long time weather data. However, the vegetation and soil data were collected in 2016 and therefore all results and conclusions were based on vegetation data collected in 2016 with a strong focus on phanerophytes.

Chapter 2: Literature review

2.1 Terrestrial vegetation and factors influencing its distribution

Plants are distributed over most of the earth’s surface either in aquatic or terrestrial environments. Each species have a smaller yet distinct distribution based on a unique evolutionary history, response to disturbances and tolerance to environmental factors. Humans often play a dominant role in the spatial and temporal distribution of vegetation. However, Scholes *et al*. (2002) stated that the physical environment also imposes different pressures that influence vegetation distribution. These constrains operate on both large and small spatial scales such as differences in rainfall patterns and soil texture respectively (Collins *et al.* 1989).

Some studies aimed at determining key factors influencing vegetation distribution have been conducted with a focus on soil variables (Ruggiero *et al.* 2002, Yue *et al.* 2008, Burke *et al.* 2009, Zou *et al.* 2011, Stein *et al.* 2017). Ruggiero *et al.* (2002)’s study on Cerrado (Brazilian savanna) and semi-deciduous forest disclosed that the relationship between vegetation and soil is much stronger at the top soil between 80 and 100 cm. Furthermore, a strong positive correlation between semi-deciduous forest and higher quantities of nutrients in the top soil layer was also noted. On the contrary, no correlation between soil fertility and Brazilian savanna’s was observed culminating into a deduction that different biomes respond differently to environmental factors. Vourlitis *et al.* (2015)’s study contrasted the findings of Ruggiero *et al.* (2002) stating that Cerrado species were distributed according to soil fertility levels. Ruggiero *et al.* (2002) emphasized that clay content especially in the top soil was the most important variable that influences vegetation vertical structure. This can be explained by the increase in soil water retention with increasing proportion of clay in the soil as opposed to sandy soils that are generally nutrient poor and retain less water (Furley 1992, Strohbach and Kutuahuripa 2014) culminating into an inference that soil texture has an influence on vegetation distribution since it determines the rate at which the soil warms up in the sun, nutrient availability and water retention. Axelsson and Hanan (2017) investigated patterns in woody vegetation structure across African savanna and revealed a unimodal relationship between crown sizes and soil texture owing to the effects of soil properties on the water cycle. However, it was concluded that woody cover, crown sizes, and woody plant densities were more strongly influenced by rainfall amounts and seasonality than by soil texture, slope and fire frequency (Axelsson and Hanan 2017).

Vegetation can affect the biophysical and chemical characteristics of the environment leading to alterations in the distribution of other plants species. It is widely accepted that trees can increase crop productivity, forage production, soil fertility, and reduce soil erosion and reverse desertification (Belsky *et al.* 1989, Barbier *et al.* 2014). This is accomplished by plants ability to intercept solar radiation, increase water infiltration, nutrients, nitrogen fixation and aluminium detoxification (Fornara and Tilman 2008, Gessner *et al.* 2010, Axelsson and Hanan 2017, Dohn *et al.* 2017). Belsky *et al.* (1989) investigated the effects of isolated mature trees of *Acacia tortilis* and *Adansonia digitata* on their environments in a semi-arid savanna west of Tsavo National Park, Kenya. It was disclosed that the canopy zones of *Acacia tortilis* and *Adansonia digitata* had lower soil temperatures and intensities of solar radiation, and received less rainfall than the nearby open zones. It was further revealed that microbial biomass, organic matter, P, K, and Ca were high in the soils under the canopy than the nearby open areas. This corroborates with Abule *et al.* (2005) who found high soil nutrients particularly soil pH, total N and organic carbon under the canopies of *Acacia tortilis* and *Balanites aegyptiaca* woody plants compared to the open grassland, in the Middle Awash Valley of Ethiopia.

2.2 Plants functional attributes in response to environmental conditions

The interaction between different environmental factors and disturbances influence trends of vegetation structure and composition, for instance the key determinants of vegetation patterns in savanna vegetation are rainfall, nutrient availability, fire and herbivory (Scholes *et al*. 2002, Zhu *et al.* 2011). These environmental factors and disturbances interact with plants functional attributes such as grass seed size (Volis 2007, 2014), plant defence strategies (Turley *et al.* 2013, Tomlinson *et al.* 2016), leaf nitrogen (Fisichelli *et al.* 2015), leaf size (Strohbach and Kutuahuripa 2014, Liu *et al.* 2017) and leaf orientation (Scholes *et al.* 2004, Grant *et al.* 2010). Volis (2007) found more but smaller seeds with increased aridity on two grass species *Hordeum spontaneum* and *Avena sterilis* along an aridity gradient in Israel. There has been an upsurge in studies aimed at determining linkages between plant physiological and morphological traits (plant functional types) for use in conceptual and mathematical models of vegetation dynamics (Paruelo and Lauenroth 1996, Fyllas *et al.* 2012, Pérez-Harguindeguy *et al.* 2013).

Plant functional attributes have been used to determine the distribution of plants and their response to environmental disturbances such as fire, overgrazing, biological invasions, soil nutrients, competition and climate change (Muller 1983, Sobrado 1986, Skarpe 1996, Gondard *et al.* 2003, Hooper *et al.* 2005, Poorter and Bongers 2006, Kunstler *et al.* 2016). de L Dantas *et al.* (2013) investigated changes in plant functional traits, soil nutrients and plant diversity attributes in response to fire along a savanna–forest gradient. It was revealed that open communities (savanna) where fire was prominent consisted mainly of short and small woody species with thick barks, tall grasses, low wood density, high grass density, thick and tough leaves, and low specific leaf areas while the opposite functional attributes were pronounced in closed communities (forest) with less fire events. Results further revealed that open communities were dominated by fire resistant woody species as opposed to closed communities that were dominated by shade-tolerant species that compensate for their lack of fire resistance by closing the canopy. Conversely, Silva *et al.* (2013) examined the influence of fire history and soil properties on plant species richness and functional diversity in a neotropical savanna and found high wood density, high leaf dry matter content, high number of re-sprouts, low plant height, low bark thickness, and basal area in high fire frequency areas. Silva *et al.* (2013) argued that under high fire frequency conditions, plants are not given enough time to accumulate bark, resist fire damage, and subsequently grow taller.

Plants have evolved many drought adaptive strategies. Deciduous plants have deep roots and tough tissues that allow them to function under low soil and plant water potentials. Deciduous plants are also known to poses small and rigidly coriaceous leaves that become even smaller with increased aridity leading to reduced evapotranspiration (Ackerly 2004, Barboni *et al.* 2004, Poorter and Markesteijn 2008). In contrast, leaves of evergreen species generally become sclerophyllous without becoming smaller (Barboni *et al.* 2004). Barboni *et al.* (2004) showed that trees are mainly needle-leaved under cool climate and broad-leaved in areas characterized by wet and cold climate suggesting that rainfall and temperature are the main environmental factors influencing leaf types and sizes. This agrees with Woodward and Williams (1987) who revealed that trees and shrubs tend to be broad-leaved and evergreen when winter temperatures increase. It was also revealed that summer-green shrubs and forbs that have photosynthetic stems become progressively abundant with increasing aridity (Barboni et al. 2004).

Environmental gradients have been widely used in attempts to determine spatial and temporal changes of vegetation and their plant functional attributes in response to environmental factors. Wana and Beierkuhnlein (2011) investigated the responses of plant functional attributes to environmental factors along an altitudinal gradient between 1000 and 3000 m in the south-west Ethiopian highlands. Their results disclosed a relationship between environmental variables and plant functional attributes. Plants with thorns and spines dominated in low altitudes subjected to drought and herbivory while plants with rhizomes and rosettes were predominant in cold and high latitude areas where grazing was common (Wana and Beierkuhnlein 2011). They further disclosed that soil variables such as organic carbon, sand fraction and surface stone cover were significantly associated with the differences in plant functional attributes across the environmental gradient. They also highlighted the significance of studies on plants functional attributes along environmental gradients given that these studies provide a better understanding of the ecological patterns of vegetation and their response to environmental gradients especially in drought-prone regions of Africa. Nonetheless, only a few studies have examined the relationships between plant functional types and environmental gradients in southern Africa, and particularly in Namibia (Skarpe 1996, Burke 2006, Strohbach and Kutuahuripa 2014).

The establishment, growth and survival of green plants and their functional attributes depends on water availability since water is a chemical reactant in photosynthesis (Pillay and Ward 2014). This is in agreement with Castellanos-Castro and Newton (2015) who stated that water availability and light are the main environmental factors associated with plant variations in tropical forests. Skarpe (1996) also revealed that temperature for the coldest month, precipitation and other variables related to soil moisture were the main environmental factors influencing the distribution of plant functional attributes such as life form, leaf size, leaf type, leaf longevity, photosynthesis and rooting depth in southern African savannas.

2.3 Vegetation studies on the Kalahari gradient

The Kalahari rainfall gradient is an extraordinary rainfall gradient on a uniform soil substrate. According to Wang *et al.* (2007), the Kalahari gradient is an ideal environment to study changes in ecosystem dynamics, vegetation composition and structure, and nutrient cycles along a spatial precipitation gradient without confounding soil effects. The significance of the Kalahari transect is well known and acknowledged since it has been designated as one of the International Geosphere–Biosphere Program (IGBP) transects designed to address global change questions at the regional scale (Koch *et al.* 1995, Scholes and Parsons 1997, Privette *et al.* 2004).

Porporato *et al.* (2003) analysed water balance and plant water stress along the 950 to 300 mm/year precipitation gradient on Kalahari sands. It was revealed that trees and grasses differ in water balance and water stress levels for example deeper-rooted trees thrives in wetter regions of the northern Kalahari while grasses are favoured in drier areas of the southern Kalahari leading to different vegetation types along the Kalahari transect. At 420 mm of rainfall during the growing season, grasses and woody plants had equal water stress signifying a possibility of tree-grass coexistence in the central sector of the Kalahari (Porporato *et al.* 2003). Contrary to Porporato *et al.* (2003), Yu *et al.* (2017) indicated that deep-rooted trees are favoured in drier environments while grasses are favoured in wetter environments. Yu *et al.* (2017) argued that in dry environments, trees have a competitive advantage over grasses because of their deeper root systems that allow them to access deep soil water resources while grasses are favoured in wet environments due to their high growth rate that allows them to take advantage of the window of opportunity existing in years with above average precipitation. This consequently increases the fuel load leading to an increased fire-induced tree mortality. Bhattachan *et al.* (2012) disclosed that the root depth of woody plants does not increase with increasing mean annual precipitation in the Kalahari.

Sekhwela (2003) investigated changes in economically important woody vegetation resources around seven settlements located along Kalahari aridity gradient in Botswana. Results disclosed an increase in total woody plant density and species richness with increasing rainfall. It was further revealed that individual species density differed at each site irrespective of rainfall suggesting that other factors such as land use play a role at a local scale. Woody plants height was also revealed to decrease with decreasing rainfall for example most trees recorded below ca. 300 mm were shorter than 2.5 m (Scholes et al. 2002).

Vegetation on the Kalahari sands is diverse. Along a line extending southeast to northwest through Botswana, the vegetation changes from fine-leaved savannas (with short woody plants and a low woody plants density) to broad-leaved woodlands (with tall woody plants and a high woody plants density) (Scholes and Walker 1993, Scholes et al. 2002). The tree and bush savannas found in the wetter central, northern and eastern areas of the Kalahari are grass dominated with widespread shrubs and belts of trees (Shaw and Thomas 1993, Thomas 2002). According to Scholes et al. (2002), the tree layer on the Kalahari is dominated by Fabaceae family specifically *Acacia* up to 400 mm mean annual precipitation. Between 400 mm and 600 mm, the Combretaceae (*Combretum* or *Terminalia*) or the Caesalpinaceae (*Colophospermum mopane*) predominate whereas in high rainfall regions > 600 mm, species belonging to the Caesalpinaceae family are predominant. This is in agreement with Wang *et al.* (2007) who stated that the Kalahari transect is covered predominantly by different types of savanna ranging from fine-leafed and nutrient-rich in the south to the broad-leafed and nutrient poor savanna in the north. On this basis, Mishra *et al.* (2015) developed a vegetation morphology map of the Central Kalahari transect.

Scholes *et al.* (2004) conducted a study on canopy structure on six savanna sites along a moisture gradient of 350 mm-1000 mm yr^{-1} on Kalahari sands. Results disclosed that plant area index for the tree canopy (stem area index plus leaf area index) declined from around 2 to 0.8 m^2 m^{-2}. It was further revealed that tree leaves changed from a horizontal orientation in high rainfall areas to a more random orientation as the aridity on the Kalahari sands increased (Scholes *et al.* 2004). Comparable results to Scholes *et al.* (2004) were recorded by Privette *et al.* (2004) who disclosed that leaf area index and canopy cover increased with increasing rainfall on about 300 to 1000 mm yr^{-1} rainfall gradient on Kalahari sands. Midgley *et al.* (2004) also revealed that leaf area and leaf size increased with increasing mean annual rainfall on the Kalahari moisture gradient in Botswana.

2.4 Grass-woody plants relationship

Namibia's economy and livelihoods highly depends on agriculture. As agricultural activities such as crop fields and/or forage for livestock increase, people exert several pressures on the vegetation around them. Such activities include but not limited to cutting down trees. According to Sala *et al.* (2001) and Archer *et al.* (2017), trees compete with grasses for space, soil moisture and nutrients, hence human cut down trees in order to reduce grass-woody plants competition and subsequently increasing forage for livestock. This is in agreement with Donzelli *et al.* (2013) who stated that in the presence of trees, grass production is generally greatly reduced depending on the kind of species, growth form and density of woody plants in that particular area. However, Scholes and Archer (1997) stated that the relationship between woody plants and grasses can either be negative (competition) or positive (facilitation).

Mean annual precipitation play a humongous role in the relationship between woody plants and herbaceous vegetation. Skarpe (1996) reported that patterns of rainfall during the year are important in the ratio of grass to woody plants in African savannas. This was substantiated by Scholes et al. (2002) who revealed that both grass cover and woody cover increased with increasing rainfall but grass cover later decreased as a result of increased competition from a high woody plants density at higher rainfall levels. Ansley *et al.* (2013) revealed similar results of an increase in C_3 annual grass production with increasing rainfall. Other factors that have been recorded to influence the relationship between woody plants and herbaceous vegetation includes climate, soil, fire, grazing/browsing and concentrations of atmospheric CO_2 (D'odorico *et al.* 2012, Archer *et al.* 2017).

Expansion of woody plants in savanna at the expense of herbaceous plants has been documented throughout the world including in Namibia (Bester 1999, Moleele *et al.* 2002, De Klerk 2004, Joubert *et al.* 2008). According to Joubert *et al.* (2008), encroachment of Namibia's rangelands by woody species such as *Acacia mellifera* can be partially attributed to poor understanding of vegetation dynamics and this highlights the significance of studying and understanding the grass-woody plants relationship and environmental factors shaping this relationship. Angassa (2005) conducted a study on the ecological impact of bush encroachment on the yield of grasses by incorporating both bush/shrub encroached and non-encroached areas in Borana rangeland ecosystem. Results showed that *Cenchrus ciliaris*, *Chrysopogon aucheri* and *Panicum coloratum* grasses were dominant in both encroached and non-encroached sites suggesting that the establishment of these grass species is not affected by bush encroachment. However, it was revealed that most of the encroached areas had a significantly lower herbage yield than the non-encroached areas (Angassa 2005). This is in agreement with Bailey and Gupta (1973) who unveiled that there is a reduction in the grass yields when grown with other plants compared to the yield of grass grown alone. The reduction in grass yield with increasing woody plants can be attributed to the ability of woody plants to alter the composition, spatial distribution, and productivity of grasses in savanna through competition (Scholes and Archer 1997).

Ratajczak *et al.* (2012) determined the consequences of woody encroachment on plant species richness by performing a meta-analysis of 29 studies from 13 different grassland/savanna communities in North America. Results depicted a decrease in species richness with an increase in woody plant encroachment in all 13 communities. However, species richness declined more in areas with higher precipitation ($r^2 = 0.81$) and where encroachment was associated with a greater change in annual net primary productivity (ANPP) ($r^2 = 0.69$) based on the strong positive correlation between mean annual precipitation and ANPP following encroachment ($r^2 = 0.87$). Ratajczak *et al.* (2012) suggested that the strong positive relationships between species richness, ANPP and MAP is because precipitation determines the magnitude of "woody release" that occurs with woody encroachment.

Contrary to the negative relationship between trees and herbaceous plants due to competition, some studies have recorded a positive relationship between woody plants, and herbaceous biomass, production and composition (Belsky *et al.* 1993, Blaser *et al.* 2013, Dohn *et al.* 2013, Archer *et al.* 2017). Belsky *et al.* (1993) examined the effect of *Acacia tortilis* and *Adansonia digitata* on the composition and productivity of herbaceous vegetation in a mesic savanna (about 750 mm annual rainfall) and xeric savanna (about 450 mm annual rainfall) in Tsavo National Park, Kenya. Results revealed a positive relationship between trees and herbaceous vegetation due to higher soil-N concentrations and lower evapotranspiration under tree canopies than open areas. It was also revealed that in the low rainfall area, herbaceous layer productivity was 95% higher under tree canopies than open areas whereas herbaceous productivity in the high rainfall area was 52% higher under *Acacia tortilis* canopies and 18% higher under *Adansonia digitata* canopies than open areas.

Belsky *et al.* (1993) postulated that differences in herbaceous vegetation under tree canopies between xeric and mesic environments may be brought about by reduced temperatures and evapotranspiration under canopies of trees in more arid environments. This is in agreement with Scholes and Archer (1997) who stated that the improved water and nutrient status under tree canopies may enhance herbaceous productivity. Weltzin and Coughenour (1990) also suggested that a reductions of understory water stress and temperature and increased nutrient concentrations may be the most important factors responsible for a decline in total herbaceous biomass with an increase in distance from tree bole to tree interspaces. It was further revealed that trees did not influence herbaceous composition beyond tree canopies (Weltzin and Coughenour 1990).

