THE EFFECTS OF NEIGHBOR, DISTANCE, AND ORGANIC FERTILIZER ON THE ESTABLISHMENT AND EARLY PERFORMANCE OF THREE WOODY SPECIES IN A RESTORATION TRIAL IN THE KUNENE REGION, NAMIBIA

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ABSTRACT

Land degradation poses a significant challenge in arid ecosystems across Africa, adversely affecting the livelihoods of many who depend on the environment. It has become an urgent priority to restore these ecosystems. While various restoration approaches have been studied globally, few have explicitly considered how neighboring plant species and plant spacing as well as organic fertilizer influence restoration outcomes. This study evaluated the effects of neighbor identity, planting distance, and organic fertilizer on the growth, survival, and leaf traits of three woody species – *Vachellia erioloba*, *Colophospermum mopane*, and *Combretum imberbe*. Experiments were conducted in outdoor and indoor environments using a "two-factor (2x9) complete randomized factorial design" with nine neighbor combinations and two levels of distance/fertilizer. Results from field experiments showed that neighbor effects varied by species. *C. imberbe* experienced improved stem length and biomass when paired with *V. erioloba*, while *C. mopane* had reduced survival when grown with *V. erioloba* at close spacing. Leaf nitrogen and surface area were generally lower when species were paired with heterospecific neighbors, with *V. erioloba* exerting the strongest influence. Wider spacing (1 m) enhanced growth and leaf traits for most species, although the impact on survival and nutrient uptake varied depending on species. In the greenhouse, manure produced mixed results, enhancing leaf traits for *C. imberbe* and *V. erioloba* when grown alone or with conspecifics, but reducing growth and survival in the presence of heterospecific neighbors. Recruitment of native species was positively associated with *C. mopane* and *C. imberbe*, especially under 1 m spacing, while *V. erioloba* showed a negative association. These findings could inform future revegetation initiatives and help design planting strategies that enhance target species performance in restoration.

Key words: Land degradation, Ecological restoration, Plant interactions, Neighbors, Distance, Fertilizer, woody species.

LIST OF CONFERENCES

1. Conference presentation: Future Rural Africa- Collaborative Research Centre TRR 228 (CRC)

- Research project proposal and preliminary results (23 September, 2022)
- Affiliation: University of Namibia

2. Conference presentation: Integrated Landscape Management National conference (ILM)

- Affiliation: NILALEG in partnership with International University of Management (IUM)

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DEDICATION

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DECLARATION

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Soini N. Akomena

1. INTRODUCTION

1.1. Background of the study

Land degradation is one of the escalating global challenges and has emerged as a major environmental issue worldwide (Ziadat et al., 2022; Prince et al., 2018). According to Nkonya et al. (2016), immediate interventions are imperative. Protecting and managing ecosystems sustainably is essential, but restoring degraded ecosystems is equally critical. Land degradation is broadly defined as the reduction in the biological productivity of land (Stavi and Rattan, 2015), encompassing declines in the productivity and complexity of forests, rangelands, croplands, and woodlands due to both natural processes and human activities (Kapalanga, 2008). It typically manifests through vegetation loss, soil erosion, and contamination.

Globally, multiple drivers contribute to degradation, including natural factors such as drought, climatic variability, and insect pests, as well as human-induced causes such as soil erosion, salinization, deforestation, overgrazing, and invasive species (Global Environment Facility, 2021; Imbaba, 2005). In sub-Saharan Africa, the impacts are particularly severe because most rural communities depend directly on natural resources for survival (Stocking, 2002). The IPCC (2007) highlights that Africa’s low adaptive capacity makes habitat degradation especially devastating, resulting in reduced agricultural productivity, water scarcity, and increased flooding (Imbaba, 2005).

Namibia, one of the driest sub-Saharan countries, is highly vulnerable to land degradation and climate change due to its arid nature (Wilhelm, 2012). Drylands, which cover most of the country, degrade easily and recover very slowly (Ndunge, 2018). Climate projections predict increasingly frequent and severe droughts (Mapaure, 2011), further intensifying existing vulnerabilities in rural and already degraded regions (Inman, 2020). In northern Namibia, degradation has steadily increased due to climatic variability, overstocking, overgrazing, deforestation, and soil erosion (Imbamba, 2005; Shanyengana, 1994). The Kunene Region is particularly affected, with unreliable rainfall, high evaporation rates (up to 80% of rainfall lost shortly after precipitation), and visible degradation in the form of bare soils, gullies, and invasive species such as Pechuel-loeschea leubnitziae (Imbamba, 2005; ILMI, 2019; Inman et al., 2020a).

These processes reduce rangeland productivity, vegetation cover, and biomass (Seware, 2015), threatening forage availability, crop yields, and rural livelihoods (Ndunge, 2018). Most rural households depend on subsistence farming, so land degradation directly undermines socio-economic stability and well-being. Consequences include food insecurity, declining agricultural production, fuelwood scarcity, and reduced quality of life (Imbaba, 2005; National Planning Commission, 2015; Hengari, 2018). At the global level, major frameworks such as the UN Decade on Ecosystem Restoration, the Bonn Challenge, the CBD, UNCCD, and UNFCCC have spurred commitments to restore over one billion hectares of degraded land (Sewell et al., 2020; UNEP, 2021). These initiatives emphasize restoration as a pathway to address land degradation, biodiversity loss, and climate change. In Africa, initiatives like the Great Green Wall demonstrate both successes and challenges, underscoring the need for context-specific research in arid and semi-arid regions.

Ecological restoration is therefore crucial for Namibia. Restoration success depends not only on species selection but also on ecological processes such as plant–plant interactions, seedling spacing, and soil fertility (Brooker, 2006; Gomez-Aparicio, 2009; Shackelford et al., 2021). Plant–plant interactions can be facilitative or competitive, influenced by environmental stress, distance, and species identity (Bertness and Callaway, 1994; Ndunge, 2018). Yet, few studies in Namibia have examined interactions among woody species during early development stages, despite their importance in restoration outcomes (Gomez-Aparicio, 2009; Inman et al., 2020).

Soil fertility is another overlooked factor in restoration. Namibian soils are nutrient-poor, particularly in Kunene (Hengari, 2018). Organic fertilizers such as goat manure improve soil structure, water retention, microbial activity, and nutrient cycling, but responses are often species-specific (Liu et al., 2011; Reganold and Wachter, 2016; Lori et al., 2017). Evaluating how organic amendments interact with plant–plant interactions is therefore vital for restoration planning. In this context, assessing the effects of neighbors (conspecific and heterospecific), distance, and organic fertilizer on the growth, survival, and leaf traits of native woody seedlings provides insights essential for restoring Namibia's degraded rangelands.

1.2. Statement of the problem

Namibia is a semi-arid country, and the rainfall patterns have been inconsistent in the recent past (Kapuka and Hlasny, 2020). In addition, droughts have become increasingly common in Namibia due to climate change (Thomson, 2021). The Kunene region is one of the impacted areas in Namibia, having experienced more than a decade of drought in a row (Inman et al., 2020a). Apart from that, there is an increased grazing pressure on the rangelands, which has resulted in rangeland degradation (National Planning Commission, 2015). This has affected the livelihoods of the inhabitants of the Kunene region, who are primarily pastoralists (Eisold, 2009; Inman et al., 2020a). The decade-long drought has culminated into a severe reduction of vegetation cover and biomass, resulting in the loss of livestock and forcing many people into poverty. With the region categorised as the most severely degraded (Eisold, 2009), and one of the poorest in the country (National Planning Commission, 2015), there is an urgent need to mitigate these challenges, and one of the strategies can be through ecological restoration. Though many restoration approaches (i.e., revegetation) have been studied globally, few have incorporated plant-plant interactions, such as using facilitation-based experiments to restore degraded habitats, necessitating the need to carry out these studies, especially in challenging environments such as the drylands of Namibia. Similarly, soil enrichment using organic fertilizers remains underutilized, especially in drylands, despite its potential to improve soil conditions and support seedling establishment. Moreover, post-planting monitoring rarely tracks the natural influx of woody seedlings around experimental plots, leaving a critical knowledge gap as to whether restored sites can generate their own next cohort of native trees. These gaps necessitate integrated studies that combine neighbor, spacing, and soil fertility effects, particularly in challenging environments like Namibia’s drylands.

1.3. Research objectives

The main objective of this study was to assess the effect of neighboring woody seedlings (conspecific and heterospecific), distance between seedlings, and fertilizer treatments on the early-stage (first 8-10 months of seedling development) performance (growth, survival, and leaf traits) of three target species; *Combretum imberbe, Vachellia erioloba,* and *Colophospermum mopane* in a restoration trial in the Kunene Region, Namibia.

Specific objectives:

1. To determine the effect of a conspecific and heterospecific neighbors on the (a) growth (biomass and stem length), (b) survival, (c) nitrogen and chlorophyll leafcontent, and (d) Surface Leaf Area of *Combretum imberbe*, *Vachellia erioloba*, and *Colophospermum mopane* (Field and Greenhouse experiment).

2. To determine the effect of distance between seedlings (conspecific or heterospecific neighbors) on the (a) growth (biomass and stem length), (b) survival, (c) nitrogen and chlorophyll leaf content, and (d) Surface Leaf Area of *Combretum imberbe*, *Vachelliaerioloba*, and *Colophospermum mopane* (Field experiment).

3. To determine the effect of fertilizer on the (a) growth (biomass and stem length), (b) survival, (c) nitrogen and chlorophyll leaf content, and (d) Surface Leaf Area of *Combretum imberbe*, *Vachellia erioloba*, and *Colophospermum mopane* (Greenhouse experiment).

4. To determine whether the neighbour-identity and distance treatments also promote natural woody regeneration, by measuring the species richness and abundance of spontaneously recruited seedlings.

1.4. Significance of the study

The successful restoration of degraded lands is affected by low rates of seedling establishment, particularly in regions with high abiotic stress. A possible tool to overcome high rates of seedling mortality in the restoration of these lands is using plant-plant interactions to ensure revegetation success, especially in stressful environments such as arid and semi-arid habitats. For example, understanding how neighbor and distance influence the growth and survival of selected woody species will aid in selecting suitable species for restoration and optimising their spatial arrangement. It will also give information on which species are good facilitators. This study will contribute important information on the facilitation and competitive abilities of the selected species. The study will also contribute to the body of scientific knowledge related to ecological interactions and vegetation dynamics in restoration ecology. This information will be useful in future revegetation initiatives in the region, and it will determine if and how the target species, all valuable to the local communities, can be used together in the restoration of degraded areas based on their performance when grown under the aforementioned treatment combinations. This study will further contribute to understanding the role of plant interactions in ecological restoration for future projects.

1.5. Delimitations of the study

The study focused on a specific location in Kunene region, which allowed the researcher to tailor the assessment to the unique characteristics and circumstances of the chosen location. There was also a temporal delimitation, the study was set for only 8 months to focus on seedling early stage performances. In addition, the study was limited to three local species in order to target data collection efforts and draw more precise conclusions about the characteristics of the target species. Furthermore, the delimitations also extend to the variables being studied, where the study delimited its scope to only consider neighbor, distance and fertilizer factors.

2. LITERATURE REVIEW

2.1 Drivers of land degradation

Land degradation and biodiversity loss are driven by a combination of direct and indirect factors that vary across ecosystems. Direct drivers include land-use change, overexploitation, pollution, invasive species, and climate change (IPBES, 2019). These are reinforced by demographic and economic indirect drivers such as population growth, globalized consumption patterns, and unsustainable development models. Among the direct drivers, unsustainable agricultural expansion, forestry, and urbanization have been identified as particularly significant contributors to the global decline in land quality (IPBES, 2018).

Globally, climate change interacts with land degradation and aggreviates other environmental stressors. According to Webb et al. (2017), the interactions between climate change and land degradation present a dual threat to ecosystems and human well-being. For instance, land degradation contributes to climate change through deforestation and the emission of greenhouse gases, particularly through the release of carbon previously stored in vegetation and soils (Hermans and McLeman, 2021). Between 2000 and 2009, an estimated 4.4 billion tonnes of CO_2 were emitted annually due to land degradation, illustrating the scale of the problem (Olsson et al., 2019).

