ASSESSMENT OF WOODY PLANT AND GRASS COMPETITIVE INTERACTIONS USING RECIPROCAL TRANSPLANTS ALONG A RAINFALL GRADIENT IN NAMIBIAN SAVANNAS

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Abstract

Savannas are mainly characterised by co-existence of woody and herbaceous vegetation. In Namibia, savannas occupy about 64% of the country’s land area. They are characterised by the arid to semi-arid climatic conditions and play a vital role in livestock and vegetation production. Most vegetation communities in savannas are influenced by rainfall and species interactions. Change in climatic pattern has shown that a decrease in rainfall can cause more frequent droughts and ultimately decrease the productivity of rangelands and can increase competition among the plants. Savannas present problems for management such as the increase in shrub thickening which can reduce grass production leading to a reduction in the carrying capacity of rangelands. However, there is no consensus yet on the main drivers of shrub encroachment, making it hard to set conservation goals and management recommendations in the savannas.

This research intended to assess competitive interactions between woody plants and grasses in the savanna’ along a rainfall gradient in Namibia using plant neighbour manipulations. Reciprocal transplant experiments were conducted at three “Options for sustainable geo-biosphere feedback management in savanna systems under regional and global change” (OPTIMASS) sites along a rainfall gradient from November 2016 to April 2017. Seeds of Senegalia mellifera (tree), Anthephora pubescens and Stipagrostis uniplumis (grasses) were collected and sown at their origin site and a neighbour drier site. Germination, survival rates and height growth were measured.

Clipping was done before seeding and within the experiment period by removing all emerging plants surrounding the respective pipes. This study revealed that clipping did not have a significant effect on the germination, survival fractions and height of all the three species. There was a higher germination fraction of S. uniplumis and S. mellifera at Tsumeb than at Okakarara. This can be attributed to the fact that high amount of rainfall was received in this area. Only S. mellifera survived in Tsumeb and significant interactions occurred in the seed origin and site with clipping. The grass plants (S. uniplumis and A. pubescens) did not survive at Tsumeb, this can be due to the clay soils found around Tsumeb and these limited the roots to penetrate deep into the soils to get water. Additionally, these species could not compete with
other perennials found in that area. The study concluded that, clipping (neighbour manipulation) does not have an effect on germination and survival fractions neither on height growth.

Furthermore, *S. mellifera* grew well despite the decrease in rainfall and steeper gradients are needed to determine the effect of severe drought conditions. There is a need to put in place interventions to control *S. mellifera*.

**Keywords:** *Anthehora pubescens*, clipping, rainfall, *Senegalia mellifera*, *Stipagrostis uniplumis*. 
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Declarations

I, Cecilia I.H.Ndunge, hereby declare that this study is my own work and is a true reflection of my research, and that this work, or any part thereof has not been submitted for a degree at any other institution.

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Cecilia.I.H.Ndunge
CHAPTER 1: INTRODUCTION

1.1 Orientation of the study

Savanna ecosystems are mainly characterised by layers of woody and herbaceous vegetation (Vetaas, 1992). Most savannas have common climatic conditions which range from hot wet seasons and warm dry seasons in a year (Woodward, 1997). In Namibia, savannas occupy about 64% of the land area (Sweet & Burke, 2000) and play a very important role in livestock and crop production. However, management of savannas has become increasingly challenging, due to a number of problems occurring in the course of global change in climate (Smit, 2004). For example, savannas have experienced an increase in the percentage of the bushes and shrubs at the expense of grasses (Vetaas, 1992). Shrub encroachment is regarded as the suppression of palatable grass species which allows an increase in abundance of some woody species which results in less palatable species available for livestock consumption (Ward, 2005). This thickening can thus decrease the productivity of the grass layer (Johnson et al. 1993; Scholes & Archer, 1997; Wong, 1979).

Several mechanisms that facilitate shrub encroachment (e.g. grazing, fire, nutrients) have been studied (de Klerk, 2004; Sheuyang et al. 2005; Vetaas, 1992). However, the main cause of shrub encroachment is not known. Moreover, climate change, which in Namibia is predicted to lead to less precipitation, higher temperatures and higher frequency of droughts (Midgley et al. 2005), also affects African savannas, and is likely to modify the balance between grasses and shrubs too. This is because grasses and shrubs have different photosynthetic pathways which affect their
sensitivity to drought. For example, the grasses in Namibia savannas are all C₄ grasses which are able to assimilate at a much higher efficiency than the C₃ shrubs or trees. Therefore, grasses should be less affected by drought than shrubs, i.e. drought could slow down shrub encroachment (Holmes & Cowling, 1997; Vetaas, 1992).

In general, understanding shrub encroachment requires an understanding of factors that determine the balance between the two life forms of grasses and woody plants. Interactions among plants are influenced by many abiotic and biotic factors. For example, plant species interact with other species within the same environment through competition for resources such as light, water and space (Ariza & Tielbörger, 2011). Competition is regarded as a limiting factor for the woody plants in the savanna, such that removal of grasses such as through grazing could favour shrub establishment (Solbrig et al. 1996). For example, the dominance of a major encroaching species, *Senegalia mellifera*, has often been explained in terms of release from competition by grasses (de Klerk, 2004; Holthuijzen & Veblen, 2015; Karuaera, 2011).

The direction of plant-plant interactions as well as their strength depends also on the availability of resources and on abiotic stress (Maestre et al. 2009). For example, it has been suggested that in highly productive environments, competition (negative interaction) would dominate over facilitation (positive interaction) among plants theory that has become known as the stress gradient hypothesis (Bertness & Callaway, 1994). Therefore, one may predict that the nature of shrub-grass interactions should change along a gradient of resource availability with positive
interactions (or less negative interactions) dominating under highly stressful conditions and competition dominating when resources are abundant. Thus, the mechanisms determining shrub encroachment could be very different along such gradients. Unfortunately, previous studies have mostly addressed single locations (Smit, 2004; Ward, 2005).

Another drawback of shrub encroachment studies that are limited to a single location is that plants adapt to local conditions. For example, different traits are developed in order to adapt to these conditions, such that plants from productive environments are more locally adapted to competition (Ghini et al. 2012). In other words, the frequencies of these traits within a population tend to improve the reproductive potential and survivorship of individuals expressing them. Therefore, studying these traits provides insights about favoured traits in the environment (Kawecki & Ebert, 2004). One way to study these traits can be by carrying out reciprocal transplants, these are experiments where organisms are moved or planted into another environment with different environmental conditions such as temperature, soil moisture and rainfall (Maranon & Bartolome, 1993). These transplants are mainly used in testing local adaptation and plant response (Maranon & Bartolome, 1993). Local adaptation is a concept whereby organisms tend to have a higher fitness in their local environment compared to other less favourable environments (Kawecki & Ebert, 2004).
1.2 Statement of the problem

Over the past years, there has been an increase in shrub densities called shrub encroachment in the central and southern parts of Namibia (Smit, 2004). This is a form of land degradation and causes a reduction in the perennial grasses and an imbalance in the grass to shrub ratio in the rangelands and eventually reduces the biological diversity and the carrying capacity of rangelands (Ward, 2005).

There is no consensus yet about the main mechanisms that drive shrub encroachment in savannas thus, recommendations concerning rangeland management are not easy to make. Effects of fire, microsites, water and nutrient availability on rangeland productivity have been investigated (de Klerk, 2004; Sheuyange, Oba et al. 2005; Vetaas, 1992) but few studies have been done on the impact of climate change on shrub encroachment. Therefore, understanding and explaining the impact of climate change on shrubs and grasses is important. In addition, little is understood on how trees and grass respond along rainfall gradients (Kulmatiski & Beard, 2013; Moustakas et al. 2013), despite the anticipated change in the interactions among plants along such gradients. Hence, this research intends to assess the effect of climate change on A. pubescens, S. mellifera and S. uniplumis by using different origins and neighbour manipulations of neighbouring plants’ aboveground biomass along a rainfall.

1.3 Aim of the study

The aim of the study was to assess competitive interactions among woody plants and grasses along a rainfall gradient in Namibian savannas in order to indirectly assess the impact of changes in precipitation on shrub encroachment.
1.4 Specific objectives

The objectives of the study were to compare the:

a) Germination fraction of *Senegalia mellifera*, *Stipagrostis uniplumis* and *Antheophora pubescens* between clipped and unclipped plots along a rainfall gradient.

b) Survival fraction of *Senegalia mellifera*, *Stipagrostis uniplumis* and *Antheophora pubescens* seedlings between clipped and unclipped plots along a rainfall gradient.

c) Height of *Senegalia mellifera*, *Stipagrostis uniplumis* and *Antheophora pubescens* seedlings between the clipped and unclipped plots along a rainfall gradient.