2.5 Climate change and its effect on vegetation

Climatic factors such as rainfall patterns, temperature, solar radiation patterns and soil moisture are the backbones through which ecosystem processes operate at various spatial and temporal scales. These factors directly or indirectly influence vegetation and are predicted to change in many parts of the world (Archer 1994, Lenihan *et al.* 2003, Archer *et al.* 2017). According to Penman *et al.* (2010), climate change will directly affect the distribution of species by shifting the location of climates to which they are adapted. Lenihan *et al.* (2003) disclosed that plant response to rising temperatures was characterized by a shift in dominance from needle-leaved to broad-leaved life-forms and by increases in vegetation productivity, especially in the relatively cool and mesic regions in California. This is in agreement with Archer (1994) and Box (2012) who stated that plants have adapted to varying climatic conditions through modification of form and foliar structures (plant functional types), physiological processes, and seasonal habits. Archer (1994) argued that climate also influences plants indirectly through its effect on soil development, and in creating conditions conducive to natural disturbances such as fire, wind-throw and flood which influence ecosystem structure and function.

Studies over the years have shown a strong relationship between climate variables and geographic difference in species richness, species diversity, species composition and vegetation type (Raunkiaer 1934, Woodward 1987, Woodward and Williams 1987, Gan *et al.* 2016, Solomou *et al.* 2017). Earth-Sun relationship and abiotic planetary factors such as atmospheric circulation and continental drift determines patio-temporal variations in climate (O'Brien 1993). O'Brien (1993) argued that climate is related to patterns of vegetation distribution because of its direct relationship to plant photosynthesis since without photosynthesis, the biological activities related to growth and reproduction cannot take place. According to O'Brien (1993), the amount and duration of available energy and moisture limits the amount and duration of photosynthesis, simultaneously limiting the amount and duration of biological activities.

Namibia's terrestrial's biomes based on dominant plant life forms are: succulent-shrub dominated Succulent Karoo, ephemeral therophyte-dominated desert, C_4 grass and shrub co-dominated Nama-Karoo, and tree and grass co-dominated savanna (Irish 1994). Each biome is affected to different extents by land use such as rangeland farming, recreation, mining and urban development (Okitsu 2005). In addition, these biomes are highly shaped by environmental factors and interactions such as climatic variables, competition, predation and herbivory which reduces the potential range of organisms. However, Cook *et al.* (2002) stated that climate is the principal determinant of vegetation distribution on a large scale.

Namibia is a generally dry and hot country with variable rainfall patterns. However, it is predicted that Namibian climate will get much drier and hotter at all locations with a greater effect in the central parts of the country (Midgley *et al.* 2005, Dirkx *et al.* 2008). This is anticipated to lead to a reduction in vegetation cover and Net Primary Productivity (NPP) throughout much of the country (Midgley *et al.* 2005, Dirkx *et al.* 2008). Namibia is highly vulnerable to the adverse effects of climate change due to its high dependence on natural resource based sectors such as agriculture, fisheries and mining (Turpie *et al.* 2010, Wilhelm 2013). Wilhelm (2013) stated that climate change threatens to significantly set back countries efforts to improve the livelihood of its people and achievement of Millennium Development Goals (MDG's) especially those aimed at poverty reduction and environmental sustainability.

Several efforts have been put in place in order to lessen problems caused by climate change. These efforts includes ratification of the United Nations Framework Convention on Climate Change (UNFCCC) in 1995 which led to Namibia becoming legally obligated to adopt and implement policies and measures designed to mitigate the effects of climate change and to adapt to such changes (Dirkx *et al.* 2008, Turpie *et al.* 2010). Such policies and measures include the National Climate Change Committee (NCCC), National Climate Change Policy (NCCP), Disaster Risk Management Act and National Climate Change Strategy and Action Plan (Midgley *et al.* 2005, Dirkx *et al.* 2008, Reid *et al.* 2008, Turpie *et al.* 2010, David *et al.* 2013). In addition, several studies on climate change adaptation have been commissioned and made freely available by the Government of Namibia through the ministry of Environment and Tourism (MET).

Chapter 3: Material and methods

3.1 Description of the study area

The study was conducted on five different sites selected along the precipitation gradient that extends from southern to north-eastern Namibia as a spatial proxy for increase water availability. All five sites form part of the greater Kalahari Basin (**Figure 1 and 2**), and thus have similar soil conditions but diverse climatic environments (**Figure 2**, **Table 1**).

3.1.1 The Kalahari

The Kalahari group also known as the Mega Kalahari in reference to its enormous size, is an extensive physiologically and sedimentologically unified area which encompasses the Kalahari Basin (Thomas and Shaw 1991). A section of the Mega Kalahari that receives less than 600 mm mean annual rainfall is known as the Kalahari desert (Scholes et al. 2002).

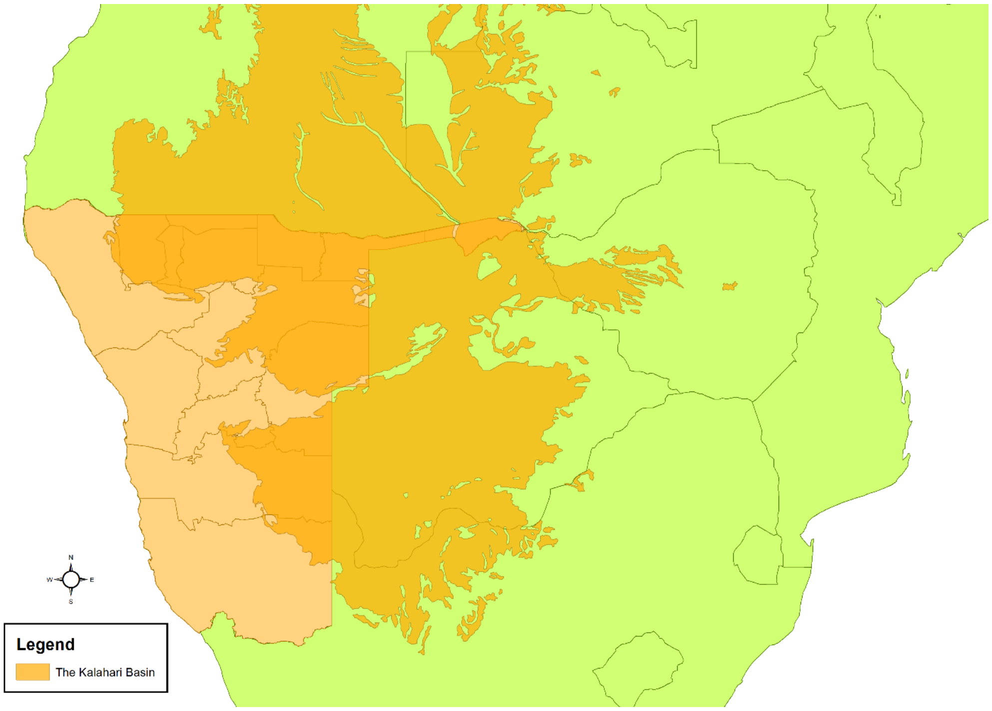


Figure 1: *Southern African countries that share the Mega Kalahari (green) and Kalahari basin (orange).*

The Mega Kalahari is shared by nine southern African countries (**Figure 1**). The topography of the Mega Kalahari sand plains is flat and slightly elevated at some points whilst the sand within the Kalahari Basin is deep with a depth of about 100-200 m in the centre of the Basin (Scholes et al. 2002, Strohbach and Kutuahuripa 2014). The deep Kalahari sands are of post cretaceous age and hold the same properties as other sand soils such as low water holding capacity and low content of basic nutrients culminating into an inference that Kalahari sands is not best fitted for agricultural activities and only a small part of the Kalahari has been transformed by humans through crop agriculture (Scholes et al. 2002).

Massive linear dune fields (up to 20 m tall) characterise the Kalahari sands, especially in the Kalahari desert. The linear dune fields have been regarded almost entirely as relict landforms illustrative of episodes of dry climate and are largely fixed by vegetation (Lancaster 1988). These dune crests, slopes and feet comprise of ferralic Arenosols with haplic Arenosols (Strohbach and Kutuahuripa 2014). The Kalahari sands further encompasses small pans and dry valleys formed as a consequence of duricrust formation and groundwater weathering (Shaw 1991). These pans and dry river valleys are more common in the south and centre of the Kalahari and contain more clay soils (Scholes et at. 2002). In addition, the Kalahari sands encompasses seasonally waterlogged, deep drainage channels commonly known as *Dambo*, *Omiramba or Vlei* (Strohbach 2008, Strohbach and Kutuahuripa 2014). These deep drainage *Omiramba* were formed during the wetter phase mostly in the early to mid-Pleistocene age and are nutrient rich (Strohbach and Kutuahuripa 2014).

The Kalahari sands is characterised by variable climatic conditions, and diverse vegetation and wildlife communities (Thomas and Shaw 1991). The northern edges of the Kalahari sands have humid tropical conditions and receive rainfall almost all year round (Thomas and Shaw 1991). However, the southern part of the Kalahari only recieves summer rainfall (Thomas and Shaw 1991). Most of the moisture in the Kalahari is from the Indian Ocean, signifying that the length of the wet season and the precipitation amount decreases in the south-westerly direction (Shaw and Thomas 1993, Thomas 2002). Humidity decreases from east to west and north to south regions of the Kalahari and is lowest during the dry seasons. Mean daily temperature on the Kalahari ranges from 20 to 24° C (Thomas and Shaw 1991).

3.1.2 Specific study sites

The present study analyzed vegetation-environment relationship on Kalahari sands in central Namibia by exploring five sites namely Mile 46, Sonop, Waterberg, Sandveld and Ebenhaezer (**Figure 2**).

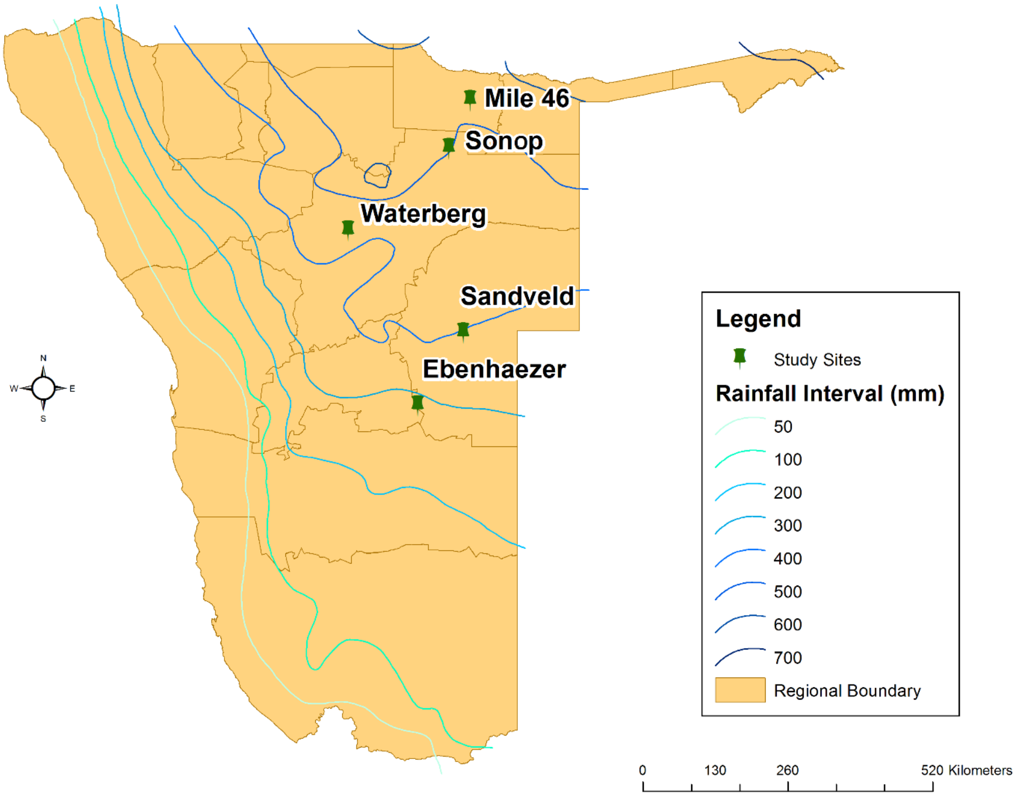


Figure 2: *Location of the five selected study sites in Namibia.*

Mile 46 biodiversity observatory

Mile 46 is a state-owned livestock farm situated on the Alex Muranda Livestock Development Centre, about 60 km southwest of Rundu in the Kavango West region in Namibia (Jürgens *et al.* 2010). Most of the Okavango West region is characterized by east-west oriented dunes, and some parts of the dune ridges are eroded (Burke 2002, Jürgens *et al.* 2010). The soil type is pure aeolian sands of the Kalahari and loamy sands associated with the old inter-dunal valleys and *Omiramba* (Jürgens *et al.* 2010), and has a dry Woodland savanna vegetation of the Northern Kalahari. It also consists of several patterns of grasses and shrubs underlying the tree layer

(Jürgens *et al.* 2010)(**Figure 3**). The dominant phanerophytes at Mile 46 are *Baphia massaiensis* Taub. ssp. *obovata Schinz*, *Combretum zeyheri* Sond., *Burkea africana* Hook., *Combretum psidioides* Welw, *Ochna pulchra* Hook. and *Terminalia sericea* Burch. ex DC. The dominant grasses are *Digitaria velutina* (Forssk.) P.Beauv, *Stipagrostis uniplumis* (Licht.) De Winter var. *uniplumis and Urochloa brachyura* (Huck.) Stapf.

Figure 3*: An example of vegetation at Mile 46 biodiversity observatory.*

Sonop biodiversity observatory

Sonop is a state-owned livestock farm situated on the Sonop Agricultural Research Station about 120 km north-east of Grootfontein in the Otjozondjupa region of Namibia (Jürgens *et al.* 2010, Kgabi *et al.* 2016). Sonop forms part of the extensive dune fields of the Northern Kalahari associated with *Omiramba* (Thomas and Shaw 1991, Strohbach and Sheuyange 2001). The dominant soil group at Sonop is arenosol whilst the inter-dunal valley soils comprise of clay and loamy soils (Strohbach and Sheuyange 2001, Jürgens *et al.* 2010). The vegetation is a typical example of a dry Woodland savanna of the Northern Kalahari with dunes having a relatively dense bushland, dominated by broad-leaved plant species (Jürgens *et al.* 2010)(**Figure 4**). The dominant phanerophytes are *Baphia massaiensis* Taub. ssp. *obovata Schinz*, *Terminalia sericea* Burch. Ex DC, *Bauhinia petersiana* Bolle ssp. *macrantha* (Oliv.) Brummitt & J, H. Ross and *Grewia* spp. The dominant grasses are *Aristida rhiniochloa* Hochst. *Stipagrostis uniplumis* (Licht.) De Winter var. *uniplumis* as well as *Urochloa trichophora* (Hochst.) Stapf.

***Figure 4**: An illustration of vegetation at Sonop biodiversity observatory.*

Waterberg Plateu Park

The WPP is a protected area situated in central Namibia about 40 km east of Otjiwarongo in Otjozondjupa region. On the north east of the park, the altitude decreases progressively towards the dip of the plateau where the mountain ultimately becomes part of the Kalahari Sandveld (Schneider 2004). The top of the plateau is made up of lithofied dunes (Mukaru 2009). Waterberg Plateau Park falls within the Tree savanna and Kalahari Woodland consisting mainly of a variety of deciduous trees and shrubs, and hard grasses (Giess 1971, Erckie 2007, Mukaru 2009)(**Figure 5**). The dominant phanerophytes are *Combretum zeyheri* Sond., *Burkea africana* Hook., *Combretum psidioides* Welw., *Terminalia sericea* Burch. Ex DC. and *Ochna pulchra* Hook. The dominant grasses are *Aristida stipitata* Hack., *Eragrostis pallens* Hack. and *Urochloa trichopus* (Hochst.) Stapf.

Figure 5: *A depiction of vegetation at Waterberg Plateu Park.*

Sandveld biodiversity observatory

Sandveld is a state-owned livestock farm situated about 40 km north-east of Gobabis in the Omaheke region of Namibia (Zedda *et al.* 2009). Its location is within the extensive Central Kalahari deep sand Basin with shallow soils on calcrete. The deep sands support open to moderately closed bushlands whilst the heavier soils often support a dense thorn-bush thicket. The vegetation is a typical example of the Camelthorn savanna of the Central Kalahari (Giess 1971, Zedda *et al.* 2009, Strohbach 2014)(**Figure 6**). The dominant phanerophytes are *Acacia erioloba* E.Mey*, Dichrostachys cinerea* (L.) Wight & Arn, *Grewia flava* DC. and *Terminalia sericea* Burch while the dominant grasses are *Aristida stipitata* Hack. *Urochloa brachyura* (Huck.) Stapf. *Stipagrostis uniplumis* (Licht.) De Winter var. *uniplumis* and *Schmidtia pappophoroides Steud.*

Figure 6: *An example of vegetation at Sandveld biodiversity observatory.*

Ebenhaezer

Ebenhaezer is a private-owned livestock farm situated about 181 km south-east of Windhoek in the southern Kalahari. It incorporates various vegetation types including grass covered dunes, saltpans, bush veldt, grassland and *Acacia* dominated savannas (Giess 1971)(**Figure 7**). The soil type is a pure aeolian sands of the Kalahari which is generally poor in nutrients. Dominant phanerophytes are *Acacia erioloba* E.Mey., *Acacia mellifera* (Vahl) Benth. ssp.*dentines* (Burch.) Brenan and *Phaeptilum spinosum* (Radlk.) S.Moore. Dominant grasses are *Stipagrostis uniplumis* (Licht.) De Winter var. *uniplumis.* as well as *Aristida stipitata* Hack.

Figure 7*: An example of vegetation at Ebenhaezer.*

Table 1*: Main characteristics of the five selected study sites along an aridity gradient.*

Study sites	**Latitude**	**Longitude**	**Altitude (m)**	**Mean annual rainfall (mm)**	**Mean annual temperature (° C)**
Mile 46	18.301826 S	19.247311 E	1180	540	22.6
Sonop	19.073818 S	18.903897 E	1236	500	23.1
Waterberg	20.461330 S	17.208133 E	1550	450	18
Sandveld	22.043351 S	19.133903 E	1523	400	19.4
Ebenhaezer	23.216666 S	18.400000 E	1340	280	21.68

3.2 Demarcation of plots

Ten 50 m by 20 m plots were randomly demarcated using stratified random sampling design at Waterberg and Ebenhaezer. According to Barbour *et al.* (1980) and Barbour *et al.* (1987) stratified random design allows the fieldworker to locate the samples randomly within each homogeneous region by subdividing the survey area or any given stand into several homogeneous regions known as strata. Barbour *et al.* (1980) stated that this design ensures that samples are dispersed throughout the entire surveyed area thus capturing key population characteristics in the sample. Another advantage of stratified random sampling is that it does not compromise the concept of random sampling (Barbour *et al.* 1980). For Mile 46, Sonop and Sandveld, sampling was done on BIOTA (50 m by 20 m) plots which were also selected on a stratified random manner. BIOTA observatory covers an area of 1 km² which is further divided into a 100 single hectare plots of 100 m × 100 m each. A 50 m by 20 m plot (where sampling was done) was demarcated in each 100 m^2 plot (Jürgens et al. 2010)(**Figure 8**).