While these patterns are evident worldwide, their impacts are often more acute in regions like sub-Saharan Africa. Here, the high dependency of rural populations on natural resources for agriculture, fuel, and livestock rearing increases their vulnerability (IPBES, 2019; Stocking, 2002). In such socio-ecological contexts, degradation not only undermines biodiversity but also threatens food security, water access, and livelihoods. Fawzy et al, (2020) emphasized that reversing land degradation can be one of the most cost-effective strategies for mitigating greenhouse gas emissions and achieving the global target of limiting temperature increases to below 2°C, as outlined in the Paris Agreement. Consequently, understanding global drivers in relation to regional contexts such as Africa’s vulnerability due to limited adaptive capacity; nesseciates the need for targeted, regionally informed ecological restoration interventions.

2.2. Possible solutions to Land degradation: Ecological restoration

Ecological restoration has emerged as a key response to land degradation and biodiversity loss globally. It is broadly defined as the process of assisting the recovery of degraded, damaged, or destroyed ecosystems (Dickson et al., 2021). Restoration can enhance ecosystem services, promote biodiversity, and improve resilience to climate change (Bullock et al., 2011). It includes a continuum of practices, from reforestation and revegetation to natural regeneration, depending on local ecological and socio-economic contexts (Dickson et al., 2021). Restoration can range from enhancing modified ecosystems to restoring degraded landscapes to a more intact natural state (Waylen et al., 2024).

Elsewhere in Africa, the Great Green Wall initiative, which spans over 20 countries in the Sahel region, has demonstrated both successes and setbacks in tree planting for land restoration (Grossnickle and Macdonald, 2018). In many instances, poor survival of planted seedlings has been linked to the exclusion of ecological context; such as spacing, soil condition, or plant compatibilityin restoration design (Grossnickle and Macdonald, 2018). These gaps highlight the need for context-specific research that tests ecological hypotheses under realistic conditions. In particular, research assessing the roles of native woody species, the influence of conspecific and heterospecific interactions, and the impact of organic fertilization on early seedling establishment is scarce in Namibian drylands.

Apart from the assisted ecosystem recovery, natural regeneration is increasingly recognized as a cost-effective and ecologically sound restoration approach (Chazdon, 2017). Chazdon (2017) emphasizes that natural regeneration relies on ecological processes such as seed dispersal, germination, and biotic interactions to drive forest recovery with minimal human input. In addition, natural revegetation can result in more structurally complex and genetically diverse ecosystems than actively planted forests, provided that the area is protected from disturbance. Crouzeilles et al. (2017) found that natural regeneration consistently increased biodiversity, vegetation structure, and ecosystem function in tropical forests compared to active restoration. While natural regeneration has shown success in tropical forests, its application in dryland ecosystems remains under-explored..

2.3. Plant interactions and neighbor effects in Restoration Ecology

The subject of plant-plant interactions is considered crucial in the restoration of degraded arid environments (Bashirzadeh et al., 2022) because such interactions shape ecosystem structure and functioning and are useful in identifying processes hindering natural recovery after disturbance (Mendez et al., 2008). These interactions whether facilitative, competitive, or neutral can alter local resource availability, microclimate, and soil conditions (Brooker, 2006). Neighboring plants may improve survival and growth by buffering stressful conditions or, conversely, suppress target species through competition (Brooker, 2006).

Although neighborhood effects have long been recognized in restoration literature (e.g., Galster et al., 2010; Graham, 2018; Maereg et al, 2024), few studies in Namibia and particularly in the Kunene Region; have assessed how neighbors and distance between seedlings influence seedling performance. Restoration experiments conducted in Namibia (e.g., Inman et al., 2020) often omit assessments of conspecific versus heterospecific effects, despite increasing global recognition of their significance. Despite documented evidence of neighbor effects globally (Filazzola et al., 2018), most studies target single interaction types (e.g., facilitation), mature plants (e.g., nurse trees), or herbaceous lifeforms. The specific case of woody-woody interactions during early life stages remains understudied, particularly in semi-arid environments where seedling establishment is a major bottleneck (Gomez-Aparizio, 2009; Barry and Dudash, 2015). Moreover, plant interactions are often studied under ideal or simplified conditions, rather than in field-based trials that reflect real-world ecological and spatial complexity.

Furthermore, while distance has been investigated in previous studies (Wettberg and Weiner, 2004; Jiang et al., 2013), results vary with species life form and stage. Evidence from Tyler and D’Antonio (1995) and Haque and Sakimin (2022) confirms that spacing influences survival and growth, yet these insights are rarely integrated into restoration practice in drylands. This study aims to fill these gaps by empirically testing how neighbor identity (conspecific vs. heterospecific) and distance between seedlings (0.5 m vs. 1 m) influence early-stage seedling performance of three native woody species. The study uniquely combines biomass, survival, and leaf trait responses under both field and greenhouse conditions, thus contributing context-specific insights essential for restoration planning in Namibia’s degraded rangelands.

In summary, the existing literature demonstrates that further exploration of plant interactions is needed, including critical examinations in both indoor and outdoor experiments. For instance, studying interactions in the open may not validate the true reflection of the target species responses. For example, a positive effect can take place between the nurse plant and target species, but ambient conditions such as rainfall, soil humidity, grazing intensity or microhabitat can influence the radiation, soil, temperature and moisture under the crown of the nurse plant, thereby changing the nursing effect and consequently the interaction nature (Ren et al., 2007). Moreover, there are limited field studies conducted to determine the role of plant-plant interactions in order to determine the local adaption of specific plant species (Lankau and Strauss 2007; Rice and Knapp 2008, cited by Ariza and Tielbörger (2011).

2.4. The influence of organic fertilizer on plant performances

Nutrient availability is a critical driver of plant growth, ecosystem productivity, and restoration outcomes (Manitoba, 2013). In Namibia, soils are characteristically nutrient-poor, with low organic carbon and high vulnerability to degradation, particularly in arid regions like Kunene (Hengari, 2018). The combination of poor soil fertility, salinity, high livestock pressure, and overexploitation of vegetation limits vegetation recovery and agricultural potential, reinforcing cycles of land degradation. The use of organic amendments such as manure is well-documented for agricultural systems (Padilla and Pugnaire, 2006), but its role in enhancing seedling performance and interacting with neighbor effects in ecological restoration has been largely overlooked (Liu et al., 2020). Although a few studies report positive effects of manure on growth and soil fertility, others highlight risks such as nutrient imbalances and species-specific responses, suggesting a need for more nuanced, context-specific trials (Kumar, 2012).

Organic fertilizers such as manure are locally available, affordable, and ecologically beneficial. They improve soil structure, water retention, and nutrient content; particularly nitrogen, through slow-release mechanisms (Bambhaneeya, 2023; Liu et al., 2020). These attributes make organic inputs a promising, sustainable option for ecological restoration in degraded drylands. However, species responses to organic inputs vary: some species thrive in nutrient-rich soils, while others may be negatively affected due to nutrient imbalances or altered competitive dynamics (Padilla and Pugnaire, 2006; Ren et al., 2007).

3. RESEARCH METHODS

3.1. Study area

3.1.1. Location

The study was conducted in Otjamaungu Village, in Epupa Constituency in Kunene Region. Kunene Region is located in north-western Namibia, bordering Angola in the north and the Atlantic Ocean to the west. The study village is situated 35 km from Ruacana hydro-power station and waterfall (NamPower, 2023). As introduced, the Kunene Region is one of the severely degraded regions in Namibia, with observable evidence of eroded areas with dongas or gullies, and abandoned fields with bare soils (Kunene Regional Development Profile, 2015).

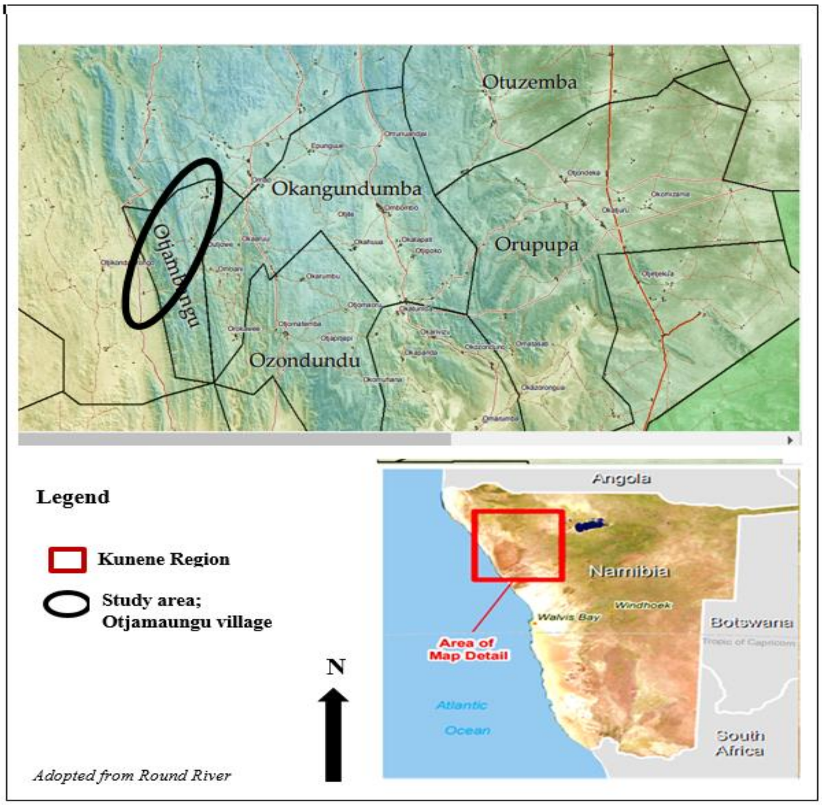

Figure 1 The location fo the study area. Otjamaungu village indicated on the upper map by a black circle and the map of Namibia showing the Kunene region (in red)(*adopted from Round River project, 2022*).

3.1.2. Climate

The region's climate is characterized by very high temperatures during summer, reaching up to 35 degrees, while during winter, the temperatures can range from an average of 5 to 26 degrees (Kunene Regional Development Profile, 2015). Annual rainfall is highly irregular, and ranges from 50 mm to 400 mm, with figures increasing from the Namib Desert in the west towards the eastern part of the region (Kunene Regional Development Profile, 2015; Schwieger et al., 2022). Furthermore, the region is susceptible to prolonged droughts which adversely affect the wildlife, livestock and inhabitant livelihoods (Inman, et al., 2020).

3.1.3. Water and Hydrological Resources

Water is the most limiting resource in many parts of Kunene region due to the landscapes' arid conditions. Even though the communities and wildlife in the region have evolved adaptations to the harsh conditions, they are heavily reliant upon the small percentage available to escape periods of drought. The water resources in the region is classified into natural (springs, seeps, or pools) or man-made (boreholes or wells). The natural sources are from the region's drainages, which provide a steady flow of ephemeral (below-ground) water throughout the year. This provides the needed water nutrients to support the large woody tree species, such as the Ana Tree and Camelthorn, that many of the native wildlife and people rely upon. The infrequent flash floods during the rainy season also create many temporary water pools that can remain for months in the rocky river beds (Shahin, 2022).

3.1.4. Geology and soils

The region comprises various ecosystems from desert to the west and mopane savannah to the east, with mountain ranges to the north near the Kunene River, which forms an international boundary with Angola; however, most northern parts of Kunene are largely mountainous (Dieckmann, 2014). The Kunene represents an incredible amount of geological diversity that supports diverse vegetation communities and landscapes. Rocky slopes and the low-lying flats provide vital grazing and calving areas for the region's wide ranging game species (Mendelsohn, 2012). The soils in the landscape area are mainly described as stony to loamy sand, characterised by low organic matter content, and their depth varies from shallow to deep (Clarke, 2021).

3.1.5. Flora

The region is reported to have endemic plants (Burke, 2003). The most abundant species, mopane species, forms a woodland savannah, with a variety of other common species in the area, such as *Catophractes alexandri, Terminalia prunioides, Boscia foetida, Commiphora glaucescens, Ziziphus mucronata, Diospyros mespiloformis, Combretum imberbe, Vachellia erioloba, Faidherbia albida, Ximenia americana,* etc. There are some succulent euphorbia species in the area such as the *virosa, damarana* and *mauritanica* species (personal observations, 2022). Furthermore, the dominant grasses in the area include; *Anthephora pubescens, Anthephora schinzi, Aristida adscensionis, Enneapogon desvauxi, Chloris virgata, Stipagrostis ciliata, Schmidtia pappophoroides, Stipagrostis uniplumis,* etc. (Eisold, 2010; Klaassen and Craven, 2003).