1.5 Null hypotheses of the study

a) There is no significant difference in mean germination fraction of *Senegalia mellifera*, *Stipagrostis uniplumis* and *Antheophora pubescens* between clipped and unclipped plots along a rainfall gradient.

b) There is no significant difference in mean survival fraction of *Senegalia mellifera*, *Stipagrostis uniplumis* and *Antheophora pubescens* seedlings between clipped and unclipped plots along a rainfall gradient.

c) There is no significant difference in mean height of *Senegalia mellifera*, *Stipagrostis uniplumis* and *Antheophora pubescens* seedlings between the clipped and unclipped plots along a rainfall gradient.
1.6 Significance of the study

Studying plant interactions is important for management strategies e.g. it will serve as basic information that can be used by farmers as to how they can manage their farms with an increase in drought frequency. Additionally, it will give an insight for farmers to make decisions if they should allow grazing to facilitate grasses growth or not. Moreover, this will inform policy makers leading to better formulation of policies and use good land management practices that can be used as adaptive measures to climate change.

1.7 Limitation of the study

Time limitation did not allow for a full factorial design to be done in the experiments (this study only focused on transplants to drier sites only and not wetter sites). This could have given an overall idea on how all the three species will perform at all the three sites. Additionally, only one shrub species was used because there were no seeds for the *Dichrostachys cinerea* during 2016. Some of the seeds were predated upon by the insects and others were removed and eaten by the birds. No information of the species and quantities of seeds that were removed is known due to the student not being full time at all the three sites to observe those actions. When the seeds germinated the researchers was not be able to determine if the seeds were the ones sown or are from the soil seed bank.
CHAPTER 2: LITERATURE REVIEW

2.1 The distribution and importance of savannas

Savanna ecosystems are mainly characterised by coexistence of grasses and woody plants (Maurin et al. 2014; Sankaran et al. 2004; Scholes & Archer, 1997; Vetaas, 1992). According to Huntley & Walker (1982), savannas are defined as continuous herbaceous layers of shrubs and trees. Savanna structure is regulated by external determinants such as climate, fire, grazing and rainfall (Solbrig et al. 1996). The savannas can have wet and dry seasons which are primarily based on rainfall and maintained by occasional fires and droughts (Scholes & Walker, 2004).

Another definition is that savannas are tropical woodlands and grasslands that are characterized by widely spaced trees and provide food for large browsing animals such as elephants. Most browsers eat and trample on tree seedlings and this can inhibit tree establishment (Woodward, 1997). These browsers turn the savannas into a grazing subclimax by debarking and knocking down trees (Holthuijzen, 2015; Ma et al. 2013). This opens up the savannas into open woodlands allowing grasses to grow and attract grazing animals such as zebra and wildebeest. When savannas are heavily grazed over long period, they can be bare and this can increase evaporation rates (D’Odorico et al. 2012). However, some woody plants such as Vachellia and Senegalia species may tolerate both overgrazing and drought (de Klerk, 2004; Smit, 2004). Tolerance allows the species to establish better than other species. This allows the tolerant species to increase in abundance and cause shrub encroachment (Ward, 2005).
Savannas cover approximately one eighth of the global land area and contribute approximately 30% of all terrestrial ecosystem gross primary productivity (Scholes & Archer, 1997). Savanna ecosystems cover about 20% of the world’s flora land and about 40% of the land in Africa. In Namibia, the savanna cover about 64% of the land surface of 824 269 km² (Sweet & Burke, 2006). The savanna is the dominant biome and vegetation in the sub-Saharan region (Baudena et al. 2015; Scholes & Archer, 1997). Savanna ecosystems can be found mostly along the tropics and subtropics, which are usually associated with wet and dry climate (Solbrig et al. 1996).

The origin of savannas is not exactly known, however, there is speculation that it can be dated to over 32 million years ago from the Oligocene period and currently it is spreading to other climates (Maurin et al. 2014). Savannas can be classified based on the height, canopy and the arrangement of the woody plants. This leads to the savanna to have complex dynamics and interactions between animals and plants (Huntley & Walker, 1982).

Rainfall in the savanna ecosystems is seasonal and plays an important role in plants, animals and the human population that directly or indirectly depends on the savanna areas. When below average rainfall is received, plants compete for water for growth and survival (Wang et al. 2015). When competition among organisms takes place there is a possible trend of either observing an increase or a decrease in competition along gradients of productivity and resource availability (Maestre et al. 2009). The stress gradient hypothesis states that as stress increases in an environment, positive
Plant–plant interactions become more significant and shift from competition to facilitation (Bertness & Callaway, 1994). Therefore, in semi-arid environments, competition is important in habitats where low abiotic stress is experienced (Fridley et al. 2007).

2.2 Tree-grass interaction models

Savanna ecosystems are mainly characterized by the coexistence of two life forms namely trees and grasses (Ward, 2005). However, the representation of these life forms varies across savanna types; some comprises of communities with continuous herbaceous, shrubs and trees. These tend to support human population and animals by providing grazing (Ward, 2005). Despite their recognized importance of the welfare and origin of humans and animals, interactions taking place in savannas are poorly understood (Sankaran et al. 2004; Scholes & Archer, 1997; Wiegand & Jeltsch, 2000). Particularly, mechanisms that allow trees and grasses to co-exist without displacing each other still remain unclear (Scholes & Archer 1997; Sankaran et al. 2004). Explanations for the coexistence of trees and grasses differ about whether it can result in a stable or unstable state (Scholes & Archer, 1997). The latter authors further stated that savanna structure is a result of factors such as climate, resource partitioning fire and herbivory that occurs at various scales.

There are two explanations for the coexistence of trees and grasses in savannas. It can be due to competition based mechanisms (Sankaran et al. 2004) which occur when there are limited resources such as water allowing the trees and grass to by partition resources (Scholes & Archer, 1997). Additionally, there are several models
that can help to understand coexistence of these plants. These models include, Walter’s two-layer; state- and-transition (de Klerk, 2004).

The Walter’s two-layer model states that if the grass layer is over-exploited, it can lose its ability to compete with trees and shrubs. In addition, water is considered to play a vital role in this model and can be limiting for both the trees and grasses (Mueller-Dombois & Walter, 1971). In this model, it is hypothesized that the removal of grass by heavy grazing can allow more water to be available for the woody plant growth in the lower layers of the soil (Wiegand et al. 2005). As a result, the woody plants increases in number, which in turn suppresses the grasses and causes bush encroachment (Mueller-Dombois and Walter, 1971). According to Walter’s two-layer model, grazing is regarded as the main cause of bush encroachment in savannas (Ward, 2005). The model suggests grass outcompetes trees in open savannas (Scholes & Archer, 1997). Grasses do this by growing fast and intercepting most of the moisture from the upper soil layers. Ultimately, this prevents trees from accessing moisture from lower soil layers where roots are mostly found (Ward et al. 2013).

When grasses are removed through grazing, soil moisture becomes available to the trees which allow more recruitment. Bush encroachment is more adverse in areas with single soil layer and where grazing is frequent (Brown & Archer, 1999). However, Walters two layer model can lead to the tree and grasses coexisting (Ward et al. 2013). Thus far, some mitigation of bush encroachment is done such as destocking livestock during low rainfall years. Nevertheless, this mitigation has
failed to reduce bush encroachment hence leading to a conclusion that causes of bush encroachment are poorly understood (Smit et al. 1996).

Walker Gillison (1982) stated that savannas have mixtures of trees and grasses in a continuous range which allow coexistence in the savanna ecosystems and leads to layers of two distinct life forms. One of the distinctions can be in their root systems. For example, most grasses absorb water from the surface of the soils whereas the shrubs absorbs water from the lower soils layers (D’Odorico et al. 2007). Another distinction can be in the different photosynthetic pathways. C₃ plants, which include most trees, are also known as temperate or cool-season plants. This means, these plants tend to become less competitive when the temperature increases. These plants can be annuals or perennials (Pearcy & Ehleringer, 1984). C₄ plants, which include most grasses, are also known as warm season plants. Compared to C₃ plants, C₄ plants tend to become more abundant when the temperature increases (Canvin, 1979; Pearcy & Ehleringer, 1984).

The predicted increase in global temperatures will favour C₄ over C₃ plants. Hence, the C₄ species have a higher rate of surviving and reproducing with the effect on climate change (Barbehenn et al. 2004; Johnson et al. 1993). The C₄ pathway allows higher fitness in warmer conditions and these species depends on the summer precipitation which enhances their establishment and allows them to be dominant in their local environment (Bond, 2008). Most of the grasses have a C₄ photosynthetic pathway and this allows them to survive in hot, sunny conditions whereas the trees and shrubs are C₃ plants and tend to do well in wet climatic conditions. C₃ plants will
suffer due to less rainfall hence they are less drought resistant and will not be
favoured when drought events occur (Pearcy & Ehleringer, 1984).

