DIVERSITY, STRUCTURE AND DYNAMICS OF AN *ACACIA ERIOLOBA* WOODLAND IN THE WINDHOEK AREA: INSIGHTS FOR THE MANAGEMENT OF URBAN HABITATS

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE
IN BIODIVERSITY MANAGEMENT AND RESEARCH

THE UNIVERSITY OF NAMIBIA and HUMBOLDT UNIVERSITAT ZU BERLIN

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March 2013

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ABSTRACT

Acacia erioloba, a tree species of great ecological and economic importance is threatened by urban expansion and a lack of sustainable management in the Windhoek area. The overall objective of this study was to determine the diversity and structure of an *Acacia erioloba* woodland and the influence of herbivory, wood harvesting, fire and physical soil properties on vegetation structure. Forty quadrats 625m^2 in size were demarcated in pairs on alternative sides of a transect line to sample trees at 50m intervals. Shrubs were sampled in 100m^2 quadrats nested in the tree quadrats and herbaceous plant cover was estimated in 1m^2 quadrats within the shrub quadrats. Mean Shannon-Wiener diversity (H') index was 1.929, and could be interpreted as reflecting moderate to low species diversity, indicative of a disturbed community. Height structure and density differed significantly between the woodland community and *A. erioloba* population. *A. erioloba* population height patterns showed an ageing population with most plants in the largest (>5m) height class. Density patterns supported this trend with higher shrub densities in the community than in the *A. erioloba* population. The HCA and DCA of plant species composition showed no a clear separation of quadrats into definable groupings. DCA axis 1 explained 46% of the variation in species composition while CCA showed environmental variables explained 19% of the observed variation in species composition. The overall test of all canonical axes was significant (F= 1.82, $p < 0.05$) with the explanatory variables fire (F= 1.82 $p < 0.05$), pH (F= 1.54 $p < 0.05$) and woodharvesting (F=1.46 $p < 0.05$) significantly influencing species composition. This illustrates that these factors are important in determining woodland structure. However, management could be facilitated by further research on more determinants of woodland structure and simulation modelling of woodland dynamics.

Key words: *Acacia erioloba* population, environmental variables, vegetation structure woodland community

DECLARATION

I, Mandene Morkel, hereby declare that this study is a true reflection of my own research, and that this work, or part thereof has not been submitted for a degree in any other institution of higher education.

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Mandene A. Morkel

DEDICATION

To my mother, a phenomenal woman, thank you for giving me Jesus. I will always love you and I will see you again.

ACKNOWLEDGEMENTS

I am indebted to my supervisor, Prof. Isaac Mapaure for his guidance throughout the course of my study. To the University of Namibia (UNAM) for granting me study leave and the UNAM Research and Publications Committee for financial assistance with soil analysis under the main project URPC/2011/249, I thank you. Mr Josef Shikeva and Ms Hileni Amadhila are acknowledged for their assistance with field work. Special thanks to the Ministry of Environment and Tourism for permission to conduct research under the Research Permit No. 1655/2011. I thank Mr David Aiyambo from the National Botanical Research Institute of Namibia (NBRI), for identification of the various plant species. Thank you to Dr. Marina Muller from the Statistics Department at UNAM, for her advice and help with the analysis of data. The City of Windhoek for the internship opportunity and the Chief of Police Mr. Abraham Kanime and Senior Superintendent Gerry Shikesho, who availed Superintendent Karl-Marx Shikongo and Constable Charles Namwaapo to protect us in the field, thank you. The MSc Programme Coordinator, Dr. John Mfune, and my collegues thank you for all your support. To my husband, mother and family, thank you for all of the love and support. Without you the realization of this work would not have been possible. Thank you all!

ACRONYMS

ABH	Area at Breast Height
CBD[1]	Central Business District
CBD[2]	Convention on Biological Diversity
CCA	Canonical Correspondence Analysis
CoW	City of Windhoek Municipality
CA	Correspondence Analysis
DCA	Detrended Correspondence Analysis
GPS	Global Positioning System
HCA	Hierarchical Cluster Analysis
ICLEI	International Council for Local Environmental Initiatives
IUCN	International Union for Conservation of Nature
SSC	Species Survival Commission
ISSG	Invasive Species Specialist Group
NBII	National Biological Information Infrastructure
NBRI	National Botanical Research Institute
n.d.	no date

NTFP	Non-timber Forest or Woodland Products
UNAM	University of Namibia
UNEP	United Nations Environment Programme
OM	Organic Matter

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CHAPTER 1

1.1 General Introduction

The genus *Acacia* represents a group of resilient plants that are synonymous with the landscapes of sub-Saharan Africa. They belong to the family Fabaceae, previously known as Leguminosae, a large and diverse taxonomic assemblage that contain many economically important tree species (Mannheimer & Curtis, 2009).

However, recent molecular and cladistic studies have revealed that *Acacia* is polyphyletic (Orchard & Maslin, 2005). Consensus has been reached for the acceptance of the proposal to conserve *Acacia* with a new type, *A. penninervis*, from the *Phyllodineae* subgenus and for the recognition of five segregate genera (Orchard & Maslin, 2005). Of these five, for the third largest group (of which *Acacia erioloba* forms part of) the name *Vachellia* is now most recent (Orchard & Maslin, 2005). For the purposes of this study however, the older classification with the genus *Acacia* has been retained.

In often erratic rainfall conditions and poor soils *Acacia* are able to thrive whilst providing people with resources ranging from medicines to fire wood (Hayward, 2004). They also maintain soil fertility and rehabilitate degraded land to increase the productivity of non-arable land (Barnes, Marunda, Maruzane & Zirobwa, 1999). The genus *Acacia* consist of 1,250 species, 170 of which are found in Africa, with 18 being more widespread whilst the remainder is more localized (Hayward, 2004). Traditionally these trees have been grown as farm trees within and adjacent to arable crops and livestock (Hayward, 2004) but recent years have seen the genus *Acacia* falling out of favor due to their invasive tendencies. However, the benefits that are associated with the genus *Acacia* far outweigh the potential damage of this threat as invasive tendencies can be controlled with proper management. The full benefits of the genus *Acacia* can only be realized once knowledge gaps on the sustainable management of natural stands for optimal production are overcome (Barnes et al., 1999). *Acacia erioloba* (Ross, 1981, cited in Seymour & Milton, 2003) is a long lived, slow growing species whose range extends from southern Angola and Namibia, parts of Botswana, southwestern Zimbabwe, the north west of South Africa and just into south west Mozambique (Barnes, Fagg & Milton, 1997). Rainfall varies over its range from less than 40mm.year^{-1} to 900mm.year^{-1} whilst daily temperatures vary from less than 15°C to 45°C, contributing to *A. erioloba's* highly variable form (Barnes et al., 1997). This plant may occur as a small spiny shrub approximately 2m high, to a tall tree up to 16m (Coates-Palgrave, 1983). Their kidney-shaped pods from which the name "erioloba" stems, which means woody lobe, sets the species apart and appear to be covered in light-grey velvet (Seymour & Milton, 2003). These pods are said to be the largest indehiscent pods recorded for any African *Acacia* (Coe, 1998). Large herbivore species such as giraffe (*Giraffa camelopardis*), elephant (*Loxodonta africana*) and livestock feeding on these pods are responsible for the dispersal of *A. erioloba* seeds. Bruchid beetles parasitize seeds whilst rodents may also consume seeds (Miller, 1995).

The benefits provided by *A. erioloba* are most readily seen when the trees become large and begin to impact soil quality, producing pods, gum, fuel wood and large patches of shade that are readily utilized by large mammals (Barnes, 2001a). Soil quality in particular is affected as nutrient leaching is reduced, increasing nutrient levels beneath large tree canopies (Materechera & Materechera, 2001), mitigating soil degradation and replenishing organic matter. Also when large, *A. erioloba* facilitates processes which maintain habitat heterogeneity (seed dispersal, site modification), suggesting that it is a keystone species in this environment (Milton & Dean, 1995). Indirect gains come from its economic and social value. The economic value of *A. erioloba* is associated with the consumption of wood as fuel and building material, increased yields from grain crops, stock weight gain or increased milk production and medicinal uses (Barnes, 2001a). Its social value is associated with aesthetics and culture, for example *A. erioloba* is considered a royal tree in Botswana (Palmer & Pitman, cited in Seymour & Milton, 2003).

Changes in tree demography resulting from various factors such as uncontrolled fire, herbivory, wood harvesting and many others however, could impair these processes, thus invalidating its role as a keystone species (Milton & Dean, 1995). Disturbances that fundamentally change the population or size structure of this species are thus likely to have detrimental effects on both biodiversity pattern and process (Seymour & Milton, 2003). Fire as a disturbance, has the greatest influence on the youngest and oldest trees within an *A. erioloba* population as it appears to be the major cause of mortality for seedlings that have yet to establish and mature large trees (Skarpe, 1991). *A. erioloba* woodlands often provide various habitats for a variety and abundance of herbivores that cause a disturbance by inhibiting growth through feeding, or outright destruction through trampling (Barnes et al., 1999). The greatest anthropogenic claims to *A. erioloba* are in the form of wood harvesting as a source of fuel (Seymour & Milton, 2003). Although coppicing from cut stumps has been observed (Morkel *pers. obs*) according to Seymour and Milton (2003) cut stumps are highly sensitive to browsing, which substantially reduces biomass and regeneration from old tree stumps. The interaction between these factors and the extent to which *A. erioloba* can tolerate repeated disturbances such as fire, herbivory and wood harvesting is not known (Seymour & Milton, 2003). Given this background, *A. erioloba* has been well recognized as an *Acacia* species that is likely to have the greatest potential for improvement through selection and better management (Barnes et al., 1999).

According to Benton-Short and Short (2008, p.4) cities are “engineered landscapes that contain urban ecosystems that can be thought of as a distinctive ecological category rather than merely disturbance sites to be unfavorably compared to pristine sites”. The combination of open space and built up areas create a patchy mosaic of habitats for plants and animals. Such open or green spaces as they are commonly referred to, are essential elements of the urban habitat in that they contribute greatly to the quality of life provided by cities for the health and well-being of citizens (Irwin & Williams Davies, 2012). Trees provide shade, help retain water and control run-off; flowering plants and shrubs beautify and attract wildlife such as birds and butterflies, and can provide shelter from winds (Irwin & Williams Davies, 2012). “The city is thus an integral part of nature and nature is intimately interwoven into the social life of cities” (Benton-Short & Short 2008, p. 5). For urban biodiversity to be maintained for residents and its fundamental value, in spite of expanding cities and increasing population pressures, requires that ecological knowledge should be better integrated into urban planning (Niemelä, 1999). The understanding of ecological processes and patterns is essential in achieving this goal (Niemelä, 1999). This background clearly illustrates the importance of *A. erioloba* and the significance of understanding ecological processes within the urban green space context. This study will attempt to provide imperative information on an *A. erioloba* woodland as a green space in the City of Windhoek so that sustainable management for the realization of this species’ complete environmental, economic and social value can be facilitated.

1.2 Statement of the problem

Biodiversity in cities is often considered to be less important than its rural counterpart because cities have been described and understood as somehow separate from the natural world (Benton-Short & Short, 2008). However, many urban areas frequently have a wide variety of plant and animal life that contribute significantly to biodiversity (ICLEI, 2008). With the majority of the world’s population calling cities their home, biodiversity in these areas is under constant threat of urban sprawl that results in habitat loss or isolation (Kong, Yin, Nakagoshi & Zong, 2010). Green space within cities represents biodiversity and in addition to enhancing the quality of life for city dwellers by providing a place for exercise, relaxation and social interaction urban green spaces also contribute to essential services including water filtration and absorption, nutrient cycling, air filtration and noise buffering (Benton-Short & Short, 2008). Green space management and conservation is in the hands of local authorities (ICLEI, 2008) and the Windhoek Municipality (henceforth the City of Windhoek or CoW) is an example of a local authority that manages various habitats and ecosystems in the form of green space. This management process is often met with many challenges of which a lack of information can be considered primary.

The City of Windhoek currently lacks sufficient information on *A. erioloba* woodland communities within its jurisdiction to ensure that such plant communities can be conserved and managed sustainably (Enviro Dynamics, 2009a). This gap in knowledge may have detrimental effects on these plant communities as well as the people that depend on them for their livelihoods. As the city expands due to rural-urban migration more people are looking to natural resources and in particular woody plant species such as *A. erioloba* for fuel wood, increasing harvesting pressure in woodland communities. Without knowledge on the diversity, structure and dynamics of *A. erioloba* woodland communities, attempts at regulating and sustainably utilizing important services provided by such a community, will be a daunting, if not impossible, task at best for the CoW.

1.3 Objectives, questions and hypotheses

The overall objective of this study was to determine the composition, diversity and structure of an *Acacia erioloba* woodland community and assess the impacts of herbivory, wood harvesting, fire and soil physical and chemical properties on the woodland.

The specific objectives were:

a) To determine the diversity, composition and richness of plant species in an *A. erioloba* woodland community.

b) To compare the structure of an *A. erioloba* population with that of the rest of the woodland community.

c) To determine the influence of wood harvesting, fire, herbivory and soil physical properties on the dynamics of an *A. erioloba* woodland community.

d) To develop a preliminary conceptual model of the dynamics of the woodland community to aid in its management.

The study aims to answer the following questions:

a) What are the diversity, composition and richness of the *A. erioloba* woodland community?

b) How does the *A. erioloba* population structure compare with that of the woodland community?

c) What is the influence of wood harvesting, fire, herbivory and soil physical properties on the dynamics of the *A. erioloba* woodland community?

The working hypotheses for the study were:

a) Diversity is expected to be relatively higher than expected due to the occasional fire disturbance which creates patchy mosaics in the woodland.

b) The *A. erioloba* population structure when compared to the woodland community is skewed towards more adult trees and fewer smaller trees and saplings due to negative impacts of fire and herbivory on propagule establishment and recruitment.

c) The diversity and structure of *Acacia erioloba* woodland community would significantly be influenced by wood harvesting, fire, herbivory and soil physical and chemical properties.