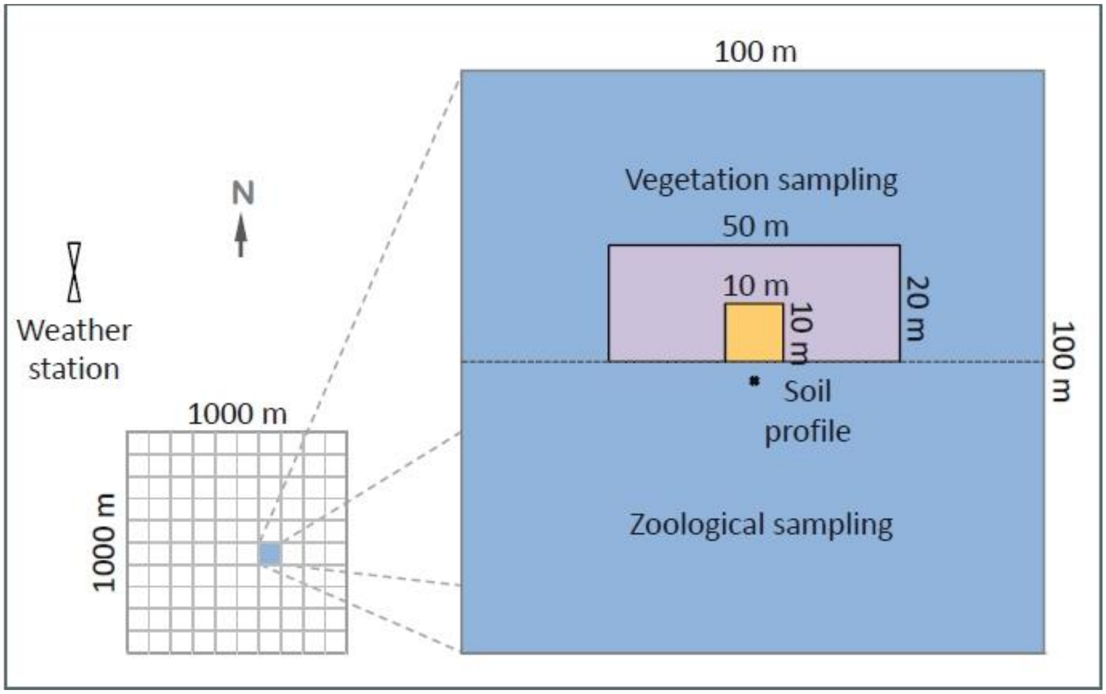


Figure 8: *A schematic layout of a BIOTA observatory in southern Africa and arrangement of different sampling areas within one of the hectare plots. Adapted from* Jürgens *et al.* (2010).

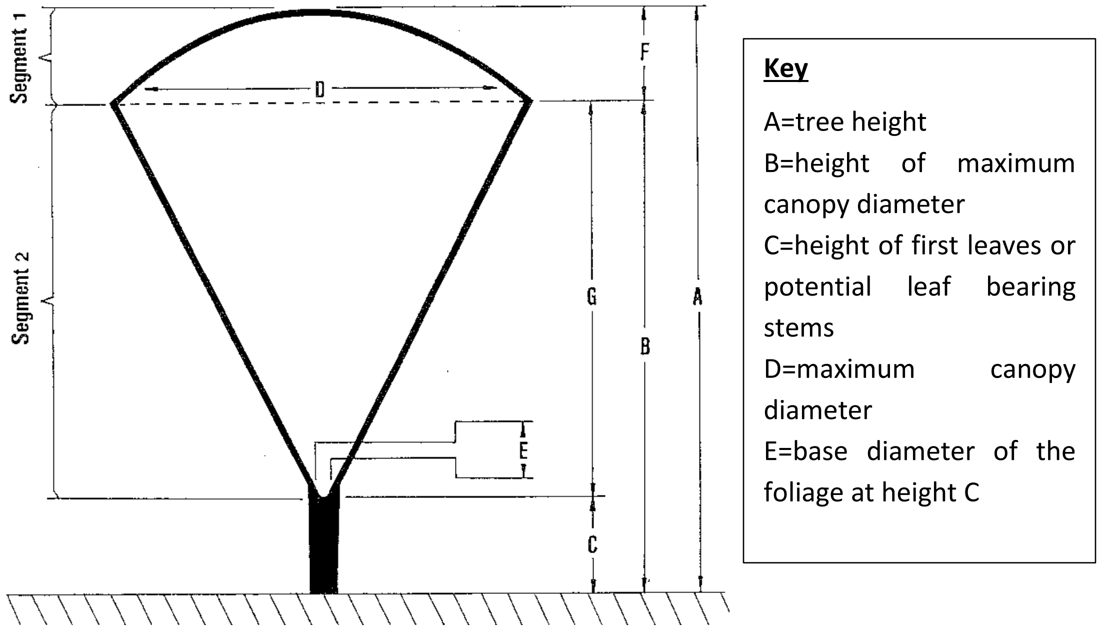
3.3 Sampling

Data used in the present study was collected from February until April 2016. Plots were set up at each site, and vegetation and soil sampling was performed. The demarcation of plots was done using measuring tapes and a GPS was used to record the position of each plot.

3.3.1 Phanerophytes measurements

Phanerophytes were divided into trees, shrubs and juveniles. Trees are self-supporting plants that are about 2 m tall, rooted and woody, possessing one or a few definite trunks that are normally branching above ground level (Edwards 1983). Shrubs are also self-supporting plants that are rooted and woody. However, shrubs are up to 5 m tall and the number of stems vary. It can either be multi-stemmed or single-stemmed when less than 2 m high or multi-stemmed and branching at or near ground level when 2-5 m high (Edwards 1983, Nangula 2007). Juveniles are all rooted woody plants up to 0.4 m high, including saplings and seedlings. All trees, shrubs and juveniles in each plot were identified and counted.

The biomass estimates from canopy volume (BECVOL) method was used to measure phanerophyte attributes (**Figure 9**). According to Smit (2014), BECVOL differs from other methods because it can provide estimates for both entire plants and plant portions. The three aspects of the agro-ecological implications of woody plants in African savanna that were considered most important in the development of BECVOL sampling method are: (1) competition with herbaceous vegetation for soil water and nutrients (bush encroachment), (2) food for browsers and (3) creation of sub-habitats suitable for desirable grass species (Smit 1989a, 2014).



Key

A=tree height
B=height of maximum canopy diameter
C=height of first leaves or potential leaf bearing stems
D=maximum canopy diameter
E=base diameter of the foliage at height C

Figure 9: *An illustration of BECVOL method for measuring trees. Adapted from Smit (1989).*

The height of phanerophytes were measured using a 3 m ranging pole which was placed as close to the tree as possible. The height of trees taller than the ranging pole was estimated. Tree basal circumference and diameter was measured using a 20 m measuring tape. Basal circumference was not recorded for shrubs and saplings with multiple stems.

3.3.2 Grass sampling

Grasses are all the herbaceous plants that are rooted, non-woody and belonging to the Poaceae family (Edwards 1983). Within each 50 m by 20 m plot, a 50 m line transect was set up using a 50 m measuring tape. At every 5 m interval, a horizontal rod was laid down across the line transect and grasses were sampled on each side of the rod following the Point-Centered Quarter (PCQ) sampling method (**Figure 10**). The PCQ sampling method was developed by Cottam and Curtis (1956) in order to determine tree and sapling compositions of woodlands in the northern Prairie-forest border region. This sampling method is very effective as it provides a means of taking rapid, yet quantitative samples of grassland vegetation which are free from subjective estimates (Dix 1961). PCQ sampling method yield both species composition and density data (Dix 1961, Stuart-Hill 1995, Sparks *et al.* 2002). All plant species (phanerophytes and grasses) which could not be identified in the field were collected and pressed, and taken to the National Herbarium of Namibia (WIND) for identification.

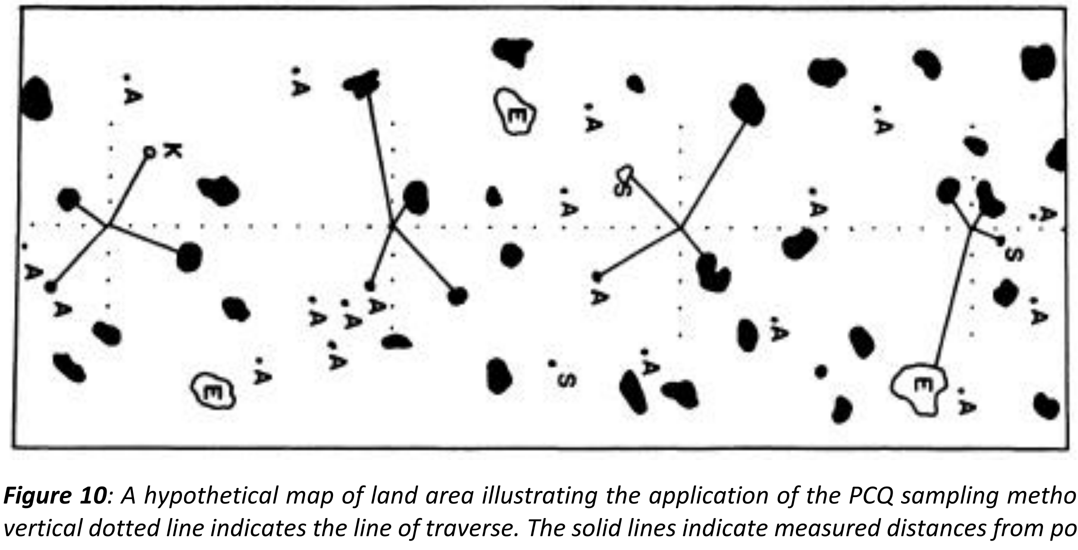


***Figure 10**: A hypothetical map of land area illustrating the application of the PCQ sampling method. The vertical dotted line indicates the line of traverse. The solid lines indicate measured distances from points to shoots (Dix, 1961).*

3.3.3 Soil sampling and chemical analysis

From each plot at each site, a composite sample of surface soil was collected from a depth of 0 – 3 cm and was done after surface litter was removed. The composite sample was prepared by combining soil samples taken from the corners and in the central point of the plot. Top soil (4 kg) was collected from each plot using a garden shovel and placed in a Ziploc bag that was labelled accordingly. Samples were then sun-dried to halt biological activities and subjected to analysis at the Ministry of Agriculture Water and Forestry (MAWF) laboratory. The analysis focused on soil pH, texture, organic matter and electrical conductivity. Soil samples were also tested for important macro elements such as; potassium, phosphorus, calcium, magnesium and sodium. Soil testing laboratory methods vary and this may influence results and adequacy ranges (Wells and Case 1995). Therefore, the sufficiency ranges in this research are only accurate for the test methods listed below.

Table 2: *Description of laboratory soil testing methods used.*

METHODS USED FOR SOIL ANALYSIS	
Sample preparation	Soil samples were dried at a temperature not greater than 35° C. A 2 mm sieve was used to sieve the soil samples, called the line earth fraction.
Phosphorus (ppm)	Ohlsen method (Olsen 1954): extraction with sodium bicarbonate. Phosphorus measured spectrophotometrically using the Phosphomolydate blue method.
extractable cations; K, Mg and Ca (ppm)	Extraction with 1M ammonium acetate at pH 7. Measurement of calcium, potassium, magnesium and sodium by atomic absorption spectroscopy (Pansu and Gautheyrou 2007, Brix 2008).
Soil texture	Dispersion of soil with sodium carbonate. Determination of silt and clay by pipette method. Sand fraction determined by sieving to retain less than 53 micron fraction. Textural Class using the USDA classification system (Wintermyer and Kinter 1955, Pansu and Gautheyrou 2007).
Organic matter	Walkey-Black method (Rowell 2000, Gelman *et al.* 2011). A factor is included in the calculations to take account of the incomplete oxidation. Organic matter content calculated as organic-C*1.74.

pH water	Measured in a 1:2.5 soil: water suspension on a mass to volume basis (Pansu and Gautheyrou 2007).
Electrical Conductivity (uS/cm)	Measurement of the supernatant of the 1:2.5 soil water suspension prior to measurement of pH (Pansu and Gautheyrou 2007).
Carbonate	Treatment of dry soil with 10% Hydrochloric acid and observation of effervescence (Pansu and Gautheyrou 2007).

3.4 Ethical considerations

This was non-destructive research. Research methodologies were explained to the farmers prior to data collection. Farm owners granted permission for the research to be performed on their farms. Permits for data collection (sampling) were obtained from the Ministry of Environment and Tourism (MET) and Ministry of Agriculture Water and Forestry. Plant parts collected and mounted were sent to the National Herbarium of Namibia (WIND) for identification and storage. All contributions made to the success of this study were acknowledged.

3.5 Data manipulation and analysis

All statistical analyses were performed with the SPSS version 23 (George and Mallery 2016) for Windows package and PC-Ord 6 (McCune *et al.* 2002). All data variables were assessed for normality using Kolmogorov-Smirnov test (K-S) (Quinn and Keough 2002). The K-S test compares observed and expected cumulative frequencies (Quinn and Keough, 2002). K-S test is suitable for comparing two frequency distributions where one distribution acts as the observed and the other act as the expected (Quinn and Keough 2002). Contrast to the Chi-square Goodness-of-fit test which depends on an adequate sample size for the approximations to be valid, K-S test itself does not depend on the underlying cumulative distribution function being tested (Quinn and Keough 2002).

3.4.1 Environmental gradient

A Nonmetric Multidimensional Scaling (NMS) ordination (Hoand 2008) was used to determine the main environmental factors influencing vegetation at selected sites along an aridity gradient. Unlike other ordination methods, Nonmetric Multidimensional Scaling (NMS) makes few assumptions about the nature of the data or the interrelationship of the samples and the link between the final output and the user's original data (Clarke and Warwick 1994, Quinn and Keough 2002, Wickelmaier 2003, Buja *et al.* 2008). NMS is relatively transparent and easy to explain. NMS has a great flexibility both in the definition and conversion of dissimilarity to distance and its rationale is the preservation of these relationships in the low dimensional ordination space (Quinn and Keough 2002, Wickelmaier 2003). It is therefore well suited for various types of data. Another advantage of NMS is that it allows the use of any distance measure of the samples, unlike other methods which specify particular measures such as implied Chi-square measure in DCA or the covariance or correlation in PCA (Holland 2008). The unique advantage of NMS is its ability to represent more complex relations accurately in low dimensional space (Buja *et al.* 2008).

The environmental data (adapted from Pitman (1980) and Mendelson *et al.* (2009)) was overlaid as a biplot to indicate the environmental gradients of interest. A second biplot was created using plant functional attributes and a third biplot was created using plant structural attributes, species diversity indices and richness as variables. The environmental factors used consisted of the following variables; annual minimum temperature, annual maximum temperature, mean annual rainfall, humidity, pH, electrical conductivity, organic matter, phosphorus, potassium, calcium, sodium, % sand, % clay and % silt.

Plant functional attributes used were leaf size (macrophyll and microphyll leaves), leaf duration (deciduous, semi-deciduous, evergreen and semi-evergreen) and plant life form (mesophanerophytes, microphanerophytes and nanophanerophytes). The leaf sizes were combined as follows: microphyll leaves with leaf sizes ≤ 2025 mm^2, and macrophyll leaves with leaf sizes ≥ 2025 mm^2 (Gillison and Carpenter 1997, Strohbach and Kutuahuripa 2014). Growth forms used in the study were defined as follows; mesophanerophytes defined as all perennial woody plants with a height from 8 m to 30 m, and microphanerophytes defined as all perennial woody plants with a height from 2 m to 8 m and nanophanerophytes defined as all perennial woody plants with a height between 25 cm and 2 m (Esten 1932, Raunkiaer 1934, Skarpe 1996). Plant functional attributes were identified using the *Tree Atlas of Namibia* (Curtis and Mannheimer 2005)*,* and the *Field guide to trees and shrubs of Namibia* (Mannheimer and Curtis 2009). Variables used in the third biplots were species richness, Shannon-Wiener diversity index, Simpsons diversity index, total phanerophytes canopy volume and leaf volume production at maximum browsing heights (MBH) of 1.5 m, 2.0 m and 5.0 m (see **sections 3.4.1, 3.4.2 and 3.4.4** for calculation formulas).

3.4.2 Phanerophyte species diversity and richness

Species diversity is the number of species and the abundance of each species present in a particular area while species richness is the number of species present in a particular area (Pielou 1975). Species diversity and richness are fundamental in determining ecosystem health. At each site, phanerophytes species richness was counted, and Shannon-Wiener diversity indices and Simpson's diversity indices were calculated using the following formulas;

Shannon-Wiener index (H’) (Peet 1974, Pielou 1975):

$$H' = -\sum_{i=1}^{s} (pi * \ln pi)$$

Pi= the proportion of individuals found in the *i*th species.

Simpson index (Peet 1974, Magurran 2013):

$$D = 1 - \left(\frac{\sum n(n-1)}{N(N-1)}\right)$$

n= the number of individuals of each different species.

N= the total number of individuals of all the species.

Shannon-Wiener diversity index and species richness were normally ditributed while Simpson diversity index was not normally distributed according to Kolmogorov-Smirnov test. Possible differences in Shannon-Wiener diversity index and species richness among the five study sites were tested using a one-way Analysis of Variance (ANOVA) (Clarke and Warwick 1994). Furthermore, a multiple comparison test, Tukey's *post hoc* range test, was used to determine the means that differed (Abdi and Williams 2010). A Kruskal-Wallis test (McDonald 2014) was used to assess significant differences in the Simpson diversity index data and a *post hoc* test using the Mann-Whitney U test analysis (Nachar 2008). The Kruskal-Wallis test also known as the H-test is a non-parametric alternative to the one-way ANOVA (Struwig *et al.* 2001). The Kruskal-Wallis test uses an ordinal scale of measurement and determines whether three or more independent groups or treatments originate from the same population (Struwig *et al.* 2001).

3.4.3 Phanerophytes density and grass sward density

Phanerophyte density was calculated based on a formula:

$$D = \frac{N}{A}$$

Where D is the density, N is the number of sampled phanerophytes and A is the size of the plot from which phanerophytes were sampled (Gotelli & Colwell 2011, Pielou 1975). Density for phanerophytes was expressed in number per hectare.