3.1.6. Fauna

The escarpment zone of Kunene, a narrow north-south band of rugged mountains and hills, has been categorized as a hotspot for endemic birds (Jarvis and Robertson, 1999) and reptiles (Griffin, 1998). This region was promoted for its contribution to Namibia's overall biodiversity goals (Bernard, 1998). Many species found in the area are classified as threatened, endangered, or endemic in Namibia's Red Data Books (Lendelvo, Sullivan, and Dieckmann, 2024). In addition to birds and reptiles, the region also supports a variety of mammalian species. Commonly observed wildlife includes Hartmann's mountain zebra (*Equus zebra hartmannae*), springbok (*Antidorcas marsupialis*), oryx (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*), and baboons (*Papio ursinus*) (Lendelvo, et al., 2024). Predators such as black-backed jackals (*Canis mesomelas*) and occasionally leopards (*Panthera pardus*) are also present. Smaller mammals like rock dassies and various rodents are widespread.

3.2. Study species

Three locally occurring woody species; *Combretum imberbe (*Combretaceae*)***,** *Vachellia erioloba* (Fabaceae), and *Colophospermum mopane* (Leguminasae-Caesalpinioideae) were used. The biology and identification of target species are detailed below:

3.2.1. *Combretum imberbe* Wawra.

C. imberbe belongs to the Combretaceae family and is commonly known as Leadwood. The magnificent Leadwood is a medium to large, semi-deciduous tree which grows up to 20 m in height. It is regarded as a slow-growing species. This is one of the protected trees in southern Africa. *C. imberbe* is widespread in Northern Namibia (Mannheimer and Curtis, 2018). The presence of Leadwood in some areas can indicate to farmers that the grazing is good, and provide nesting sites for birds (Mtsweni, 2006). It is fairly drought resistant but could be damaged by frost (Mtsweni, 2006). It occurs in various habitats but mostly along dry rivers and on plains. It grows in sand, loam, calcrete, stony and rarely on rocky areas (Van Wyk and Gericke, 2000).

C. imberbe has many medicinal properties; the smoke from burning leaves relieves coughs, colds and chest complaints, leaves are believed to have magical powers, and roots are prepared as a decoction to treat diarrhoea and stomach pains (Mtsweni, 2006). The ash is traditionally used as toothpaste. Moreover, Leadwood is known for its hard and tough wood which is used to build houses, furniture, fencing, tools, charcoal, etc. The trees also have good shade, and the branches provide food for game and livestock (Mtsweni, 2006).

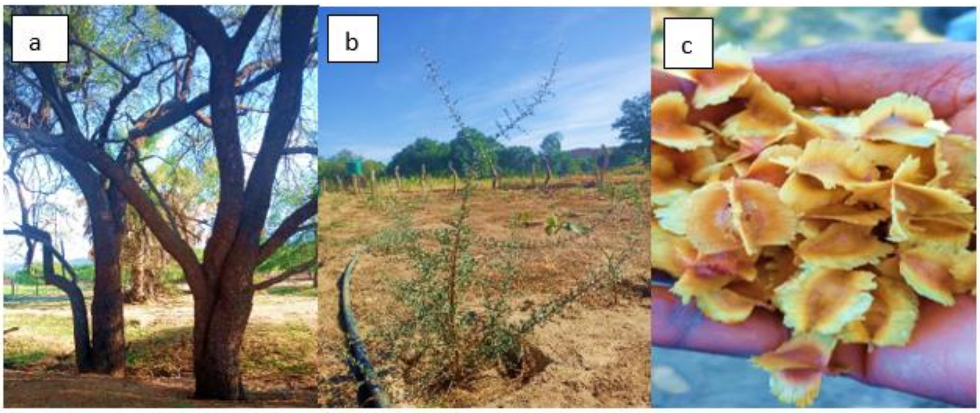

Figure 2(a) Mature *C. imberbe* trees (in the field), (b) *C. imberbe* seedlings (from current study), and (c) *C. imberbe* seeds.

3.2.2. *Vachellia erioloba* (Meyer), Camel thorn

Vachellia erioloba, previously known as *Acacia erioloba*, belongs to the Fabaceae family (Toivo, 2021). It is native to Africa; in Namibia, it occurs throughout the country. The camel thorn (common name) is a single stemmed evergreen tree that grows up to 12 m in height with a canopy diameter of 22 m (Hassan and Hamdy, 2021). It has ecological values of erosion control and acts as an indicator of groundwater. It also improves soil quality by providing Nitrogen (*V. erioloba* is a Nitrogen fixer). This species has deep taproots that penetrate soil to great depths (more than 45 m) to obtain water (Merwe et al., 2019). The wood is resistant to termites (personal communication: local community, 2022).

The camel thorn is a pioneer species that thrive in various habitats; woodland, hillsides/slopes, grassland, and floodplains. The altitude ranges from 120-1675 m asl. It can grow in rocky gravels/stony areas, alluvial soils, sandy, clayey, and dry soils. However, on rocky outcrops in Namibia, it grows mainly as shrubs of 1 - 3 m high. *V. erioloba* is adapted to aridity conditions, dry seasons, frost tolerant, and desert environmental conditions such as scarcity of water, extreme temperatures and nitrogen-poor soil (Mannheimer and Curtis, 2018). It thrives in areas with annual rainfall ranging from 40-900 mm.

V. erioloba provides food, medicine, shelter, and niches for many animals and harbours plant species below the canopy (Seymour, 2008; Seymour and Milton, 2003). Both wild and domestic animals browse the leaves, flowers, young shoots and pods which are highly nutritious. In Namibia, it is regarded as excellent firewood because it burns slowly and provides hot coals (Dlamini, 2005). The pods are heated to treat embers and swellings, while roots heal heart ailments. There is an increase in quantities of firewood and charcoal imported into South Africa from Namibia, which has a potential danger of over-exploiting the resource; hence it is protected by the Forestry Ordinance.

Figure 3 *V. erioloba* seedling (Obtained from study site).

3.2.3. *Colophospermum mopane* (kirk ex Benth). Kirk ex J. Leonard

C. mopane (butterfly tree) is a Leguminous species in a subfamily of Caesalpinioideae. The butterfly/mopane tree grows in hot, dry, low-lying areas in the far northern parts of southern Africa (Makhado, Potgieter, and Luus-Powell, 2018). It is one of the dominant and valuable species in the Kunene region, known for its termite-proof timber, which is good for fencing and firewood (Mapaure, 1994), medicinal properties, and animal fodder. In Namibia, mopane stretches southwards from the Kunene River towards the Ugab and North-eastwards towards Namutoni. It is found in a variety of soil types, however, its distribution is more influenced by rainfall, with short shrubs found in areas of less than 100 mm and tall trees in 500-600 mm or along rivers (Teshirogi et al., 2017). It prefers well-drained soil, though it can tolerate some water logging. It is very drought resistant and adapted to tolerate water stress and high temperature conditions (Makhado et al., 2018).

Seeds are removed from ripe pods to speed up the germination and best sown in river sand. *C. mopane* is commonly associated with *Terminalia prunoides, Combretum* *imberbe, Ximenia americana, Berchemia discolor, Acacia reficiens, Boscia foetida, Catophractes aexandrii, Commiphora sp*., etc. (Teshirogi et al., 2017).

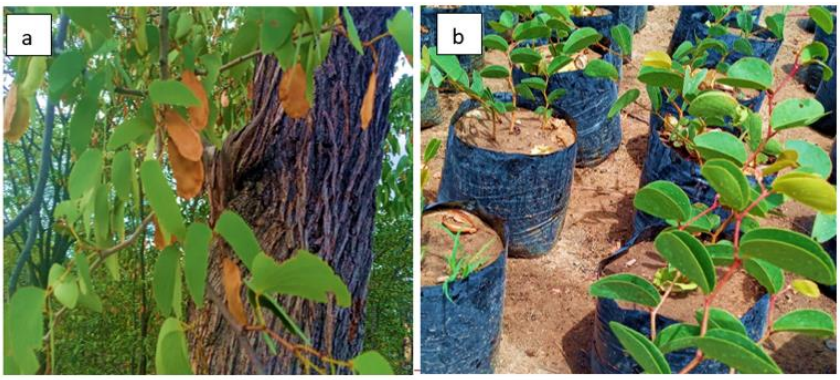

Figure 4. (a) Mature *C. mopane* tree with seeds and (b) mopane seedlings from the study.

3.3. Research design

3.3.1. Overview

To increase the reliability of the findings, the study conducted two experiments concurrently; a greenhouse experiment and an outdoor/common garden experiment to test the effects of distance, neighbor, and fertiliser on the performance of selected species. The study employed a “two-factor (2x9) complete randomised factorial design” in each experiment (greenhouse and field). The treatments included nine neighbor levels (single individuals- alone standing, conspecific neighbors, and heterospecific neighbors of *Combretum imberbe, Vachellia erioloba,* and *Colophospermum mopane*) and two levels of distance (50 cm or 1 m between neighbors) for the field experiment. The treatments for the greenhouse experiment included nine neighbor levels and two levels of fertilizer treatment (With and Without fertilizer). Each experiment is detailed below.

3.3.2. Outdoor/common garden experiment

In this experiment, two levels of distance treatment were crossed with nine neighbor treatments (Fig. 3.5). Three replicate blocks for distance 1 and distance 2, were demarcated respectively (Fig. 3.5). Each neighbor treatment (nine neighbor levels) was replicated 5 times in each block, and so for each treatment there were 15 observations in total. A distance of 2 meters was left between the blocks (Fig. 3.5). Each neighbor treatment was demarcated in a mini plot of 1 m ×1.5 m, and these were kept at 1.5 m apart in each block. The mini-plots were arranged in 9 rows and 5 columns to form a block, and these were randomised across the block, as illustrated in Fig. 3.5. A mesh fence was placed over the experimental site to exclude livestock.

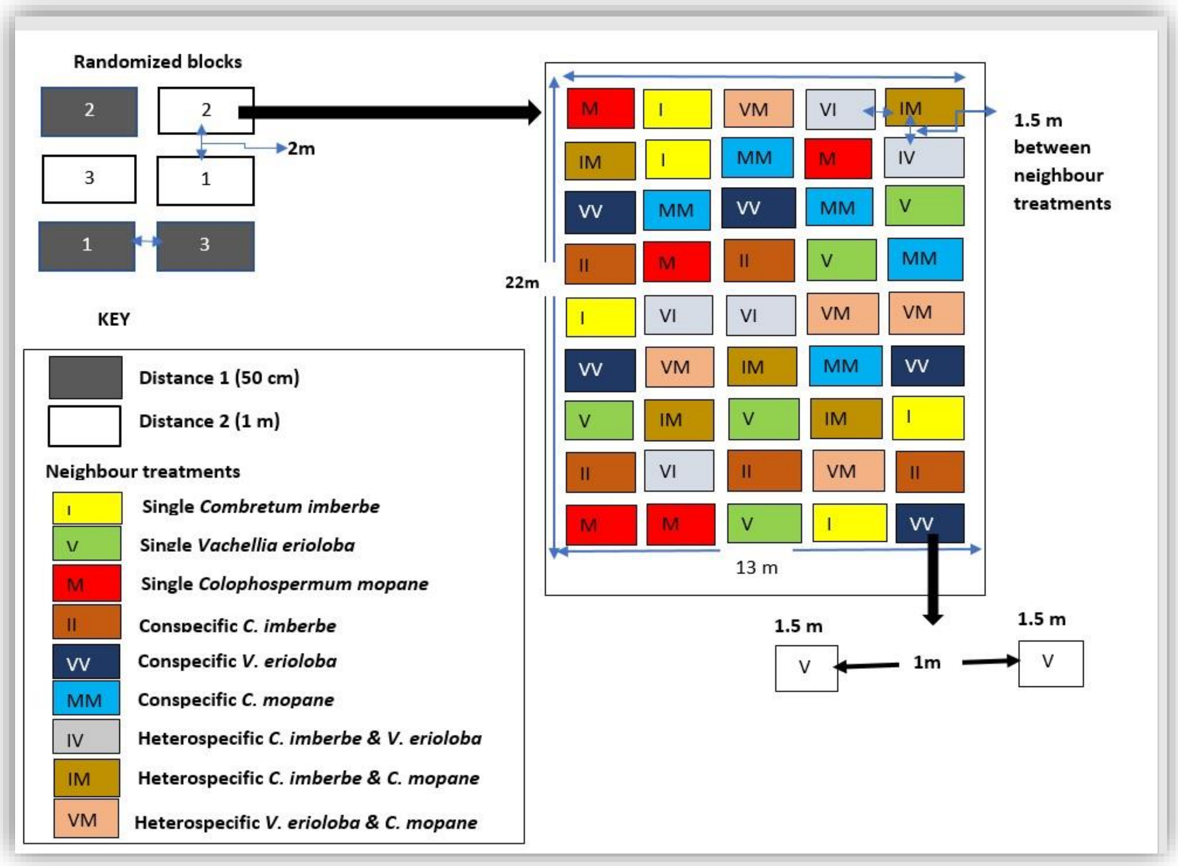

Figure 5 Field Experimental design (common garden) to study neighbor and distance effect on target species in a degraded area in Kunene Region.