CHAPTER 2

LITERATURE REVIEW

2.1 Overview of extent, value and ecology of woodlands in Namibia

Forests and woodlands occupy an estimated 650 million ha or 21.8% of the land area in Africa (UNEP, 2006). In Namibia, areas defined as woodlands cover approximately 50% of the country and in a country that is generally arid “the value of each individual tree is relatively greater than in a wetter, more wooded environment” (Mendelsohn & el Obeid, 2005, p.6). This may be because as perennial plants in dry areas, trees are more buffered against environmental variations, making them more dependable as a resource (Mendelsohn & el Obeid, 2005). The most important factors determining the abundance and distribution of trees in Namibia are: water availability, soil conditions, fire, elevation and historical and human influences (Mendelsohn & el Obeid, 2005).

Woodlands provide Namibians with habitats to live in and resources to live by. Resources such as food, timber and non-timber forest or woodland products (NTFP’s) are important contributors to wealth from the household to regional level. Human induced processes such as the frequent burning of trees, land-clearing for crop cultivation and bush encroachment, have led to some major losses of woodlands and forests in Namibia (Mendelsohn & el Obeid, 2005). The significance of these habitats must thus be recognized, valued and celebrated as the loss of this resource can have far reaching adverse impacts on nesting birds and poverty struck communities alike. The recognition and promotion of the importance of these habitats is thus vital to their survival and sustainable management practices key.

2.2 Direct and Indirect use values of *Acacia erioloba* woodlands

The *A. erioloba* woodland community under investigation was observed to be utilized by the local people, particularly those from nearby informal settlements for woodharvesting and pod harvesting activities. Such activities were thus evidence of the direct use value of this resource.

Direct use value is when money is made or “saved” directly from buying or selling a natural resource (Primack, 2006). In Namibia more wood is used for fuel than any other purpose (Table 1) and *A. erioloba* is no exception because this species when compared with other fuel woods, has the greatest density, lowest moisture content and highest heat capacity which are all characteristics of good fuel wood (Raliselo, 2002). Though harvesting of *A. erioloba* wood is illegal (Nature Conservation Amendment Act No. 5, 1996) it does not appear to be well enforced in Namibia as many people are still seen to harvest fuel wood (Morkel *pers. obs*.).

The other major use of indigenous wood in Namibia is for creating fencing and building homes as shown in Table 1. *A. erioloba* wood is readily used as building material as it is dense and heavy with medium to fine texture and the heartwood resistant to fungal, borer and termite attacks (Timberlake, Fagg & Barnes, 1999). A major source of revenue from woodlands comes from the commercial production of charcoal. In recent years Namibia's annual production of charcoal has ranged between about 40 000 and 50 000 tons whilst approximately 240 000 m^3 (Table 1) of wood is consumed to produce this charcoal (Mendelsohn & el Obeid, 2005). In 2004, the industry was valued to be between N$75 and N$100 million (Mendelsohn & el Obeid, 2005).

Table 1: Approximate quantities of indigenous wood used in Namibia each year (m^3)

Use or product	Domestic consumption	Commercial consumption
Fuel wood	983 000	100 000
Charcoal	0	240 000
Building material/ fencing	316 000	0
Carving	0	440

Source: Mendelsohn & el Obeid (2005)

Indirect use value refers to the aspects of woodlands that are not harvested or destroyed for economic gains (Primack, 2006). It is thus essentially the biological diversity that we often do not think of but without which we could not have those resources from which we get direct use values. According to Milton and Dean (1995) *A. erioloba* is often the only large tree in its environment and functions as a crucial structural component of the savanna vegetation. Large *A. erioloba* trees have been described as "nutrient islands" that act as a nursery for many other plants whilst the shade provided by these trees creates an advantageous microclimate for many large herbivores that seek to escape the heat of the midday sun (Anderson & Anderson, 2001).

It is thus clear that *A. erioloba* basically increases habitat heterogeneity by increasing species richness through the provision of habitats and services for a variety of plants and animals (Milton & Dean, 1995). Changes in vegetation structure of woodlands such as *A. erioloba* woodlands may thus imply a negative impact on biodiversity as large trees are crucial for many faunal and floral communities.

2.3 Legal status of *A. erioloba*

The legal frame work for the protection and conservation of *A. erioloba* has international roots with the Convention on Biological Diversity (CBD[2]**)** signed by Namibia on 12 June 1992. Under the Convention, States are obliged to conserve biodiversity and regulate sustainable use of its component resources (Ruppel & Ruppel-Schlichting, 2011). *Acacia erioloba* is one example of such a component resource and is thus protected under this International law. In 2003 the revised African Convention on the Conservation of Nature and Natural Resources (The Algiers Convention) was signed by Namibia. As its main aim the revised Convention strives “to enhance environmental protection, foster conservation and sustainable use of natural resources,…” (Ruppel & Ruppel-Schlichting, 2011, p. 131) and addresses vegetation cover in Article V(iii), protected species in Article X and sustainable development and natural resources in Article XIV. All of these articles represent the regional framework for the conservation and sustainable management of a plant species such as *A. erioloba*.

At national level, the major biodiversity related law in Namibia is the Nature Conservation Ordinance No.4 of 1975, which later became the Nature Conservation Amendment Act No. 5, of 1996 as it governs conservation of wildlife, indigenous plants and protected areas (Ruppel & Ruppel-Schlichting, 2011). Chapter VI of the Ordinance deals with the protection of indigenous plants and provides Schedules that list *A. erioloba* as a protected species. This law is thus primary in the conservation of *A. erioloba* as it explicity gives *A. erioloba* its protected species status in the country. Additionally the Forest Act no. 12 of 2001, the Environmental Management Act No.7 of 2007 and the Traditional Authorities Act No. 17 of 1995 more broadly make provision for the conservation of *A. erioloba*. The Forest Act no. 12 of 2001 focuses on sustainable forest management and forest resource management and development (Ruppel & Ruppel-Schlichting, 2011). This Act refers to forests but by the definition of forests, woodlands could arguably by included in this context. The Environmental Management Act No.7 of 2007, Section 2 (d) states that: "..functional integrity of ecological systems must be taken into account to ensure sustainability of the systems.." (Ruppel & Ruppel-Schlichting, 2011, p.131). By compromising *A. erioloba* in woodlands, ecosystem integrity can be compromised as this species may act as a keystone species, thus rendering the ecosystem incapable of providing services such as pod production. Furthermore, section 2 (f) states: "Sustainable development must be promoted in all aspects relating to the environment.", so that by studying *A. erioloba* community structure and dynamics the foundations for recommendations can be laid for sustainable management and community resource utilization practices**.** Finally**,** customary law through the Traditional Authorities Act No. 17 of 1995, stipulates how natural resources in particular large trees such as *A. erioloba* should be governed (Hinz & Ruppel, 2008). Unfortunately many customary laws are difficult to apply in the city as indigenous peoples in the city are difficult to regulate by traditional authorities that are primarily based in the rural areas.

2.4 Geographic distribution and species description

Acacia erioloba is a southern African species and in Namibia it is widely distributed preferring sandy soils, depressions and dry riverbeds where it can grow up to 20m high (Mannheimer and Curtis, 2009). “The branches are often drooping forming a crown or umbrella shape” (van Wyk & van Wyk, 1997, p. 168). The bark is highly fissured, rough and grey to blackish-brown (Coates-Palgrave, 1983). The straight, rigid thorns are paired at the nodes and grey-white with black flecks and often with pale brown tips. Older thorns are often noticeably thickened at the base (Mannheimer & Curtis, 2009). Leaves are bipinnately compound, spirally arranged with 2-5 pairs of pinnae (Timberlake et al., 1999). “Each pinna has 6-15 leaflet pairs and the leaf margin is entire” (Mannheimer & Curtis, 2009, p. 92). The flowers are golden yellow balls, whilst the pods are indehiscent and ear shaped with a velvety covering. Pods are spongy on the inside with irregularly placed seeds (Barnes et al., 1997). The ecology of the species suggests that it is adapted to sandy soils that can sometimes be alkaline and are deep to shallow with rooting systems accessing deep water with dissolved nutrients (Barnes, 2001a). As sandy soils may offer a competitive advantage to a species with an initial rooting system that can rapidly expand it may serve as a reasonable explanation as to why it can be preferred as a substrate (Barnes, 2001a).

2.5 Germination and Seed predation

Many laboratory experiments have been done in an attempt to establish optimal germination conditions in *Acacia* species and results often supported the idea that germination rates increase with physical or chemical damage to the seed coat so as to open up the seed. Clemens, Jones and Gilbert (1997) showed the effect of seed treatments such as hot water on germination to be less effective than manual chipping. In the case of Miller (1995, p. 95) “Ingested seeds exhibited a greater germination than uningested seeds when germinated on filter paper or in dung and soil media. Seed germination in soil exceeded that in dung whereas seedling growth in dung and soil did not differ.” Additionally rodent predated *Acacia* seeds germinated better than seeds that were not chewed on (Miller, 1995). However, Seymour and Milton (2003) suggests that field studies conducted on *A. erioloba* germination rates may be more valuable as low water holding capacity of Kalahari sands may influence the observed outcome. Though the issue of germination speed remains unresolved, what is clear is that seeds that have been digested by herbivores germinate faster than those that have not (Barnes, 2001a).

A. erioloba seeds are parasitized by a range of bruchid beetles (Seymour & Milton, 2003) which influence seedling establishment but is thought to be less significant than abiotic factors such as amount and pattern of rainfall where studies have shown seedling emergence to be low or zero in years of drought (Barnes et al., 1999). Additionally, satisfactory conditions are needed for a substantial period in order to ensure not only establishment but survival as well (Seymour & Milton, 2003). The impact on germination by bruchid beetle larvae is determined by larval development, though no conclusive studies have been done as to the extent of such an impact and whether it serves to increase or decrease germination rates (Miller, 1995). "During the first five years the species is slow growing, but thereafter growth is reasonably fast for a long lived tree" (Timberlake et al., 1999, p.147). According to Barnes et al., (1997), *A. erioloba* has an estimated lifespan of 300 years and starts to flower at the age of approximately 10 years whilst producing regular large pods at the age of 20 years.

2.6 Effects of disturbance factors on woodland dynamics

Various disturbance factors can influence woodland dynamics to varying degrees. The impact of such factors may have important consequences for woody species' diversity, composition and population size structure (Seymour & Huyser, 2008). This study focused on and will now review the effects of herbivory, fire and woodharvesting in greater detail as important determinants of woodland dynamics.

2.6.1 Effects of herbivory

Acacia erioloba is an important source of forage for wildlife (Barnes, 2001b) and livestock. Elephant browsing alone can prevent woodland regeneration (McNaughton, Ruess & Seagle, 1988) whilst small browsers can suppress growth in seedlings, delaying growth to reproductive maturity and keeping them vulnerable to fire (Barnes, 2001b). Augustine and McNaughton (2004) emphasized that the effects of small browser herbivory can be important when they found impacts of small browsers to be equivalent to a 6-fold reduction in shrub recruitment from the <0.5m height class to the 0.5-1.5m class.

Invertebrates have also been found by Shaw, Keesing and Ostfeld (2002) to have a pronounced influence on seedling survival in savanna ecosystems dominated by large *Acacia* trees. This was illustrated when they conducted experiments were seedling exposure to rodent and invertebrate herbivores did not cause greater damage than that found in seedlings exposed only to invertebrates, suggesting that invertebrates caused most of the damage to the seedlings. In a second experiment conducted by Shaw, Keesing and Ostfeld (2002), 63% of seedlings exposed to all herbivores (large mammals, rodents, and invertebrates) suffered major damage or mortality in 14 days. Seedlings exposed to only rodents and invertebrates, however, suffered damage at a faster rate than did seedlings exposed to rodents, invertebrates, and large mammals, suggesting that small herbivores (rodents and invertebrates) might be compensating for the removal of large herbivores (Shaw, Keesing & Ostfeld, 2002). Herbivory not only influences *A. erioloba* woodlands by inhibiting growth through feeding but also by damage or destruction resulting from trampling (Barnes et al., 1999). So even when seeds are able to germinate in years of good rains their survival is still hinged on determinants such as herbivory.

To defend against herbivory many *Acacia* species have developed thorns in high density on branches that are regularly browsed on as these have been found to deter herbivory by browsers like giraffes (Milewski, Young & Madden, 1991). Others make use of aggressive symbiotic ants such as those found in the genus *Crematogaster* that occupy and actively defend shoot tips, the preferred plant parts of many large herbivores (Madden & Young, 1992). Whatever the form of defense, the significance of herbivory in many *Acacia* woodlands is evidently undeniable.

2.6.2 Effects of fire

Fire has been a common, natural phenomenon in African savanna systems and can be seen as one of the determinants of savanna ecosystem structure and functioning (Gandiwa & Kativu, 2009). Fire occurrence has been increasing with expanding human populations (Mapaure & Moe, 2009). The effect of fire on natural ecosystems involves a reduction in the regeneration and recruitment of plants whilst "promoting the establishment and maintenance of grassland vegetation by preventing development of taller, fire-resistant stages of plants" (Mapaure & Moe, 2009).

Generally in woodland savannas the overall effect of the type of fire is that surface head fires have the potential to have the greatest effect on trees (Trollope & Trollope, 2004). This is because the heat is released above ground level away from the growing points of the grasses and closest to the growing points of the trees. The overall effect of fire intensity on trees is that they are sensitive to increasing fire intensities because their growing points are generally exposed to the release of heat energy in the canopy of the trees (Trollope & Trollope, 2004). These effects explain why intense fires favor the development of grassland and open savannas and vice versa (Trollope & Trollope, 2004).

Studies on responses of *A. erioloba* demography to uncontrolled natural fires have found diverse patterns (Seymour & Huyser, 2008). This variation in responses can be attributed to the highly variable nature of fires that is difficult to replicate and is determined by factors such as fire intensity, fuel load, regime and prevailing weather conditions. For example, van der Walt and Le Riche (1984) found that a third of all trees in their study sites were killed as a result of fire of which large trees constituted about 75%. On the other hand Barnes (2001b) found very few *A. erioloba* dying in her study at Savuti, Botswana with even seedlings surviving fires that swept the area. Others such as Seymour and Huyser (2008) found that resprouting was most prominent in the <6.5m high trees whilst the largest size class of 8-12m height suffered the highest mortality rates. What is agreed upon is that the species is thought to be fire sensitive with large trees either dying or suffering minor damage (Seymour & Huyser, 2008, van der Walt & le Riche 1984) whilst established seedlings have been found to be able to survive (Barnes, 2001b). Fire is also thought to shape woodland structure particularly as *A. erioloba* is a long lived and slow-growing large tree that is a keystone actor instrumental in maintaining biodiversity pattern and process (Seymour & Huyser, 2008).