Grass sward density was calculated using the formula:

$$Mean\ distance = \frac{\mathrm{d1 + d2 + d3 + \cdots dn}}{36}$$

Where d was the distance to the nearest grass, 36 was the number of distances recorded in a plot. Density for grasses was expressed per 100 m^2. Grass sword density formula was based on the formula developed by(Dix 1961).

$$Grass\ density\ per\ 100\ m^2 = \frac{100}{(mean\ distance)^2}$$

Density data for phanerophytes and grasses at the five study sites were not normally distributed according to the Kolmogorov-Smirnov test. A Kruskal-Wallis test (McDonald 2014) was used to assess significant differences in the density data and a *post hoc* test using the Mann-Whitney U test analysis was used to determine where the significant differences were.

3.4.4 Phanerophyte canopy volume

Total phanerophyte canopy volume

In order to calculate the volume of any phanerophyte, volume formulas of; an ellipsoid, a right circular cone, a frustum of a right circular cone or a right circular cylinder is used depending on the shape of the phanerophyte (Spiegel 1968, Smit 1989b). In addition to the measurements A, B, C, D and E previously described in **Figure 9**, the following dimensions were necessary for phanerophyte canopy volume calculations (**Figure 11**).
F=Height of tree crown (A-B)
G=Height of tree base (B-C)

Depending on the shape of the phanerophyte, any one or more or a combination of more than one volume formula(s) indicated below were used to calculate total phanerophyte canopy volume. If the shape of the phanerophyte resembled parts of two different shapes, the canopy volume of that phanerophyte was calculated in two parts. The first part was located above the level of the maximum canopy diameter (B), and the other below this level (B) (Smit 1989b).

Volume of phanerophyte segment I and II (Smit 1989b)***:***

$$Volume = \frac{(22/7) * \mathrm{D}{}^\wedge 2 * \mathrm{F}}{6}$$

Volume of phanerophyte segment III and IV (Spiegel 1968, Smit 1989b):

If E was equal to D, the volume was calculated as:

$$Volume = (22/7) * (\mathrm{D}/2)^2 * \mathrm{G}$$

If E was equal to 0, the volume was calculated as:

$$Volume = (1/3) * (22/7) ** (\mathrm{D}/2)^2 * \mathrm{G}$$

If E was bigger than 0, but smaller than D, the volume was calculated as:

$$Volume = (1/3) * (22/7) * \mathrm{G} * ((\mathrm{D}/2)^2 + (\mathrm{D}/2) * (\mathrm{E}/2) +* (\mathrm{E}/2)^2)$$

Leaf volume production at different mean browsing height (MBH)

Leaf volume production of phanerophyte below 1.5 m, 2 m and 5 m mean browsing height (MBH) were calculated. The height of 1.5 m represented the MBH of a Boer goat (*Capra aegagrus hircus)* and impala (*Aepyceros melampus*) (Aucamp 1976, du Toit 1990), while 2.0 m and 5.0 m heights represented the MBH of a kudu (*Tragelaphus strepciseros*) and giraffe (*Giraffa camelopardalis*) respectively (du Toit 1990). Leaf volume production was calculated depending on the height of the MBH in relation to the phanerophyte height (Height A) (**Figure 9 and 11**):

(i) When MBH was above A, the volume of a complete tree was used (Spiegel 1968, Smit 1989b).

(ii) When MBH was below C, the available browse was zero (Spiegel 1968, Smit 1989b).

(iii) When MBH was above B but below A (**Figure 11a**), tree segments **I** and **II** were divided by the MBH. The parts above the MBH were calculated and deducted from the complete volume of that particular plant (Spiegel 1968, Smit 1989b).

$$Volume\ above\ MBH = \frac{(22/7) * \mathrm{H}^2 * \mathrm{I}}{6}$$

Where

$$\mathrm{H}^2 = \frac{\mathrm{D}\hat{}2 * (\mathrm{F}^2 - \mathrm{J}^2)}{\mathrm{F}^2}$$

(iv) When MBH was below B but above C (**Figure 11**), Segments **III** and **IV** were divided by the MBH. The volume below the MBH was calculated directly. To calculate this volume, the new height L and new radius K (**Figure 11)**, were determined (Spiegel 1968, Smit 1989b).

$$\mathrm{L} = MBH - C$$

Determination of K:

$$\mathrm{M} = \frac{\mathrm{D} - \mathrm{E}}{\mathrm{G}}$$

$$\mathrm{N} = M * L$$
$$\mathrm{K} = N + E$$

Values K and L then replace D and G in the appropriate volume expression (Spiegel 1968, Smit 1989b).

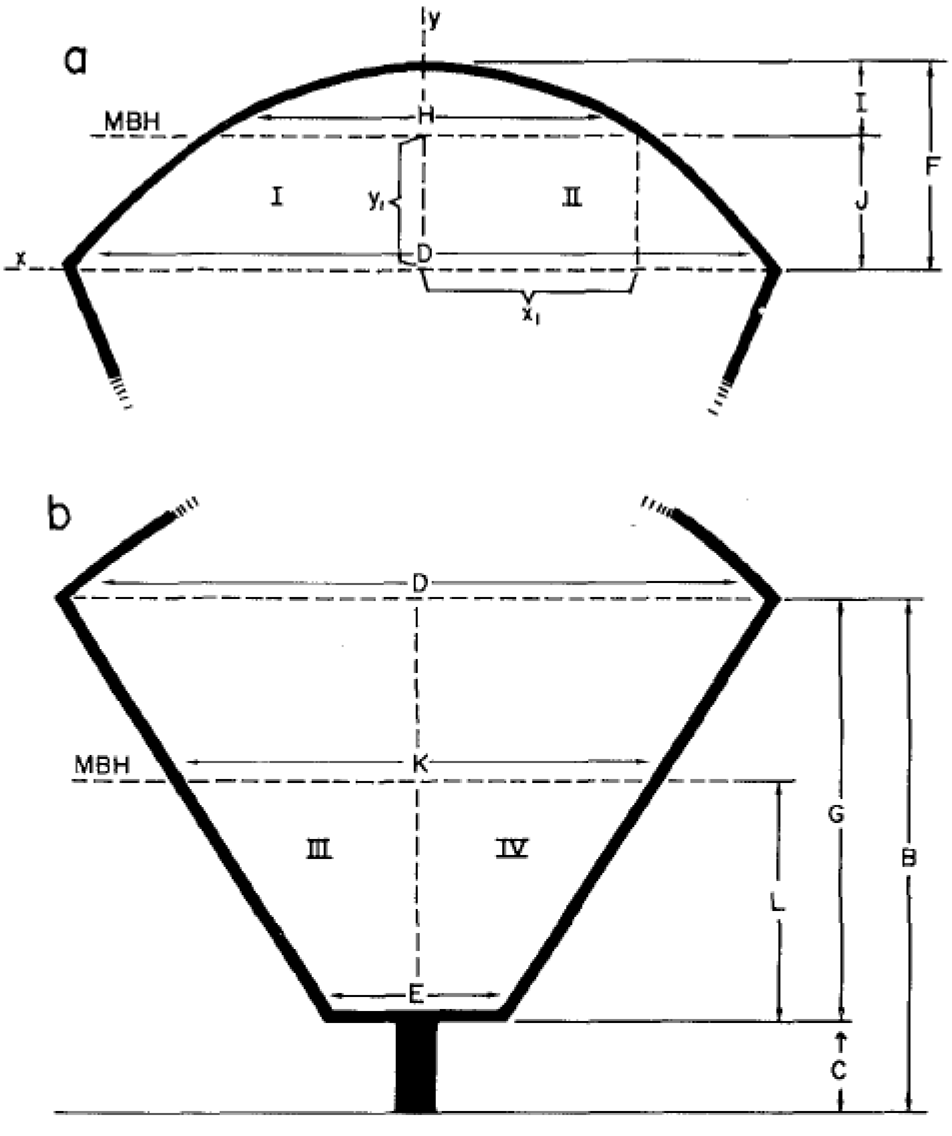


Figure 11*: Examples of (a) tree segments* **I** *and* **II** *divided by the MBH, and (b) segments* **III** and **IV** *divided by the MBH. Adapted from Smit (1989b).*

3.4.5 Phanerophytes heights

All height values of phanerophytes at the different study sites along the aridity gradient were arranged into the following height classes: <0.5, 0.5-1.5, 1.6-2.5, 2.6-3.5, 3.6-4.5, 4.6-5.5, 5.6-6.5, 6.6-7.5, 7.6-8.5, 8.6-10.5, 10.5-15.5, and >15.6 (m). A Pearson's Chi-square (χ2) test (Runyon *et al.* 2000) was used to test for differences in distribution patterns of height classes among the study sites. The observed and expected frequencies were compared to indicate where the differences were.

3.4.6 Phanerophytes basal area

The basal area of each phanerophyte was calculated from basal circumference using the formula:

$$BA = \frac{\mathrm{C}^2}{4\;x\;\pi}$$

Where BA was the basal area and C was the circumference. The basal area formula was used with an assumption that the stems were circular. Basal area values of all phanerophytes per plot were added together to give a total basal area per plot. The total basal area for each study site was then calculated.

The Kolmongrov-Smirnov test indicated that the data for phanerophyte mean basal area was not normally distributed hence, a Kruskal-Wallis test was used to test for significant differences in the mean basal area at the five study sites along the aridity gradient. Mann-Whitney U test was used to determine where the significant differences were.

Chapter 4: Results

4.1 Environmental gradient

A Kolmogorov-Smirnov test for normality indicated that all the environmental variables were not normally distributed ($P < 0.05$). Multivariate statistics specifically Nonmetric Multidimensional Scaling (NMS) was used to determine vegetation-environment relationship. NMS ordination procedure was done using Sørensen (Bray-Curtis) distance measure. Number of runs used with real data was 200. After 500 number of iterations a final solution was reached with a stress of 13.310 and a final instability of 0.000001. A varimax Rotation of the results was requested. The resulting ordination graph was overlaid as a biplot (**Figure 12**). In addition, second and third biplots were created using plant functional attributes (**Figure 13**) and phanerophyte structural attriutes (**Figure 14**) respectively.

According to **Figure 12**, humidity (r= 0.855, tau= 0.631) and mean annual rainfall (r=0.835, tau=0.631) were positively correlated with ordination Axis 1 whilst annual minimum temperature (r=-0.565, tau=-0.067) and pH (r= -0.448, tau=-0.290) were negatively correlated with Axis 1. A strong positive correlation between phanerophyte distribution, and mean annual rainfall and humidity was revealed (**Figure 12)**. However, humidity and rainfall are very closely related, it was therefore logical to set mean annual rainfall as a spatial proxy for differences in vegetation across the five selected study sites along an aridity gradient.

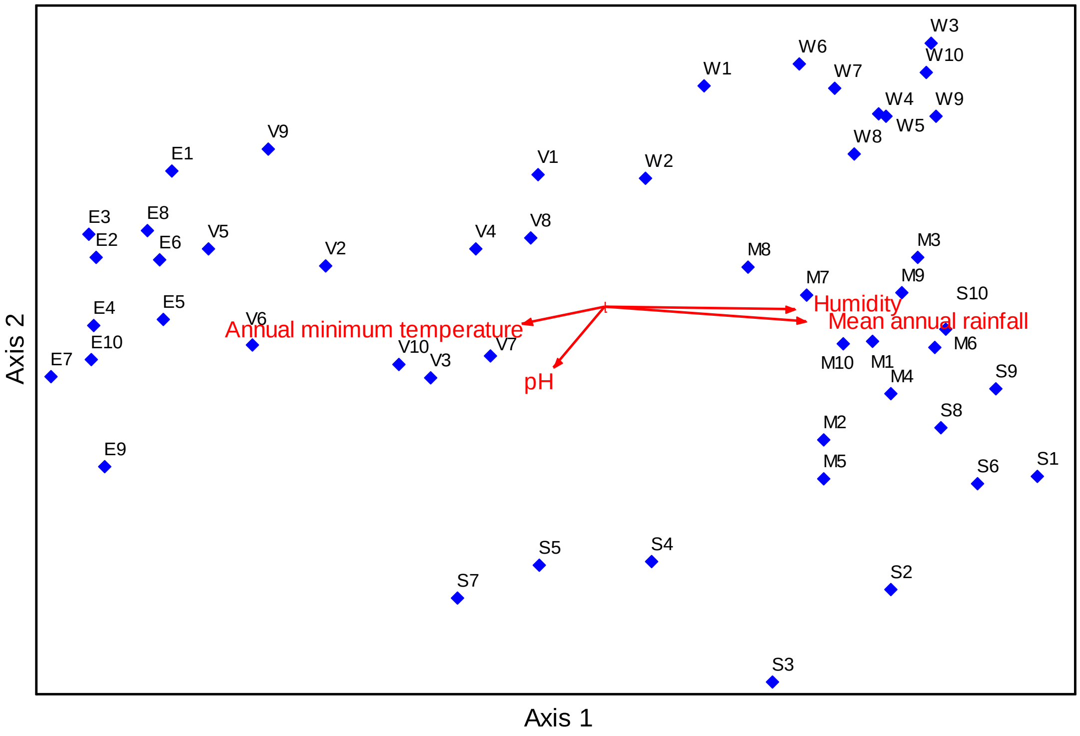


Figure 12: *NMS result of phanerophyte data illustrating a biplot overlaid with environmental factors (M=Mile 46, S=Sonop, W=Waterberg, V=Sandveld and E=Ebenhaezer).*

The change in key plant functional attributes were determined on the NMS ordination (**Figure 13).** Inferring to **Figure 13**, the main aridity gradient manifests itself in a gradual change from evergreen plants (r=0.631 and tau=0.499) and plants with macrophyll leaves (r= 0.658 and tau=0.518) in high rainfall areas to deciduous plants (r= -0.567 and tau=-0.462) and plants with microphyll leaves (r=-0.645 and tau=-0.530) in low rainfall areas.

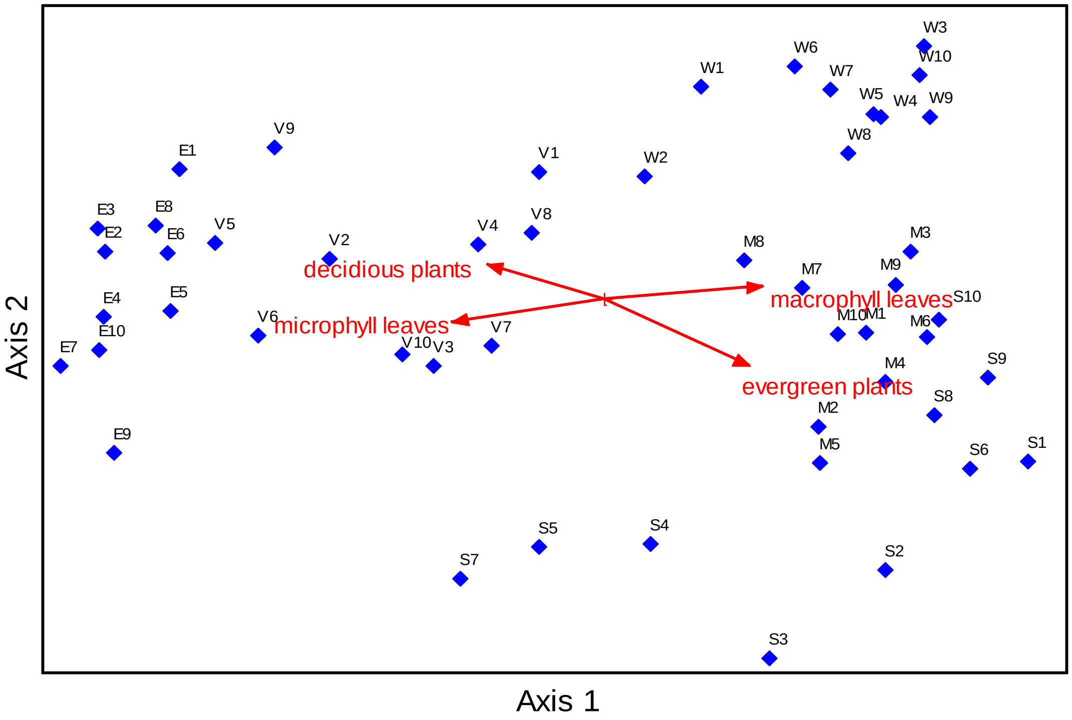


Figure 13: *NMS ordination diagram overlaid with plant functional attributes as biplots (M=Mile 46, S=Sonop, W=Waterberg, V=Sandveld and E=Ebenhaezer).*

NMS ordination (**Figure 12)** was overlain with vegetation structural attributes such as, phanerophyte total canopy volume, leaf volume production at diferent MBH, diversity indices and species richness data. It was disclosed that phanerophyte total canopy volume (r= 0.503, tau=-0.489), leaf volume production at 5 m MBH (r= 0.549, tau=-0.525), species richness (r= 0.643, tau=0.474) and Shannon-Wiener index (r= 0.638, tau=-0.422) were positively correlated with mean annual rainfall (**Figure 14**). Also refer to **Figure 15, 16, 18, and 19**.