The state-and-transition model is an idea that deals with rangeland vegetation, which
exhibits multiples states that involves transitions. However, for this concept to be
operational, detailed vegetation dynamics of a specific area has to be described
(Briske et al. 2003). The state-and-transition model which emphasizes that savanna
ecosystems are event-driven and bush encroachment is a reversible event, depending
on favourable management and environmental conditions (Bestelmeyer et al. 2017).
This model is driven by fire suppression, browse exclusion and annual rainfall
variability (de Klerk, 2004). This model involves the identification of the vegetation
state, linkage in the states and defining the transitions from the “normal” savanna to
the bush encroached savannas (Briske et al. 2003).

This model involves plant communities and how changes can occur in these
communities. These changes can alter the abundance of species and are caused by
external factors. These factors can be heavy continuous grazing, that causes change
in rangelands by changing grass dominated areas into shrub dominated areas (Briske
et al. 2003). The heavy grazing facilitates in spreading invasive species such as a S.
mellifera, by providing dispersal pathway for seeds and reducing competition by
removing grasses. Therefore reduced competition may allow shrub establishment and
growth (de Klerk, 2004).
2.3 Bush encroachment in savannas

Bush encroachment is broadly defined as the reduction of palatable grasses and herbs replacing them with unpalatable species to the livestock and other animals in the long run. Bush encroachment can affect the human livelihood where it occurs (de Klerk, 2004). According to Ward (2005) and De Klerk (2004), it is evident that savannas are being altered by bush encroachment. De Klerk (2004) stated that bush encroached areas are about 26 million ha of the savanna in Namibia and the combined effects of shrub encroachment and climate change can result in loss of land productivity and causes a reduction in the carrying capacity of farms lands. Additionally, when the capacity of rangelands is reduced, this negatively affects the livelihoods of some farmers and the economy as a whole.

Bush encroachment is mainly caused by interlinked factors such as incorrect grazing practices, lack or misuse of fire, and absence of browsing animals (Ward, 2005). Bush encroachment rates may differ due to climate change. Savannas are predicted to have an increase in bush encroachment with an increase in atmospheric carbon dioxide concentrations (Bond & Midgley, 2012). An increase in atmospheric carbon dioxide is expected to benefit the *Vachellia* and *Senegalia* species by improving their water-use efficiency and increasing carbon uptake. The most dominant species causing bush encroachment in Namibia are *Senegalia mellifera* (previously known as *Acacia mellifera*) subsp. *detinens* (black thorn), *Dichrostachys cinerea* (sickle bush), *Terminalia sericea* (silver Terminalia), *Terminalia prunioides* (purple pod terminalia), *Senegalia erubescens* (blue thorn), *Vachellia reficiens* (false umbrella thorn) and *Colophospermum mopane* (mopane) (de Klerk, 2004).
2.4 Trends and predictions of climate change for savanna in Namibia

Climate is the long-term weather conditions experienced in a specific region. However, in the past years the earth’s climate has changed and this is referred to as climate change (Intergovernmental Panel on Climate Change, 2007). Climate change occurs normally due to the natural variabilities in the long –term weather conditions but it has intensified due to human activities that have increased emissions of greenhouse gases such as carbon dioxide and methane. The change in climate can have adverse effects on both humans and natural ecosystems. For instance, changes in weather patterns can influence rainfall, resulting in severe droughts or floods. This decrease food production leading to less food being available and can adversely affect the health of humans and animals (Intergovernmental Panel on Climate Change, 2007).

Namibia is known to be among the countries in the sub Saharan Africa that are most vulnerable to the effects of climate change (Serdeczny et al. 2016). The effects of climate change will vary in Namibia due to the different regions such as desert and grasslands. Climatic conditions in Namibia are predicted to become warmer and less rainfall is expected in some parts of the country (Mapaure, 2011). It is predicted that Namibia will be hotter than usual, the predicted temperature rises between 1°C and 3.5°C in summer and 1°C to 4°C in winter during 2046–2065 (Midgley et al. 2005). Furthermore, the other major predicted impacts will be an increase in the frequency and the severity of droughts. Grasses tend to be drought resistant leading them to suffer less and thus can ultimately help in combating shrub encroachment (Parmesan & Hanley, 2015; Ward, 2005).
Forage in Namibia is vulnerable to climate due to the variability that might occur between seasons (Midgley et al. 2005). Namibia is a semi-arid area and receives on average low and variable rainfall (Mendelsohn et al. 2002). The Namibian economy largely depends on its natural resources for income generation. Climate change is predicted to cause changes in the vegetation structure (Intergovernmental Panel on Climate Change, 2007; Midgley et al. 2005). Vegetation cover and net primary production are expected to decrease and this will ultimately affect livestock production.

Kgope et al. (2010) pointed out that climate change will affect natural resources and suggests that Namibia can lose about 6 percent of Gross Domestic Product (GDP) if no actions are taken to adapt to climate change. It is suggested that the increase of carbon dioxide in the atmosphere can reduce rangelands net productivity (Reeves et al. 2014). Rangelands’ are known to provide benefits such as fuel wood and protein. When rangeland productivity decreases, the vegetation cover and biomass decreases leading to larger portions of land being bare (Midgley et al. 2005). Ultimately, this will affect the amount of forage availability to livestock and wildlife. This will lead to low livestock and wildlife that affect the agricultural sector as a whole which contributes largely to the GDP of Namibia (Midgley et al. 2005).

2.5 Possible approaches to studying plant responses to climate change

There are several possible approaches of studying the effect of climate change on the responses of plants. Firstly, rain-out shelters are used in manipulative field experiments to mimic drought stress by intercepting rainfall. They are transparent
roofs that blocks out rainfall and have minimal effects on other environmental variables (Yahdjian & Sala, 2002). Secondly, observations of plant responses along a temperature/rainfall gradient can be done. Lastly, a combination of observations along a temperature/rainfall gradient can be used including reciprocal transplant experiments.

Reciprocal transplants are experiments where one or more organisms are moved from their native environment to a new environment; the new environment usually have different environmental conditions to that of the native (Liu & van Kleunen, 2017). Reciprocal transplants is a concept borrowed from evolutionary studies (Ariza & Tielbörger, 2011); and is hardly used in climate change studies. Only few studies have actually combined reciprocal transplants with neighbour manipulations by manipulating density of plants that are neighbours to the focal plant (Ariza & Tielbörger, 2011; Vuorisalo & Mutikainen, 1999). However, these experiments often fail to separate abiotic from biotic components of local adaptation, therefore, inferring how climate change affects these interactions is difficult.

There are limited field studies conducted to determine the role of plant-plant interactions in order to determine the local adaption of specific plant species (Sambatti & Rice 2006; Lankau & Strauss 2007; Rice & Knapp 2008, cited by Ariza & Tielbörger (2011)). According to Petru & Tielbörger (2008), there are few experimental studies that have attempted to test for the response of plants by separating environmental variables such as soil type and rainfall. Therefore, drought should play a key role in shrub encroachment but experimental evidence is missing.
in the field and rare in common gardens, and interactions between drought and factors amenable to manipulation, namely adaptive management of fire, grazing, and nutrients, are unknown (Holthuijzen, 2015).
CHAPTER 3: MATERIALS AND METHODS

3.1 Research design
Experiments were conducted at field sites, namely Tsumeb, Okakarara and Ebenhaezer along a steep annual rainfall gradient range in Namibia. The experiment followed a factorial design in order to study the effect of plant species, origin of seeds, planting site and neighbour treatment on germination, survival and growth of a focal shrub and grasses.

3.2 Study species
The study focused on three species, namely Senegalia mellifera, Stipagrostis uniplumis and Anthephora pubescens. These grasses (S. uniplumis and A. pubescens) are perennial and were chosen due to their importance of grazing to livestock and wild animals.

A. pubescens has a high grazing value due to digestible, nutritious and high dry matter production and a good indicator of good veld conditions and it is drought resistant (Zimmermann, 2007). It is mostly found on sandy or gravelly soils and is more tolerant of low phosphorus levels than other grasses. In addition, it can grow up to 1000 mm high and has a panicle inflorescence which ranges from 5cm to 500mm long (Zimmermann, 2007). Whereas, S. uniplumis is an indicator of poor soils and sometimes can act as an indicator of overgrazing.
It is mostly found on granitic soils. These grasses can grow up to 850 mm high and has a leaf blade that is rolled. It has inflorescence that can be up to 300 mm long.

*S. mellifera* (previously known as *Acacia mellifera*) was chosen because it is among the high encroacher species in Southern Africa. It produces papery pods and has white creamy flowers. *S. mellifera* has twigs and pods that are very nutritious to livestock and game such as black rhino, kudu, eland and giraffe and these animals help with seed dispersal. The rapid spreading leads to forming impenetrable thickets (Rohde & Hoffman, 2012). Furthermore, *S. mellifera* is a small-sized tree with almost round-shaped canopy and has paired curved thorns. Its height ranges from 3 m to 4 m.