2.6.3 Effects of wood harvesting

Wood clearing practices in the southern Kalahari of Southern Africa that included the removal of *A. erioloba*, were initially established by the local farmers to restore potential for savanna rangelands. The wood removed was then a by-product of this larger practice and used for domestic purposes only (Tewsa, Esther, Milton & Jeltsch, 2006). More recently however this trend has changed significantly with the primary purpose becoming the removal of large, solitary trees as oppose to thicket forming shrubs for the commercial harvest of charcoal and firewood (Anderson & Anderson, 2001). This may be because *A. erioloba* like other *Acacia* species could be described as ideal for firewood and charcoal production as it occurs in almost mono-specific stands in high densities over vast areas, it coppices readily when harvested or top-killed by fire and its hard wood makes good quality charcoal (Okello, O'Connor & Young, 2001).

Although *A. erioloba* has been found to multiply from root suckers and also to be able to coppice even from cut stumps and fallen over partly dead trees, this ability varies with size, time of harvesting, herbivory or fire, amount of rainfall and land use (Seymour & Milton, 2003). In some areas of the southern Kalahari commercial harvest of firewood and charcoal has resulted in the disappearance of the typical 'parkland' aspect provided by *A. erioloba* (Anderson & Anderson, 2001).

This uncontrolled and irresponsible utilization of *A. erioloba* and many other large tree species can benefit from the re-introduction of positive management to the large “neglected” or undermanaged woodlands (Rippengal & Bright, 2002). Such management practices can then in turn result in social, economic and environmental benefits which forms the foundation for sustainable utilization of these and other such resources.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Area

3.1.1 Location and extent

The study was carried out in the outskirts of Windhoek (Fig. 1) between S 22. 46ˈ 85″ E0 17. 08ˈ 55″ and S 22. 47ˈ 614″ E0 17. 08ˈ 692″. This site is opposite the Brakwater suburb (Fig. 1) and 15km north east of the Windhoek Central Business District (CBD[1]). More generally it is south-west of the first weigh bridge that is found on the B1 highway coming from Windhoek and approximately 1 km^2 in size (Fig. 2).

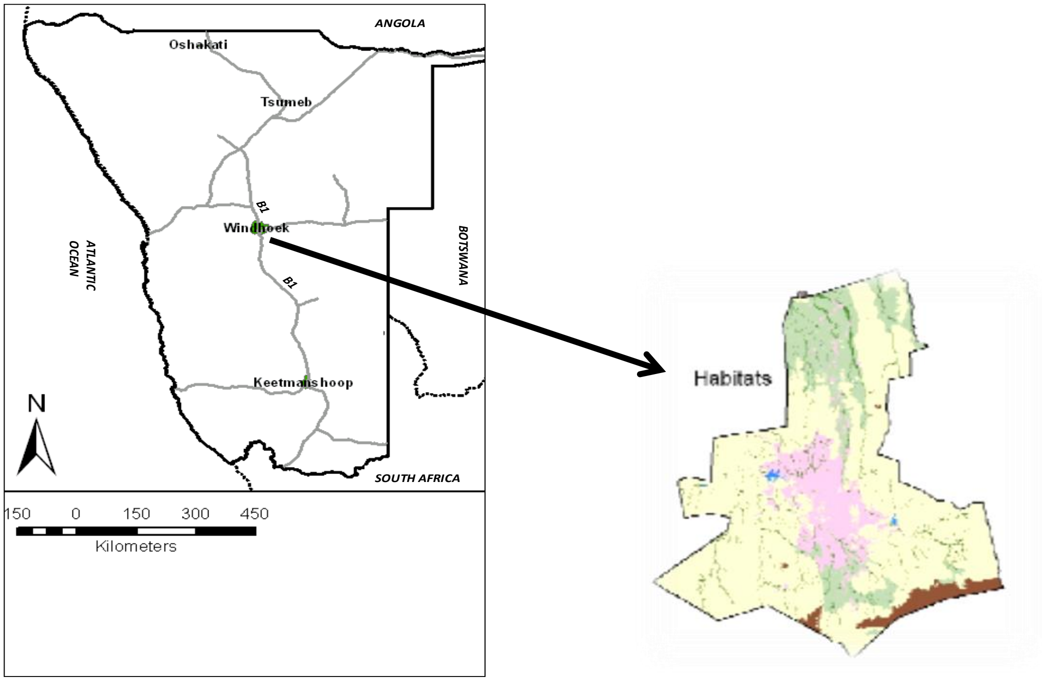

Figure 1. Map of Namibia showing the city of Windhoek and the extent of its municipal district (Source: Enviro Dynamics, 2009b).

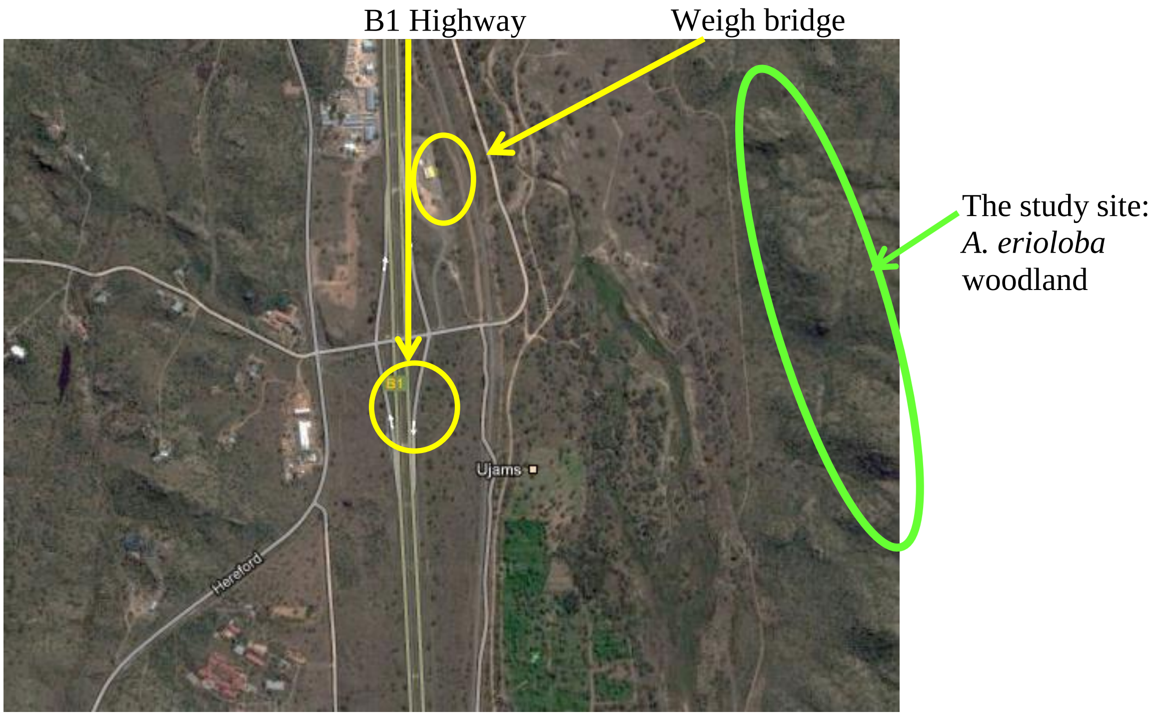

Figure 2. Location of the study site, an Acacia erioloba woodland, east and south east of the first weigh bridge that is found on the B1 highway that exits the city of Windhoek Namibia. (Google maps, 2012)

3.1.2 Climate

As part of a Tree and Savanna biome (Barnard 1998, p. 26), Windhoek’s climate can generally be described as semi-arid with a summer season stretching from October to February. The maximum temperatures range between 26°C and 32°C (Fig. 3) with November being the warmest month on average (Government of the Republic of Namibia, Ministry of Works and Transport: Meteorological Services Division, n.d.). The winter months of the year are May to August, with July being the coldest month on average (Fig. 3). Minimum temperatures range between 5°C and 18°C (Government of the Republic of Namibia, Ministry of Works and Transport: Meteorological Services Division, n.d.). Windhoek, like most of the country, receives summer rains whilst the driest months of the year are in the winter. January is reported to be the wettest month of the year and August the driest month (Fig. 3) with the mean annual rainfall in the area ranging between 300-360mm (Barnard 1998, p. 17)

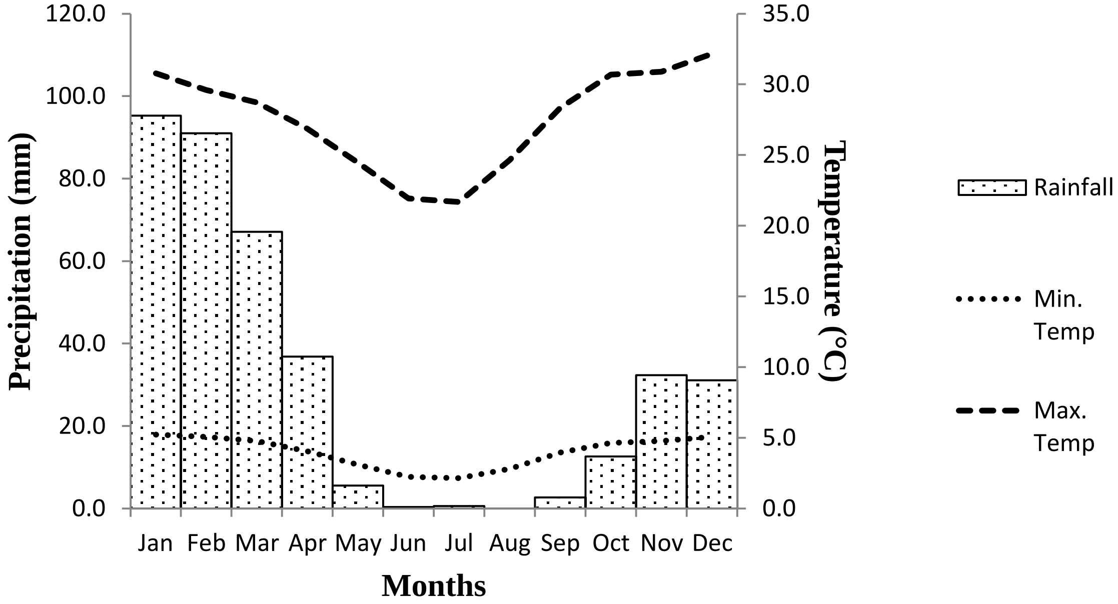

Figure 3. Mean monthly rainfall and maximum and minimum temperatures for Windhoek from 1990-2010. (Data source: Republic of Namibia Ministry of Works and Transport: Meteorological Services, 2012)

3.1.3 Flora

According to Enviro Dynamics (2009a) the study site is situated in a habitat known as the Windhoek Valley. The vegetation of this habitat according to Mannheimer, Hochobes and Greyling (2009) consists of 172 plant species, including three protected tree species, *Acacia erioloba*, *Boscia albitrunca* and *Searsia lancea*. This habitat also supports a high diversity of herbaceous and geophytic vegetation (Enviro Dynamics, 2009a). One protected herb, *Harpagophytum procumbens* (Devil's claw) as well as the endemic species *Peristrophe hereroensis*, *Senecio windhoekensis*, *Ondetia linearis Benth*, *Crotalaria dinteri*, *Bulbostylis mucronata* and the two near endemic species *Vahlia capensis* subsp. *capensis*, *Selago dinteri* subsp. *dinteri* are known to occur (Mannheimer et al., 2009).

The Windhoek Valley can be divided into the lowlands and the alluvial plains (Strohbach & Seely, 2003). The lowlands are usually dominated by *Acacia mellifera* with *Leucosphaera bainesii* also being very common, whilst the alluvial plains serve as the preferred habitat of large specimens of *Acacia erioloba* (Mannheimer et al., 2009). Thirty-six alien species occur in the valley habitat, those of concern being (in order of importance), *Prosopis glandulosa*, *Nicotiana glauca*, *Argemone ochroleuca*, *Datura ferox*., *Datura inoxia*, *Arundo donax* and *Pennisetum clandestinum* (Mannheimer et al., 2009).

3.1.4 Fauna

The Windhoek valley is further characterized by plains animals as well as sand burrowing animals (Strohbach & Seely, 2003). Relevant plains animals include medium to large herbivores that comprise of the antelopes *Alcelaphus buselaphus* (Red Hartebeest), *Sylvicapra grimmia* (Common Duiker) *Antidorcas marsupialis*

(Springbok), *Raphicerus campestris* (Steenbok), Oryx gazelle (Oryx) and *Tragelaphus strepsiceros* (Kudu). Small mammals make up most of the sand burrowing animals found in the habitat and the estimated diversity and endemism is between 61-75 species and 5-6 species respectively Cunningham (2009). Endemic species include the Hairy-footed gerbil, *Gerbillurus paeba* and the Koakoveld ground squirrel, *Xerus princeps*. Other plains animals include 126 species of arthropods recorded by Lamprecht (2009) of which 8 are endemic or near endemic and *Mantophasma zephyra* is the most publicized. Amphibians and reptiles also occur in a high diversity with 3 amphibian and 19 reptile species endemic to the area.

3.1.5 Geology, soils and physical features

The geology of Windhoek though highly varied due to historical folding, thrusting, faulting and rifting episodes forms part of the major geological division known as the Damara Supergroup and Gariep complex (Africon & EnviroNomics, 2004). Biotite schist, (a moderately course-grained foliated crystalline rock with monoclinic biotite minerals), of the Kuiseb formation, characterize the majority of the geology of the area. It can be observed on the slopes of many of the road cuts in and around Windhoek and is known for its rather rapid rate of weathering, especially when exposed (Brink, 1981). In the Windhoek Valley habitat along rivers and defined drainage lines, biotite schist is intersected by a north-south running band of sand calcrete gravel and alluvium (Africon & EnviroNomics, 2004). Sand calcrete gravel is an unconsolidated surficial deposit consisting of sand and calcrete and acts as an infiltration medium for surface water. It is highly permeable and the presence of calcrete indicates seasonal perched water.