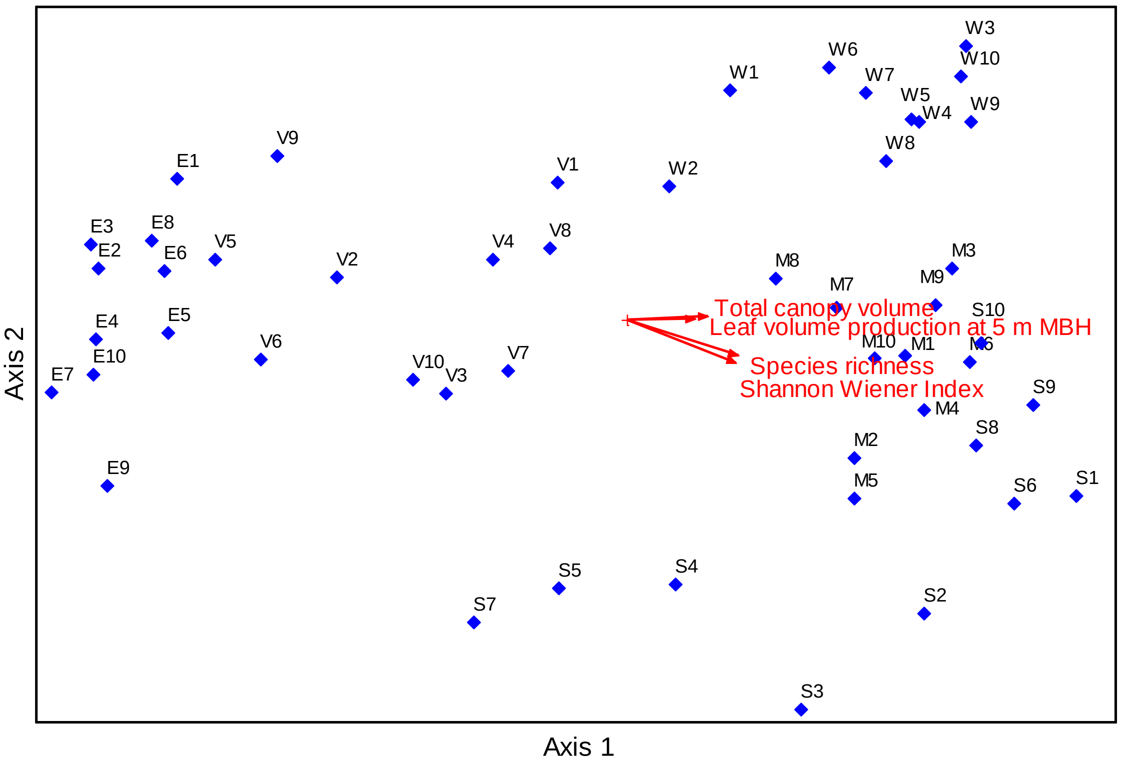
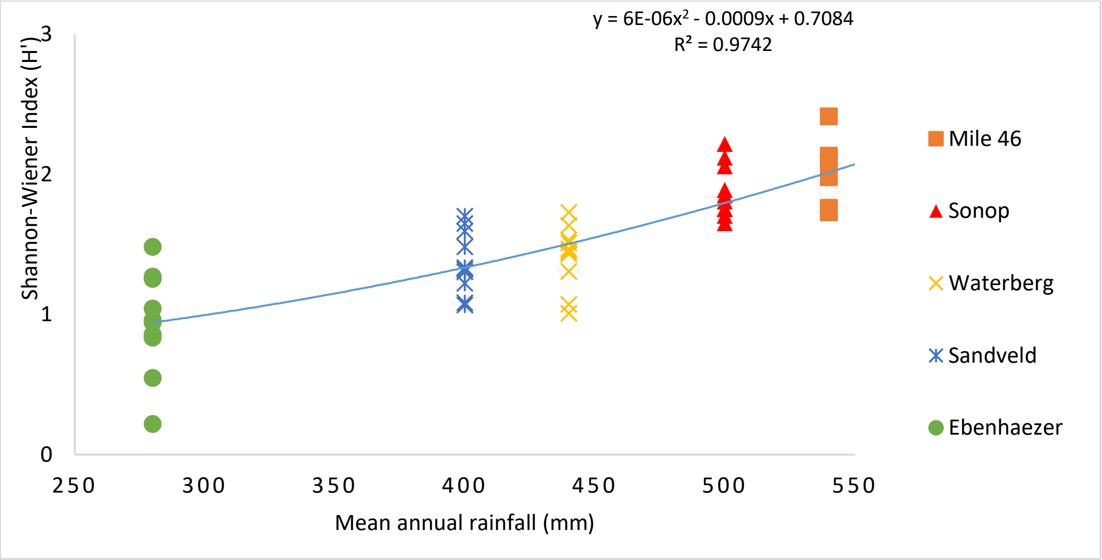


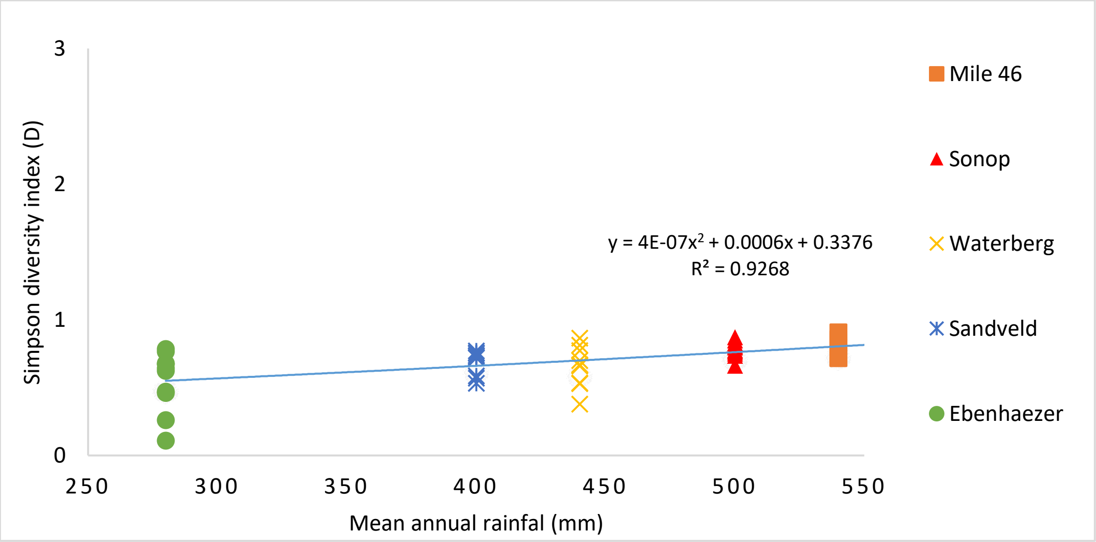
***Figure 14**: NMS ordination diagram with plant structural attributes as biplots (M=Mile 46, S=Sonop, W=Waterberg, V=Sandveld and E=Ebenhaezer).*

4.2 Species diversity and richness

The Kolmogorov-Smirnov test was used to determine whether the diversity indices and species richness data followed a normal distribution. The Kolmogorov-Smirnov test indicated that Shannon-Wiener Index (H') data for the five study sites along an aridity gradient were normally distributed ($P > 0.05$) while Simpson Index data were not normally distributed ($P < 0.05$). It was noted that there was a significant difference in species diversity among the selected study sites along an aridity gradient; Shannon-Wiener Index (H’) using the one-way ANOVA (F = 27.105, df = 4, P < 0.001) and Simpson Index using Kruskal-Wallis test (H = 19.280, df = 4, P < 0.005). However, Tukey’s HSD test indicated that there was no significant difference in Shannon-Wiener Index recorded at Waterberg and Sandveld (P > 0.05). According to **Figure 14** and **15**, there was a general increase in species diversity with increasing mean annual rainfall.



a)



b)

Figure 15: *Change in phanerophyte species diversity (a) Shannon-Wiener index (H’) and (b) Simpson Index along an aridity gradient.*

Species richness

The Kolmogorov-Smirnov test indicated that species richness data for the five selected study sites along an aridity gradient were normally distributed ($p = 0.102$). The one-way ANOVA indicated a significant difference in species richness at the five study sites along an aridity gradient ($F = 29.627$, $df = 4$, $P < 0.001$). There was a general increase in species richness with an increase in mean annual rainfall (**Figure 14 and 16**). However, Tukey's HSD test indicated that there was no significant difference in species richness recorded at Waterberg and Sandveld ($P > 0.05$).

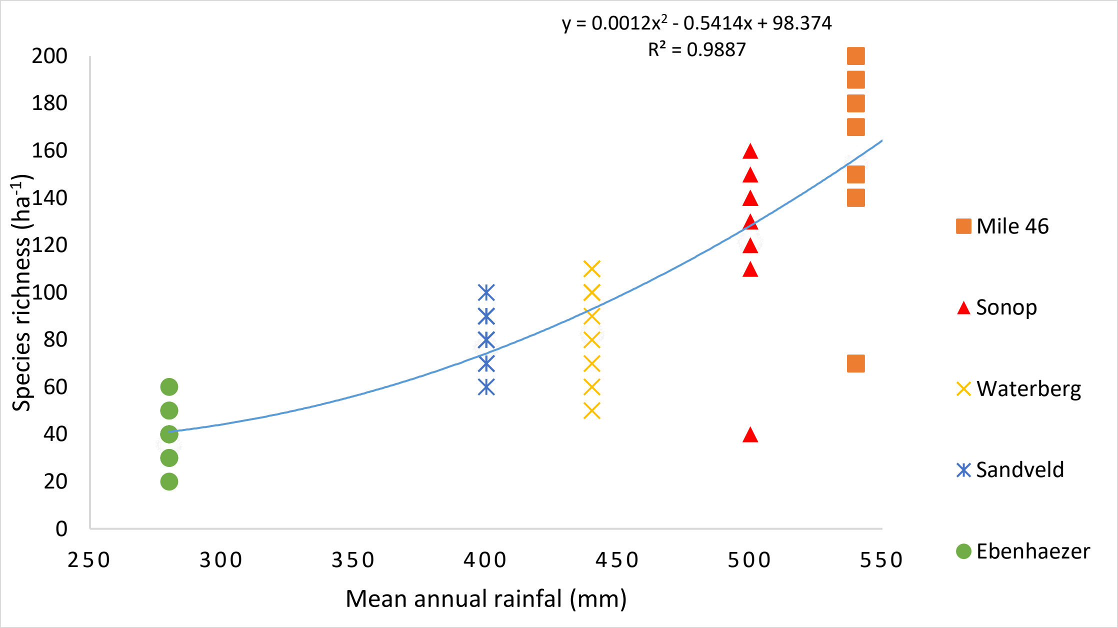
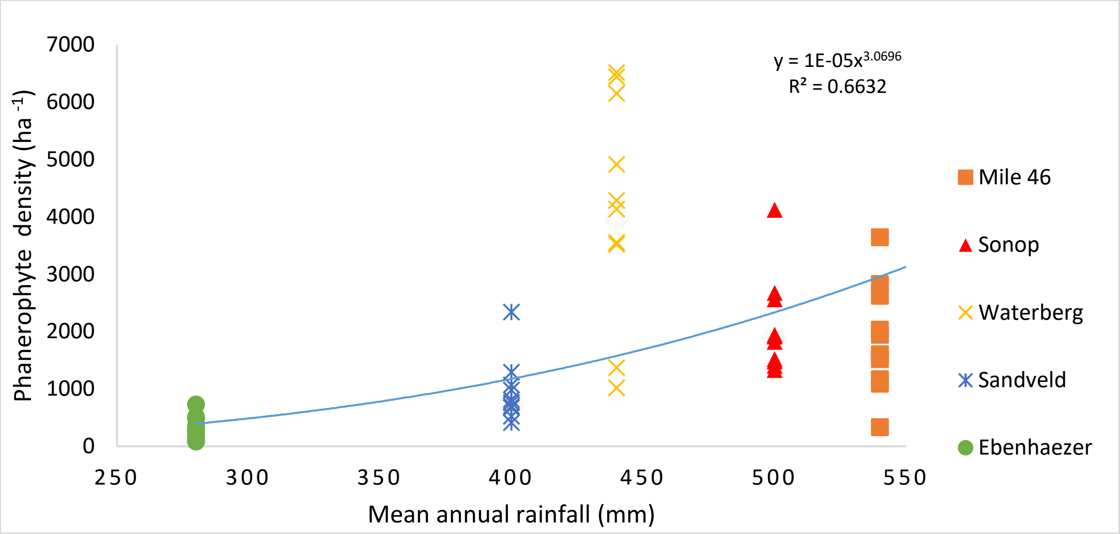


Figure 16: *The relationship between species richness and Mean annual rainfall on Kalahari sands.*

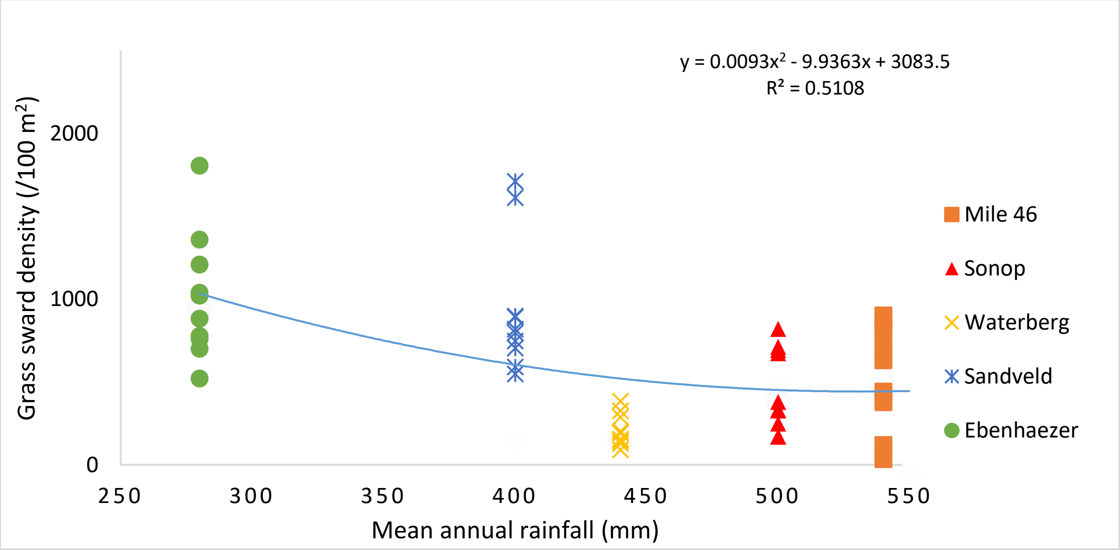
4.3 Density

Phanerophyte density per hectare and grass sward density per 100 m^2 at five different study sites along the Kalahari sands aridity gradient were calculated and plotted **(Figure 17a)**. According to the Kolmogorov-Smirnov test, phanerophyte density and grass sward density were not normally distributed ($P< 0.05$). The highest phanerophyte density was recorded at mean annual rainfall of 440 mm (Waterberg) while the lowest phanerophyte density was recorded at mean annual rainfall of 280 mm (Ebenhaezer), and the opposite was true for grass sward density (**Figure 17b**). In addition, Kruskal-Wallis test revealed a significant difference in phanerophyte density (H =

34.365, df = 4, P < 0.001) and grass sward density (H = 19.280, df = 4, P < 0.005) at the five selected study sites along the aridity gradient.



a)



b)

Figure 17*: Change in (a) Phanerophyte density (ha $^{-1}$) and (b) Grass sward density at the five study sites along an aridity gradient.*

4.4 Phanerophyte total canopy volume

Total canopy volume was calculated for all the five selected study sites along the aridity gradient and plotted (**Figure 18**). According to the Kolmogorov-Smirnov test, total canopy volume at the five selected study sites along an aridity gradient was not normally distributed (P < 0.05). A nonparametric Kruskal-Wallis test showed that there was a significant difference in the total canopy volume recorded at the five selected study sites along an aridity gradient (H = 24.298, df = 4, P < 0.001). Total canopy volume increased with increasing mean annual rainfall (**Figure 14 and 18**).

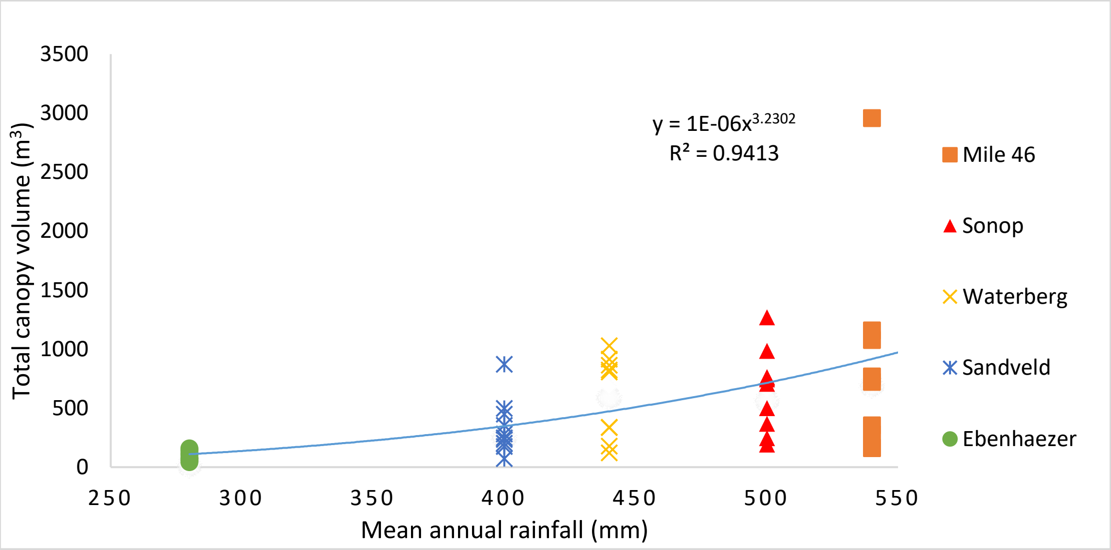
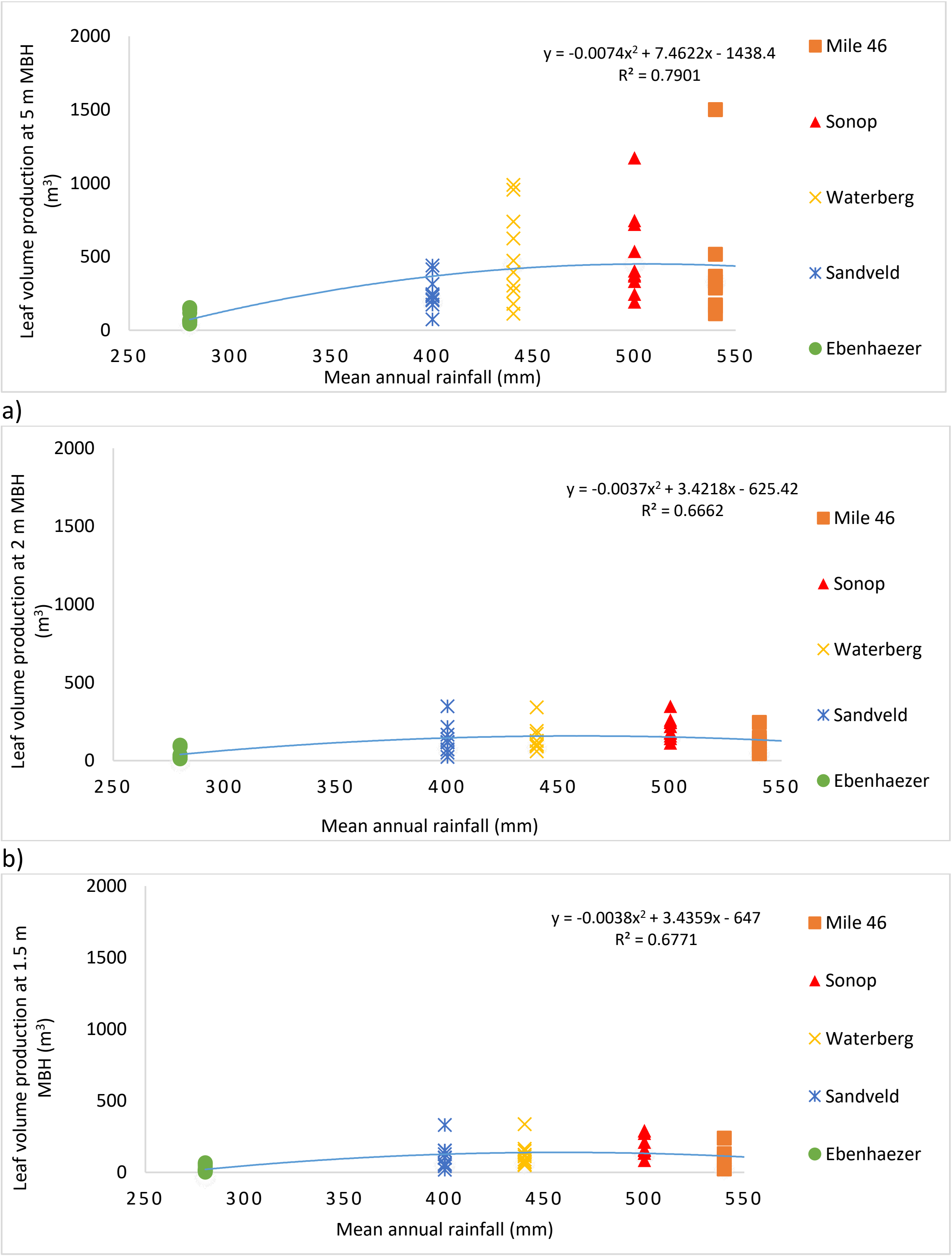