3.3.3. Indoor/greenhouse experiment

For the greenhouse experiment, two greenhouses of 2m by 3m were used. There were 3 blocks (1.8 m by 0.80 m) in each greenhouse, randomly arranged in three layers on a concrete floor. Each neighbor treatment (single individuals, conspecific neighbors, and heterospecific neighbor) was replicated 5 times in each block, randomised in 5 columns and 9 rows as illustrated in Fig 2. Each neighbor treatment was allocated to one polythene pot (21 cm diameter), and the pots were kept at 10 cm apart. The seedling pots were placed in fixed positions for the duration of the experiment (Hartung et al., 2019). Iron sheets were added to the floor to prevent root penetration into the ground.

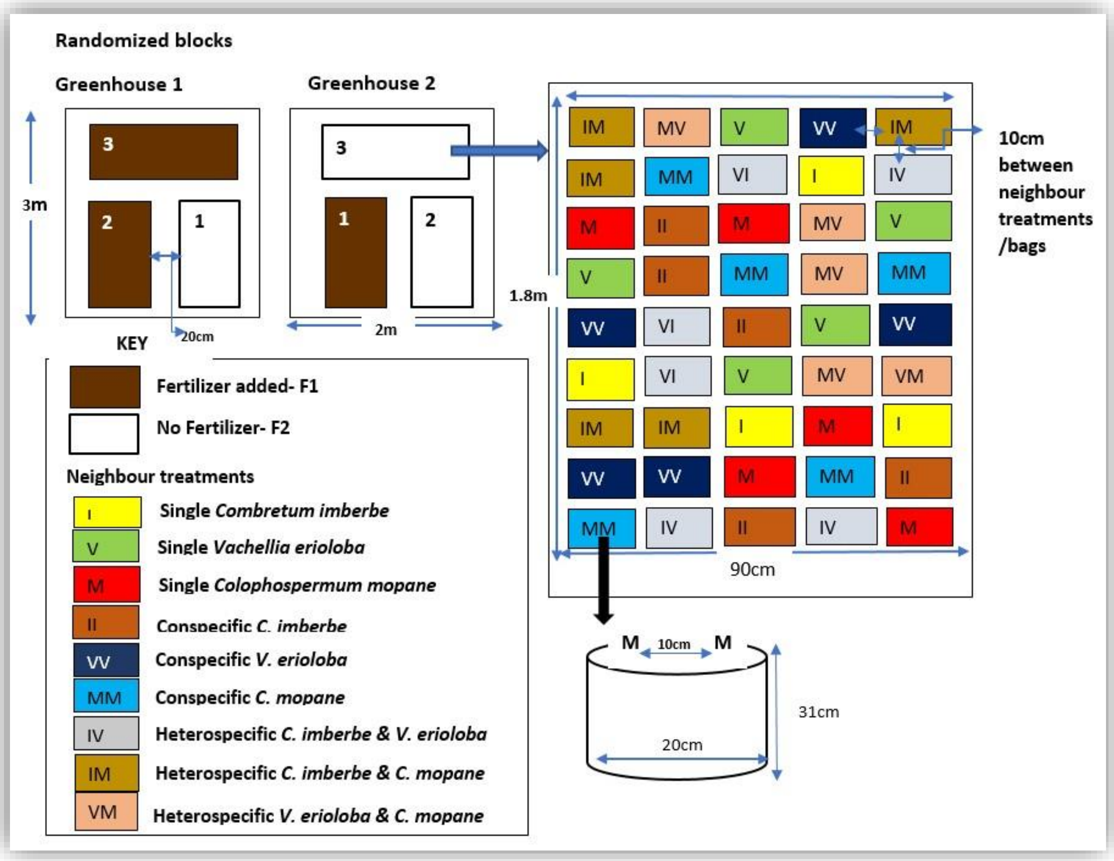

Figure 6 Greenhouse Experimental design to study neighbor and fertilizer effect on target species in a degraded area in Kunene Region.

3.4. Seed collection, seed treatment and germination

Seeds of *Combretum imberbe, Vachellia erioloba*, and *Colophospermum mopane* were collected by hand from branches or from the ground in Otjamaungu village and the surrounding areas. The seeds were tested for viability by picking out the infested seeds and those that floated in the water test. The seed pretreatment methods applied in this study were selected based on the seed coat structure and dormancy mechanisms of each species. *Vachellia erioloba* seeds have a hard, impermeable testa that imposes physical dormancy; therefore, concentrated sulphuric acid scarification has been widely used to enhance germination by softening the seed coat (Tybirk, 1993; Dlamini and Boatwright, 2019). In contrast, *Colophospermum mopane* seeds possess a semi-permeable seed coat that responds well to warm water soaking, which improves germination rates (Nekongo, Kwembeya and Chinsembu, 2020). For *Combretum imberbe*, which has seeds enclosed in a woody pericarp, manual removal is necessary. However, it was discovered during the process that steaming the seeds or enclosing them in a zipped plastic bag exposed to the sun helps soften the outer layer and facilitate safe coat removal. These methods were selected to maximize germination success while minimizing seed damage.

Sowing was carried out from early October 2022 until early December 2022. Seeds were germinated in 13 cm deep polythene bags. For sowing, the polythene bags were filled with a combination of soil from the experimental site and sand soil. The ratio of 50% of soil from the experimental site to 50% sand soil was mixed before filling the bags. To enhance the chances of germination, four seeds were planted per bag. The polythene bags were placed in their respective experimental settings from onset; outside and in a greenhouse.

3.5. Site preparation and greenhouse soil preparation

In the field experiment, the field was prepared before transplanting the seedlings. This involved clearing the area of any debris, weeds, or other unwanted vegetation that may compete with the seedlings for nutrients and water. Next, the seedling holes were dug at appropriate intervals and depths according to the specified design (depth of 0.5 m and size of 0.5 m by 0.4 m).

The soil from the experimental site (loamy-silt) and river sand was used for transplanting in the greenhouse. The same soil mixture was used for both fertilized and non-fertilized treatments in the following; ratio of 50% soil from the experimental site and sand: 50% river sand. A ration of 20% goat manure was added to the fertilized blocks, as adopted from a common procedure (Mupambwa et al., 2024). A wheelbarrow was utilized to ration the amount of soil mixture, derived from the volume of plastic bags to be used in the study (33cmx21cm). One wheelbarrow was filled up by a total number of nine full plastic bags. Fifteen wheelbarrows were required per treatment to fill 135 bags. Furthermore, the manure was crushed with a traditional pounding stick “omushi” to get close to a consistent mixture. The soil treatments were initially mixed by smaller portions (i.e. two wheelbarrows at a time), and later on mixing the smaller portions with each other, on a hard cleaned surface.

3.6. Seedling transplanting

In the field experiment, the seedlings were watered thoroughly to reduce transplant shock. The seedlings were also carefully handled to avoid damaging their delicate roots and shoots. After placing the seedlings in the holes, they were gently covered with soil and tamped down to ensure good soil-to-root contact. The seedlings were watered again after transplanting to help them settle into their new environment and support root establishment.

In the greenhouse experiment, seedlings were carefully removed from their original growing bags, taking care not to damage the roots. Each seedling was gently placed into their respective plastic bags as per the design, ensuring that the roots were spread out and not cramped within the bag. The seedlings were positioned at the appropriate depth and distance within the plastic bag, with neighbor pairs spaced at 10cm.

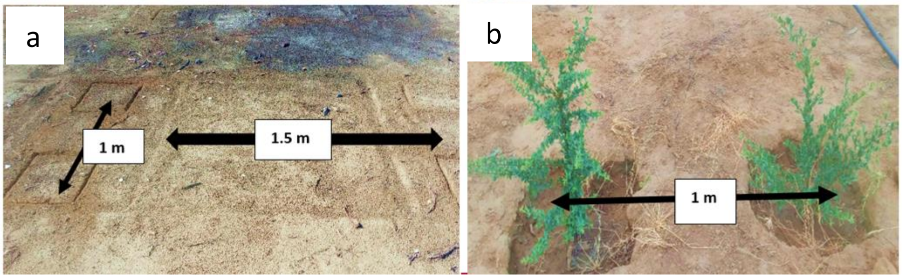

Figure 7 Field experimental plots (a) 1.5 m distance between neighbor pairs and (b) example of a transplanted conspecific pair of *C. imberbe* at 1 m distance interval treatment.

Figure 8 Greenhouse experimental bags (a) transplanting neighbor pairs in a plastic bag with 10cm between seedlings and (b) example of a transplanted seedlings in the greenhouse experimental block.

3.7. Monitoring and Data collection

3.7.1. Monitoring

Seedlings in the outdoor experiment were hand watered with low pressure 20 mm pipes, while seedlings in the greenhouse were watered with a sprinkler irrigation system for 8 months. No water was applied for the outdoor experiment if it had rained in the previous 24 hours. The watering was progressively reduced; every two days, once a week, after 2 weeks, once a month, and then eventually the plants were left to strive on their own. Each watering intensity period lasted for about two months. The data was recorded monthly, for 8 months.

3.7.2. Data collection

Seedling growth was assessed by measuring seedling height (from the stem base at ground level to the highest point of the central branch), cumulative stem length (the combined length of all branches), and diameter at the root collar using a ruler. Additionally, seedling survival was also determined by counting the number of surviving seedlings in each treatment at every monitoring session. Furthermore, Nitrogen content and Surface Leaf Area was measured at the end of the study using the Chlorophyll SPAD meter and Leaf Area software application, respectively. An average reading of five simple leaves per seedling sample was used to determine seedling's nitrogen content. A leaflet was used to measure Nitrogen content for species with smaller leaves, in order to maximize the chances of leaf detection (i.e. *V. erioloba*). Moreover, seedling recruitment was recorded in the field experiment. Species richness, abundance, and composition of all the self-recruited woody plants were recorded at every monitoring session. The blocks were weeded to avoid the accumulation of herbaceous cover, which may affect the study of woody interactions.

3.8. Data processing and analysis

Seedling biomass was determined using a non-destructive method, Allometric equations, by estimating biomass from seedling measurements such as diameter at root crown (DRC), plant height, and cumulative stem length (Amadhila, 2012; Beets et al., 2012; Henry et al., 2011; Condit, 2008; Kuyah, et al., 2012, Voster, and Evangelista, 2020). In addition, the recorded seedling survival was converted to percentage proportions (number of seedlings at each monitoring session/initial number of seedlings per treatment *100). The growth (biomass and cumulative stem length), survival, nitrogen leaf content, and Surface Leaf Area data was tested for normality using Shapiro Wilk test and skewness in R, and the skewed data was then log-transformed (log10) prior to the GLM analysis.

3.8.1. Estimation of Biomass

The biomass estimation method used for this study was adapted from Brown (1997), where general equations applicable to tropical dry ecological zones were used. The Above-ground biomass (AGB) and Below-ground biomass (BGB) was estimated using the following equations, adapted from Brown (1997);

- Equation 1: Above-ground biomass (AGB) = VOB x WD x BEF
- Equation 2: Below-ground biomass (BGB) = AGB x 0.24

To estimate Above-ground biomass (AGB), Equation 1 was used where VOB is the estimated merchantable volume per hectare (m3/ha). This was calculated using Smit's (1996) formula for trees and shrubs that had a stem diameter at root crown bigger than zero, but smaller than the maximum canopy diameter.