According to Mannheimer & Curtis (2009), *S. mellifera* is mainly found on clayey soils and does not require larger amounts of water to survive. Furthermore they stated that this species can survive in extreme dry conditions. The shoots are too spiny and the animals such as sheep and cattle tend not to browse on them and this allows *S. mellifera* to grow much faster than woody plants that are (Mannheimer & Curtis, 2009).

### 3.3 Study areas

The experiments were conducted at three research OPTIMASS sites along a rainfall gradient from Tsumeb, Okakarara and Ebenhaezer (Figure 1).
**Figure 1:** Map of Namibia showing the three study sites.
3.3.1 Tsumeb

3.3.1.1 Location
Tsumeb is located at S19°14´31" and E17°43´47" in Oshikoto Region, and is about 1320 metres above mean sea level (Mendelsohn et al. 2002). The research was done at the Tsumeb Geophysical Research Station about 12 km northwest of Tsumeb. The station is owned by the government under the supervision of the Ministry of Mines and Energy. According to the Geological Survey of Namibia (2017), this station primarily focuses on monitoring seismic activity as part of the Global Seismological Network (GSN). Cattle farming take place at the station.

3.3.1.2 Climate
The climate of this area is considered as semi-arid. The mean annual rainfall is between 500-550mm and the rainy season extends from November to April (Mendelsohn et al. 2002), with most of rain falling in January and February. The average annual temperature for Tsumeb is between 20°C and 22°C. The maximum temperatures range from 32°C to 34°C during summer, while in winter, temperatures range from 6°C and 8°C (Mendelsohn et al. 2002).

3.3.1.3 Geology and soils
According to Mendelsohn et al. (2002) Tsumeb has high soil fertility which makes the place suitable for crop production. Soils consist of Mollic latosols on various landscapes. Most areas in Tsumeb have rock outcrops that consist of limestone and Chromic Luvisols and Chromic Cambisols (Mendelsohn et al. 2002).
3.3.1.4 Flora

The vegetation in this area is classified as the Acacia tree-and shrub savanna (Kartsveld) made up of mixed woodlands (Mendelsohn et al. 2002). The experimental site was dominated by woody species such as *Combretum apiculatum*, *Dichrostachys cinerea*, *Vachellia* species and *Senegalia* species. The most abundant grasses in this area are *Mellinis repens Aristida congesta*, *Enneapogon cenchroides*, *Setaria verticillata*, *Stipagrostis uniplumis*, *Chloris virgata*, *Eragrostis trichophora*, *Heteropogon contortus*, *Panicum kalaharense* and some wild Sorghum species. The main bush encroaching species are *D. cinerea* and *S. mellifera* (Mendelsohn et al. 2002).

3.3.1.5 Fauna

Although the Seismic Station is mainly used for research, it is also home to large herds of cattle and wild life such as kudu, springbok and warthog (Mendelsohn et al. 2002). Predators such as jackals roam on the farm but in camps that are far away from the station buildings. Small animals such as porcupines and ground squirrels can also be found at the Seismic Station. The farm is home to a variety of birds such as the Cape turtle and laughing doves.

3.3.2 Okakarara

3.3.2.1 Location

The study site is located about 12 km north of Okakarara town in Otjozondjupa Region at the Kahengombe and Son’s Stud Farm (S20°30’46”, E17°27’55”). This
farm is owned by Mr. Brian Kahengombe and it is about 1347 metres above mean sea level (Mendelsohn et al. 2002).

3.3.2.2 Climate

The climate of this area is considered as semi-arid and has a mean annual rainfall of about 425mm and the rainfall season extends from November to April with most of the rainfall experienced in January and February. The average annual temperature for Okakarara ranges from 20°C to 22°C. The maximum temperatures ranges from 32°C to 34°C during summer, while in winter the minimum temperatures range from 6°C and 8°C (Mendelsohn et al. 2002).

3.3.2.3 Geology and soils

According to Mendelsohn et al. (2002), Okakarara soils are of medium fertility. Okakarara occurs on the rocky central plateau of Namibia and has various soil types. Okakarara is has 200-m high sandstone with deep sand (Mendelsohn et al. 2002). Okakarara is near the Waterberg plateau which is approximately 4100 km² sandstone uplift geological feature of this area (Mendelsohn et al. 2002).

3.3.2.4 Flora

The vegetation in this areas is classified as Thornbush (Mendelsohn et al. 2002). Thornbush savanna consists of dominant woody plant genera such as Senegalia, Vachellia, Dichrostachys, Grewia, Terminalia, and Boscia species. This area has changed over the last century due to the synergistic effects of human disturbance and
the change in climatic (Mendelsohn et al. 2002). In some parts of the farm, bush encroachment is evident. The dominant encroachers are Senegalia mellifera and Terminalia sericea which occur as dense thickets. The farm showed different forms of degradation due to certain land use ranging from the grassland with few woody plants to more heavily encroached as you move away from the farm house.

Part of the farm where the experiment was done comprises mostly Terminalia sericea, Combretum collinum, Combretum psidioides, Grewia flava, Philenoptera nelsii, Ochna pulchra, Ziziphus mucronata, Acanthospermum hispidium and Abutilon species. Grass species commonly found on the farm are Eragrostis species and Digitaria seriata.

3.3.2.5 Fauna

The farm is mainly for cattle, goats and sheep raising for breeding purposes but there are few herds of game species such as kudu, springbok, steenbok and warthog. Predators such as jackals also freely roam on the farm. There are also antbears, pangolins, porcupines, scrub hares, and ground squirrels.

3.3.3 Ebenhaezer

3.3.3.1 Location

Ebenhaezer Farm occurs in Omaheke region, about 160km south-east of Windhoek. Ebenhaezer is a privately owned commercial livestock farm in the Western Kalahari and is located at S23°12′57″ and E18°27′22″, south west of Gobabis town and close
to a settlement called Nina. It is about 1400 metres above sea level (Mendelsohn et al. 2002).

3.3.3.2 Climate

The climate of Ebenhaezer is semi-arid. Ebenhaezer and neighbouring farms receive about 250 mm of rainfall annually. The annual temperature is between 20°C and 22°C. The average the average maximum temperature is between 32-34°C and the mean minimum temperature is between 2 and 4°C (Mendelsohn et al. 2002). The hottest months are experienced during summer whereas the coldest months are experienced during winter mostly in June and July (Mendelsohn et al. 2002).

3.3.3.3 Geology and soils

The Western Kalahari is known to have flat scattered dunes that may contain a variety of rock types (Mendelsohn et al. 2002). The area has sandy soils of low fertility and the dominant soil type is ferralic arenosols (Mendelsohn et al. 2002). The topography is characterised by low longitudinal dunes (Vinte, 2015).

3.3.3.4 Flora

The vegetation of Ebenhaezer is categorised as the Acacia Tree-and –Shrub Savanna (Mendelsohn et al. 2002), with Senegalia species as the dominant woody components and the most dominant grasses such as Stipagrostis, Aristida and Eragrostis species in the herb layer. The dominant species on the Ebenhaezer farm were Vachellia erioloba, Senegalia mellifera, Vachellia hebaclada, Grewia flava,
*Albizia anthelminthica, Boscia albitrunca* and the most dominant grasses are *Stipagrostis uniplumis, Aristida meridionalis, Aristida stipitata, Eragrostis* species and some perennial herbs such as *Senna italica* and *Pollichia campestris* (Vinte, 2015).

### 3.3.3.5 Fauna

Livestock at Ebenhaezer farm include cattle, sheep, goats and horses. The farm is adjacent to the Kuzikus wildlife farm and movement of kudu, springbok, steenbok and warthog between farms occurs (Vinte, 2015). In addition, predators such a foxes and jackals are also occasionally seen on the farm. Small animals such as porcupines and ground squirrels are found on the farm.

### 3.4 Seed collection and sorting

This study was part of a larger project called Options for sustainable geo-biosphere feedback management in Savanna systems under regional and global change (OPTIMASS) that took place from November 2016 to April 2017. Seeds of *Anthehphora pubescens* and *Stipagrostis uniplumis* were collected from 30 random individuals at each of the three sites and put in paper bags during April and May 2016. Seeds of *Senegalia mellifera* were collected during October and November 2016. Seeds were sorted in the laboratory by putting ten seeds of each grass species and five seeds of each woody species in paper bags.
3.5 Reciprocal transplant experiment

The reciprocal experiment involved sowing of seeds in their home location and at an away drier location. Seeds (five seeds of *S. mellifera*; ten seeds of the *A. pubescens* and *S. uniplumis*) were sown at its local site and the close proximity drier site. Such that Tsumeb site has only one seed origin, while Okakarara and Ebenhaezer has two origins (Appendix 2). To test for local adaptation of *Stipagrostis uniplumis*, *Anthephora pubescens* and *Senegalia mellifera*, a 30 m by 30 m area representing the whole area’s vegetation was selected for the experiments. A combination of a cattle proof fence and a chicken mesh wire of 30 m by 30 m were erected at Tsumeb and Okakarara. No fence was erected at Ebenhaezer because the fencing would have interfered with the movement of horses on the farm.