Figure 18: *Relationship between phanerophyte total canopy volume and Mean annual rainfall on the Kalahari sands.*

4.4.1 Leaf volume production

Leaf volume production at 5 m, 2 m and 1.5 m mean browsing height (MBH) was calculated and plotted (**Figure 18**). According to the Kolmogorov-Smirnov test, leaf volume production at 5 m, 2 m and 1.5 m MBH data at the five selected study sites along an aridity gradient was not normally distributed (P < 0.05), P < 0.05, and P < 0.05 respectively). Furthermore, Kruskal-Wallis test showed a significant difference in leaf volume production at all the mean browsing heights recorded at the five selected study sites along an aridity gradient; 5 m (H = 25.652, df = 4, p < 0.001), 2 m (H = 24.044, df = 4, P < 0.001) and 1.5 m (H = 25.694, df = 4, P < 0.001).



a)

b)

c)

Figure 19: Change in leaf volume production at 5 m MBH (a), 2 m MBH (b), and 1.5 MBH (C) along an aridity gradient.

4.4 Phanerophyte height distribution and basal area

The proportion of phanerophyte at different rainfall areas was recorded depending on their respective height class (**Table 3**). There was a significant difference in height proportions of phanerophyte along an aridity gradient ($\chi2=4461.097$, df= 4, $p < 0.001$).

Table 3*: Comparisons of phanerophyte height proportion patterns along an aridity gradient.*

	MEAN ANNUAL RAINFALL				
Height class	**280 mm**	**400 mm**	**440 mm**	**500 mm**	**540 mm**
<0.5	12.9	6.8	174.3	37.1	58.8
0.5-1.5	8.6	56.7	197.2	102.7	67.2
1.6-2.5	5.9	27	13.8	61	31.8
2.6-3.5	2.1	6.7	6.8	11.1	4.1
3.6-4.5	2.7	2.2	4.5	3.5	3.5
4.6-5.5	0.6	2.3	4.7	0.9	1.9
5.6-6.5	0.7	0.8	5.9	0.5	1.4
6.6-7.5	0.2	0.5	5.5	0.3	0.9
7.6-8.5	0.1	1.2	1.7	0.4	1.1
8.6-10.5	0.2	0.3	2.3	1.1	0.7
10.6-15.5	0	0.1	0.9	0.5	1.6
>15.6	0	0	0.4	0.2	0.8

There was a significant difference in height proportions of phanerophyte along an aridity gradient ($\chi2=4461.097$, df= 4, $p< 0.001$).

Basal area

According to the Kolmogorov-Smirnov test, phanerophytes basal area at the five selected study sites along the aridity gradient was not normally distributed ($P < 0.05$). In addition, Kruskal-Wallis test revealed that the distribution of phanerophytes basal areas is not the same across the five study sites along the aridity gradient ($H = 17.685$, df = 4, $P < 0.005$). Conferring to **Figure 20**, the highest phanerophyte basal area was recorded at 540 mm mean annual rainfall (Ebenhaezer) while, the lowest basal area was recorded at mean annual rainfall of 280 mm (Waterberg). Generally **Figure 20** depicted an increase in basal area with increasing mean annual rainfall.

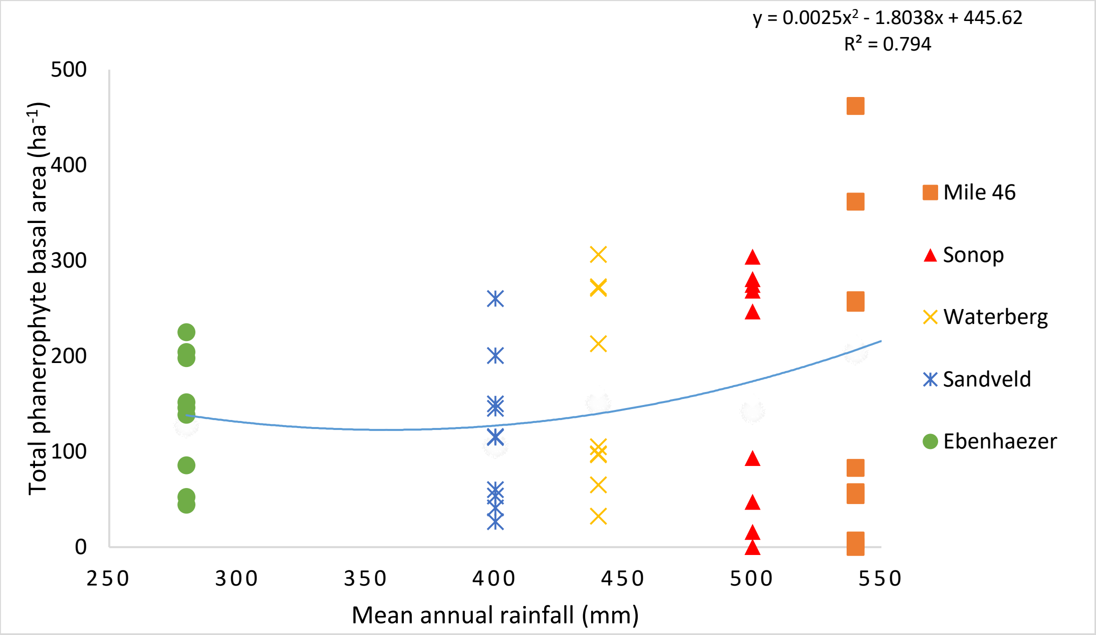


Figure 20: *Relationship between phanerophyte basal area and Mean annual rainfall.*

Chapter 5: Discussion

5.1 Environmental gradient

The present study found that mean annual rainfall was the main environmental factor influencing vegetation distribution (**Figure 11 & 12**). Rainfall plays a significant role in plant growth, development and survival, hence excess or lack of water can be detrimental to plant species depending on their tolerance level. Rainfall has been reported to be the main environmental factor influencing vegetation distribution in other studies (O'Brien 1993, Skarpe 1996, Scholes et al. 2002, Pillay and Ward 2014, Strohbach and Kutuahuripa 2014, Axelsson and Hanan 2017). Inferring to **Figure 12**, the rainfall gradient was demonstrated from low rainfall areas (Ebenhaezer and Sandveld) to high rainfall areas (Waterberg, Sonop and Mile 46).

Irrespective of all plots at Sonop receiving similar mean annual rainfall, plot S5 and S7 were plotted differently from other Sonop plots due to a positive correlation between with soil pH. It can be inferred that pH has an effect on species distribution over a relative short spatial scale. Soil pH is essential to vegetation as it exerts an effect on the solubility of plant nutrients through controlling the presence or activities of many micro-organisms. McLean (1982) also disclosed a significant positive correlation between species richness and density, and soil pH. Differences among plots at Sonop also possibly reflected local variations in species structure since pH is highly associated with plant succession (Collins *et al.* 1989).

Sandveld and Ebenhaezer were positively correlated with minimum annual temperature (**Figure 12**). Sandveld and Ebenhaezer experience many cold days compared to the other study sites. According to Mendelson *et al.* (2009), Sandveld and Ebenhaezer receive on average about 20 to 30 days of frost in a year whereas Mile 46, Sonop and Waterberg receive less than 5 days of frost in a year. This highlights the significance of temperature in plants survival and distribution. This is in agreement with Haferkamp (1988) who stated that each vital process is restricted to a certain temperature range and has an optimum temperature on each side of which performance decline. Woodward (1988), Skarpe (1996) and Wakeling *et al.* (2012) also revealed minimum temperature as one of the environmental factors influencing vegetation distribution. Not all species have the ability to tolerate and survive many days of frost especially juveniles and short shrubs (Wakeling *et al.* 2012), corroborating with the low abundance of phanerophyte juveniles recorded at Sandveld and Ebenhaezer (**Table 3**). It has been suggested that a number of broad leaved phanerophyte are frost sensitive (Skarpe 1996), this is confirmed by the present study's results (**Figure 13**) that showed; microphyll leaves in areas subjected to low temperature and many days with frost (Sandveld and Ebenhaezer), and macrophyll leaves (broad leaved species) in areas exposed to less frost days (Mile 46, Sonop and Waterberg). In addition, Wakeling *et al.* (2012) stated that savanna trees grow more slowly in cooler sites compared to warmer sites.

5.1.1 Plants functional attributes along the aridity gradient

Over decades, plants have evolved various adaptive features in response to changes in environmental factors and disturbances. Plants are known to quickly detect changes in their environment and deploy necessary survival mechanisms. For example, many plants slow down or completely stop growing when conditions are not favorable and resume growth when conditions are propitious (Skarpe 1996). Gillison and Carpenter (1997) and Burke (2006) also stated that high water use efficiency by plants such as *Acacia erioloba*, dual water obtaining strategies found in species such as *Faidherbia albida* and photosynthetic layer under the translucent bark (cortic photosynthesis) of *Commiphora* species are some of the strategies that help plants adapt in xeric environments. The present study was conducted on Kalahari sands. Strohbach and Kutuahuripa (2014) argued that high hydraulic conductivity of sandy soils leads to less time of water in the upper soil layer through fast water infiltration. The fast water infiltration on sandy soils culminates into more water being accessible to deeper rooted plants compared to shallow rooted plants as water only stays for a short time in the upper soil layer (Strohbach and Kutuahuripa 2014).

The present study revealed a decrease in leaf size with decreasing mean annual rainfall. Leaf size is one of the main mechanisms employed by plants in response to water availability because leaf size influences the amount and rate of transpiration. Larger leaves have a huge surface area and are known to develop thicker boundary layers of still air compared to smaller sized leaves. This results in larger leaves shedding heat more slowly, leading to overheating (Givnish 1984, McDonald *et al.* 2003). Since transpiration is essential for heat shedding, studies have shown that smaller sized leaves are more suitable in low rainfall areas compared to high rainfall areas (Meier and Leuschner 2008). In the present study, the changes from microphyll leaves in low rainfall areas to macrophyll leaves in high rainfall areas (**Figure 13**) happened over a relative short rainfall gradient of about 270 mm mean annual rainfall. Comparable results have been recorded in high rainfall gradients of approximately 588 mm and in lower rainfall gradients of less than 150 mm mean annual rainfall (Strohbach and Kutuahuripa 2014). Strohbach and Kutuahuripa (2014) attributed the differences in plant leaf sizes to changes in soil moisture availability due to changes in the soil texture.

The results of the present study further showed a relationship between mean annual rainfall and leaf type demonstrated by evergreen leaves in high rainfall areas to deciduous plants in low rainfall areas (**Figure 13**). Deciduous plants are well adapted to low rainfall through investing less energy in leaf production and shedding off leaves when conditions become unfavourable, consequently reducing moisture loss (Skarpe 1996, Wana and Beierkuhnlein 2011) as opposed to evergreen leaves with high leaf production and maintenance. In contrast, Chabot and Hicks (1982) argued that as water availability decreases, it may be more economical to retain leaves throughout the year than to shed and replace seasonally. Orians and Solbrig (1977) complemented Chabot and Hicks (1982) by stating that evergreen leaves are known to favour plants through improving carbon balance, nutrient conservation, and a general balance to environmental stress.

5.2 Phanerophyte species diversity and richness

For many community ecologists and conservation biologists, measuring species richness and diversity has been a fundamental objective since it can be used to determine and explain vegetation-environment relationships (Gotelli and Colwell 2011). In the present study, it was noted that species richness and diversity increased with increasing mean annual rainfall. Similar results were reported by Poorter (2004), Adler and Levine (2007), Jianshuang *et al.* (2012) and Rutherford and Powrie (2013). However, studies have also indicated the importance of other environmental factors such as pH (Adler and Levine 2007, Dingaan *et al.* 2017) and soil fertility (Gentry 1988, Enright *et al.* 1994, Harpole and Tilman 2007) as main environmental variables influencing species diversity and richness.

Pourbabaei *et al.* (2014) emphasized the importance of rainfall by studying the effect of drought on species richness and diversity in the Oak forests of Western Iran. It was revealed that species richness and diversity decreased significantly due to drastic declines in total annual precipitation from about 430 mm in 2007 to 210 mm in 2008. Results further disclosed a significant increase in species richness and diversity when total annual precipitation increased from about 210 mm in 2008 to 360 mm in 2009. Different species have different ecological niches for moisture as demonstrated in the present study, *Terminalia sericea* was recorded at study sites with 540 mm, 500 mm, 450 mm and 400 mm but not at 280 mm suggesting that 280 mm mean annual rainfall is not conducive for the growth and survival of *Terminalia sericea*. The absence of *Terminalia sericea* at 280 mm contributed to the low species diversity and richness recorded at 280 mm (Ebenhaezer).

Other species that contributed to the decrease in species richness and diversity with decreasing mean annual rainfall are *Ochna pulchra*, *Burkea africana*, *Combretum collinum* and *Combretum psidioides* not recorded at and below 400 mm as well as; *Baphia massaiensis, Commiphora africana* and *philoneptera nelsii* not recorded at or below 450 mm (see **Appendix 2**). It is therefore logical to state that under the projected change in climate, species diversity and richness are anticipated to decline in many parts of the country. This is substantiated by Bakkenes *et al.* (2006) who stated that future climatic changes have the potential to aggravate the loss of species, with severe effects on species with strict climate and habitat requirements. Other studies also revealed a decrease in species richness and diversity due to change in climate (Hao *et al.* 2000, Pourbabaei *et al.* 2014). The present study's increased species diversity and richness with increasing mean annual rainfall led to a deduction that high rainfall favours a wide range of species and reduces inter-specific competition, bush encroachment and extirpation.

5.3 Phanerophyte density and grass sward density

The current study disclosed an inverse relationship between phanerophyte density and grass density (**Figure 17**). A general increase in phanerophyte density with an increase in mean annual rainfall and a decrease in grass density with an increase in mean annual rainfall was also revealed (**Figure 17**). Similar density trends were observed in other studies (Bailey and Gupta 1973, Scholes and Archer 1997, Scholes 2003, Donzelli *et al.* 2013, Kulmatiski and Beard 2013a). Rainfall determines plant development, growth and survival. Therefore, as rainfall at a particular site increases, the potential for that site to support plants especially phanerophytes also increases (Ratajczak *et al.* 2012, Sankaran *et al.* 2005), leading to a decrease in grass density as depicted in **Figure 17**. It can therefore be argued that the observed decrease in grass density with a decrease in mean annual precipitation is due to competition from increasing density of phanerophytes. Low rainfall events are known to reduce the density of phanerophytes through only moistening the upper soil layer (Neilson *et al.* 1992) whereas large rainfall events especially on sandy soils percolate the soil rapidly, recharging soil moisture at deeper lengths not accessible to grasses and consequently increasing the density of deep-rooted phanerophytes (Strohbach and Kutuahuripa 2014). The effect of high rainfall on grass density in the presence of phanerophytes is said to be exacerbated if occuring during grass dormancy (Kulmatiski and Beard 2013b, 2013a).

The present study recorded an increase in phanerophyte density and a decrease in grass sward density along a rainfall gradient from 280 mm to 540 mm (**Figure 17**). Studies disclosed that the increase in woody plants density only goes up to 650 mm mean annual rainfall and becomes asymptotic at 650 mm (Archer *et al.* 2017). Scholes et al. (2002) also disclosed that both grass cover and woody cover increases with rainfall but grass cover only increases with rainfall up to 600 mm mean annual rainfall, and then decreases due to increased competition from woody plants at higher rainfall levels.

Regardless of the general increase in phanerophyte density and a decrease in grass density with an increase in mean annual rainfall observed in this study, outlier density values (very high phanerophyte density and very low grass sward density) were recorded at 440 mm mean annual rainfall (Waterberg) (**Figure 17**). One of the most important factors that contributed to a very high phanerophyte density and a very low grass sward density at Waterberg was fire suppression. According to MET (2016), fire exclusion policies at Waterberg can be dated back to the 1960's and has continued as the backbone of fire management. A lightning fire occurred in 2011 but did not have a significant effect on vegetation because its spread was suppressed by management. MET (2016) further argued that the low frequency of fire occurrence at Waterberg have impacted the vegetation by thickening of woody cover, degradation of the ecosystems, change in vegetation structure and species composition, reduced ecosystem productivity and reduced species diversity. The findings of this study agree with Mapaure (2001) who revealed an increase in shrub density in the Sengwa wildlife research area due to reduced fire intensities. Silva *et al.* (2013) stated that species abundances are more strongly influenced by soil variables when fire is infrequent.

Axelsson and Hanan (2017) concluded that woody plant densities are significantly influenced by rainfall amounts and seasonality than by soil texture, slope and fire frequency. However, their conclusion was based on large scale data across African savannas. At a local scale, the significant influence of fire, browsing, soil texture and soil depth have been acknowledged and documented (Archer 1994a, Eamus and Palmer 2008, Archer *et al.* 2017). Bond (2008) argued that in the absence of fire, semi-arid and sub-humid savanna would transition to a community dominated by woody plants.