Therefore;

$$\text{VOB} = (\frac{1}{3}) \times (\frac{22}{7}) \times G \times ((\frac{D}{2})^2 + (\frac{D}{2}) \times (\frac{E}{2}) + ((\frac{E}{2})^2$$

Whereas;

G = height of tree (height)

D = maximum canopy length (cumulative stem length)

E = base diameter of the seedling (diameter at root crown)

The WD notation in Equation 1 signifies the mean wood density for Africa (0.58 t/m3), whereas BEF is the biomass expansion factor which is calculated using the formula: BEF = EXP {3.213-0.506 x ln (BV)} (Shifa, 2017). Furthermore, BV in the BEF formula is the biomass of inventoried volume calculated as the product of wood density and inventoried volume (BV = VOB (m3/ha) x WD (0.58 t/m3) (Brown 1997; Amadhila, 2012). Estimated merchantable volume (VOB m3/ha) was converted to oven-dry mass, using Africa's mean wood density (WD) of 0.58 t/m3 (Brown 1997). The merchantable growing stock was then expanded to account for non-merchantable components of the tree with the Biomass Expansion Factor (BEF- the ratio of above-ground oven-dry biomass density to the oven-dry biomass density of the inventoried). According to Henry et al. (2011) and Button, Liao, Filley and Archer (2009), below-ground biomass is a function of above-ground biomass. Since the indirect method of estimating biomass was used, the biomass obtained using Equation 1 was that of above-ground only. Where 0.24 is the constant coefficient ratio of below ground biomass to above-ground biomass (Amadhila, 2012).

3.8.2. The statistical analysis for neighbor and distance effect (field experiment).

For each target species, a Generalized Linear model (GLM) procedure in R (version 4.2.1 of 2022) was used to determine significant differences in seedling (a) growth (biomass and stem length), (b) survival, (c) nitrogen and chlorophyll leaf content, and (d) Surface Leaf Area between the different neigbour treatments. Growth, survival, nitrogen and chlorophyll content, as well as Surface Leaf Area were treated as response variables and were tested separately. Neighbor treatment was considered as a predictor. After transformation, a normal distribution family with an identity link was used for growth, leaf nitrogen content and leaf surface area, except for seedling survival where a poisson distribution was used (the data was still skewed). Multiple pairwise comparisons were done using Tukey's hsd test.

Furthermore, Generalized Linear model (GLM) procedure in R (version 4.2.1 of 2022) was used to determine if there were significant differences in cumulative stem length, estimated biomass, survival, leaf nitrogen content and leaf surface area of seedlings between the distance treatments for each target species used in the field experiment. The interaction effect between neighbors and distance treatments were also determined. The growth data and seedling survival was positively and negatively skewed respectively, therefore, the data was log(10) transformed and the distribution was improved close to normality. However, the survival data still did not follow a normal distribution, hence, a Poisson family distribution for non-normal count data was used in GLM to determine if there were significant differences in mean survival proportions. On another hand, Leaf Nitrogen content data and leaf surface area was normally distributed from a Shapiro-wilk test, therefore, a normal distribution family was used for GLM testing.

3.8.3. The statistical analysis for the effect of fertilizer (greenhouse experiment).

A Generalized Linear model-GLM was also used to test for significant differences in seedling cumulative stem length, biomass, Nitrogen contents, and survival between different fertilizer treatments for each target species in the greenhouse experiment. The same procedures used in the field experiment was used to test for the effect of neighbors and fertilizer on the seedling cumulative stem length, estimated biomass, Nitrogen contents, surface leaf area and seedling survival of *C.mopane*, *C.imberbe* and

V. erioloba. Multiple pairwise comparisons were also carried out using the Tukey's hsd test.

3.8.4. Natural woody recruitment (field experiment)

To assess whether neighbor and distance treatment promoted natural regeneration, we monitored the spontaneous recruitment of woody seedlings throughout the eight-month experiment. At each monthly census, all newly emerged or persistent woody individuals around each planted seedling were identified to species and counted. From these data, we derived species richness (S) and total abundance (N).

4: RESULTS

4.1 The effect of neighbor treatments on the growth of target species (field experiment).

4.1.1 Growth of seedlings

(a) Cumulative stem length

In the field experiment, the Generalized Linear Model revealed that there was no significant difference in cumulative stem length of *C. mopane* seedlings among neighbor treatments under both 0.5 m distance treatment (F=0.8, df = 3, *p*>0.05) and 1 m distance treatment between seedlings (F=0.3, df = 3, *p*>0.05). There was also no significant difference in cumulative stem length of *C. imberbe* seedlings among neighbor treatments when 0.5 m distance between seedlings was used (F=1.7, df = 3, *p*>0.05). However, when grown with *V. erioloba* under the 1 m distance treatment, there was a significant difference in the cumulative stem length of *C. imberbe* seedlings (F=4.3, df3, *p*<0.05). The presence of *V. erioloba* neighbors has positively influenced the cumulative stem length of *C. imberbe* seedlings. In addition, there was no significant difference in cumulative stem length of *V. erioloba* seedlings among neighbor treatments under 0.5 m distance treatment (F=0.6, df3, *p*>0.05) and 1 m distance treatment between seedlings (F=3, df3, *p*>0.05).

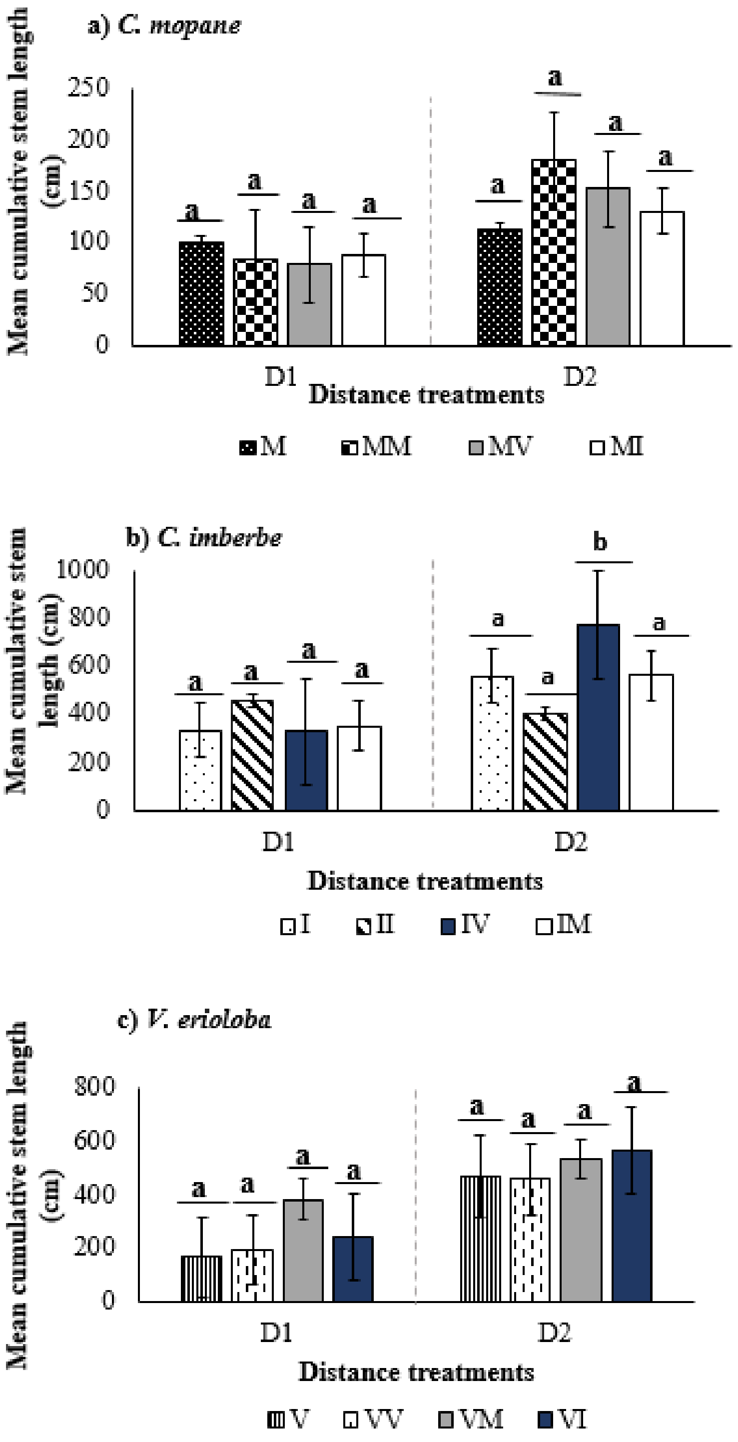

Figure 8 Mean cumulative stem length (cm) of (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings among single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-0.5 m and D2-1 m). The neighbor comparisons for each target species were within

distance treatments, separated by the faded lines. Different letters on the bars (for example. a, b, c) indicate significant differences ($p < 0.05$).

(b) Estimated total biomass

The results indicate that there were no significant differences in the total estimated biomass of *C. mopane* seedlings among different neighbor treatments at distances of 0.5 m (F=0.08, df3, p>0.05 and 1 m (F=0.2, df3, p>0.05). Similarly, there were no significant differences in the total estimated biomass of *C. imberbe* seedlings at 0.5 m distance (F=0.4, df3, p>0.05). However, there was a significant difference in estimated biomass when *C. imberbe* was grown with *V. erioloba* at a 1 m distance (F=7.22, df3, p<0.05), indicating an increase in seedling biomass in the presence of *V. erioloba*. Additionally, there were no significant differences in the total estimated biomass of *V. erioloba* seedlings among neighbor treatments at 0.5 m distance (F=1.5, df3, p>0.05) and 1 m distance (F=0.29, df3, p>0.05).

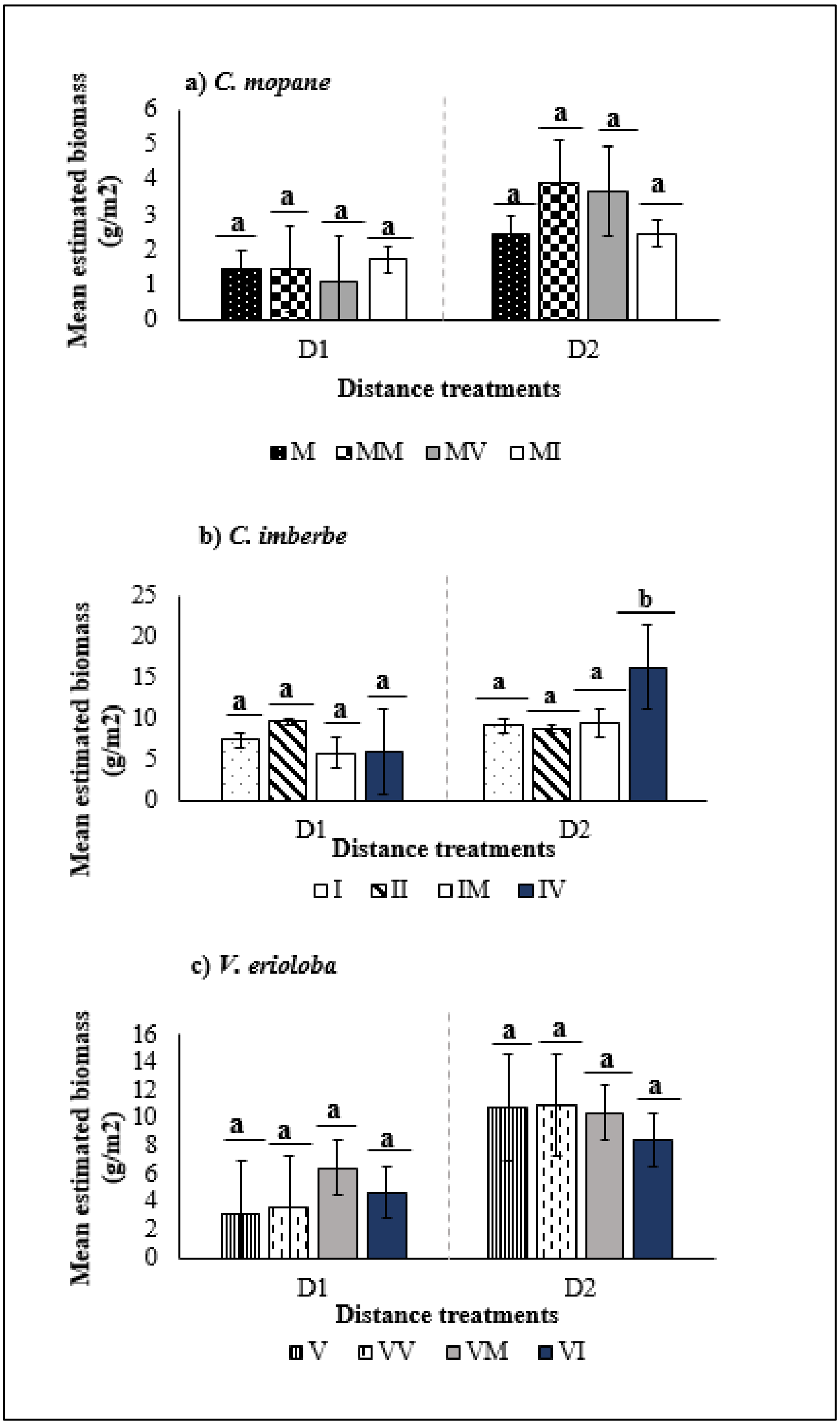

Figure 9 Mean total estimated biomass of (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The neighbor comparisons for each target species were within

distance treatments, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.1.2. Seedling survival