**Figure 2:** Design of plots and the measurements at Tsumeb.
Figure 3: Design of plots and measurements at Okakarara and Ebenhaezer.

Within the 30 m by 30 m fence, a distance of 1 m (shown by the arrows in the above diagrams) was systematically measured out from the fence and pipes with a 50 mm diameter (the pipes were referred to as plots) were laid down on the ground as blocks (group of pipes) (Figure 2 and 3), with 4 cm above ground and 3 cm below ground with a distance of 10 cm between them. Neighbour treatments was done by clipping (before seeding and within the experiment period) or removing all emerging plants surrounding the respective pipes where clipping treatments was applied according to the keys in figure 2 and 3. Another 1 m was measured out randomly by interspersing from the first block of species and the second paired species plots were measured out. This was done for all the remaining species (Figure 2 and 3) and it was repeated 30 times (n=30). The experiment consisted of 240 plots in Tsumeb and 480 plots in Okakarara and Ebenhaezer. Overall, 1200 plots were used in this study.
In each the demarcated block, the polyvinyl chloride (PVC) pipes were labelled according to the keys in Figure 2 and 3. The grass species were sown two months prior to adding woody plant seeds by turning the soil and to cover the seeds.

3.6 Data analysis
Germination fraction was expressed as mean percentage of total number of seeds that germinated per number of seeds that was sown. Survival proportion was expressed as mean percentage of the total number of seedlings that survived at the end of the experiment per total number of seeds that germinated. Height was measured by measuring the height of 1-2 emerging seedlings per plot using a ruler.

3.7 Statistical analysis
Generalised Linear Models (GLMs) were used to test for germination, survival interactions with binomial distribution and logit link function. Two analyses were made for the site pair’s example Tsumeb vs. Okakarara and Okakarara vs Ebenhaezer. An automatic selection of the best generalized linear model with a logit link function was used in Statistical Package for the Social Sciences (SPSS). Some GLMs involved choosing a stepwise approach. The analysis was firstly done by fitting the model with all the variables (site, seed origin and clipping) and all the interactions (site and seed origin, site and clipping, seed origin and clipping, site, seed origin and clipping). This was followed by removing the four-way interactions that were not significant, then the three–way interactions, two-way interactions and so on, until the best (most parsimonious) model was obtained. Parsimony was tested by comparing the Akaike information criterion (AIC) between the models, leading to
the model with the smallest value to be chosen as the best model. The same procedure was applied to the height data but with a normal distribution and log link function was applied to the model.

All statistical analyses were performed using SPSS 22 (IBM SPSS Statistics for windows, Version 22).
CHAPTER 4: RESULTS

4.1 Comparison of germination fractions

4.1.1 Stipagrostis uniplumis

Mean germination fractions were similar between clipped and unclipped plots and there was no statistically significant differences in clipped plots of Tsumeb-Okakarara and Okakarara-Ebenhaezer (Generalised linear model: \( p = 0.387 > 0.05, \) df = 1, \( p = 0.495 > 0.05, \) df = 1, respectively). Seeds from Okakarara had a higher germination fraction at Ebenhaezer than at Okakarara between both clipped and unclipped plots. Overall, seeds from Okakarara had a higher germination fraction than seeds from Tsumeb and this was statistically significant (df = 1, \( p = 0.010 < 0.05 \)).

There was a significant difference in the mean germination fraction between Okakarara and Ebenhaezer (df = 1, \( p = 0.000 > 0.05 \)) (Figure 4). There was a positive interaction between the site and seed origin in Tsumeb-Okakarara (df = 1, \( p = 0.000 > 0.05 \)) (Appendix 2).
Figure 4: Comparisons of mean (±SE) germination fraction (%) of *S. uniplumis* seeds collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbour drier site in clipped and unclipped plots.

4.1.2 *Anthophora pubescens*

Mean germination fractions were similar between clipped and unclipped plots in Tsumeb-Okakarara and Okakarara-Ebenhaezer (df = 1, p = 0.895 > 0.05 and df = 1, p = 0.730 > 0.05, respectively). Seeds from Tsumeb had a higher germination
fraction at Okakarara than at Tsumeb in both clipped and unclipped plots. However, this was not statistically significant (Generalised linear model: \( df = 2, p = 0.180 > 0.05 \)).

Seeds from Okakarara had a higher germination fraction at Ebenhaezer than at Okakarara in both clipped and unclipped plots. Overall, the seeds sown at the neighbouring drier sites had a higher germination fraction than the seeds sown in their native sites. This trend was statistically significant in Tsumeb-Okakarara (T-O) and Okakarara-Ebenhaezer (O-E) sites (\( df = 1, p = 0.005 < 0.05 \), \( df = 1, p = 0.001 < 0.05 \), respectively) (Figure 5).
**Figure 5**: Comparisons of mean (±SE) germination fraction (%) of *A. pubescens* seeds collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.

### 4.1.3 Senegalia mellifera

Seeds from Tsumeb had a higher germination fraction at Tsumeb than at Okakarara in both clipped and unclipped plots. Seeds that originated from Okakarara had a significantly higher germination fraction than to Tsumeb ($p = 0.034 < 0.05$). Overall, the seeds sown at their local sites had a higher germination fraction than those seeds
sown at their neighbouring drier sites (Appendix 4). The Generalised Linear Model showed a statistically significance in sites (df=1, p=0.000 < 0.05 and df=1, 0.004 < 0.05 for T-O and O-E respectively).

Overall, germination fractions increased from the wet to the drier sites (Figure 6). There was a significant interaction between site and seed origin in Tsumeb-Okakarara (p=0.0005 < 0.05) (Appendix 4). Clipping had no significant effect on germination fraction for Tsumeb-Okakarara and Okakarara-Ebenhaezer (df = 1, p = 0.425 > 0.05 and df = 1, 0.176 > 0.5 respectively) (Figure 6).
Figure 6: Comparisons of mean (±SE) germination fraction (%) of *S. mellifera* seeds collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.

4.2 Comparison of seedlings survival fraction

4.2.1 *Stipagrostis uniplumis*

There were no seedlings that survived from Tsumeb that were sown in Tsumeb in both clipped and unclipped plots. Additionally, there were no seedlings that survived from Tsumeb that were sown in Okakarara (away site) in the clipped plots. Overall,
there was a higher mean survival fraction in Okakarara than to Tsumeb (Figure 7). There was a statistically significant difference in the seed origin of Tsumeb-Okakarara ($p = 0.010 < 0.05$): the S. uniplumis seedlings from Okakarara had a higher mean survival fraction at Okakarara in the clipped plots than in the unclipped plots where no germination took place. Overall, there was a higher mean survival fraction in the clipped plots than to the unclipped plots (Figure 7) though this was not statistically significant ($p = 0.345 > 0.05$ and $0.225 > 0.05$ for T-O and O-E respectively). Overall, competition with neighbours was not significant in T-O and O-E ($p=0.345 > 0.05$, O-E; $0.225 > 0.05$, respectively). There was a negative interaction between the site and clipping in O-E (df = 1, $p = 0.356 > 0.05$) (Appendix 5).
Figure 7: Comparisons of mean (±SE) survival fraction (%) of *S. uniplumis* seedlings collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped.

4.2.2 Anthephora pubescens

There were no seedlings that survived from Tsumeb that were sown in Tsumeb in both clipped and unclipped plots. Seedlings from Okakarara had a higher survival at Okakarara than at Ebenhaezer in both clipped and unclipped plots. Seedlings from Ebenhaezer had a higher survival fraction in the unclipped plots than the clipped
plots which had zero survival fractions (Figure 8). Okakarara had the highest survival fraction than Tsumeb and Ebenhaezer \((p = 0.009 < 0.05, p = 0.012 < 0.05\) respectively). Overall, competition with neighbours was not significant in T-O and O-E \((p=0.089 > 0.05, O-E; 0.698 > 0.05,\) respectively). There was a negative interaction between the site and clipping in O-E \((df = 1, p = 0.356 > 0.05)\) (Appendix 6).

**Figure 8:** Comparisons of mean (±SE) survival fraction (%) of *A. pubescens* seedlings collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.
4.2.3 Senegalia mellifera

Seedlings from Tsumeb had a higher mean survival fraction at Okakarara than at Tsumeb in both clipped and unclipped plots. Seedlings from Okakarara had a higher survival fraction than Ebenhaezer and the GLM showed that this was significant for T-O and O-E (p = 0.000 < 0.05 and p = 0.000 < 0.05 respectively) (Figure 9). Competition with neighbours was not significant in the paired sites (T-O and O-E) (p = 0.403 > 0.05 and p = 0.065 > 0.05 respectively) (Figure 9). There was a significant interaction between transplantation site and clipping (df = 1, p = 0.001 < 0.05 and df = 1, p = 0.001 < for T-0 and O-E respectively), and seed origin and clipping (df = 1, p = 0.012 < 0.05 and df = 1, p = 0.005 < 0.05 for T-O and O-E respectively) in S. mellifera (Appendix 7).
Figure 9: Comparisons of mean (±SE) survival fraction (%) of *S. mellifera* seedlings collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.