Another factor that ostensibly contributed to a high phanerophyte density and low grass sward density at Waterberg was the presence of a porous aeolian sandstone of the Etjo formation. According to Schneider (2004), rainwater rapidly percolates down into the porous sandstones leading to less water in the upper soil layer thereby disadvantaging shallow rooted species. The rainwater that rapidly seeps into the soil reappears in numerous springs at the boundary between the sandstone and the dense mudstones (Schneider 2004). Sherratt (2013) argued that high woody plants density in any given area translates into the existence of high and dense roots as well as organic matters in the soil, leading to increased water seepages into the ground forming a vicious cycle. Browsing did not probably contribute a significant role since no disturbances were observed on sampling plots at Waterberg. Mukaru (2009) only recorded browsers effect on vegetation density near water points at Waterberg.

The present study observed the occurrence of bush encroachment at 440 mm (Waterberg). This observation is not an exception to the vast parts of the country in which bush encroached areas have been recorded to lie between 300–450 mm mean annual rainfall (De Klerk 2004). Bush encroachment in Namibia is coupled with high evaporation and evapotranspiration rates (De Klerk 2004). It is therefore logical that if bush encroachment is not controlled, it will worsen water shortages in the country since bush encroachment is known to lead to a rapid loss of soil moisture and a reduction of groundwater recharge through evapotranspiration (Grygoruk *et al.* 2014, Strohbach *et al.* 2015, Honsbein and Lindeque 2017).

5.4 Phanerophyte canopy volume and leaf volume production

Canopy volumes are used as indicators of growth, health and overall productivity of a particular tree and area at large (Colaço *et al.* 2017). Canopy volumes have further been proved to be the most reliable predictor of browse production per species and per area (Penderis and Kirkman 2014). The present study recorded an increase in phanerophyte total canopy volume and leaf volume production at 5 m MBH with an increase in mean annual rainfall (**Figure 18**). However, leaf volume production at 2m and 1.5 m MBH was high at 440 mm (Waterberg) and 400 mm (Sandveld) mean annual rainfall. Since canopy volume is highly associated with productivity (Thorne 1998), it can be inferred that overall phanerophyte productivity was high in increased rainfall areas and low in reduced rainfall areas. The high canopy volume and leaf volume production at 5 m MBH in high rainfall areas can be explained by Woodland savanna vegetation types present in high rainfall areas compared to Camelthorn savanna vegetation types (at 400 mm) and Grassland/*Acacia* dominated savanna vegetation types (at 280 mm) in low rainfall areas.

The present study recorded a very high phanerophyte density at 440 mm (Waterberg) compared to other study sites (**Figure 17**, see also Section 5.3). However, it is evident that high phanerophyte density (bush encroachment) did not lead to a high phanerophyte total canopy volume and leaf volume production at 5 m MBH. It is therefore logical to state that there is no direct relationship between phanerophyte density, and phanerophyte total canopy volume and leaf volume production at and above 5 m MBH especially in bush encroached areas. This agrees with Axelsson and Hanan (2017) who urgued that crown size responded more strongly to rainfall than woody density. Hence the commonly observed relationships of increasing woody cover with mean annual rainfall less than 700 mm in African savannas is due to increasing sizes of trees rather than tree density (Axelsson and Hanan 2017). In addition, the high phanerophyte density at Waterberg was also due to a high number of Juveniles and shrubs (**Table 3**) which have small canopy volumes compared to trees at or above 5 m tall. The high number of juveniles and shrubs at Waterberg contributed to a high leaf volume production at 2 m and 1.5 m MBH. No logical explanation was found to explain a high leaf volume production recorded at 400 mm (Sandveld).

5.5 Phanerophyte basal area

The present study revealed a direct relationship between phanerophyte total basal area and mean annual rainfall. This emphasised the importance of rainfall in plant lifecycles. According to Toledo *et al.* (2011) and Lempereur *et al.* (2015), climate variables in particular water availability is the strongest driver essential for tree growth. The present study's increase in phanerophyte basal area with rainfall agrees with and Scholes *et al.* (2004), Nath *et al.* (2006), da Costa *et al.* (2010) and Lempereur *et al.* (2015). Scholes *et al.* (2002) found an increase in basal area with increasing mean annual precipitation across a 200 to 1000 mm.yr^{-1} aridy gradient on the Kalahari sands.

The low rainfall areas recorded in the present study are known to experience more frost days compared to high rainfall areas (Mendelson *et al.* 2009) which may lead to reduced photosynthetic activity and consequently slow growth. It is therefore logical to state that the high number of frost days in low rainfall areas are also responsible for the low phanerophyte total basal area recorded in these areas. Feng and Cao (2005) also stated that cold fronts cause injury, reduced photosynthesis and growth of tropical trees. Furthermore, the low total phanerophyte basal area recorded in low rainfall zones were due to a low total stem density. This agrees with Honda and Durigan (2016) who noted an increase in basal area with increasing wood density. Honda and Durigan (2016) disclosed that a 0.9% decrease of rainfall reaching the ground as total basal area increases by 1 m^2 ha^{-1} led to less soil moisture, and low overall groundwater recharge which can be exacerbated in bush encroached areas.

It was also noted that a high abundance of slow growing species contributed to a low phanerophyte basal area in low rainfall areas that experience inter- and intra-annual growth patterns in response to water availability. This agrees with Markesteijn (2010) who stated that plants in drier areas have a reduced hydraulic conductance and slow growth as adaptive mechanisms to seasonal and limited water availability. Conversely, Hanson *et al.* (2001) did not find a strong relationship between the variation of rainfall in growing seasons and annual basal area growth of large trees ostensibly indicating that soil water content was never low enough to be unreachable by deep rooted species and to thereby limit their basal growth. However, results indicated that small-stature plants were very sensitive to reductions in precipitation and soil water content. The lower than expected total phanerophyte basal area recorded at Sonop was probably due to lack of a basal area in plot S4 and S5. S4 and S5 were mostly colonised by shrubs, juveniles and saplings of *Cataphractes alexandrii* and *Grewia* species. In addition, plot S4 and S5 had a lot of dead wood indicating signs of herbicide treatment.

Trends of increasing phanerophytes basal area with mean annual rainfall correlated well with canopy volume, leaf production, leaf size, density, richness and diversity, and by inference biomass and productivity on Kalahari sands. Under projected climate change scenarios, it can be postulated that there will be a reduction in the above ground biomass and productivity due to predicted decrease in mean annual rainfall. According to Midgley *et al.* (2005), Dirkx *et al.* (2008) and Archer *et al.* (2017), the decrease in rainfall is coupled with extreme temperatures, high intensity and freequency of fire, and increasing seasonality of rainfall. Species with restricted ecological niche such as *Commiphora africana* (only recorded in high rainfall areas) are most likely to be adversely affected. Furthermore, increasing phanerophytes biomass and productivity, and decreasing grass sward density with rainfall suggests that there is more food for browsers in high rainfall areas and more food for grassers (e.g. livestock) in low rainfall areas.

Chapter 6: Conclusion and recommendation

The findings of the present study led to the conclusions that mean annual rainfall is the main environmental factor influencing vegetation distribution on Kalahari sands in central Namibia primarily owed to its role in plant establishment, growth and survival. Plants in low rainfall areas on Kalahari sands have adapted decidious characteristics allowing them to reduce water loss while those in high rainfall areas display evergreen traits, confirming that plants functional atributes varies in response to mean annual rainfall. Species richness, diversity, density,total basal area, total canopy volume, and leaf volume production at 5 m, 2 m and 1.5 m MBH of phanerophytes increases with mean annual rainfall confirming that phanerophyte productivity on Kalahari sands increases with mean annual rainfall. In addition, grass sward density decreases with mean annual rainfall mainly due to competition from increasing phanerophyte density with mean annual rainfall.

Furthermore, Waterberg is bush encroached primarily by fire suppression which contributes to high evapotranspiration in Namibia. Rainfall is projected to decrease in many parts of the country under future climate change, and this study asserts that phanerophytes species richness, diversity, total basal area, total canopy volume and leaf volume production will decrease while grass density will increase on Kalahari sands in central Namibia.

It is therefore recommended that the importance of species diversity and richness should be conversed to farmers and the general public in order to preserve the ecological health of the country. Farmers plays a substantial role in maintaining the country’s economy and food provision hence this study recommends that farmers should be involved in climate change research especially studies aimed at determining vegetation-environment relationships as this will help them manage and maintain their farms even under the projected change in climate. It will also help farmers to avoid detrimental environmental threats such as bush encroachnment. This study futher suggests that fire suppression on savannas should be avoided as it is one of the causative factors of bush encroachnment, and information from this study should be used as a baseline for conservation and restoration attempts especially in adressing ecological concerns such as bush encroachnment.

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Appendices

Appendix 1 Field Sheet for Data Collection

***Table 4**: Field data sheet for phanerophyte using BECVOL sampling method.*

Site: **Date:**										
Plot #	**GPS**	**Species name**	**# of stems**	**A**	**B**	**C**	**D**	**E**	**Basal Diameter**	**Basal Circumference**

***Table 5**: Field data sheet for grasses sampling using PCQ sampling method.*

Site **Date**			
Plot #	**Point (m)**	**Species name**	**Distance to species (m)**

Appendix 2 List of species recorded at the five study sites

***Table 6**: List of phanerophyte species recorded at Mile 46.*

plots	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**M10**
Acacia ataxacantha DC.	0	1	0	0	0	0	0	0	0	0
Acacia erioloba E.Mey	0	0	0	0	1	0	0	0	0	1
Acacia erubescens Oliv.	0	0	0	1	1	0	0	0	1	0
Acacia reficiens subsp. *reficiens* Wawra	0	1	0	0	1	0	0	0	0	0
Baphia massaiensis Taub. Ssp. *obovata* (Shinz) Brimmitt var. *obovata*	1	1	0	1	1	1	1	0	1	1
Bauhinia petersiana Bolle ssp. *macrantha* (Oliv.) Brummitt & J,H.Ross	1	1	1	1	1	1	1	0	1	1
Baikiaea plurijuga Harms	1	0	0	0	0	1	0	0	0	0
Burkea africana Hook.	1	0	1	1	0	1	1	1	1	1
Combretum collinum Fresen.	1	1	1	1	1	1	1	1	1	1
Combretum engleri Schinz	1	1	1	1	0	0	0	0	0	0
Combretum Zeyheri Sond.	0	0	0	1	0	0	0	0	1	1

Commiphora africana (A. Rich.) Engl.	0	0	0	1	0	0	0	0	0	0
Commiphora angolensis Engl.	0	1	1	1	1	0	0	0	0	0
Combretum psidioides Welw.	0	1	1	1	0	1	0	1	0	1
Croton gratissimus gratissimus Burch.var. *gratissimus*.	0	1	0	0	1	0	0	0	0	0
Dichrostachys cinerea (L.) Wight & Arn	0	1	0	0	1	1	0	0	0	0
Diplorhynchus condylocarpon (Mull.Arg.)	1	0	1	1	0	1	0	0	1	1
Diospyros chamaethamnus Mildbr.	1	0	0	0	1	0	1	0	0	0
Ehretia alba. Retief & A.E.van Wyk	0	0	1	0	0	0	0	0	0	0
Grewia retinervis DC	0	0	0	0	1	0	0	0	0	0
Grewia flava DC.	0	1	0	0	0	0	0	0	0	0
Grewia flavescens Juss. var *flavescens*	1	1	0	1	1	0	1	1	1	0
Grewia olukondae Juss. var *olukondae*	0	0	1	0	0	0	0	0	0	0
Grewia avellana Hiern	0	0	1	0	1	0	0	0	0	0
Guibourtia coleosperma (Benth.) J.Leonard	0	0	1	1	0	1	1	0	1	1
Ochna pulchra Hook.	1	0	1	1	0	1	1	1	1	1
Ozoroa schinzii (Engl.) R. & A.Fern.	0	0	0	0	1	0	1	0	1	1
Peltophorum africanum Sond.	0	1	0	0	1	1	1	0	1	0
Philenoptera nelsii (Schinz) Schrire	0	1	1	1	1	1	1	0	1	1
Pterocarpus angolensis DC.	1	0	0	1	0	0	1	1	1	1
Searsia tenuinervis (Engl.) Moffett.	0	1	0	1	1	0	0	0	1	1
Schinziophyton rautanenii (Shinz) Radcl.-Sm	0	0	0	0	0	0	0	0	0	1
Strychnos pungens Soler.	1	0	0	1	0	0	1	0	1	1

Strychnos cocculoides Baker	0	0	0	0	0	0	1	0	1	0
Terminalia sericea Burch. Ex DC.	1	1	1	1	1	1	1	1	1	1
Ximenia americana L.	0	1	0	0	1	1	0	0	0	0
Ximenia caffra caffra Sond.	0	1	0	0	0	0	0	0	0	0

***Table 7**: List of grass species recorded at Mile 46.*

plots	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**M10**
Aristida stipitata Hack.	1	0	0	0	0	0	0	0	0	1
Digitaria seriata Stapf.	0	0	0	1	1	1	1	1	1	0
Eragrostis rigidior Pilg.	0	0	0	0	1	0	0	0	0	0
Melinis repens (Willd.) Zizka ssp. *grandiflora/repens* (Hochst.) Zizka	1	0	1	1	0	0	1	1	0	1
Panicum coloratum L.	1	0	1	1	0	0	0	0	0	0
Schmidtia pappophoroides Steud.	0	1	0	1	0	1	0	0	1	0
Sporobolus fimbriatus (Trin.) Nees	0	1	0	0	0	0	0	0	0	0
Stipagrostis uniplumis (Licht.) De Winter var.*uniplumis*	1	1	1	1	0	1	1	0	0	0
Tragus berteronianus Shult.	0	0	0	0	0	0	0	0	0	0
Urochloa brachyura (Hack.) Stapf	1	1	1	1	1	1	1	1	1	1

Table 8: *List of phanerophyte species recorded at Sonop.*

Plots	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**
Acacia ataxacantha DC.	0	1	0	0	0	1	0	1	0	1
Acacia erioloba E.Mey.	0	0	0	0	1	0	1	0	0	0
Acacia fleckii Shinz	1	1	1	0	0	0	1	0	1	1
Acacia hebeclada DC. ssp. *hebeclada*	0	0	0	1	1	0	0	0	0	0
Acacia mellifera (Vahl) Benth. ssp.*dentines* (Burch.) Brenan	0	0	0	1	1	0	1	0	0	0
Baphia massaiensis Taub. Ssp. *obovata* (Shinz) Brimmitt var. *obovata*	1	1	1	0	0	1	0	1	1	1
Bauhinia petersiana Bolle ssp. *macrantha* (Oliv.) Brummitt & J,H.Ross	1	1	1	0	0	1	0	1	1	1
Burkea africana Hook.	1	1	1	0	0	1	0	1	1	1
Catophractes alexandri D.Don.	0	0	0	1	1	0	0	0	1	0
Combretum collinum Fresen.	1	1	1	0	0	1	1	1	1	1
Combretum engleri Schinz	1	1	0	0	0	1	0	1	0	0

Combretum Zeyheri Sond.	0	0	1	0	0	1	0	0	1	1
Commiphora africana (A. Rich.) Engl.	1	1	0	1	0	1	1	1	1	1
Commiphora angolensis Engl.	0	0	0	1	0	0	1	0	0	0
Croton gratissimus gratissimus Burch.var. *grat issimus*.	1	1	0	0	1	0	0	1	1	0
Dichrostachys cinerea (L.) Wight & Arn	0	0	1	1	1	0	0	0	0	0
Ehretia alba. Retief & A.E.van Wyk	0	0	0	0	0	0	1	0	0	0
Grewia retinervis DC	1	1	1	1	1	1	1	1	1	1
Grewia falcistipula K.Shum.	0	0	1	0	0	0	1	0	0	0
Grewia bicolor Juss.	0	0	0	1	1	0	0	0	0	0
Grewia flava DC.	0	0	0	1	0	0	0	0	0	0
Grewia flavescens Juss. var *flavescens*	1	0	0	0	0	0	0	0	0	0
Mundulea sericea (Willd.) A. Chev.	1	1	0	1	1	1	1	1	0	0
Ochna pulchra Hook.	0	1	1	0	0	0	0	1	1	1
Ozoroa paniculosa (Sond.) R. & A.Fern.	0	0	0	1	0	0	1	0	0	0
Ozoroa schinzii (Engl.) R. & A.Fern.	1	0	0	1	0	0	1	1	0	1

Peltophorum africanum Sond.	0	0	0	0	0	0	1	0	0	0
Philenoptera nelsii (Schinz) Schrire	0	1	1	0	1	0	1	1	1	1
Psydrax livida (Hiern) Bridson	1	1	0	0	0	1	1	0	1	0
Pterocarpus angolensis DC.	1	0	1	0	0	0	0	0	0	0
Searsia tenuinervis (Engl.) Moffett.	0	0	0	1	1	0	1	0	0	0
Strychnos pungens Soler.	0	0	0	0	0	0	0	0	0	1
Terminalia sericea Burch. Ex DC.	0	1	1	0	0	1	0	1	1	1
Ziziphus mucronata Willd.	0	0	0	0	0	0	1	0	0	0

Table 9*: List of grass species recorded at Sonop.*

plots	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**
Aristida meridionalis Henrard	1	0	0	0	0	0	0	0	0	0
Aristida rhiniochloa Hochst.	1	1	1	0	0	1	0	1	1	1
Brachiaria deflexa (Shumach.) C.E.Hubb.ex Robyns	0	0	0	1	1	0	0	0	0	0
Digitaria eriantha Steud.	0	1	1	0	0	0	0	0	0	0
Digitaria seriata Stapf.	1	1	1	0	0	1	1	1	1	1
Eragrostis porosa Nees.	0	0	0	1	0	0	0	0	0	0
Eragrostis lehmanniana Nees	0	1	1	0	0	0	0	0	0	0
Eragrostis trichophora Coss. & Durieu	0	0	0	1	1	1	1	0	0	1

Melinis repens (Willd.) Zizka ssp. *grandiflora/repens* (Hochst.) Zizka	1	1	0	0	0	1	0	1	1	1
Panicum coloratum L.	0	0	1	0	0	0	0	0	0	0
Pogonarthria fleckii (Hack.) Hack	0	0	0	1	1	0	0	0	1	1
Schmidtia kalahariensis Stent.	0	0	0	0	0	0	1	0	0	0
Stipagrostis uniplumis (Licht.) De Winter var.*uniplumis*	0	1	1	1	1	0	1	1	1	1
Tragus berteronianus Shult.	0	0	0	1	1	1	0	0	0	0
Urochloa trichopus (Hochst.) Stapf	1	1	0	1	1	0	1	1	0	0
Triraphis schinzii Hack.	0	1	1	0	0	0	0	0	0	1