Significant differences were observed in the survival of *C. mopane* among neighbor treatments under 0.5 m distance treatment (F=0.7, df3, p<0.001). However, there was no significant difference in seedling survival of *C. mopane* among neighbor treatments when 1 m distance between seedlings was used (F=0.01, df3, p>0.05). The presence of *V. erioloba* had a negative impact on the survival of *C. mopane* seedlings when they were placed at a 0.5 m distance from neighboring plants (F=2.1, df3, p<0.001). Similarly, significant differences were found in the survival of *C. imberbe* seedlings under both 0.5 m (F=3.4, df3, p<0.001) and 1 m (F=3.6, df3, p<0.001) neighbor treatments. *C. imberbe* seedlings' survival was lower when they were grown alone (F=11.2, df3, p<0.05) or paired with *C. mopane* (F=5.3, df3, p<0.01) under 0. 5 m, whereas seedling survival of *C. imberbe* decreased in the presence of neighbors under the 1 m distance (fig.4.3b). Additionally, significant differences were observed in the seedling survival of *V. erioloba* between neighbors when 0.5 m distance between seedlings was used (F=9.1, df3, p<0.01) and also under 1 m distance treatment (F=4.3, df3, p<0.001). There was a decrease in seedling survival of *V. erioloba* in the presence of heterospecific neighbors *C. mopane* (F=4.1, df3, p<0.05) and *C. imberbe* (F=3.7, df3, p<0.001) under the two distances, respectively (fig.4.3c).

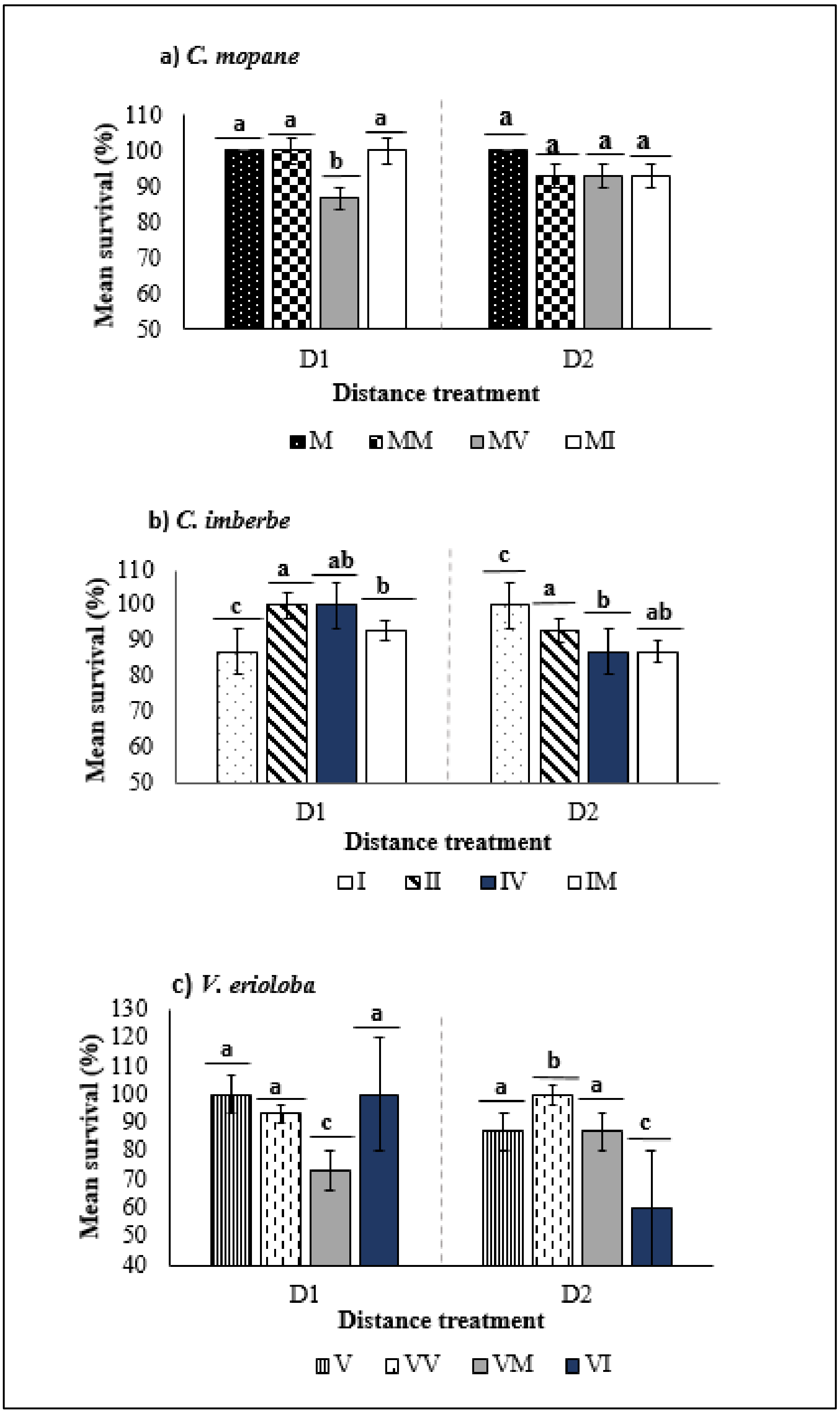

Figure 10 Average percentage survival of(a) *C. mopane*- M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The neighbor comparisons for each target species were within

distance treatments, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.1.3 Leaf Nitrogen content

The GLM procedure showed no significant difference in leaf nitrogen content of *C. mopane* seedlings among neighbor treatments when a 0.5 m distance between seedlings was used (F=0.3, df3, p>0.05). However, there was a significant difference in leaf nitrogen content of *C. mopane* among neighbor treatments when 1 m distance was used (F=11.9, df3, p<0.001). There was a decrease in seedling leaf nitrogen content of *C. mopane* when it was grown with conspecific neighbors (F=8.4, df3, p<0.001), *C. imberbe* (F=11, df3, p<0.001), and with *V. erioloba* (F=9, df3, p<0.001). In addition, there was no significant difference in leaf nitrogen content of *C. imberbe* among neighbor treatments when 0.5 m distance was used (F=0.18, df3, p>0.05). However, there was a significant difference in leaf nitrogen contents of *C. imberbe* among neighbor treatments when 1 m distance treatment was used (F=6.4, df3, p<0.05). There was a decrease in seedling leaf nitrogen content of *C. imberbe* under 1 m distance treatment when it was grown with *V. erioloba* (F=2.3, df3, p<0.05). Additionally, there was a significant difference in leaf nitrogen content of *V. erioloba* among neighbor treatments when 0.5 m distance (F=5.2, df3, p<0.001) and 1 m distance treatment (F=3.2, df3, p<0.05) were used. The seedling leaf nitrogen decreased when *V. erioloba* was grown with *C. mopane* (F=4.8, df3, p<0.05) or with *C. imberbe* (F=5.2, df3, p<0.001). under 0.5 m. While under 1 m distance treatment, seedling leaf nitrogen decreased when *V. erioloba* was grown with *C. imberbe* (F=3, df3, p<0.05) (fig. 4.4c).

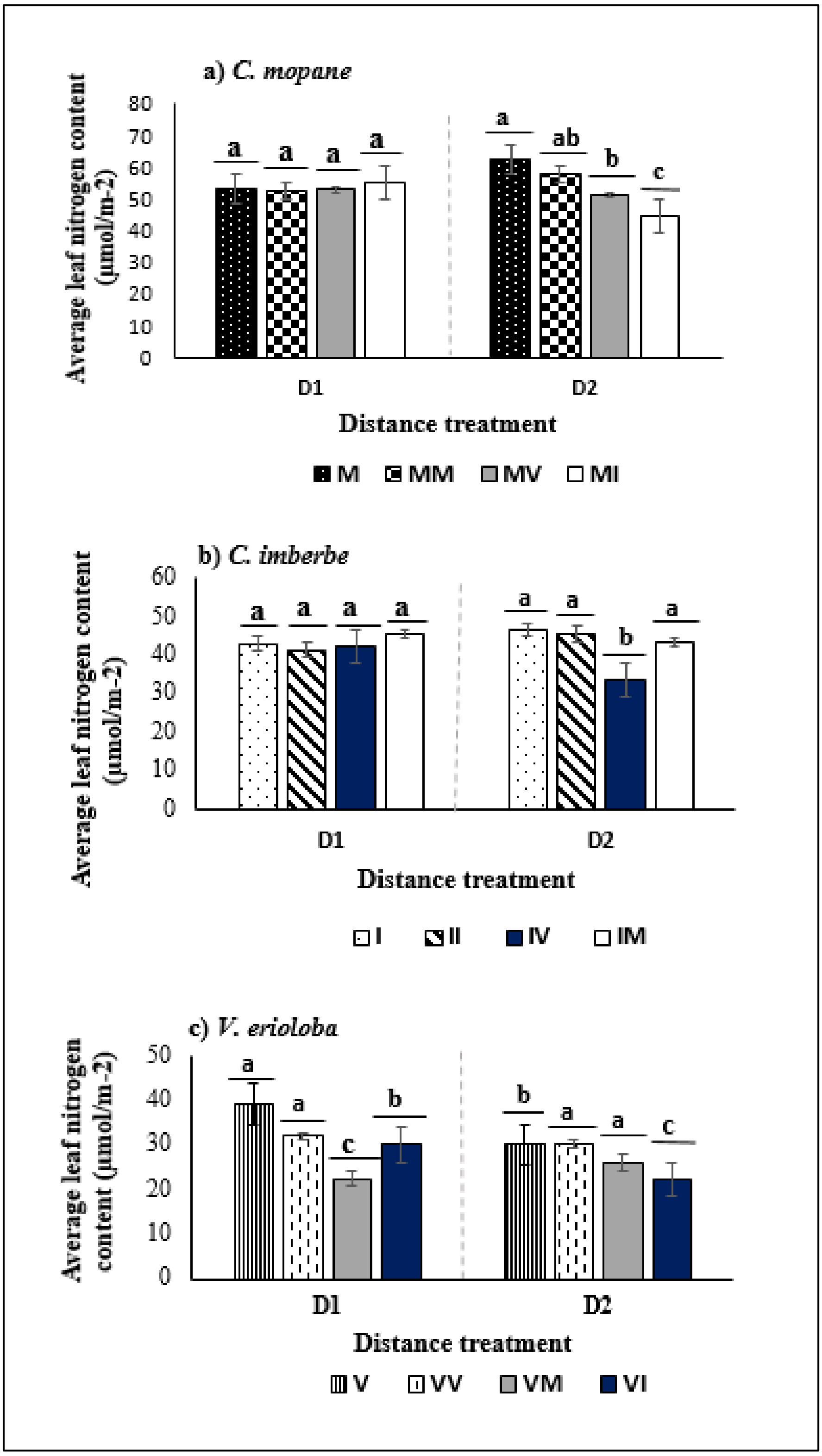

Figure 11 Average Leaf Nitrogen content (µmol m-2) of (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The neighbor comparisons for each target species

were within distance treatments, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.1.4 Leaf surface area