4.3 Comparison of seedlings height

4.3.1 *Stipagrostis uniplumis*

There were no seedlings at Tsumeb. Overall, unclipped plots had a higher mean height than the clipped plots but this trend was not statistically significant (df = 1, p = 0.106 > 0.05 and df = 1, p = 0.061 > 0.05 for T-O and O-E, respectively).
Seedlings form Okakarara had a higher mean height than Ebenhaezer seedlings in both clipped and unclipped plots and this was statistically significant (df = 1, p = 0.022 < 0.05) (Figure 10). Overall, competition with neighbours was not significant in T-O and O-E (p=0.106 > 0.05, O-E; 0.061 > 0.05, respectively). The GLM did not show interactions for *Stipagrostis uniplumis* (Appendix 8).

**Figure 10:** Comparisons of mean (±SE) height (%) of *S. uniplumis* seedlings at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.
4.3.2 *Anthephora pubescens*

There was no survival for Tsumeb seedlings in Tsumeb. Seedlings from Tsumeb had a higher height than Okakarara; seedlings from Okakarara had a higher height than Ebenhaezer. This trend was statistically significant (df = 1, \( p = 0.002 < 0.05 \) and df = 1, \( p = 0.001 < 0.05 \) for T-O and O-E respectively). Seedlings from Okakarara had a higher height in clipped plots at Okakarara than at Ebenhaezer. Whereas, seedlings from Okakarara had a higher height in unclipped plots at Ebenhaezer than at Okakarara. Overall, competition with neighbours was not significant in E-O and O-E (\( p=0.551 > 0.05 \), O-E; 0.391> 0.05, respectively) (Figure 11). Although the main effect of clipping was not significant, there was a significant interaction between the site and clipping for both T-O and O-E (\( p = 0.001 < 0.05 \) and 0.002 < 0.05 respectively). There was no significant interaction in seed origin and clipping in T-O (\( p=0.734 > 0.05 \)) (Appendix 9).
Figure 11: Comparisons of mean (±SE) height (%) of *A. pubescens* seedlings collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.

4.3.3 *Senegalia mellifera*

Seedlings from Tsumeb had a higher mean height at Tsumeb than at Okakarara in both clipped and unclipped plots (df = 1, p = 0.805 > 0.05). There was no significant difference in mean height of seedlings of Okakarara origin between Okakarara and Ebenhaezer (df = 1, p = 0.739 > 0.05). Overall, Tsumeb seedlings had a higher mean
height than Okakarara seedlings but not significant (df = 1, p = 0.065 > 0.05). Also, Okakarara seedlings had a higher height than Ebenhaezer and this was not statistically significant (df = 1, p = 0.653 > 0.05) (Figure 12). Overall, competition with neighbours was not significant in T-O and O-E (p=0.427 > 0.05, O-E; 0.610 > 0.05, respectively). There were no positive interactions in transplantation site and seed origin, transplantation site and clipping and seed origin and clipping for *Stipagrostis uniplumis* (See Appendix 10).

Figure 12: Comparisons of mean (±SE) height (%) of *S. mellifera* seedlings collected at three sites: very dry (E=Ebenhaezer), dry (O=Okakarara), and wet (T=Tsumeb) and sown at the home and neighbouring drier site in clipped and unclipped plots.
5.1 Comparisons of germination fraction

The mean germination of *S. uniplumis* seeds of Okakarara was higher when planted at a drier site (Ebenhaezer) than at a wetter site (Okakarara) when clipping was not considered. This allowed the seeds from a wet site to perform much better in the area where less rain is expected. The possible explanation for this can be because in 2017, the rainfall in Ebenhaezer occurred more frequently despite the amount being less (J. Heblack\(^1\), personal communication, 12 January, 2017) unlike in Okakarara where the rainfall was high but did not occur frequently (S. Gabriel\(^2\), personal communication, 14 April, 2017). This is consistent with the stress gradient hypothesis (Maestre *et al.* 2009), which suggests that plant species to perform much better in stressed conditions due to facilitation. Facilitation can occur when species are moved from favourable environments and exposed to less favourable conditions. According to Cranston *et al.* (2012), facilitation can allow some plant species such as *S. uniplumis* to inhabit new environments that are less favourable and this can allow for greater fitness, abundance and range expansion.

\(^1\)J. Heblack is a student on the OPTIMASS project studying at Potsdam University (Germany) who did some experiments in Ebenhaezer.

\(^2\)S. Gabriel is a foreman at Kahengombe Farm, Okakarara.
Overall, *S. uniplumis* seeds germinated more when sown in their local site (Okakarara) than when planted in a neighbouring dry site (Ebenhaezer) in both clipped and unclipped plots. This variation in seed germination can be considered as an adaptive response of plant species to adjust to their environmental conditions. This allows seeds to perform better than when planted in a foreign site by breaking the dormancy when favourable conditions occur (Fernández-Pascual *et al.* 2013).

Local response of *S. uniplumis* can also be a reason why there was a higher mean germination fraction when seeds were planted in their local sites than in the neighbouring dry sites. Donohue *et al.* (2010) suggested that environmental-cued germination can be a reason why home seeds had a higher germination fraction. Plant species tend to have mechanisms that allow germination to be delayed when environmental conditions are not favourable. *S uniplumis* had the highest mean germination at Ebenhaezer in both clipped and unclipped plots. Ebenhaezer has shallow sandy soils and *S. uniplumis* is known to perform well when in reddish sandy soils (Huntley & Walker, 1982) and the variations in the soil nutrients at each specific site can play a vital role in germination when neighbours are removed; it is more likely that there was less competition over limited resources such as sunlight, water and other resources.

The results of this study have shown a significant difference in the mean germination of *A. pubescens* between the Tsumeb seeds planted in Tsumeb and in Okakarara. This grass species germinated at higher rates despite being planted in drier sites because rainfall did not perhaps play a major role in the germination rate but some
other factors such as the soil type and temperature at the community level influenced the germination hence allowing the species to perform better (Rysavy et al. 2014). *A. pubescens* seeds from Okakarara had a higher mean germination when planted in Ebenhaezer than the seeds that are from Ebenhaezer and planted in Ebenhaezer.

There was a significant interaction effect between transplantation site and seed origin. According to Beckmann *et al.* (2011), and Gillard *et al.* (2017) some seeds that are planted away from their home environments have wide ranges of conditions which can allow them to grow. Seeds from Ebenhaezer did not have a high mean germination despite being planted at the home site. This is because some seeds may be dormant and germinate when the conditions are favourable. Such conditions may have been available in the neighbouring site but not at Ebenhaezer during the experimental period. Another reason why *A. pubescens* was recorded with the high mean germination fraction at the wetter site is because this species grows quite well where the mean annual precipitation is about 550 mm (Zimmermann, 2007).

Mean germination fraction did not differ in *A. pubescens* between the experiment sites but tended to be higher when sown in their local sites in both clipped and unclipped plots. Moreover, there was an indication of local adaptation along the rainfall gradient indicated by the significant interactive effect between site and seed origin. Species performances along environmental gradients are often associated with the decrease in the performances when the rainfall decreases. However, in this study not all the results supported this hypothesis. In the drier site of Ebenhaezer, mean seed germination was higher than at the wetter site, Okakarara. This can be due to
different responses of species to the environmental changes that occurred at the respective local scales (Liu & van Kleunen, 2017).

Down the rainfall gradient from Tsumeb to Ebenhaezer, *S. mellifera* germination continued to increase. de Klerk (2004) suggested that *S. mellifera* has a high resilience and is adapted to harsh environments such as low rainfall. Furthermore, this species has a high competitive ability and is known to have extensive and well developed tap and lateral roots that can reach deep in the soil to obtain water and nutrients (de Klerk, 2004).

Results of this study show that there was a significant difference in the seeds grown at their local than in the neighbouring drier sites of Tsumeb and Okakarara for *S. uniplumis* and *S. mellifera*. Seeds from Tsumeb had a higher mean germination rate than those from Okakarara because the amount of rainfall received during the experimental period may have been sufficient to elicit high germination rates at the respective sites in spite of the lower long-term mean rainfall. These patterns can occur due to the geographical region where the seeds came from and due to the home environment that can have a positive influence on germination due to local adaptation. Another reason can be the temperature difference between the two sites. Tsumeb experiences higher mean temperature of about 27°C than Okakarara which had a mean temperature of about 21°C (Accuweather, 2017). According to Gillard *et al.* (2017), environmental temperature can be the primary regulator for seed germination and can change seed dormancy and the germination responses in plant species. *S. mellifera* had a higher mean germination rate and this can be linked with
its encroaching characters. Many *Senegalia* species have aggressive root systems which allow the plants to grow and most of the time allows them to invade other areas.