***Table 10**: List of phanerophyte species recorded at Waterberg.*

plots	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
Acacia ataxacantha DC.	0	0	1	1	1	1	0	1	0	0
Acacia erioloba E.Mey.	0	1	0	0	0	0	0	0	0	0
Acacia fleckii Shinz	1	0	0	0	1	0	0	0	0	0
Bauhinia petersiana Bolle ssp. *macrantha* (Oliv.) Brummitt & J,H.Ross	0	0	1	1	1	1	1	1	1	0
Burkea africana Hook.	0	0	1	1	1	1	1	1	1	1
Combretum collinum Fresen.	0	1	0	0	0	0	0	1	0	1
Combretum Zeyheri Sond.	1	1	1	1	1	0	1	1	1	0

Combretum psidioides Welw.	1	0	0	1	1	1	1	1	1	1
Grewia flava DC.	0	0	0	1	1	1	1	1	0	0
Grewia flavescens Juss. var *flavescens*	1	1	1	1	0	0	0	1	0	0
Grewia olukondae Juss. var *olukondae*	0	0	0	0	0	0	1	0	0	0
Mundulea sericea (Willd.) A. Chev.	1	0	0	0	0	0	0	0	0	0
Ochna pulchra Hook.	0	1	1	1	1	1	1	1	1	1
Ozoroa paniculosa (Sond.) R. & A.Fern.	0	0	1	0	0	0	0	0	0	0
Ozoroa schinzii (Engl.) R. & A.Fern.	0	1	0	0	0	0	0	0	0	0
Peltophorum africanum Sond.	1	1	1	0	0	0	0	0	0	0
Searsia tenuinervis (Engl.) Moffett.	1	0	0	0	1	0	0	1	0	0
Terminalia sericea Burch. Ex DC.	1	1	1	1	1	1	1	1	1	1
Ximenia caffra caffra Sond.	1	1	1	0	0	0	0	0	0	0
Ziziphus mucronata Willd.	1	1	1	0	0	0	0	0	0	0

Table 11: *List of grass species recorded at Waterberg.*

plots	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
Andropogon chinensis (Nees) Merr.	0	0	1	0	0	0	0	0	0	0
Aristida congesta Roem. & Schult. Spp. *congesta*	0	1	0	0	0	0	0	0	0	0
Aristida meridionalis Henrard	0	0	1	0	0	0	0	0	0	0
Aristida stipoides Lam.	0	1	1	0	0	0	0	0	0	0
Aristida stipitata Hack.	1	1	0	1	1	1	0	1	1	1
Digitaria seriata Stapf.	0	0	1	1	1	1	1	1	0	1
Eragrostis lehmanniana Nees	0	1	0	0	0	0	0	0	0	0
Eragrostis jeffreysii Hack.	0	0	0	0	0	1	1	0	0	0
Eragrostis nindensis Ficalho & Hiern	0	1	0	0	0	0	0	0	0	0
Eragrostis pallens Hack.	0	0	1	1	1	1	1	1	1	1
Eragrostis superba Peyr.	1	0	0	0	0	0	0	0	0	0
Leptochloa fusca (L.) Kunth.	1	1	0	0	0	0	0	0	0	0
Melinis repens (Willd.) Zizka ssp. *grandiflora/repens* (Hochst.) Zizka	0	0	0	0	0	0	0	1	0	0
Panicum lanipes Mez.	0	0	0	0	0	1	1	0	0	0
Panicum maximum Jacq.	1	0	0	0	0	0	0	0	0	0
Panicum stapfianum Fourc.	0	1	0	0	0	0	0	0	0	0
Perotis patens Gand.	1	0	0	0	0	0	0	0	0	0
Pogonarthria fleckii (Hack.) Hack	1	0	0	0	0	0	0	0	0	0

Schmidtia pappophoroides Steud.	0	1	0	0	0	0	0	0	0	0
Stipagrostis uniplumis (Licht.) De Winter var.*uniplumis*	1	1	1	1	1	1	1	1	1	1
Tragus berteronianus Shult.	1	1	0	0	0	0	0	0	0	0
Urochloa brachyura (Hack.) Stapf	1	1	0	0	0	0	0	0	0	0
Triraphis schinzii Hack.	0	0	0	0	1	1	1	0	0	0

***Table 12**: List of phanerophyte species recorded at Sandveld.*

Plots	V1	V2	V3	V4	V5	V6	V7	V8	V9	V10
Acacia ataxacantha DC.	0	0	0	1	0	0	0	0	0	0
Acacia erioloba E.Mey.	1	1	1	1	1	1	1	1	1	1
Acacia hebeclada DC. ssp. *hebeclada*	1	1	1	1	1	1	0	0	1	0
Acacia mellifera (Vahl) Benth. ssp.*dentines* (Burch.) Brenan	0	1	0	0	1	1	1	1	1	1
Dichrostachys cinerea (L.) Wight & Arn	1	0	1	0	0	1	1	1	1	1
Diospyros lycioides Desf.	0	1	0	1	0	0	0	0	1	0
Grewia flava DC.	1	1	1	1	1	1	1	1	1	1
Ozoroa paniculosa (Sond.) R. & A.Fern.	0	1	1	1	1	1	1	1	0	1

Searsia tenuinervis (Engl.) Moffett.	0	0	1	0	0	0	0	1	0	0
Tarchonanthus camphoratus L.	1	1	1	1	1	0	1	0	1	1
Terminalia sericea Burch. Ex DC.	1	1	1	1	0	0	1	1	0	1
Ziziphus mucronata Willd.	0	1	1	1	0	1	0	1	1	1

Table 13*: List of grass species recorded at Sandveld.*

plots	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	**V8**	**V9**	**V10**
Aristida congesta Roem. & Schult. Spp. *congesta*	1	1	0	0	0	0	0	1	0	0
Aristida meridionalis Henrard	0	1	0	0	1	0	0	0	0	1
Aristida stipitata Hack.	1	1	1	1	1	1	1	1	1	1
Eragrostis echinochloidea Stapf	0	0	0	0	0	0	0	0	1	0
Eragrostis cylindriflora Hochst.	0	0	0	0	0	1	0	0	0	0
Eragrostis porosa Nees.	0	1	0	0	0	0	0	0	1	0
Eragrostis trichophora Coss. & Durieu	1	1	0	1	0	0	1	1	1	0
Melinis repens (Willd.) Zizka ssp. *grandiflora/repens* (Hochst.) Zizka	1	1	1	1	1	1	1	1	1	1
Pogonarthria fleckii (Hack.) Hack	0	1	0	0	1	0	0	0	0	1
Pogonarthria squarrosa (Roem. & Schult.)	1	0	0	0	0	1	0	1	0	0

Schmidtia pappophoroides Steud.	0	1	0	0	0	0	0	0	0	0
Schmidtia kalahariensis Stent.	0	1	1	0	0	1	0	1	1	0
Stipagrostis uniplumis (Licht.) De Winter var.*uniplumis*	1	1	1	1	1	1	1	1	1	1
Tragus berteronianus Shult.	0	0	0	0	1	0	0	0	0	0
Urochloa brachyura (Hack.) Stapf	1	1	1	1	1	1	1	1	1	1
Triraphis schinzii Hack.	0	0	1	1	0	0	1	1	0	1

***Table 14:** List of phanerophyte species recorded at Ebenhaezer.*

Plots	E1	E2	E3	E4	E5	E6	E7	E8	E9	E10
Acacia erioloba E.Mey.	1	1	1	1	1	1	1	1	1	1
Acacia hebeclada DC. ssp. *hebeclada*	0	0	0	0	1	0	1	1	0	1
Acacia mellifera (Vahl) Benth. ssp.*dentines* (Burch.) Brenan	1	1	1	1	1	1	1	1	1	1
Boscia albitrunca (Burch.) Gilg & Gilg-Ben.	0	1	1	0	0	1	0	1	0	0
Boscia foetida. Schinz	0	0	0	0	1	0	0	0	0	0

Grewia flava DC.	0	0	0	0	1	1	0	1	0	0
Grewia flavescens Juss. var *flavescens*	1	0	0	0	0	0	0	0	0	0
Phaeoptilum spinosum (Radlk.) S.Moore	1	1	1	1	1	1	1	1	0	0

Table 15*: List of grass species recorded at Ebenhaezer.*

Plots	**E1**	**E2**	**E3**	**E4**	**E5**	**E6**	**E7**	**E8**	**E9**	**E10**
Aristida congesta Roem. & Schult. Spp. congesta	0	0	0	0	0	0	0	0	1	1
Aristida stipitata Hack.	1	1	1	1	1	1	1	0	1	1
Enneapogon cenchroides (Roem. & Shult.)C.E. Hubb	1	0	1	1	1	1	1	1	0	0
Eragrostis bicolor Nees.	1	0	0	0	1	0	1	0	0	0
Eragrostis porosa Nees.	0	0	0	0	1	0	1	1	1	1
Pogonarthria fleckii (Hack.) Hack	0	1	1	0	0	0	0	0	0	1
Stipagrostis uniplumis (Licht.) De Winter var.uniplumis	1	1	1	1	1	1	1	1	1	1

Appendix 3 Soil data

***Table 16**: Soil analysis results from the five selected study sites (M=Mile 46, S=Sonop, W=Waterberg, V=Sandveld and E=Ebenhaezer).*

Plots-	PHw	Ecw uS/cm	OM %	P ppm	K ppm	Ca ppm	Mg ppm	Na ppm	Sand %	Silt %	Clay %
M1	6.25	212	1.1	0.6	38	339	57	0	96.2	2	1.8
M2	6.2	169	0.36	0.4	0	81	21	0	96.9	1.8	1.3
M3	6.35	226	1.08	1.5	77	595	82	0	94.3	3.6	2.1
M4	6.07	144	0.36	0.9	0	85	27	0	95.9	2.9	1.2
M5	6.32	218	1.16	0.6	0	25	14	0	93.6	2.7	3.7
M6	6.51	103	0.44	0	34	376	76	0	96.6	1.4	2
M7	6.22	182	0.95	1	29	525	76	0	96.3	2.3	1.4
M8	6.46	160	0.99	0.1	0	119	39	0	96.7	2.1	1.2
M9	6.05	142	0.5	0.3	0	90	30	0	96.8	2.3	0.9
M10	6.23	177	0.56	3.5	0	127	15	0	96.6	1.7	1.7
S1	5.65	232	0.78	3.6	21	179	32	0	95.6	3.5	0.9
S2	6.53	198	1.05	2.5	28	359	78	0	97.1	1.1	1.8
S3	5.98	127	0.35	0	21	57	14	0	96.7	1.3	2
S4	6.32	228	0.88	2.8	0	20	11	0	89.9	5.3	5
S5	6.69	215	0.78	5.2	38	489	82	0	97.2	1.6	1.2
S6	6.82	150	0.51	3.2	0	508	29	0	97.6	1.9	0.5
S7	5.76	200	0.45	0.3	30	201	43	0	93.8	4.6	1.6
S8	5.91	230	0.69	0.9	60	607	83	0	96.6	2.3	1.1
S9	6.86	217	0.41	0	55	642	91	0	97.5	1.3	1.2
S10	6.15	151	0.42	0.1	0	25	10	0	97.1	1.7	1.2
W1	5.33	337	2.76	37.2	262	3149	342	0	79.1	13.2	7.7
W2	5.26	182	1.72	16	15	331	69	0	91.6	4.7	3.7
W3	4.97	105	0.61	0	0	36	8	0	95.4	2.6	2
W4	5.32	283	0.75	0	20	39	10	0	93.9	5.1	1
W5	5.97	996	1	0	6	22	26	0	94.9	2.6	2.5
W6	5.06	167	1.13	0	2	14	22	0	94.5	4.3	1.2
W7	5.06	167	1.13	0	2	19	25	0	95.3	4	0.7
W8	4.5	135	0.76	21	44	29	6	0	92.8	6.1	1.1
W9	4.72	101	0.82	0	13	325	38	0	94.6	3.5	1.9
W10	5.39	620	1.92	30	163	675	322	0	95.2	4.1	0.7
V1	6.25	212	1.1	0.6	38	339	57	0	89.6	7.2	3.2
V2	6.76	236	0.76	0.5	43	201	60	0	90	6.9	3.1
V3	5.98	127	0.35	0	21	57	14	0	94.3	3.6	2.1
V4	5.81	169	0.36	0.4	0	81	21	0	94.9	4	1.1
V5	6.69	215	0.78	1	38	489	82	0	93.7	4	2.3
V6	6.65	226	1.08	1.5	77	595	82	0	92.8	5	2.3
V7	6.28	230	0.89	0.7	0	29	21	0	91.9	6.9	1.2

V8	6.36	144	0.63	0.9	0	85	27	0	94.2	2.3	3.3
V9	6.86	217	0.55	0	59	642	91	0	93.5	4.9	1.6
V10	6.53	151	0.42	0.3	0	25	10	0	95.1	3.2	1.7
E1	5.65	220	1.3	0.39	23	130	20	0	94.4	2.3	3.3
E2	6.55	132	1.1	0.9	0	239	63	0	94.8	4.2	1
E3	6.79	180	0.78	0.65	32	260	19	0	94.3	3.1	2.6
E4	6.6	126	1	2.8	40	325	56	0	95.2	2.1	2.7
E5	6.68	134	1.16	0.6	0	264	14	0	95.6	2.6	1.8
E6	6.51	103	0.44	0	34	376	76	0	96.8	2.3	0.9
E7	6.44	122	0.39	0	0	129	46	0	95.1	3.2	1.7
E8	6.46	160	0.99	0.1	0	119	39	0	94.2	4	1.8
E9	6.65	177	0.56	2.3	0	127	30	0	94	2.8	3.2
E10	6.37	100	1.22	0.64	29	300	69	0	93.7	3.3	3

Appendix 4 Plant functional attributes

Table 17*: Key phanerophytes functional attributes, expressed as percentage of all species found in the relevant plot.*

	leaf size		**leaf duration**				**life form**		
Plots	macrophyll	microphyll	deciduous	semi-deciduous	evergreen	semi-evergreen	mesophanerophytes	microphanerophytes	nanophanerophyte
M1	97.4	2.58	33.62	0.86	51.72	0	62.93	23.28	13.7
M2	78.13	21.25	18.75	11.25	60	0	44.38	43.75	1.25
M3	91.24	0.09	86.08	2.58	11.34	0	84.02	15.98	0.52
M4	88.16	5.92	46.05	0.66	53.29	0	80.92	19.08	0
M5	76.71	23.01	16.44	15.07	68.22	0	68.22	45.48	1.92
M6	98.94	1.06	30.74	0.71	68.55	0	51.24	43.11	0
M7	87.15	12.84	69.72	19.27	19.27	0	52.29	24.77	22.94
M8	78.78	21.21	100	0	0	0	51.52	48.49	0
M9	95.57	1.97	65.02	0.49	33	0	53.69	22.83	1.48
M10	97.32	2.67	48.09	0	46.56	0	74.43	28.63	0.76
S1	92.14	7.86	1.43	6.43	61.42	0	24.29	74.29	1.43
S2	94.66	5.34	33.49	2.67	61.65	0	24.27	73.05	2.67
S3	92.76	72.36	78.95	0	20.39	0	41.45	19.74	8.55

S4	34.08	32.58	97	0.37	0.37	0	2.25	42.32	55.43
S5	56.59	43.41	92.86	1.09	6.04	0	7.14	24.73	68.13
S6	83.78	12.84	6.08	6.76	59.46	0	24.32	69.59	6.08
S7	76.67	23.31	80.45	6.76	8.27	1.5	9.02	65.41	24.06
S8	84.02	15.97	39.17	9.28	48.97	0	38.67	52.58	5.05
S9	92.19	7.32	25.13	0	68.59	0	14.65	74.35	4.71
S10	96	3.91	50.78	0	49.22	0	16.4	51.17	1.95
W1	97.08	2.91	87.59	5.83	0.73	5.83	0.58	39.42	0
W2	82.23	17.64	90.19	7.84	0	1.96	66.66	17.65	15.69
W3	100	0	9.38	0.31	2.15	0.15	49.92	50.08	0
W4	90.22	9.78	77.17	0	22.83	0	75	22.98	0.78
W5	93.64	6.36	83.03	0	16.97	0	71.13	27.57	1.14
W6	62.95	37.05	99.76	0	0.24	0	52.78	31.96	15.25
W7	80.85	19.14	97.35	0	3.1	0	72.91	23.39	7.13
W8	79.91	7.76	88.78	0	9.81	0	57.24	28.27	1.17
W9	83.66	16.34	94.37	0	5.63	0	53.8	46.19	0
W10	89.49	10.51	100	0	0	0	74.71	25.28	0
V1	81.25	19.59	92.78	7.21	0	0	85.57	11.34	3.09
V2	42.11	57.89	65.79	28.94	0	5.26	21.05	57.89	21.05
V3	6.98	93.02	92.24	5.43	0.77	1.55	13.95	58.14	27.91
V4	48.55	51.43	57.14	40	2.86	4.27	25.71	70	4.29
V5	62.69	37.31	76.12	23.88	0	0	17.91	80.59	1.49
V6	69.23	30.76	96.15	0	0	1.92	23.08	71.15	5.79
V7	17.39	79.13	17.39	0	0	0	10.43	79.69	7.39
V8	64.19	35.8	95.06	0	1.23	3.7	66.66	22.22	11.11
V9	81.57	18.42	76.32	0	0	5.26	9.21	80.26	10.53
V10	19.44	15.74	88.88	10.18	0	0.93	13.88	75.92	9.26
E1	87.76	12.24	100	0	0	0	8.16	87.76	4.08

E2	75	25	95.83	0	4.16	0	25	70.83	4.16
E3	75.86	24.14	96.55	0	3.45	0	17.24	72.41	10.34
E4	37.5	62.5	100	0	0	0	43.75	37.5	0
E5	37.93	85.71	96.55	0	3.44	0	31.03	37.93	31.03
E6	50.98	49.02	94.11	0	5.88	0	39.22	45.01	15.68
E7	50	50	100	0	0	0	50	37.5	12.5
E8	39.73	60.28	95.89	0	4.11	0	56.16	34.25	9.59
E9	5.71	94.28	100	0	0	0	94.29	5.71	0
E10	50	50	100	0	0	0	60	40	0