Alluvium, on the other hand, is a general term used to describe transported material such as riverine deposits (Africon & EnviroNomics, 2004).

Windhoek generally has poorly developed thin topsoil that is the product of alluvial and colluvial deposition of mainly fine sands and silts intermixed with residual quartz pebbles. River alluvium along ephemeral river courses and valleys comprising sand, gravel and stones form the thickest soils. (Africon & EnviroNomics, 2004)

3.2 Site selection

The site was chosen because it is a large area where the vegetation is dominated by *A. erioloba* and it is also an area where this protected species of main concern may be lost due to urban development pressures. This woodland is also a highly utilized area by Windhoek's poor and marginalized for activities such as wood and pod harvesting and is furthermore exposed to annual uncontrolled fires. No data exist on the impacts of these activities on the area making the management of the site extremely challenging for local authorities. There is thus a need to gather information on this *A. erioloba* woodland that may inform management practices.

3.3 Experimental design

A line transect was placed within the centre of the woodland patch in a South-North direction. The transect had to be divided into two sections due to practical considerations. The first section started at S 22. 46ˈ 859″ E0 17. 08ˈ 558″ and ended at S 22. 47ˈ 206″ E0 17. 08ˈ 639″ and covered a distance of 425m. At 25m intervals along the transect, on opposite sides, the closest *A. erioloba* was identified and such trees were used as the starting corners of the quadrat. On the opposite side the same distance would be moved as measured to the closest *A. erioloba* to start a quadrat that would not necessarily include *A. erioloba*. Thus one quadrat in a pair focused on *A. erioloba* and the other was at the same distance on the opposite side of the transect. This was done to ensure that *A. erioloba* as the focus species would be included in at least half of the quadrats. During the first 175m of the transect, a distance of 25m between successive quadrats was used but this was adjusted to 50m from 175m to ensure that quadrats would not overlap.

The second section started at the 425m mark of the first section of the transect, when the transect was moved 30m from S22.47 ' 206″ E017. 08' 639″ to S22.47' 216″ E0 17. 08' 611″. This was done to avoid a gravel road that occurred in the woodland at this point as a disturbance to the natural behavior of the vegetation in the area. From this point on the transect stretched to a distance of 825m and at every 50m mark a pair of quadrats were done in the same manner as the first part of the transect (Fig. 4).

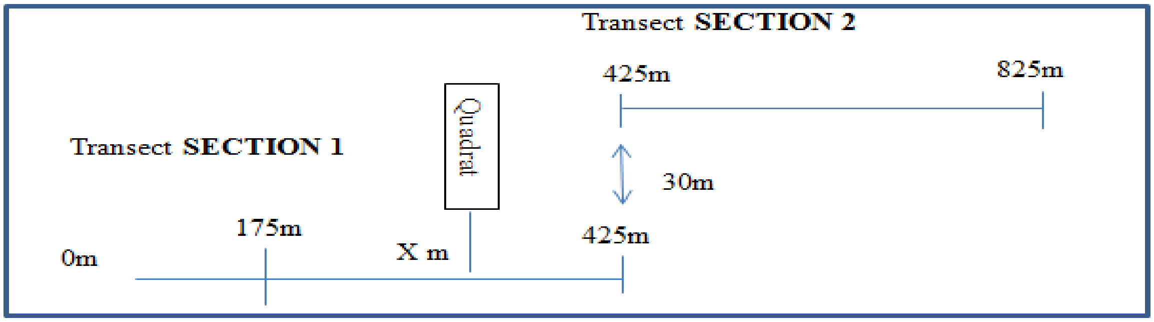

Figure 4. An illustration of how sampling was done in the field. X meters in each case represents the various distances that was moved from the transect to establish quadrat locations. In each case such distances were determined by the closest *A. erioloba* tree on alternative sides of the line transect (not drawn to scale).

Along the transect at the various distances, forty nested quadrats of 25m x 25m, 10m x 10m and 1m x 1m were demarcated (Fig. 5). Comparable studies have used similar quadrats justifying the use of the suggested quadrat sizes (see Mapaure & Mhlanga, 1998). For each quadrat GPS coordinates were recorded at the reference corner, to enable similar studies to be done at approximately the same place (Appendix 1).

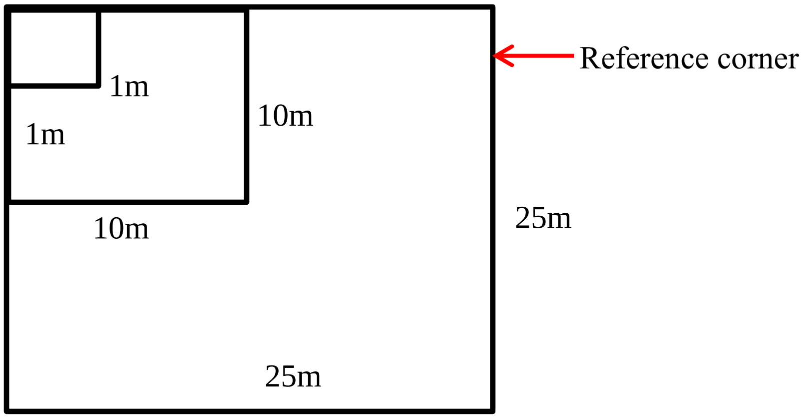

Figure 5. The nested quadrat design used to record data on trees, shrubs and herbaceous plants in 25m x 25m, 10m x 10m and 1m x 1m respectively as well as soil sample collection.

3.4 Measurement of plant attributes

Woody plants with a basal circumference ≥ 15cm were regarded as trees (Mapaure & McCartney, 2001, p. 139; Gandiwa, 2009, p. 4). In the case of multi-stemmed trees, stems were counted and the circumference at breast height of each stem was measured using a tape measure, with the plant qualifying as a tree if any one of the stems met the above criteria. An individual tree was considered to be in a quadrat if the center of its base was included in the quadrat. All trees were identified to species level in the 25m x

25m quadrats. The heights of individuals were estimated and recorded using a 2m ranging pole by placing the ranging pole as close to the tree as possible. Wherever trees were taller than 2m, height was estimated to the nearest 0.5m.

Shrubs and saplings were defined as having a basal circumference < 15cm. Shrubs and saplings could be single or multi-stemmed. For *A. erioloba* individuals, both single and multi-stemmed, circumference at breast height was measured using a tape measure and recorded. Whilst for all other species, only the number of stems were recorded and not the circumference. Species-level identification was done for all shrubs and saplings in the 10m x 10m quadrat and the heights of individuals were estimated and recorded using a 2m ranging pole. This was done by placing the ranging pole as close to the shrub or sapling as possible.

In the 1m x 1m quadrat grasses and forbs were identified to species level and cover was visually estimated using a modified Braun-Blanquet scale (0-25%, 25-50%, 50-75% & 75-100%) as described by Mueller-Dombois and Ellenberg (1974). Species were also ranked from 1 to 3 according to their dominance with 1 denoting the most dominant species and 2 and 3 denoting the second and third most dominant species, respectively. When there were more than three species, the ranking was still done and all other species that fell outside of the ranking were simply recorded. All plants not identified in the field were collected for identification at the National Botanical Research Institute (NBRI) in Windhoek. A complete list of all plant species collected was compiled

(Appendix 2). The *Acacia erioloba* woodland population (hence forth the *Acacia erioloba* population) was defined as a consisting of the trees, shrubs and saplings of the species *A. erioloba*. The *Acacia erioloba* woodland community was then defined as the *Acacia erioloba* population as well as all other vegetation found in the woodland.

3.5 Determination of wood harvesting, herbivory and fire

Each *A. erioloba* was assessed as to whether it was dead or alive and damage by wood harvesting, herbivory and fire was recorded. Extent of damage was visually assessed, classified and noted (Appendix 3). Classification was done using a coding system as suggested by Burke, Juola and Korhonen (1996) where 0= no damage, 1= mild damage, 2= moderate damage and 3= serious damage. Where stumps remained as a result of wood harvesting such stumps were counted and identified to species level unless such stumps were severely impacted by fire in which case identification was not possible. Leaves and leaf stalks were assessed to detect both insect and large mammal herbivory. Insects would mainly damage leaves whilst large mammals would remove leaves completely sometimes leaving behind leaf stalks or nodes where leaves were once attached. In this woodland insect herbivory was mainly detected and thus assessed (Appendix 3). The trunk and branches of trees and shrubs were assessed for fire scars and charcoal to evaluate fire damage (Appendix 3).

3.6 Soil sampling

In each quadrat top soil samples were collected at a reference corner (Fig. 4) to a depth of 10cm with a small garden/hand shovel. A total of 40 samples were collected in brown paper bags that were clearly marked with the date and quadrat number from where it was collected. All samples were sun dried and then analyzed for chemical (Organic matter and pH) (Hendershot, Lalande, & Duquette, 1993) (Schulte, Kaufmann, & Peter, 1991) physical (% sand, clay and silt) (Miller & Miller, 1987) properties.

3.7 Data manipulation and analyses

3.7.1 Plant species diversity and composition

Plant species diversity was calculated as follows for each quadrat using the Shannon-Wiener diversity index (H').

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

Where, '*s*' is the species richness, p*i* is the proportion of abundances belonging to the *i*th species '*i*' and ln is the natural logarithm (Sagar and Sharma, 2012). Species richness (S) was calculated as well as the means and standard errors for H' and S.

3.7.2 Vegetation structure

For all comparisons done between *A. erioloba* population and *A. erioloba* woodland community, the woodland community data included the *A. erioloba* population data. To compare height distribution patterns between the *A. erioloba* population and woodland vegetation community data were placed into the following height categories: 0-0.5m, 0.5-1m, 1-1.5m, 1.5-2m, 2-3m, 3-4m, 4-5m and >5m and differences in the height structure were tested using a χ^2 test.

Area at breast height was calculated for all trees in the woodland community and for *A. erioloba* shrubs, using the formula:

$$ABH = \pi * r^2$$

Where ABH is the area at breast height and r is the radius. The area at breast height for multi-stemmed trees was obtained by calculating the area at breast height for each stem separately and adding them together to get the total area at breast height for individual trees and *A. erioloba* shrubs. Stem cross-sections were assumed to be circular. To compare tree and shrub area frequency distribution patterns in the woodland community and *A. erioloba* population, data were tested for differences using a χ^2 test.

Individual plant and stem densities (trees and shrubs) were obtained in 25m x 25m and 10m x 10m quadrats respectively and means and standard errors calculated. To compare mean individual tree and shrub densities in the woodland community data were tested for normality using the Kolmogorov–Smirnov test and found to be normally distributed. An independent two sample T-test was then used to test for differences. To compare mean stem and individual tree densities in the woodland community, data were tested for normality using the Kolmogorov–Smirnov test and also found to be normally distributed and a paired T-test was used to test for differences.

3.7.3 Vegetation composition and dominance

3.7.3.1 Vegetation classification

A species-by-quadrat matrix was compiled that consisted of 40 species and 40 quadrats. A Hierarchical Cluster Analysis (HCA) using species binary data and the Average Linkage Cluster statistic was used to test if composition differs across the area. HCA is a method that sequentially pairs variables, clusters or variables and clusters to produce a unique set of categories (Bridges, 1966). Pairing is initiated from less inclusive clusters through larger more inclusive clusters and is continued until all variables are divided into a single group. Dendrograms are graphs which are then used to show the class-inclusive relations between clusters and the value of the clustering criterion associated with each (Bridges, 1966).

3.7.3.2 Grass composition and dominance

Median grass cover and the proportion of grasses in the various cover classes were calculated. Frequency of occurrence (as a percentage) was calculated to indicate the rate of recurrence of a species when sampling was done. The following formula was used to calculate percentage frequency of occurrence:

$$\text{\% Frequency of occurrence} = \frac{\sum(\text{Rank 1}+\text{Rank 2}+\text{Rank 3})}{40} \text{ x } 100$$

Where rank denotes dominance (1 = most dominant, 3 = least dominant) and is thus the summation of the number of times an herbaceous species was ranked 1, 2 or 3 and 40 reflects the total number of quadrats used for this assessment. Rank percentage was calculated as a proportion of the number of times a species was ranked 1, 2, or 3 from the total number of times it was ranked (Appendix 4).

3.7.4 Determinants of vegetation composition

Ordination is a collective term for multivariate techniques that arrange sites along axes on the basis of data on species composition (Jongman, ter Braak & van Tongeren, 1996). This technique results in a diagram in which sites are represented by points in two dimensional spaces with the aim being to have points with similar species composition close together and species that are dissimilar represented by points that are far apart (Jongman et al., 1996). It could thus be used extremely effectively to illustrate the overlaps in species composition in the various quadrats.

Detrended Correspondence Analysis (DCA) is an indirect gradient analysis or ordination technique that was used on presence/absence data of plant species to show similarities between the various plant associations within the sampled quadrats. In indirect gradient analysis species data alone are used to determine what the most important gradients are that dictate associations. To determine the extent of influence of fire, herbivory, soil properties and wood harvesting on vegetation a direct gradient analysis technique was used. Canonical Correspondence Analysis (CCA) as a direct ordination method is designed to detect the patterns of variation in the species data that can best be explained by observed environmental variables (Jongman et al., 1996). The resulting ordination diagram expresses not only a pattern of variation in species composition but also the main relations between the species and each of the environmental variables thus combining aspects of regular ordination with aspects of regression (Jongman et al., 1996).

In the CCA the same species data set was used as for the DCA with the addition of the environmental variables. For the environmental variables fire, wood harvesting and herbivory, mean damage extent scores were calculated for each quadrat. These midpoint values were than incorporated into the species data matrix as well as the percentage values obtained from soil properties (sand, Organic Matter and pH) analyses.

CHAPTER 4

RESULTS

4.1 Plant species diversity and richness

The mean, range and standard error of the species diversity index (H') and richness were obtained and summarized (table 2). Plant species recorded totaled 40 which consisted of 15 woody species and 25 herbaceous (grasses, forbs and sedges) species.