The mean germination of *S. mellifera* in Okakarara seeds was higher in Ebenhaezer than at Okakarara because this species has a high resilience and can adapt well in new environments (de Klerk, 2004). These results were similar to those of Donohue *et al.* (2010), that highlighted that germination is a plant trait and can evolve fast in new environments compared to their native environments. In Tsumeb, seeds germinated at greater rates than at Okakarara and this may be attributed to local adaptation. Based on similar findings by Liancourt & Tielbörger (2011), along a rainfall gradient, the ecotypes from the more favourable sites (wetter) are better adapted to competition. It is hypothesised that species will have a high germination rate at home sites due to local adaptation and would be better competitors than at the drier site. There are many factors that explain germination responses and this may include the seed size and the nutrient reserves. In the case of *S. mellifera*, they have bigger seeds and high nutrient reserves hence this can lead to an increment in the germination rate (Souza & Fagundes, 2014).

Low seed germination occurred in all species especially *S. mellifera*. This can be because field observations showed that some seeds were dug out by the small mammals and birds and this led to less seeds being able to germinate. Furthermore, the effect of germination fraction was negligible for local adaptation when compared to the effects of local sites, drier neighbouring sites (experiment sites) and clipping.
5.2 Comparisons of seedling survival fraction

The number of seedlings of *S. uniplumis* from Okakarara in the clipped plots was higher at Okakarara than Ebenhaezer. This is because most plant species growth rates tend to increase when neighbouring plants are removed (Primack, 1978). This process is mainly attributed to less competition that occurs in the surroundings when other plants are removed. Removal of neighbouring plants allows more sunlight to reach the soil and increase the microsites that can be suitable for seed germination and establishment of the species (Aarssen & Epp, 1990). This may have occurred due to the increase in the water availability which aided the establishment and survival of plant species and could explain the high survival rates between Tsumeb and Okakarara.

No survival was recorded for both grass species of Tsumeb when planted at Tsumeb because of the type of the soils found at the experimental site. The Tsumeb site had loamy to clayey vertisols soils. This type of soil usually has high content of clay minerals that shrinks and cracks when there is low water content and swells when there is a high content of water. Tsumeb receives the highest rainfall among the three study sites hence the grasses did not survive due to waterlogging that took place while *S. mellifera* survived because the roots may have penetrated the soil much to deeper layers (Amadhila, 2011; Sahungwa, 2015). Grasses usually obtain moisture from the topsoil and cannot survive long periods of drought when soil moisture drops. In a similar study by Duane & Scott (2001) that was done along an environmental gradient using neighbour manipulation, some of the grasses survived. This was because in this study, less competition occurred and allowed this species to grow and establish itself without competition for resources that are needed for
survival. Overall; plants in the unclipped plots of A. pubescens had a higher survival than plants in clipped plots. According to Callaway (1995), the presence of other plants tends to provide more favourable habitats for survival.

*S. mellifera* can survive in the clayey soils in Tsumeb since the species has inherently slow growth rates and have high root elongations with an increase in acidity (Önemli, 2004). As proposed by Kidd & Proctor (2001), soil aridity can play a major role as a limiting factor for plant growth. Generally, grasses have low tolerance to low pH which is found in clayey soils and this can lead to lower survival. In addition, the grass species did not survive in Tsumeb because there are other perennials such as *Mellinis repens* Aristida congesta and *Enneapogon cenchroides* that were well adapted to the clayey conditions and may have outcompeted the two experimental grass species. A study by Önemli (2004) showed that soil types and environmental conditions can increase germination rates and also survival of seedlings. When there was an increase in the soil organic matter, there was also an increase in the seedling emergence due to the greater water content in the soil. As a result, the seeds receive sufficient rainfall to break dormancy and germinate. However, if inadequate rainfall is received after germination, the plants may die and this can cause a low survival fraction. Inadequate rainfall can also be an explanation why low survival fraction was recorded in *S. uniplumis* and *A. pubescens* along the rainfall gradient (Rysavy, 2013). In addition, when plant species experience changes in water availability, they may have less potential to regulate responses in the changing environments hence they do not perform well and survivorship decreases as the rainfall decreases (Rysavy, 2013).
There was a significant interaction between transplantation site and clipping, and seed origin in *S. mellifera* for both paired sites because facilitation occurred allowing *S. mellifera* to survive despite less rainfall being received. These results corresponded to a study done by Rysavy *et al.* (2014) where the seedlings had a high survival in response to neighbour presence along a rainfall gradient. Generally, the pattern in *S. mellifera* of having a high survival fraction at the wet areas and then low and lower at the dry and very dry areas was because of higher rainfall and high competitive abilities which allows *S. mellifera* to get sufficient resources needed for growth and survival. This pattern supports the stress gradient hypothesis which states that stress decreases if the most limited resource such as water is increased causing an improvement in survival and leading to high establishment success. This corresponds with a study done by Michalet *et al.* (2006) who stated that competition should first be moderate in the intermediate rainfall site along the environmental gradient and finally decreases drastically at the end of the gradient where the environmental conditions are harsh.

The survivorship and establishment of seedlings may depend directly on the environmental conditions after germinating (Gillard *et al.* 2017). High survival fraction occurred in Okakarara seeds planted at Okakarara for *S. mellifera* because local individuals maximise their survival success as seedlings under the favourable conditions and at the same time reduces the exposure to harsh environmental conditions. *S. mellifera* interactions were positive since interactions changed along the gradient and increased with the environmental stress of less rainfall. When interactions occur more frequently in plants, local adaptation can occur and allows
the species to compete for resources such as water that limits the growth and survival of the species (Kawecki & Ebert, 2004).

Overall, there were negative interactions at Okakarara and Ebenhaezer because of competition, especially for moisture, which might have been increased when less rainfall was received. According to Maalouf et al. (2012), in places where neighbours are removed, plants tend to suffer more from drought than when the neighbours were not removed. Overall, competition with neighbours was not significant in the three species and there were no interactive effects. Plant growth and survival are not entirely dependent on the presence of neighbours. Therefore, positive interactions mostly occur in stressful, abiotic environments and allows plants to establish in such environments in the presence of neighbours (Bertness & Callaway, 1994).

5.3 Comparisons of seedling height

Mean height of *S. uniplumis* seedlings was greater at Okakarara than at Ebenhaezer. There was a significant difference in the mean height of *S. uniplumis* seedlings between Okakarara and Ebenhaezer. This can be because grass species tend to invest more in the outside structures such as high height for better dispersal of seeds. It can be that the species in the very dry areas may be locally adapted to dry conditions (Jump & Peñuelas, 2005).

There was a significant interaction between site and clipping in *A. pubescens* seedlings. Plants tend to grow faster when there is less competition for resources such as water and sunlight (Nagashima & Hikosaka, 2011). Additionally, there was
no significant difference in the mean height of *A. pubescens* seedlings between Tsumeb-Okakarara and Okakarara-Ebenhaezer. According to findings by Nagashima and Hikosaka, (2011). *A. pubescens* regulated its height similar to that of the neighbours, thus reducing the probability of being spotted and grazed first. Hence, *A. pubescens* maintains a height similar to that of its neighbours. In contrast, a similar study by Li *et al.* (2017) it was found that species in the unclipped enclosure were taller and had greater leaf area which demonstrated that these species acquired more sunlight compared to the other species. The latter authors also concluded that the presence of neighbours is not necessarily advantageous as plants try to keep their height similar to that of neighbours to avoid overtopping other species since they can be easily spotted by herbivores. The significant interaction between site and clipping found here may suggest a higher competitive advantage in neighbouring drier sites than at the local sites.