There was no significant difference in the leaf surface area of *C. mopane* seedlings among neighbor treatments when 0.5 m distance between neighbor pairs was used (F=2.3, df3, p>0.05). However, there was a significant difference in the leaf surface area of *C. mopane* seedlings among neighbor treatments when a 1 m distance between seedlings was used (F=41.3, df3, p<0.001). The presence of heterospecific neighbors decreased the leaf surface area of *C. mopane* seedlings; when grown with *V. erioloba* (F=12.6, df3, p<0.001) or *C. imberbe* (F=24, df3, p<0.001) (fig.4.4a). For *C. imberbe,* there was a significant difference in seedlings' leaf surface area among neighbor treatments when 0.5 m distance treatment (F=4.2, df3, p<0.05) and 1 m distance treatment (F=7.1, df3, p<0.001) were used. The leaf surface area of *C. imberbe* seedlings was lower in the presence of *V. erioloba* when 0.5 m distance was used (F=4.2, df3, p<0.05), while *C. imberbe* seedlings had bigger leaves when grown with their conspecific neighbors under the 1 m distance treatment (F=3.8, df3, p<0.001) (fig4.5b). In addition, there was a significant difference in the leaf surface area of *V. erioloba* among neighbor treatments when 0.5 m distance between seedlings was used (F=8.3, df3, p<0.05). However, there was no significant difference in the leaf surface area of *V. erioloba* among neighbor treatments when 1 m distance between seedlings was used (F=4.8, df3, p<0.05). The presence of *C. imberbe* has improved the seedling leaf surface area of *V. erioloba* (F=6.4, df3, p<0.05), while there was a decrease in leaf surface area when grown with *C. mopane* (F=2.9, df3, p<0.05) under 0.5 m distance treatment (fig.4.5c).

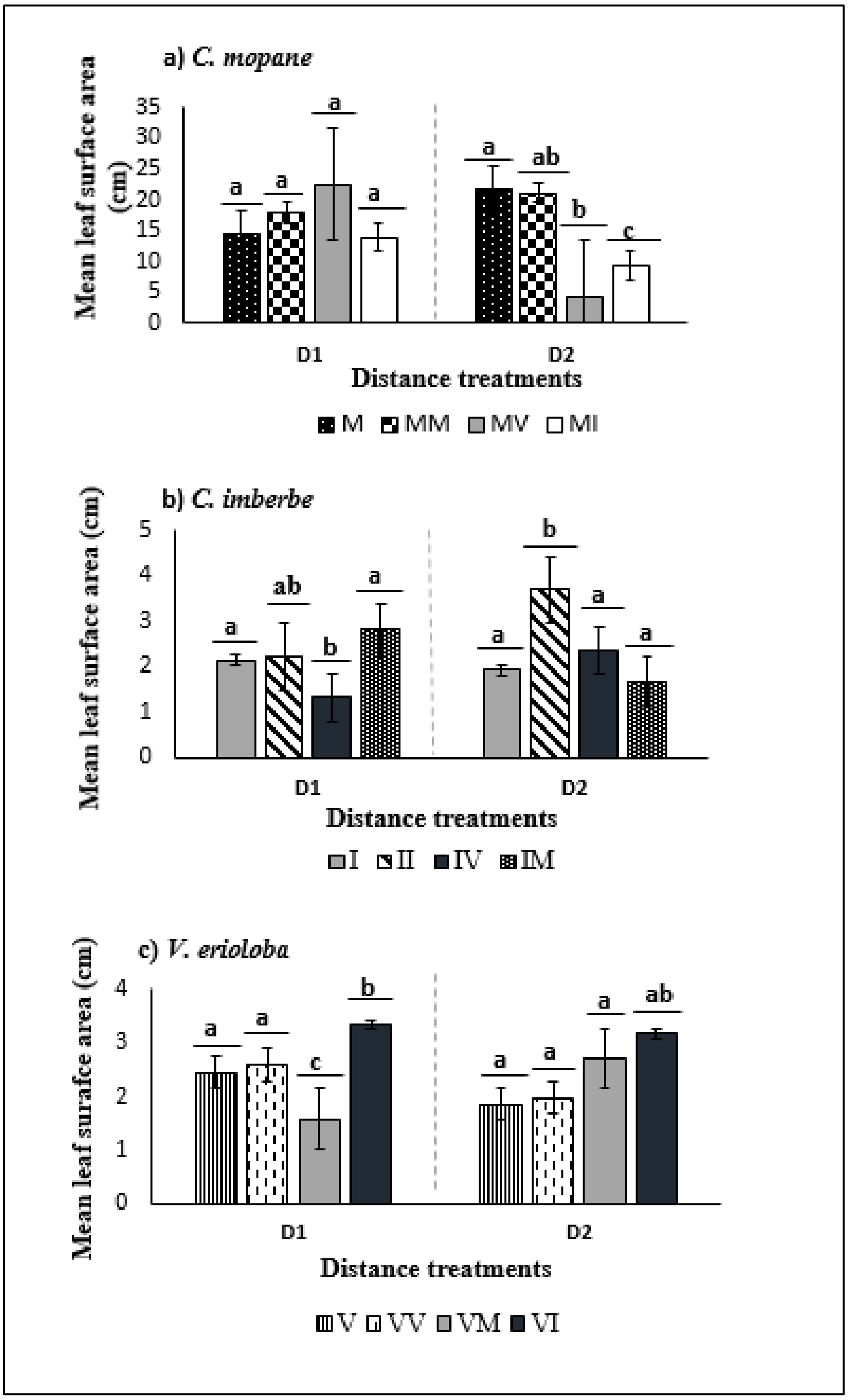

Figure 12 Average Leaf surface area (cm) of (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The neighbor comparisons for each target species were within distance treatments, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.2 The effect of distance between neighbors on seedling performance

4.2.1 Growth of seedlings

(a) Cumulative stem length

There was a significant difference in cumulative stem length of *C. mopane* seedlings between distance treatments when it was growing with its conspecific neighbors ($F=2.3$, df3, $p<0.05$) and with *V. erioloba* ($F=3.1$, df3, $p<0.05$), but not when it was grown alone ($F=0.17$, df3, $p>0.05$), or with *C. imberbe* ($F=2.7$, df3, $p>0.05$). *C. mopane*'s cumulative stem length was higher under the 1m distance when grown with conspecific neighbors ($F=2.3$, df3, $p<0.05$) and with *V. erioloba* ($F=3.1$, df3, $p<0.05$). Additionally, there was a significant difference in cumulative stem length of *C. imberbe* seedlings between distance treatments when they were grown alone ($F= 3.2$, df1, $p<0.01$), and when grown with *V. erioloba* neighbors ($F=4.1$, df1, $p<0.01$). Higher cumulative stem length was observed under 1 m distance between seedlings, when *C. imberbe* was grown alone ($F= 3.2$, df1, $p<0.01$), with *V. erioloba* neighbors ($F=4.1$, df1, $p<0.01$), or with *C. mopane* neighbors ($F=3.03$, df1, $p<0.05$). However, there was no significant difference in cumulative stem length of *C. imberbe* seedlings when they were grown with their conspecific neighbors ($F=0.01$, df1, $p>0.05$). Moreover, there was a significant difference in cumulative stem length of *V. erioloba* seedlings between distance treatments when they were growing alone ($F=4.7$, df3, $p<0.05$) and with *C. imberbe* ($F=3.9$, df3, $p<0.05$), but not when it was grown with conspecific neighbors ($F=0.1$, df3, $p>0.05$) or with *C. mopane* ($F=0.2$, df3, $p>0.05$). Higher cumulative stem length for *V. erioloba* seedlings was also observed under 1 m distance treatment when they were growing alone ($F=4.7$, df3, $p<0.05$) or with *C. imberbe* ($F=3.9$, df3, $p<0.05$) (fig. 4.6c).

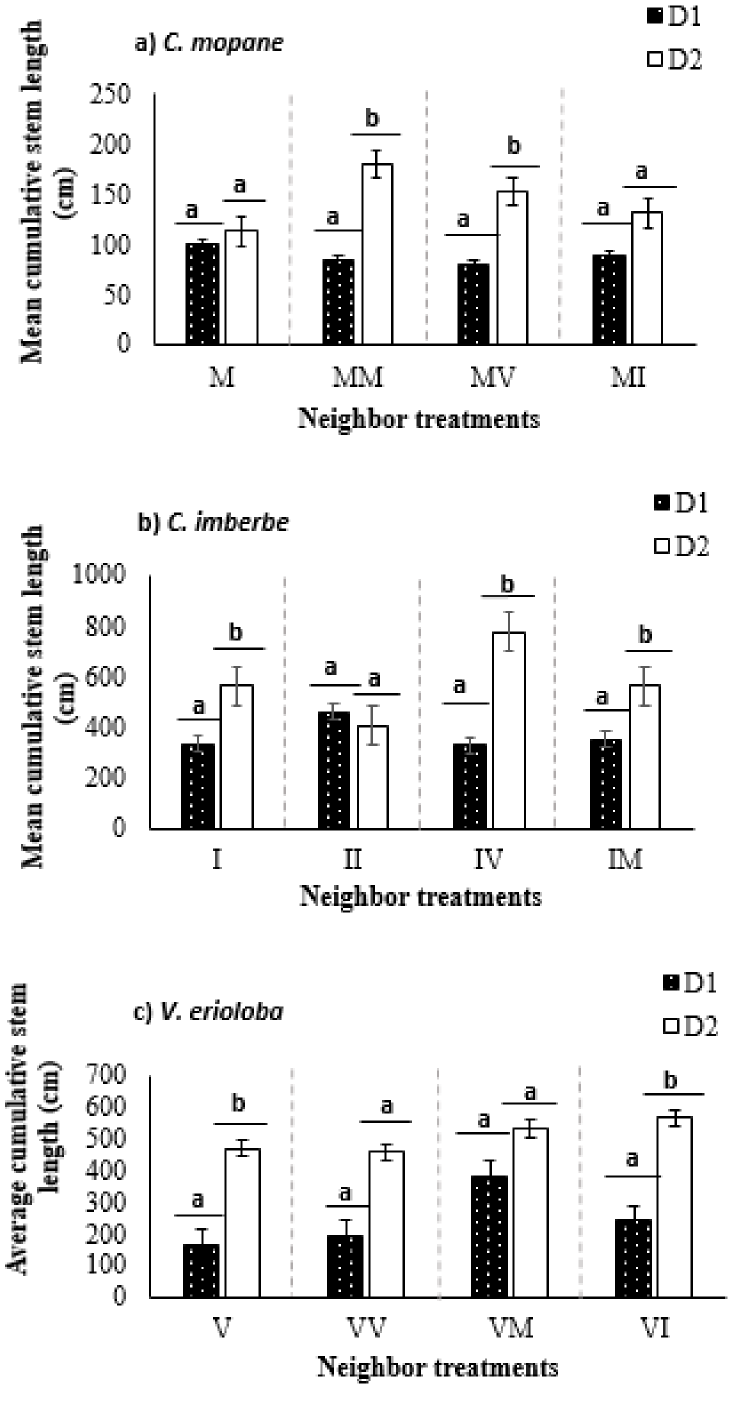

Figure 13 Mean cumulative stem length (cm) of (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The comparisons between distance treatments for

each target species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

(b) Estimated biomass

The GLM test shows that there was a significant difference in the total estimated biomass of *C. mopane* between distance treatments when it was grown with its conspecific neighbors (F=6.1, df1, $p<0.05$) or with *V. erioloba* (F=11, df1, $p<0.05$), but not when *C. mopane* was grown alone (F=1.3, df1, $p>0.05$), or with *C. imberbe* (F=0.8, df1, $p>0.05$). Furthermore, there was no significant difference in the total estimated biomass of *C. imberbe* seedlings between distance treatments when it was growing alone (F=1.2, df1, $p>0.05$), with its conspecific neighbors (F=0.3, df1, $p>0.05$), and with *C. mopane* (F=0.3, df1, $p>0.05$). However, there was a significant difference in seedling total estimated biomass between distance treatments when it was grown with *V. erioloba* (F=7.9, df1, $p<0.05$), where the highest biomass of *C. imberbe* was recorded under the wider distance of 1 m (F=3.1, df3, $p<0.05$) (fig.4.7b). Moreover, there was significant difference in estimated biomass of *V. erioloba* seedlings between distance treatments when *V. erioloba* was growing alone (F=4.6, df1, $p<0.05$), when it was grown with its conspecific neighbors (F=2.9, df1, $p<0.05$), and *C. mopane* (F=0.5, df1, $p>0.05$), but not when it was grown with its heterospecific neighbor of and *C. imberbe* (F=0.3, df1, $p>0.05$). The highest biomass was recorded under the 1 m distance treatment when *V. erioloba* was growing alone (F=4.6, df1, $p<0.05$), with its conspecific neighbors (F=2.9, df1, $p<0.05$), and when it was grown with *C. mopane* (F=0.5, df1, $p>0.05$).