Table 2. Summary of descriptive statistics obtained for the species diversity and richness in the *A. erioloba* woodland community.

Attribute	Mean	Range	Standard Error (SE)
Species diversity	1.929	1.39 – 2.4	±0.01
Species richness	7.13	4 – 11	±0.05

4.2 Vegetation structure

A total of 285 trees and 282 shrubs and saplings were assessed in this study (Table 3). *A. erioloba* constituted 76% of all trees assessed and 12 % of all shrubs and saplings assessed. Of the 217 *A. erioloba* trees assessed there was 1 live stump and 4 dead trees.

Table 3. The number of alive and dead trees, shrubs and saplings assessed in the A. erioloba woodland community.

Vegetation assessed	Alive	Dead	Total
Trees	277	8	285
Shrubs and saplings	260	22	282

Comparisons of woody plant height structure showed a significant difference between the woodland community and *A. erioloba* population ($\chi^2 = 113.69$, df=7, $p < 0.001$). In the woodland community there was much higher observed than expected plants in the height classes: 0.5-1m, 1-1.5m, 1.5-2m, whilst in the >5m height class there was a much lower observed than expected number (Fig. 6). The height distribution pattern for the woodland community does not conform to the expected inverse J pattern as substantial numbers of trees were found in the largest height class which is atypical of the inverse J pattern (Fig. 6). There were much lower observed than expected plants of the *A. erioloba* population in the 0.5-1m, 1-1.5m, 1.5-2m height classes. In the >5m height class for the *A. erioloba* population there was a much higher observed than expected numbers. This height distribution pattern for the *A. erioloba* population is contrary to the expected inverse J pattern, instead it can be described as a unimodal height pattern with most of the plants occurring in the largest height class.

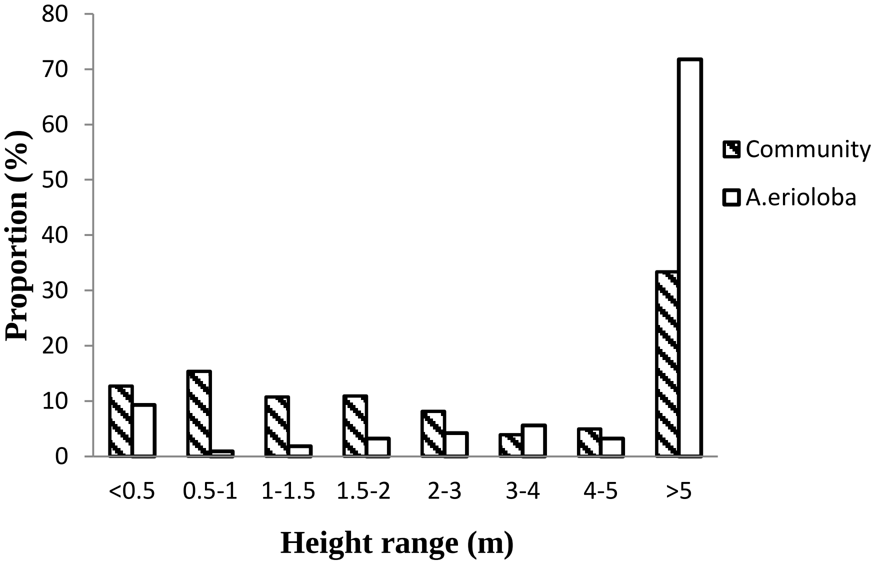

Figure 6. A comparison of woody plant height frequency distribution patterns between the woodland community and the *A. erioloba* population.

There was no significant difference in the woody plant area at breast height distribution patterns between the woodland community and *A. erioloba* population ($\chi^2 = 4.084$, df= 7, $p = 0.77$). Observed and expected values for both the *A. erioloba* population and the woodland community were very similar (Fig. 7). The general breast height distribution pattern can be described as bimodal with two peaks that occur in both the woodland vegetation community and the *A. erioloba* population. This pattern is also contrary to the expected inverse J pattern.

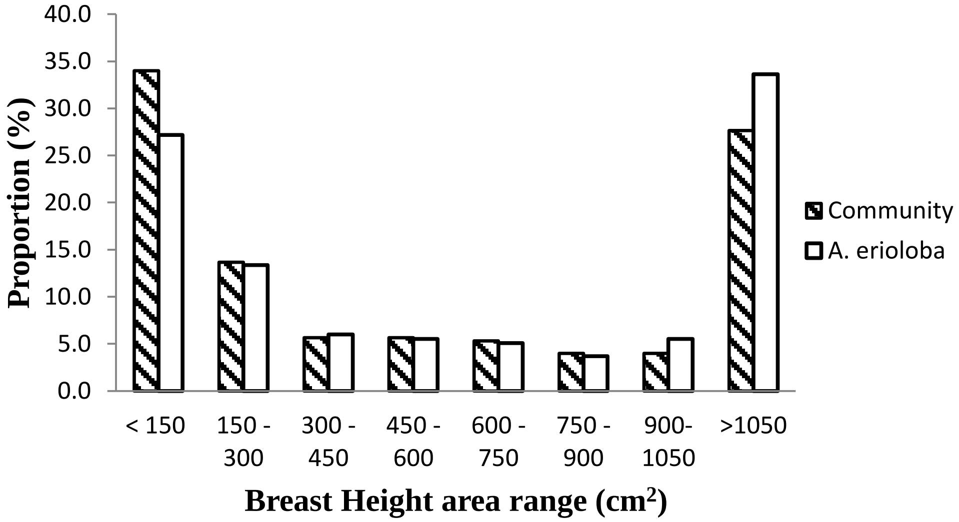

Figure 7. A comparison of tree breast height area frequency distribution patterns between the Woodland community and the *A. erioloba* population.

There was a significant difference in tree and shrub densities in the woodland community ($t = 5.1$, df = 40, $p < 0.001$) with shrub densities significantly higher than tree densities (Table 4). Similarly, density comparisons between individual tree and stem counts showed a significant difference (t= 4.8, df = 39, p< 0.001) with stem densities significantly higher than individual tree densities (Table 4).

Table 4. Comparisons of densities of individual trees, shrubs and stems of trees and shrubs in *A. erioloba* community in Windhoek.

	Trees (per hectare)	Shrubs (per hectare)	Difference
Stems	4.6	263.4	p < 0.001
Individuals	2.3	19.9	p < 0.001
Difference	p < 0.001	p < 0.001	

4.3 Vegetation composition and dominance

4.3.1 Vegetation classification

The Hierarchial Cluster Analysis separated the quadrats into 3 main clusters based on differences in plant species composition (Fig. 8). Cluster 1 is separated from the other two clusters at 27% similarity whilst cluster 2 and 3 are 34% similar. Generally similarity ranges from 27% to 85%. Heterogeneity is thus relatively high as seen from the level of similarity.

Cluster 1 was formed by six quadrats and had *A. erioloba* as a common woody species. *A. erioloba* occurred primarily as a tree in all six quadrats with its only occurrence as a sapling restricted to quadrats 27 and 30. Two forb species were also common to this floristic association, namely *Bulbostylis densa* and *Tribulus zeyheri*. subsp. *zeyheri*.

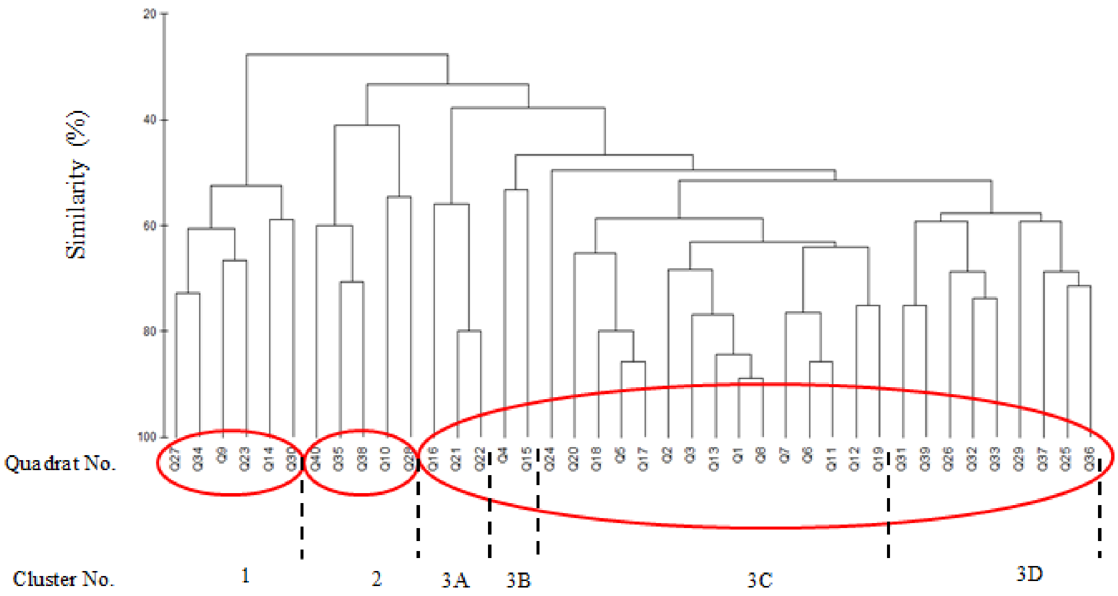

Figure 8. Hierarchial Cluster Analysis (HCA) dendrogram illustrating the classification of vegetation into 3 main clusters based on species presence/absence data.

Cluster 2 consisted of five quadrats that had the shrub *Pechuel-Loeschea leubnitziae* as a common woody species. No grass species were commonly found either, however the forb species and *Nidorella resedifolia* subsp. *resedifolia* was shared by this cluster.

Cluster 3 was generally associated with plots that all contained *A. erioloba* either as a tree, sapling or both and was further divided into four sub-clusters based on the species they had in common.

***Sub-cluster* 3A** was formed by three quadrats forming a very small cluster with *A. erioloba* as a common woody species. *A. erioloba* occurred primarily as a tree in all three quadrats with its occurrence as a sapling found in two out of the three quadrats. Two grass species were found to be common to this cluster, namely *Sporobolus fimbriatus* and *Urochloa oligotricha*. This subcluster basically differs from cluster 1 by differences in grasses.

***Sub-cluster* 3B** was the smallest of all of the sub-clusters consisting of only two quadrats. This association had *A. erioloba* which occurred mainly as a tree and *Lycium eenii* which occurred as a shrub species as common woody species. The forb species *Commelina benghalensis* and the grass species *Urochloa oligotricha* was common to this floristic association as well as. These 2 sub-clusters differ mainly in the herbaceous layer. They also differ from cluster 1 through differences in the herbaceous layer.

***Sub-cluster* 3C** was the largest of the sub-clusters formed by fifteen quadrats and primarily had *A. erioloba* as a common woody species with the exception of one quadrat. Another prominent woody species, though not common to all quadrats, was *Ziziphus mucronata* as it occurred in more than eighty percent of the quadrats. The grass species *Sporobolus fimbriatus* primarily occurred as the most common herbaceous species across all quadrats.

***Sub-cluster* 3D** mainly had *A. erioloba* as a common woody species with the exception of one quadrat. Two forb species were common to this floristic association, namely *Bidens biternata* and *Nidorella resedifolia* subsp. *resedifolia*.

4.3.2 Grass composition and dominance

Median grass cover ranged from 12.5- 87.5% in the study area. The largest proportion (35% of the quadrats) of grass cover fell in the 50-75% scale whilst the 75-100% scale contained the smallest proportion (13%). The second largest proportion of grasses fell into the 25-50% scale (27%) whilst the remainder (25%) was in the 0-25% scale. Thus, in general the area had a moderate grass cover (25-75%).

The grass *Sporobolus fimbriatus* (with a frequency of occurrence as a primary measure) was found to be most dominant (52.5% frequency of occurrence) in this *A. erioloba* woodland followed by the forbs *Bidens biternata* (47.5%), *Commelina benghalensis* (32.5%) and *Nidorella resedifolia* subsp. *resedifolia* (27.5%). Dominance rankings indicated that where *Sporobolus fimbriatus* and *Nidorella resedifolia* subsp. *resedifolia* occured they were most likely to be the most dominant. The forbs *Bidens biternata* and *Commelina benghalensis* were mostly ranked the 2nd most dominant where they occurred (Table 5).

Table 5. Grass and forb ranking, with frequency of occurrence indicating the rate of recurrence of a species in each sampled quadrat when grasses and forbs were sampled in the woodland. Rank (%) is an indication of how often a species was ranked as 1 (dominant), 2 (less dominant) and 3 (least dominant) of the top 3 should the species be encountered. (G= Grass, F= Forb, S=Sedge).

Species	**Life form**	**Frequency of occurrence (%)**	**Rank 1 (%)**	**Rank 2 (%)**	**Rank 3 (%)**
Sporobolus fimbriatus	G	52.5	61.9	0.3	28.6
Bidens biternata	F	47.5	0.0	0.6	57.9
Tribulus zeyheri subsp. *zeyheri*	F	17.5	28.6	0.4	42.9
Commelina benghalensis	F	32.5	7.7	0.5	46.2
Urochloa oligotricha	G	25.0	60.0	0.2	20.0
Nidorella resedifolia subsp. *Resedifolia*	F	27.5	63.6	0.3	27.3
Schimdtia kalahariensis	G	17.5	42.9	0.1	14.3
Bulbostylis densa	S	15.0	16.7	0.3	33.3
Sesamum capense	F	5.0	0.0	1.0	100.0
Monandrus squarrosus	F	2.5	100.0	0.0	0.0
Pollichia campestris	F	5.0	50.0	0.0	0.0
Mollugo cerviana	F	5.0	0.0	0.5	50.0
Dactyloctenium aegyptium	G	2.5	0.0	1.0	100.0
Pogonarthria fleckii	G	2.5	100.0	0.0	0.0
Cenchrus ciliaris	G	2.5	0.0	0.0	0.4
Eragrostis tricophora	G	2.5	100.0	0.0	0.0
Laggera decurrens	F	2.5	0.0	0.0	0.0
Chenopodium amboanum	F	5.0	100.0	0.0	0.0
Helichrysum candolleanum	F	5.0	50.0	0.0	0.0
Geigeria ornativa	F	2.5	0.0	1.0	100.0
Setaria verticillata	G	2.5	0.0	0.0	0.0
Ocimum americanum var. *americanum*	F	5.0	0.0	0.5	50.0
Hermannia tomentosa	F	2.5	0.0	0.0	0.0

4.4 Determinants of vegetation composition

Detrended Correspondence Analysis (DCA) separated the quadrats into two main groups along DCA axis 1. Group 1 largely corresponds to cluster 1 of the HCA with a slight overlap with quadrat 35 that forms part of cluster 2 of the HCA (Fig. 9).