Overall, the mean height of *S. mellifera* seedlings was similar between the two paired sites. This may be because the species invest more energy in the roots to enhance the uptake of below-ground water than investment in other physical structures such as leaves (Padilla & Pugnaire, 2007). Moreover; they allocated more biomass to roots, which might contribute to improvement of water availability leading to them having more or less the same height (Padilla & Pugnaire, 2007). This shrub species reduces its stem diameter when young and increases its root mass fraction which contributes to mechanical stability. Competition with neighbours was not significant in *S. mellifera*. This is because competition in *S. mellifera* mainly takes place underground despite neighbour removals. This species grows very long tap roots as seedlings to avoid direct competition with neighbours, as shown in previous studies (e.g.
Amadhila 2011 and Sahungwa 2015). Overall, along the gradient *S. mellifera* had a higher competitive ability, which allowed it to survive much better in low rainfall areas. *S. mellifera* plants tend to invest more on their physical structures such as thorns and elongated roots which may help to keep away browsers and get water from underground respectively when rainfall decreased (Padilla & Pugnaire, 2007).
CHAPTER 6: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusion

Germination fraction

Competition with neighbours was not significant in *S. uniplumis*. The study concluded that there was a statistically significant difference between germination of Tsumeb-Okakarara and Okakarara-Ebenhaezer in *S. uniplumis*. This is due the amount, frequency and duration of rainfall received during the experimental period. Furthermore, the study found statistically significant difference in the mean germination of *A. pubescens* seeds sown in neighbouring drier sites than seeds sown in their local sites. Perhaps rainfall did not play a major role in germination but some others factors such as soil type and temperature influenced germination. The study also concluded that there was a significantly higher mean germination of *S. mellifera* at seeds sown at their local sites than those in neighbouring sites. Therefore, interventions to clear and manage *S. mellifera* in order to strike a balance between trees, shrubs and grasses need to be put in place by both farmers and decision-makers. Additionally, this species may have adapted to harsh conditions of less rainfall and may also have greater competitive ability.

Seedling survival fraction

The study found that no grass species survived in Tsumeb. The high clay content in the soil did not allow the grass roots to penetrate deep and acquire water and nutrients from the soil. This grass species did not survive because the perennials in Tsumeb had a high competitive ability for resources. The present study concluded
that there was also a significant difference in the mean survival of seedlings sown at their local sites than those in neighbouring sites in *S. mellifera*. This was because of its ability to have tap roots to get water from underground and this can lead to the capacity to perform better with the predicted scenarios of climate change. Overall, competition with neighbours was not significant in all the three species.

**Seedling height**

The study concluded that seedlings at Okakarara were significantly taller than seedlings at Ebenhaezer in *S. uniplumis*. Additionally, seedlings at Okakarara were significantly taller than seedlings at Ebenhaezer in *A. pubescens*.

The present study concluded that there was no significant difference among the paired sites. The study also concluded that there was no significant difference in *S. mellifera* mean height of seedlings among the seed origin. This occurred because shrubs invest their energy similarly in roots, which helps them to be stable and provides them with more water. Therefore, when less rainfall is experienced the grass growth especially height will be more or less same in the farms occurring in this vicinities. Overall, competition with neighbours was not significant in the three species since the height were similar despite neighbour removals.

Overall, this study did not find any consistent evidence for predictions of germination behaviour in response to a rainfall gradient and to neighbour manipulations. However, it revealed how some individual species respond to lower rainfall or to drought. The present study concluded that clipping did not have a significant effect on the germination fraction, survival fraction and height across the
rainfall gradient in all the three species. Therefore, species will have the same responses despite neighbour manipulations and farmers do not have to remove all the emerging plants to facilitate grass germination nor survival.

6.2 Recommendations

a) If climate changes, the survival of grass species will be low and this can negatively affect the rangeland productivity. Therefore, full factorial experiments should be done to investigate how all the species performances along the rainfall gradient. This will provide insights on how individual species will under predictions of low rainfall at the three sites.

b) Further studies should aim to determine seedling performance along the rainfall gradient and concentrate on seedling establishment, rates of growth and survival over longer periods of time because these are critical life stages that are prone to drought.

c) Soil properties, plant-plant and plant–soil factors can affect the response of plants’ ability to adapt to the predictions of climate, and further research needs to be done on these factors.

d) Since S. mellifera survival was high along the rainfall gradient. Control of seedlings need to be done during early developmental stages and further research can be done along a steeper rainfall gradient to examine how
they will perform with much lower rainfall that mimics severe drought conditions.


Li, J., Zheng, Z., Xie, H., Zhao, N. & Gao, Y., 2017. Increased soil nutrition and decreased light intensity drive species loss after eight years grassland enclosures. Scientific Reports. doi: 10.1038/srep44525.


CHAPTER 8: APPENDICES

Appendix 1: The respective seed origin, experiment sites and home/away used in the study

<table>
<thead>
<tr>
<th>Seed origin</th>
<th>Experiment site</th>
<th>Home/Away for experiment site</th>
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<td>Tsumeb</td>
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Appendix 2: Germination fraction (%) statistical table of results for Generalised Linear Model on *Stipagrostis uniplumis* at the two paired sites. Significant results (p <0.05) are reported in boldface type.

<table>
<thead>
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<th>SPECIES</th>
<th><em>Stipagrostis uniplumis</em></th>
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<tbody>
<tr>
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<td>Tsumeb-Okakarara</td>
</tr>
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73
Appendix 3: Germination fraction (%) statistical table of results for Generalised Linear Model on *Anthephora pubescens* at Tsumeb-Okakarara and Okakarara-Ebenhaezer. Significant results (p < 0.05) are reported in boldface type.

### SPECIES

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#### MAIN EFFECTS OF THE MODEL

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#### INTERACTIONS

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Appendix 4: Germination fraction (%) statistical table of results for General Linear Model on *Senegalia mellifera* at the two paired sites. Significant results (p <0.05) are reported in boldface type.

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<td>INTERACTIONS</td>
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Appendix 5: Survival fraction (%) statistical table of results for Generalised Linear Model on *Stipagrostis uniplumis* at Tsumeb-Okakarara and Okakarara-Ebenhaezer. Significant results (p <0.05) are reported in boldface type.

<table>
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<td>Okakarara-Ebenhaezer</td>
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### Appendix 6: Survival fraction (%) statistical table of results for Generalised Linear Model on *Anthephora pubescens* at Tsumeb-Okakarara and Okakarara-Ebenhaezer.

Significant results (p <0.05) are reported in boldface type.

<table>
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**Appendix 7:** Survival fraction (%) statistical table of results for Generalised Linear Model on *Senegalia mellifera* at Tsumeb-Okakarara and Okakarara-Ebenhaezer. Significant results (p < 0.05) are reported in boldface type.

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**Appendix 8:** Mean height (cm) statistical table of results for Generalised Linear Model on *Stipagrostis uniplumis* at Tsumeb-Okakarara and Okakarara-Ebenhaezer. Significant results (p < 0.05) are reported in boldface type.

<table>
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<tr>
<th>SPECIES</th>
<th>Stipagrostis uniplumis</th>
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<td>Tsumeb-Okakarara</td>
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<td>df</td>
</tr>
<tr>
<td><strong>MAIN EFFECTS OF THE</strong></td>
<td></td>
</tr>
</tbody>
</table>
**Appendix 9**: Mean height (cm) statistical table of results for Generalised linear model on *Anthephora pubescens* at Tsumeb-Okakarara and Okakarara-Ebenhaezer. Significant results (p <0.05) are reported in boldface type.

<table>
<thead>
<tr>
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<td><strong>MAIN EFFECTS OF THE MODEL</strong></td>
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</tr>
<tr>
<td>Site</td>
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</tr>
<tr>
<td>Seed origin</td>
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</tr>
<tr>
<td>Clipping</td>
<td>1</td>
</tr>
<tr>
<td><strong>INTERACTIONS</strong></td>
<td></td>
</tr>
<tr>
<td>Site * clipping</td>
<td>1</td>
</tr>
<tr>
<td>Seed origin * clipping</td>
<td>1</td>
</tr>
</tbody>
</table>
Appendix 10: Mean height (cm) statistical table of results for Generalised linear model on *Senegalia mellifera* at Tsumeb-Okakarara and Okakarara-Ebenhaezer.

Significant results (p <0.05) are reported in boldface type.

<table>
<thead>
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<td>Tsumeb-Okakarara</td>
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<td><strong>MODEL</strong></td>
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<tr>
<td>Site</td>
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<td>Seed origin</td>
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<tr>
<td><strong>INTERACTIONS</strong></td>
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<tr>
<td>Site * Seed origin</td>
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<td>Site * clipping</td>
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<tr>
<td>Seed origin * clipping</td>
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</tr>
</tbody>
</table>
Appendix 11: Research permission letter

RESEARCH PERMISSION LETTER

Student Name: Cecilia I. Ndunge

Student number: 201175215

Programme: MSc Biological Sciences

Approved research title: ASSESSMENT OF WOODY PLANT AND GRASS RESPONSES IN SAVANNAS USING RECIPROCAL TRANSPLANTS ALONG A RAINFALL GRADIENT IN NAMIBIA

TO WHOM IT MAY CONCERN

I hereby confirm that the above mentioned student is registered at the University of Namibia for the programme indicated. The proposed study met all the requirements as stipulated in the University guidelines and has been approved by the relevant committees.

The proposal adheres to ethical principles as per attached Ethical Clearance Certificate. Permission is hereby granted to carry out the research as described in the approved proposal.

Best Regards

Dr Marius Hedimbi
Director: Centre for Postgraduate Studies
Tel: +264 61 2063275
E-mail: mhedimbi@unam.na
Appendix 12: Ethical clearance certificate