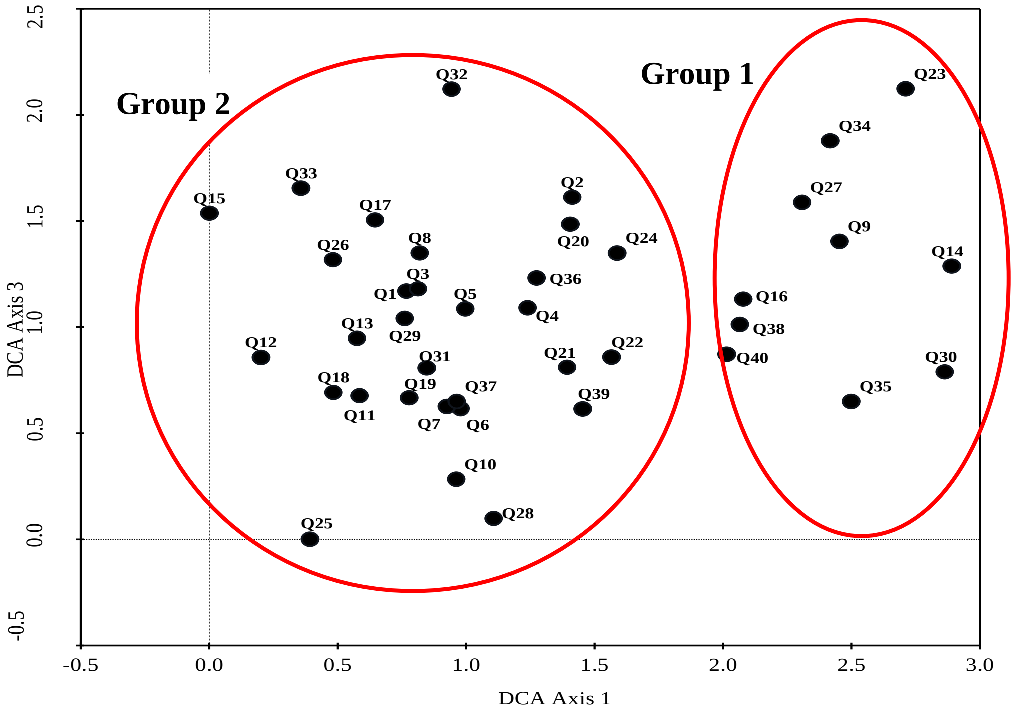

Figure 9. Detrended Correspondence Analysis (DCA) ordination diagram based on plant species presence/absence data illustrating the separation of quadrats into two groups along DCA axis 1.

Group 2 combined all of the other quardrats excluded from Group 1 thus including all of the other clusters of the HCA (Fig. 9). Overlaps thus occur in the association of quadrats from different clusters of the HCA. DCA axis 1 explained 46% of the variation in species composition, whilst DCA axes 2 explained 31% of the variation.

Along axis 1, the hypothesized gradient was fire damage, which seemed to have been more in Group 2 plots.

The measured environmental variables used in the CCA analysis explained 19% of the observed variation in species composition. CCA axis 1 explained 23.6% of the variation, whilst CCA axes 2, 3 and 4 explained 16.9 %, 13.9%, 11.4% of the variation respectively. The explanatory variables that significantly influenced species composition were fire ($F= 1.82$ $p< 0.05$), pH ($F= 1.54$ $p< 0.05$) and woodharvesting ($F=1.46$ $p< 0.05$). The gradient along CCA axis 1 was significant ($F= 1.95$, $p < 0.05$) while the overall test of all canonical axes was also significant ($F= 1.295$, $p < 0.01$).

Along CCA axis 1 the explainable variation in species composition was positively correlated with fire, sand, wood harvesting and pH and negatively correlated with herbivory and organic matter (OM). CCA axis 3 was positvely correlated with wood harvesting, sand and pH and negatively correlated with fire, herbivory and OM.

The direction and influence of environmental variables indicate that along CCA axis 3, fire, herbivory and OM strongly influenced species composition in Group 1 (Fig. 10). This group was thus strongly correlated with high levels of fire, herbivory and OM. For Group 2, there were no measured environmental variables that showed a clear, strong positive influence on species composition, but were associated with lower levels of pH, fire and woodharvesting. Species composition in Group 3 was associated with high levels of sand and woodharvesting (Fig. 10) which corresponds with Group 3 of the

HCA (Fig. 8) and Group 2 of the DCA (Fig.9). Quadrat 13 was not inlcuded in any of the groups as it was an outlier that was positively influenced by pH.

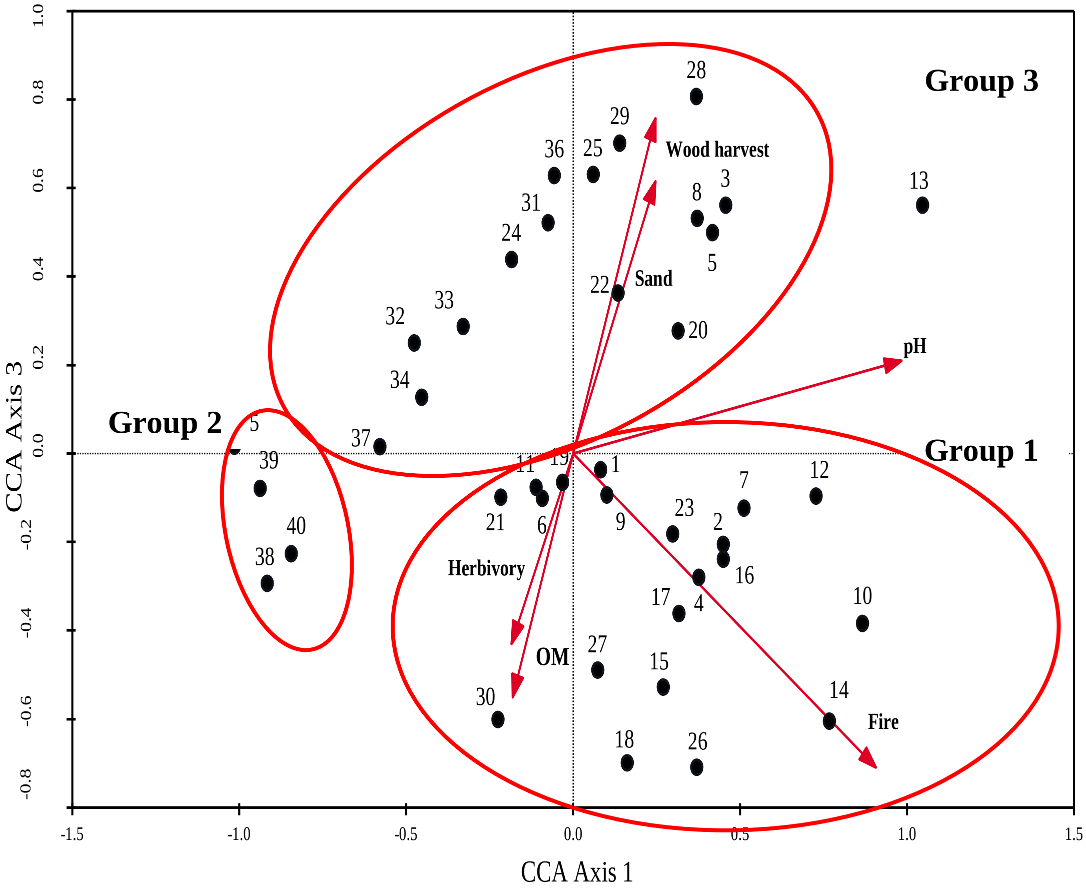

Figure 10. Canonical Correspondence Analysis (CCA) ordination diagram illustrating the influence of the measured environmental variables on species composition in an *A. erioloba* vegetation community.

CHAPTER 5

DISCUSSION

5.1 Vegetation structure

Comparisons of tree and shrub height in the woodland community and *A. erioloba* population indicated significant differences between the woodland community and the *A. erioloba* population. Neither of them tended to conform completely to the inverse-J pattern, typical of uneven-aged populations, where all size classes are represented and most of the plants belong to the relatively smaller size classes (Fajardo, Quiroz, & Cavieres, 2008). Instead the woodland community showed a height structure that illustrated that there is a high level of sapling and shrub recruitment and retention with much higher observed than expected values in the height classes: 0.5-1m, 1-1.5m, 1.5-2m. However, there was a decline in the number of such trees in the 2-3m, 3-4m and 4-5m height classes which resulted in lower observed than expected frequency in the 5m height class. This decline may be as a result of human induced disturbances, in particular fire that the CCA ordination has shown to be significant.

Fire is known to have a widespread effect across woodlands which could result in extensive tree loss (Ben-Shahar, 1996). The *A. erioloba* population on the other hand had a unimodal height pattern as most of the plants could be found in the largest size class. This shows that this is an ageing population with very few to no new plants being recruited. A low sapling and shrub frequency suggests less than optimal germination conditions for initial seedling establishment (Rocky & Mligo, 2012). No sign of large herbivores, such as faecal matter, were observed in the woodland during the study period. Their movement into the area may be restricted by farm fencing on the woodland’s southern border that would otherwise have served as a natural corridor into the woodland and human activity in the area that could have conditioned the animals not to frequent the area. Unfavorable germination conditions could thus be attributed to a lack of large herbivores in the woodland as it has been established that seeds that have passed through the gut of herbivores germinate faster than those that have not (Barnes, 2001a).

Pod harvesting was also observed in the woodland which could also impact germination as pods were removed from the area thereby reducing the number of seeds that could potentially have germinated. Pods are collected by locals in poverty stricken suburbs to sell and so generate income. Other contributing factors to these less than optimal microhabitat conditions may again include disturbances such as fire, herbivory and woodharvesting which are fully discussed in the section below. Also, this may be a contributing factor to such high recruitment in the woodland as a lack of *A. erioloba* recruitment and establishment can mean more resources and space available to other species in the community. Should this situation continue indefinitely and no new plants are added, the population could become extinct in this area.

There was no significant difference between the tree and shrub area at breast height distribution patterns in the woodland community and *A. erioloba* population. This pattern indicates that the woodland is dominated by smaller and larger trees with disproportionately fewer individuals in the middle-size classes which is evidence of the impact of fire that perhaps prevents the survival of smaller trees into the middle size classes as smaller trees are known to be more vulnerable to fire (Seymour & Huyser, 2008), further emphasizing the significance of fire in the area as shown by the CCA ordination. It also demonstrates that *A. erioloba* is dominant in terms of stem area such that it's influence on the community us unparalled, resulting in similar patterns between the community (which includes *A. erioloba*) and the *A. erioloba* population.

Comparisons between tree and shrub density in the woodland community showed shrub densities were significantly higher than tree densities. Shrub recruitment may be enhanced by the occurrence of fire as this disturbance may create space for opportunistic invaders giving shrubs a competitive advantage over trees. *Lycium eenii* that was observed to be particularly prevalent in the woodland can serve as an example of such an opportunistic invader. This shrub is known to occur in the shade of other trees and bushes (Mannheimer & Curtis, 2009) and may have benefited from the removal of vegetation from under trees by fire that created a gap for them to move in.

Density comparisons between individual tree and stem counts showed a significant difference with stem densities significantly higher than individual tree densities. The results indicate that most individual trees in the woodland community were multi-stemmed whilst *A. erioloba* is usually single stemmed, which can be interpreted as a disturbance to the plant whilst it is growing (Mapaure, 2006). The high stem density may be a survival strategy in reaction to a disturbance like fire, where species may be more reliant on resprouting than recruitment for population persistence (Mapaure, 2006). When fires occur saplings are often killed, however, sprouters are able to survive by rapidly regenerating stems. Multi-stemming is also evidence that this woodland is subjected to significant woodharvesting (Mapaure, 2006).

5.2 Species richness, diversity and composition

The diversity index recorded in this woodland community was 1.929 (SE ±0.0067), and the mean species richness of 7.125 (SE ±0.0461). Generally Hˈ values range from 0 (only one species present with no uncertainty of what species each individual will be) to about 4.5 (high uncertainty as species are relatively evenly distributed). In theory, the H’ value can be much higher than 4.5, although most real world estimates of H’ range from 1.5 to 3.5. (*Estimating Species Richness and Diversity and Assessing Stream Quality: A Survey of the Macro-invertebrates in Boulder Creek*, n.d.)**.** High species diversity indicates a complex community in which a high degree of species interaction is possible. For this reason, communities with higher diversities typically have higher levels of energy transfer (food webs), predation, competition and niche availability (*Theory of Species Diversity*, n.d.)**.** Species diversity has been construed as a measure of community stability in which low or changing species diversity may indicate a stressed or unstable environment (*Theory of Species Diversity*, n.d.). The Hˈ and species richness recorded in this study could be interpreted as reflecting a moderate to low species diversity and is thus indicative of a disturbed and less stable environment. According to the intermediate disturbance hypothesis it would be expected that should the area have been moderately disturbed it would have a high diversity (Roxburgh, Shea, & Wilson, 2004), which is not the case. Instead, disturbance in the area could be interpreted as being moderately high given this H' and richness. Pieters and Laamanen (2002) recorded a species richness of 9 for trees in the Rehoboth Acacia Park, a similar woodland but where *A. erioloba* constitutes 31% of the total number of trees found in the area. The diversity index in the Park was calculated to be 1.688 which could also be interpreted to be a moderate to low species diversity and richness (*Estimating Species Richness and Diversity and Assessing Stream Quality: A Survey of the Macro-invertebrates in Boulder Creek*, n.d.). Though not directly comparable this species diversity is very similar to the *A. erioloba* woodland community of this study, which could be attributed to human disturbances as both the Rehoboth Acacia Park and woodland community are extensively utilized by the local communities surrounding these areas. The hypothesis that diversity is expected to be relatively higher than expected due to the occasional fire disturbance which creates patchy mosaics in the woodland is thus not supported by the species diversity and richness.

The clusters formed by the vegetation in this study did not represent a clear separation of the quadrats according to their position along the transect or on the landscape. Instead, cluster associations could be more reflective of the type of disturbance that has impacted that particular area in the woodland (Mapaure, 2006). The specie *Pechuel-*

Loeschea leubnitziae found in cluster 2 is known to often invade disturbed ground (Mannheimer & Curtis, 2009). Its presence as a common woody specie could be used in support of the argument that cluster associations are disturbance based. This is supported by the DCA ordination analyses which showed Group 1 mainly corresponding to cluster 1 of the HCA and Group 2 corresponding to the rest of the HCA clusters. DCA axis 1 explained 46% of the variation in species composition. Depending on the type of disturbance or combination thereof various microhabitats could have been formed selecting for either competitive K-selected or opportunistic r-selected species to fill the different niches that were created as a result of the disturbances. These clusters are a mere representation of heterogeneity found in the vegetation community and not different vegetation types. The explanatory environmental variables in the CCA accounted for 19% of the observed variation in species composition. Fire, woodharvesting and soil pH showed a significant influence on plant composition. Fire was the most important variable influencing species compostioin along CCA axis 1 followed by wood harvesting.

According to Seymour and Huyser (2008) *A. erioloba* is fire sensitive, in particular unestablished seedlings and mature trees in the largest size class (8-12m height) where large tree mortality rates can be attributed to “large well-developed assemblages of flammable subcanopy plants producing a bonfire beneath trees.” In this woodland where the source of ignition for fires is thought to be mainly anthropogenic with people using the woodland as a recreactional barbeque area (Morkel *pers. obs*) the frequency and intensity with which they occur, though not recorded, could prevent seedling establishment and thus the regeneration of *A. erioloba* as a keystone species. Furthermore, fires could also destroy highly sensitive mature trees that currently dominate the woodland. However, vegetation structure patterns showed mature *A. erioloba* trees in the woodland had a higher than expected value which could be attributed to the fire behaviour in the area. Fire could thus be preventing the regeneration of *A. erioloba* in the woodland and could also potentially destroy existing mature *A. erioloba* trees.

In addition to uncontrolled fires, unregulated woodharvesting exerts more pressure on the intergrity of the ecosystem as the CCA ordination found this practice to significanlty influence species composition. Shrubs when they occur also suffer greatly as their easily accesible branches are possibly harvested more readily leaving them more vulnerable and less likely to survive frequent fires. Soil pH generally had a siginificant influence on species composition as well although this was not clearly illustrated by the CCA ordination diagram (Fig. 10) with none of the quadrats that were closely associated with the pH gradient. This influence may be attributed to a conceivably high incidence of fire in the woodland as soil pH have been found to increase with increased burn frequency (Mitros, McIntyre, & Moscato-Goodpaster, 2002). The long-term impacts of such fires on soil properties including pH, is determined by burn severity which is a product of the peak temperature and duration of the fire (Certini, 2005). Low to moderate severity fires promote the renewal of the dominant vegetation by increasing soil pH and plant available nutrients. In contrast severe fires can cause extensive soil damage ranging from the removal of organic matter and the loss of nutrients to leaching and erosion (Certini, 2005).

This shows that variation in diversity and composition could be attributed to human disturbance which further supports the justification that plant diversity found in the *A. erioloba* woodland community is low. However, the low species diversity found in the area was not only due to differences in human utilization but other factors associated with DCA axis 2 (Mapaure, 2006). These factors may include more complex biotic and abiotic interactions than simply the determinants suggested by this study. Such interactions may include small mammal activity that can range from burrowing and thus turning the soil so impacting soil quality to herbivory on seedlings that include the complete removal of the plant and the dispersal and germination of seeds. Evidence of such activity was noted throughout the woodland and could thus be significant in determing vegetation species composition throughout the woodland. An abiotic factor that may also have been important was the amount of rainfall that the area had received, as this would impact especially the biomass of grasses and forbs which have been found to have a positive relationship with precipitation (Ni, 2003).

This study site was characterized by a mean grass cover of 46.3%. Species of grasses and forbs that dominated the area can be viewed in terms of two main functional groups namely fire promoted opportunistic invaders of disturbed areas and climax plants.

Opportunistic invaders of disturbed areas include the species *Bidens biternata* and *Commelina benghalensis* the second most dominant non-woody species (Fig. 9 & Table 5) in the woodland community. *Bidens biternata* is a cosmopolitan, annual herb which originates from tropical and Central America. What is characteristic of this functional group as that species possess over explosive reproductive potential and an ability to thrive in almost any environment such as in the case of *Bidens biternata* (National Biological Information Infrastructure (NBII) & IUCN/SSC Invasive Species Specialist Group (ISSG), 2010). Such species thus thrive in disturbed areas that include a range of habitats from grasslands to roadsides and *Commelina benghalensis* as an example have been listed as one of the world's worst weeds (Webster, Burton, Culpepper, York, & Prostko, 2005) due to its great affinity for invading disturbed areas. *B. biternata*, as an opportunistic invader is capable of surviving severe droughts but it is not fire tolerant however it is known to quickly invade burnt areas (National Biological Information Infrastructure (NBII) & IUCN/SSC Invasive Species Specialist Group (ISSG), 2010). This characteristic can thus make it part of the fire promoted functional group as the presence of frequent fires can be seen to encourage the invasion of this species. The presence of this species in this dominance ranking could be used to argue in support of fire as an important determinant of species composition in this woodland. This further underlines the importance of disturbances such as fire and perhaps wood harvesting in the area in determining the floral make-up of this woodland community. Other more prominent species found in the area that also form part of this functional group is the grass *Schimdtia kalahariensis*. The high frequency of occurrence of such invasive species could be contributing to the moderate species diversity in the area that would otherwise have been low and perhaps a more accurate depiction of the level of disturbance in the area.

Climax plants are characterized by their strong competitive ability which enables them to establish themselves in the presence of other plants (van Eck, 2007). Furthermore they are known to be efficient utilizers of water, an attribute that makes them relatively drought tolerant. Climax plants, such as the perennial grass *Sporobolus fimbriatus* which occurred as the most dominant non-woody species in the woodland community, indicate ecosystem recovery after the disappearance of a disturbing factor like fire (van Eck, 2007). This once again emphasizes the significance of the influence of fire as a disturbance factor in the woodland. Their competitive ability is what facilitates climax plant species dominance over opportunistic invader, hence the reason that *Sporobolus fimbriatus* was ranked most dominant where it occurred (Fig. 9 & Table 5). Other more prevalent species that also formed part of this functional group include the perennial grass *Urochloa oligotricha*.

5.3 Preliminary Conceptual model of the dynamics of *A. erioloba* population

In the absence of frequent hot fires or any other major disturbance, regeneration of the *Acacia erioloba* woodland would occur naturally with an expected inverse J pattern. Three stages of regeneration can be identified in this woodland (Fig. 11): Initial recruitment (normal) or regrowth stage (after disturbance); tall sapling stage; and mature woodland stage (Frost, 1996). The influence of the disturbances that were found to be significant in this study (fire, woodharvesting) as well as soil pH and precipitation is discussed in detail below.

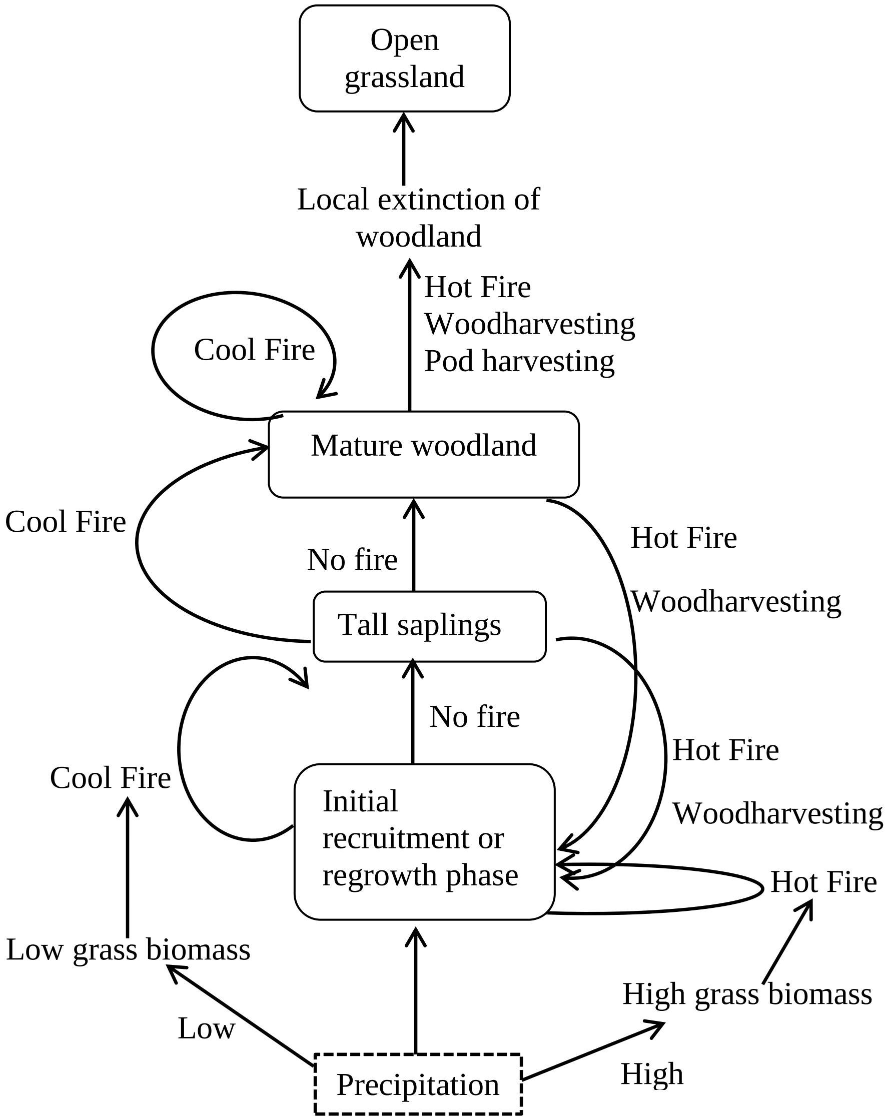

Figure 11. A preliminary Conceptual Model of the *A. erioloba* population dynamics under the influence of fire, woodharvesting and precipitation. The qualitative descriptors of 'Hot' and 'cold' refer to fire line intensities of about >1000 and <1000 W m-1, respectively (Frost, 1996).

In the initial recruitment or regrowth stage is where woody vegetation is less than 1m tall (Frost, 1996) *A. erioloba* will regenerate by recruitment of new propagules from seeds, coppicing from cut stumps or multiplying from root suckers (Seymour & Milton, 2003). Intense, late dry season frequent fires or ‘hot’ fires can prevent the development of the tall sapling stage by suppressing woody vegetation recovery to the initial stage (Frost, 1996). In resilient ecosystems, this would result in formation of “gullivers” which are low-growing, fire–suppressed woody plants (Gambiza, Bond, Frost, & Higgins, 2000). However, *A. erioloba* is known to be fire sensitive (Seymour & Huyser, 2008, van der Walt & le Riche, 1984) so that ‘hot’ fires could kill saplings, prevent resprouting in trees and turning pods into charcoal (Materechera & Materechera, 2001). In so doing tree densities are reduced and recruitment is negatively impacted as seeds are rendered unviable. On the other hand cool early dry season fires or no fire can allow for the development of a subsequent tall sapling phase with woody vegetation 3-6m high and a mature woodland stage (Frost, 1996) capable of producing more seeds. Should the fire regime change to ‘hot’ fires during the tall sapling stage, vegetation may be forced back into the regrowth stage (Fig. 11). Fire alone does not alter the development of woodlands though it may impede it (Frost, 1996).

Fire can have secondary impacts on soil that can in turn influence the vegetation in an area. In ‘cool’ fire regimes soil pH is reduced promoting the renovation of the dominant vegetation by facilitating the release of plant nutrients from the soil to both trees and saplings (Certini, 2005). In contrast late, intense dry season fires cause the removal of organic matter as intense burning of fallen logs renders the soil hydrophobic, leading to increased run-off from and an increase in soil pH. These effects can result in restriction of plants to the initial or regrowth phase (Fig. 11).

Precipitation is also extremely important in *A. erioloba* recruitment as studies have shown seedling emergence to be low or zero in years of drought (Barnes et al., 1999) and that satisfactory rainfall conditions are needed for a substantial period in order to ensure not only establishment but survival as well (Seymour & Milton, 2003). When precipitation is high (above average rainfall for the season) in the absence of any fires the woodland will develop naturally and if precipitation is low (below average rainfall for the season) under the same other conditions, woodland recruitment and resprouting vigour will be negatively impacted. However, when fire is present as a disturbance in an ecosystem along with high precipitation the fuel load and the time of year at which a fire occurs will determine fire intensity. Burning in the early dry season when precipitation was high during the previous wet season will produce a less intense cool fire than burning at the same time under low precipitation conditions. This is because although the fuel load or vegetation produced would be high as a result the high availability of water the moisture content in the vegetation would still be high in the early dry season which would smother a fire keeping it cooler.

In contrast fire in the late dry season with high precipitation in the preceeding wet season will produce a more intense hot fire than burning at the same time under low precipitation conditions beacause a higher and drier fuel load will be available for burning. *A. erioloba* could thus benefit from high precipitation patterns in its initial recruitment or regrowth phase as long as fire occurrence is minimised, or totally excluded during the dry season. However such precipitation that produces high fuel loads in the form of saplings and herbaceous plants could result in tall saplings returning to the initial stage should a fire occur in the late dry season. Cool, fires in contras, can result in sapling survival into the mature woodland stage (Fig. 11) even though growth may be momentarily retarded.

Woodharvesting in many woodlands results in specific sized mature trees being targeted (Mapaure, 2006) which are often trees with great reproductive potential. The density of such trees is thus reduced as well as their biomass since trees are often harvested in full if they are of medium bole size. When these trees are removed the consequence is that there are fewer pods produced and less seeds that can be released into the environment for recruitment. Reduction in tree density would in turn lead to more grass cover which provides more fuel for fire (with consequences discussed above). In the absence of woodharvesting the woodland can develop to maturity unhindered. When partially harvested trees and tall saplings are exposed to cool fires they are able to survive whilst fully harvested trees and tall saplings can regenerate from stumps by coppicing.

In contrast trees and saplings can be made more vulnerable by woodharvesting in the presence of hot fires which could result in fatalities due to the fire sensitive nature of *A. erioloba* causing it to revert back to the initial recruitment or regrowth stage (Fig. 11). Long term unregulated woodharvesting and pod harvesting (Morkel *pers. obs*) along with hot fires can result in the local extinction of the woodland and its transition into open grassland. This would result in a loss the primary ecosystem services associated with this woodland.

Hence, any management plan that should be put in place must focus on managing woodharvesting, pod harvesting, and fire since these are secondary determinants and we can exercise control over them. In managing these secondary determinants, cognizance should be taken of the importance of primary determinants such as precipitation (which influences soil moisture) and soil chemical and physical properties. When all such aspects are properly quantified, simulation models can be built with different scenarios based on the relationships discussed above.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

Vegetation structure aspects investigated; in particular height distribution patterns supported the hypothesis that *A. erioloba* community structure is skewed towards more adult trees and fewer smaller trees and saplings. A t-test showed the difference in tree and shrub densities in the woodland community to be significant with shrub densities that were much higher. Shrub recruitment was thought to be enhanced by the occurrence of fire as this disturbance may create space for opportunistic invaders giving shrubs a competitive advantage over trees. The t-test on density comparisons between individual tree and stem counts also showed a significant difference with stem densities significantly higher than individual tree densities. Multi-stemming was used as evidence for the influence of disturbance, in particular fire and woodharvesting, on the plant whilst it was growing as this response is often associated with such disturbances. The CCA ordination showed that fire and woodharvesting were significant disturbance factors which further supported the remainder of the hypothesis which stated that this pattern could be due to negative impacts of fire and wood harvesting (rather than herbivory) on establishment and recruitment.

Species diversity and richness recorded in this study were interpreted as reflecting a moderate to low species diversity and is thus indicative of a disturbed and less stable environment. The Rehoboth Acacia park woodland community showed a similar H' and species richness and though not directly comparable this species diversity is very similar to the *A. erioloba* woodland community of this study. This similarity was attributed to similar land use practices as both the park and woodland community are extensively utilized for human activities ranging from recreation to the harvesting of Non-timber Forest or Woodland Products. The hypothesis that diversity is expected to be relatively higher than expected due to the occasional fire disturbance which creates patchy mosaics in the woodland is thus not supported by the findings.

The HCA revealed that the clusters formed by the vegetation did not represent a clear separation of the quadrats according to their position along the transect or on the landscape. Instead there were other factors at work which was then explained by the DCA and CCA ordinations. It was clear from the DCA and CCA that fire played a significant role in determining species composition. The hypothesized gradient along DCA axis 1 was fire and the importance of this was further emphasized by the CCA which showed fire, wood harvesting soil pH to be significant environmental variables influencing diversity and structure of *Acacia erioloba* woodland community. Herbivory and other physical soil structure properties (OM, %clay, sand and silt) that were also measured were not significant. This study site was characterized by a mean grass cover of 46.3%. Species of grasses and forbs were divided into two main functional groups namely fire promoted opportunistic invaders of disturbed areas and climax plants. Both functional groups were indicators of ecosystem response to fire as a disturbance, re-emphasizing its importance. Additionally, the high frequency of occurrence of grasses and forbs in the area were thought to contribute to the moderate species diversity that would otherwise have been low and a more accurate depiction of the level of disturbance in the area.

Based on these three environmental variables alone it is clear that current conditions that allow for unregulated woodharvesting and fires present an undeniable threat to the survival of this *A. erioloba* woodland community. A lack of proper management measures will thus in all likelihood result in the local extinction of this woodland. Other measured variables did not have a significant influence on species compostion as anticipated, suggesting that perhaps other environmental variables not measured may have an important role to play. Alternatively, the quantification of measured variables may be revised as this may also have impacted results that were obtained.

6.2 Recommendations

a) This study has shown that fire and wood harvesting have significantly influenced the structure and composition of this *A. erioloba* woodland community. Management goals should therefore focus on the development of a short term and long term conservation action plans. Short term plans should be aimed at addressing these issues as an immediate threat whilst long term conservation goals should focus on developing community based natural resource management.

b) Sustainable development should form the backbone of all conservation efforts keeping in mind that the Intermediate Disturbance Hypothesis could be employed to allow for disturbances such as wood harvesting and fire to continue but in a regulated fashion. This will encourage the development of high species diversity and also benefit the poorest residents of the City that mainly utilize these woodlands.

c) This study could also benefit from more detailed simulation modeling as conceptual models represent a tool for understanding the connections between the components of complex systems, but simulation modeling allows for understanding both the dynamics of these systems and the possible outcomes of various interventions in them (Campbell, Frost, Goebel, Standa-Gunda, Mukamuri, & Veenan, 2000).

d) The extent of damage may be quantified to boles and canopy rather than using qualitative scales of “moderate” and “serious”. This may be particulary important for a variable such as herbivory as studies have shown small browser (Augustine & McNaughton 2004) and invertebrate herbivory (Shaw, Keesing, & Ostfeld, 2002) to be significant in *A. erioloba* woodlands.

e) Pod harvesting may also be included as an aspect that can influence *A. erioloba* recruitment however, careful consideration must be given to the practical process of quantifying such data. Pods are collected and taken from the woodland by various collectors and at different times of the year making quantification challenging. Other variables could also be included that can provide valuable insights into woodland functioning such as chemical soil properties (that was excluded due to financial constraints).

f) Seasonal variation in plant species composition can also be an important aspect to look at as time and resources in this study did not allow for this aspect to be included. This information could enable a more complete depiction of the woodland dynamics which could especially be important for the management of the woodland as it will influence management goals and strategies.

g) The identification of sources of ignition should also be invetigated as this will help to come up with a fire management plan for the area.

h) Human impacts on the vegetation can effectively be solved by addressing the bigger issues of people’s needs in the City, especially those living in impoverished “informal” settlements.

i) Finally, a similar study should be conducted in a prestine *A. erioloba* woodland community that can serve as a control so that more comparative studies can be done that can also facilitate management strategies and practices in these woodlands.

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APPENDICES

Appendix 1. The GPS coordinates of all of the quadrats

Quadrat no.	Distance from starting point along the transect	Degrees South	Degrees East
1	25m	S 22°. 28149	E017°. 05135
2	50m	S 22°. 46941	E017°. 08549
3	75m	S 22°. 46857	E017°. 08545
4	100m	S 22°. 46965	E017°. 08490
5	25m	S22°. 46910	E017°. 08457
6	50m	S22°. 46912	E017°. 08514
7	75m	S22°. 46968	E017°. 08541
8	100m	S22°. 46991	E017°. 08491
9	125m	S22°. 47001	E017°. 08535
10	125m	S22°. 47011	E017°. 08516
11	150m	S22°. 47027	E017°. 08547
12	150m	S22°. 47024	E017°. 08516
13	175m	S22°. 47048	E017°. 08528
14	175m	S22°. 47041	E017°. 08557
15	225m	S22°. 47081	E017°. 08574
16	225m	S22°. 47089	E017°. 08538
17	275m	S22°. 47129	E017°. 08559
18	275m	S22°. 47126	E017°. 08559
19	325m	S22°. 47174	E017°. 08606
20	325m	S22°. 47178	E017°. 08574
21	375m	S22°. 47236	E017°. 08589
22	375m	S22°. 47211	E017°. 08610
23	425m	S22°. 47231	E017°. 08659
24	425m	S22°. 47282	E017°. 08623
25	475m	S22°. 47307	E017°. 08635
26	475m	S22°. 47294	E017°. 08667
27	525m	S22°. 47333	E017°. 08685
28	525m	S22°. 47353	E017°. 08637
29	575m	S22°. 47401	E017°. 08668
30	575m	S22°. 47378	E017°. 08701

31	625m	S22°. 47421	E017°. 08623
32	625m	S22°. 47435	E017°. 08671
33	675m	S22°. 47488	E017°. 08683
34	675m	S22°. 47464	E017°. 08732
35	725m	S22°. 47507	E017°. 08710
36	725m	S22°. 47520	E017°. 08674
37	775m	S22°. 47584	E017°. 08681
38	775m	S22°. 47555	E017°. 08735
39	825m	S22°. 47609	E017°. 08727
40	825m	S22°. 47614	E017°. 08692

Appendix 2. Plant species list of plants recorded in the *A. erioloba* woodland

1	*Acacia hebeclada DC.* (O.B. Miller) A. Schreiber
2	*Acacia erioloba* E. Mey.
3	*Acacia mellifera* (Vahl) Benth. subsp. *mellifera*
4	*Acacia reficiens* Wawra subsp. *reficiens*
5	*Acacia sp.*
6	*Bidens biternata* (Lour.) Merr. & Sherff
7	*Bulbostylis densa* (Wall.) Hand.-Mazz
8	*Cenchrus ciliaris* L.
9	*Chenopodium amboanum* (Murr) Aellen
10	*Commelina benghalensis* L.
11	*Crotalaria argyraea* Welw. ex Baker
12	*Dactyloctenium aegyptium* (L.) Wild.
13	*Enneapogon cenchroides* (Roem. & Schult.) C.E.Hubb.
14	*Eragrostis tricophora* Coss. & Durieu
15	*Geigeria ornativa* O. Hoffm
16	*Helichrysum candolleanum* H. Buek
17	*Hermannia tomentosa* (Turcz.) Schinz ex Engl
18	*Indet (Species J)*
19	*Laggera decurrens* (Vahl) Hepper & J.R.I. Wood
20	*Lycium bosciifolium* Schinz
21	*Lycium eenii* S. Moore
22	*Lycium villosum* Schinz
23	*Melinis repens* (Willd.) Zizka subsp. *repens*
24	*Mollugo cerviana* (L.) Ser. ex DC
25	*Monandrus squarrosus* (L.) Vorster ined.
26	*Nidorella resedifolia* DC. subsp. *resedifolia*
27	*Ocimum americanum* L. var. *americanum*
28	*Pechuel-Loeschea leubnitziae* (Kuntze) O.Hoffm
29	*Pergularia daemia* (Forssk.) Chiov. var. *leiocarpa*
30	*Pogonarthria fleckii* (Hack.) Hack
31	*Pollichia campestris* Aiton
32	*Prosopis sp*
33	*Schimdtia kalahariensis* Stent.
34	*Sesamum capense* Burm.F.
35	*Setaria verticillata* (L.) P.Beauv
36	*Solanum capense L*
37	*Sporobolus fimbriatus* (Trin.) Nees

38	*Tribulus zeyheri* Sond. subsp. *Zeyheri*
39	*Urochloa oligotricha* (Fig. & De Not.) Henrard
40	*Ziziphus mucronata* Willd

Appendix 3. Photographic depictions of herbivory, fire and woodharvest damage assessment scales.

Damage	Herbivory	Fire	Woodharvest
1= Mild			
2= Moderate			
3= Serious			

Appendix 4. Grass and forb species list with ranking, 1 indicating the most dominant species, 2 less dominant and 3 least dominant.

Species	**Rank 1**	**Rank 2**	**Rank 3**	**Frequency of occurrence**	Pi 1	%	Pi 2	%	Pi 3	%
Sporobolus fimbriatus	13	6	2	52.5	0.619	61.90	0.286	28.57	0.095	9.52
Bidens biternata	0	11	8	47.5	0.000	0.00	0.579	57.89	0.421	42.11
Tribulus zeyheri subsp. zeyheri	2	3	2	17.5	0.286	28.57	0.429	42.86	0.286	28.57
Commelina benghalensis	1	6	6	32.5	0.077	7.69	0.462	46.15	0.462	46.15
Urochloa oligotricha	6	2	2	25	0.600	60.00	0.200	20.00	0.200	20.00
Nidorella resedifolia subsp. resedifolia	7	3	1	27.5	0.636	63.64	0.273	27.27	0.091	9.09
Schimdtia kalahariensis	3	1	3	17.5	0.429	42.86	0.143	14.29	0.429	42.86
Bulbostylis densa	1	2	3	15	0.167	16.67	0.333	33.33	0.500	50.00
Sesamum capense	0	2	0	5	0.000	0.00	1.000	100.00	0.000	0.00
Monandrus squarrosus	1	0	0	2.5	1.000	100.00	0.000	0.00	0.000	0.00
Pollichia campestris	1	0	1	5	0.500	50.00	0.000	0.03	0.500	50.00
Mollugo cerviana	0	1	1	5	0.000	0.00	0.500	50.00	0.500	50.00
Dactyloctenium aegyptium	0	1	0	2.5	0.000	0.00	1.000	100.00	0.000	0.00
Pogonarthria fleckii	1	0	0	2.5	1.000	100.00	0.000	0.00	0.000	0.00
Cenchrus ciliaris	0	0	1	2.5	0.000	0.00	0.000	0.40	1.000	100.00
Eragrostis tricophora	1	0	0	2.5	1.000	100.00	0.000	0.00	0.000	0.00
Laggera decurrens	0	0	1	2.5	0.000	0.00	0.000	0.00	1.000	100.00
Chenopodium amboanum	2	0	0	5	1.000	100.00	0.000	0.00	0.000	0.00
Helichrysum candolleanum	1	0	1	5	0.500	50.00	0.000	0.00	0.500	50.00
Geigeria ornativa	0	1	0	2.5	0.000	0.00	1.000	100.00	0.000	0.00
S. verticulata	0	0	1	2.5	0.000	0.00	0.000	0.00	1.000	100.00
Ocimum americanum var. americanum	0	1	1	5	0.000	0.00	0.500	50.00	0.500	50.00
Hermannia tomentosa	0	0	1	2.5	0.000	0.00	0.000	0.00	1.000	100.0