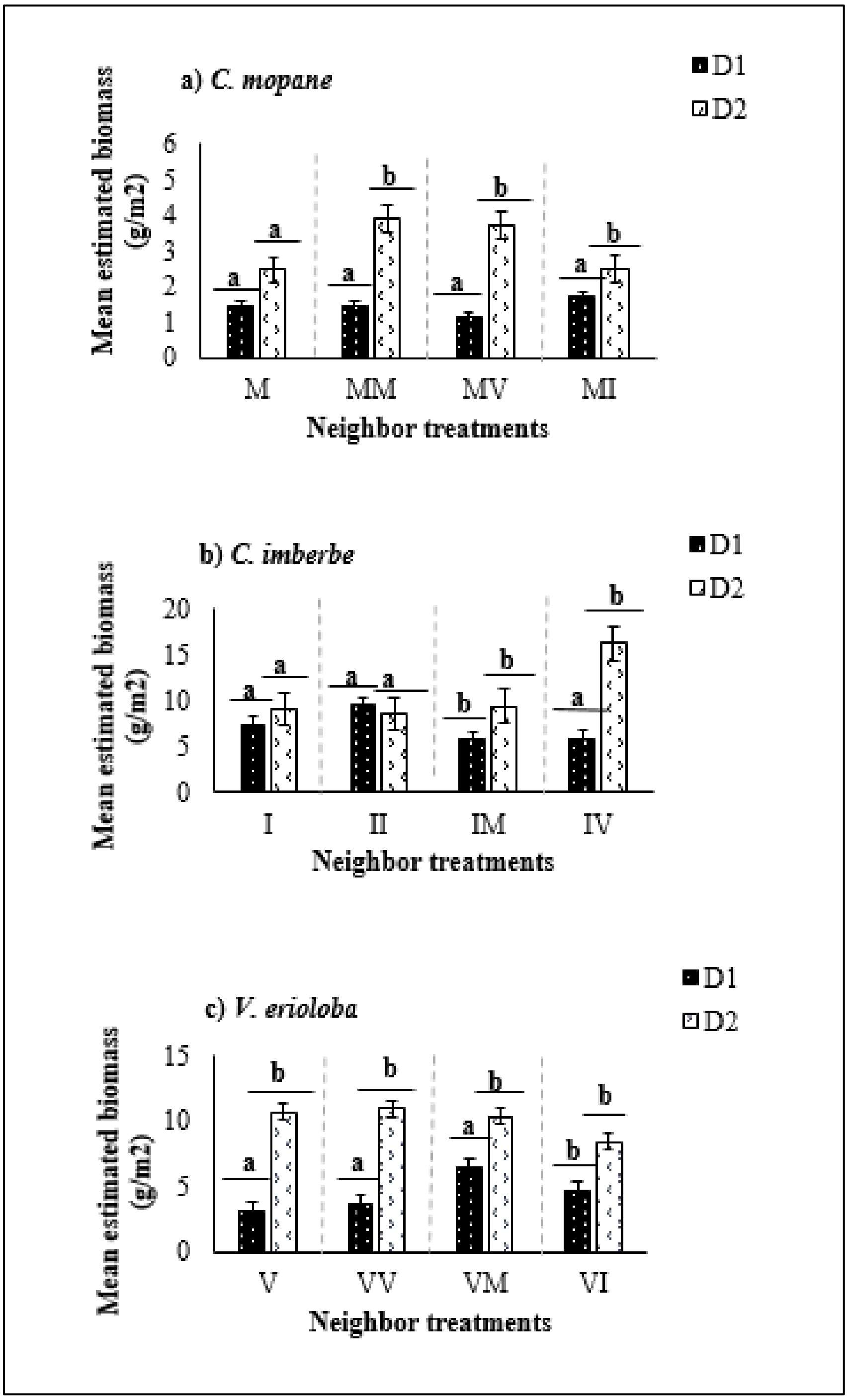

Figure 14 Mean total estimated biomass of the three study species: (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The comparisons between distance treatments for each target species were within neighbor combinations, separated by the

faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.2.2 Seedling survival

There was no significant difference in seedling survival of *C. mopane* between distance treatments; when *C. mopane* was grown alone (F=1, df1, p>0.05), with its conspecific neighbors (F=0.9, df1, p>0.05), with *V. erioloba* (F=1.8, df1, p>0.05), and with *C. imberbe* (F=1.9, df1, p>0.05). Furthermore, there was a significant difference in the seedling survival of *C. imberbe* between distance treatments; when it was grown alone (F=3.6, df1, p<0.001) and when it was grown with *V. erioloba* (F=2.9, df1, p<0.001), but not when *C. imberbe* was growing with its conspecific neighbors (F=0.01, df1, p>0.05) or with *C. mopane* (F=0.06, df1, p>0.05). Higher seedling survival of *C. imberbe* was observed under 0. 5 m distance treatment when it was grown alone (F=3.6, df1, p<0.001) and when it was grown with *V. erioloba* (F=2.9, df1, p<0.001), however, individual seedlings of *C. imberbe* preferred a more spaced area of 1 m distance (fig.4.8b). There was also a significant difference in seedling survival of *V. erioloba* between distance treatments when it was grown alone (F=2.5, df1, p<0.001), with *C. mopane* (F=2.9, df1, p<0.001), and with *C. imberbe* (F=9.1, df1, p<0.001), however, there was no significant difference between distance treatments when *V. erioloba* was growing with its conspecific neighbors (F=1.8, df1, p>0.05). The seedling survival of *V. erioloba* increased under 1 m distance treatment when it was grown with *C. mopane* (F=4.2, df1, p<0.001), but decreased under 1 m distance in the presence of *C. imberbe* (F=6..7, df1, p<0.001) (fig.4.8c).

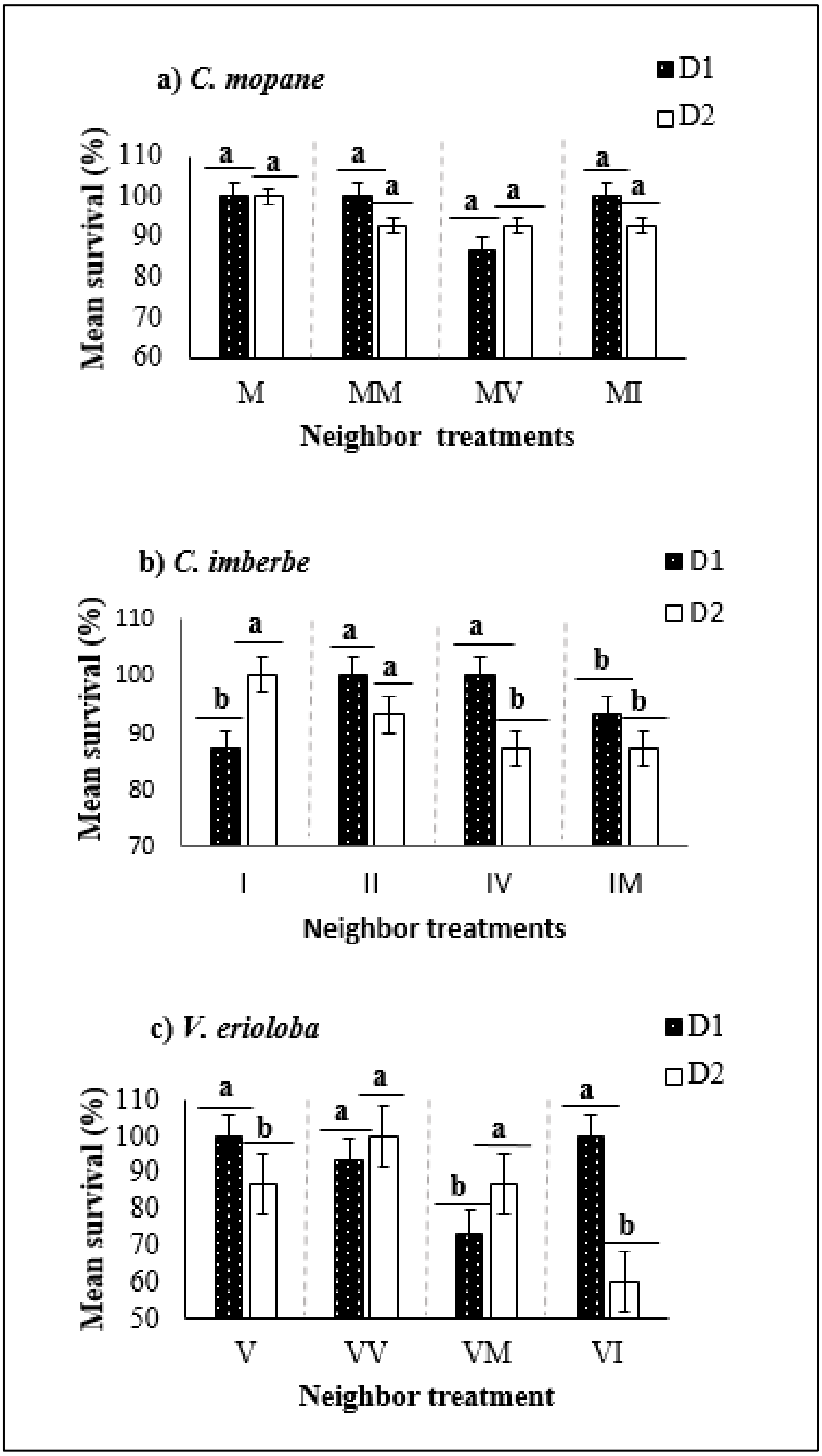

Figure 15 Average percentage survival of (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The comparisons between distance treatments for each target

species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.2.3. Leaf Nitrogen content

There was a significant difference in leaf nitrogen content of *C. mopane* seedlings between distance treatments when it was grown alone (F=10.3, df1, p<0.01) and when it was grown with *C. imberbe* (F=12, df1, p<0.01). Seedling leaf nitrogen content was lower under 1 m distance treatment when *C. mopane* was grown with *C. imberbe* (F=3.7, df1, p<0.01). However, there was no significant difference in leaf nitrogen content of *C. mopane* between distance treatments when it was grown with its conspecific neighbors (F=1.6, df1, p>0.05) and when it was grown with *V. erioloba* (F=0.2, df1, p>0.05). Additionally, there was a significant difference in leaf nitrogen content of *C. imberbe* between distance treatments when it was grown with *V. erioloba* (F=4.8, df1, p<0.05), but not when it was grown alone (F=0.17, df1, p>0.05), with its conspecific neighbors (F=0.7, df1, p>0.05) or with *C. mopane* (F=0.12, df1, p>0.05). The seedling leaf nitrogen content of *C. imberbe* was higher under 0.5 m distance treatment when it was grown with *V. erioloba* (F=2.2, df1, p<0.01). Moreover, there was a significant difference in leaf nitrogen content of *V. erioloba* between distance treatments when it was grown alone (F=4.2, df1, p<0.001) and when it was grown with *C. imberbe* neighbors (F=4.5, df1, p<0.05). However, there was no significant difference in leaf nitrogen content of *V. erioloba* when it was grown with its conspecific neighbors (F=0.2, df1, p>0.05) or with *C. mopane* (F=1.2, df1, p>0.05). The 0.5 m distance treatment had a positive influence on the seedling leaf nitrogen content of *V. erioloba* (fig.4.9c).

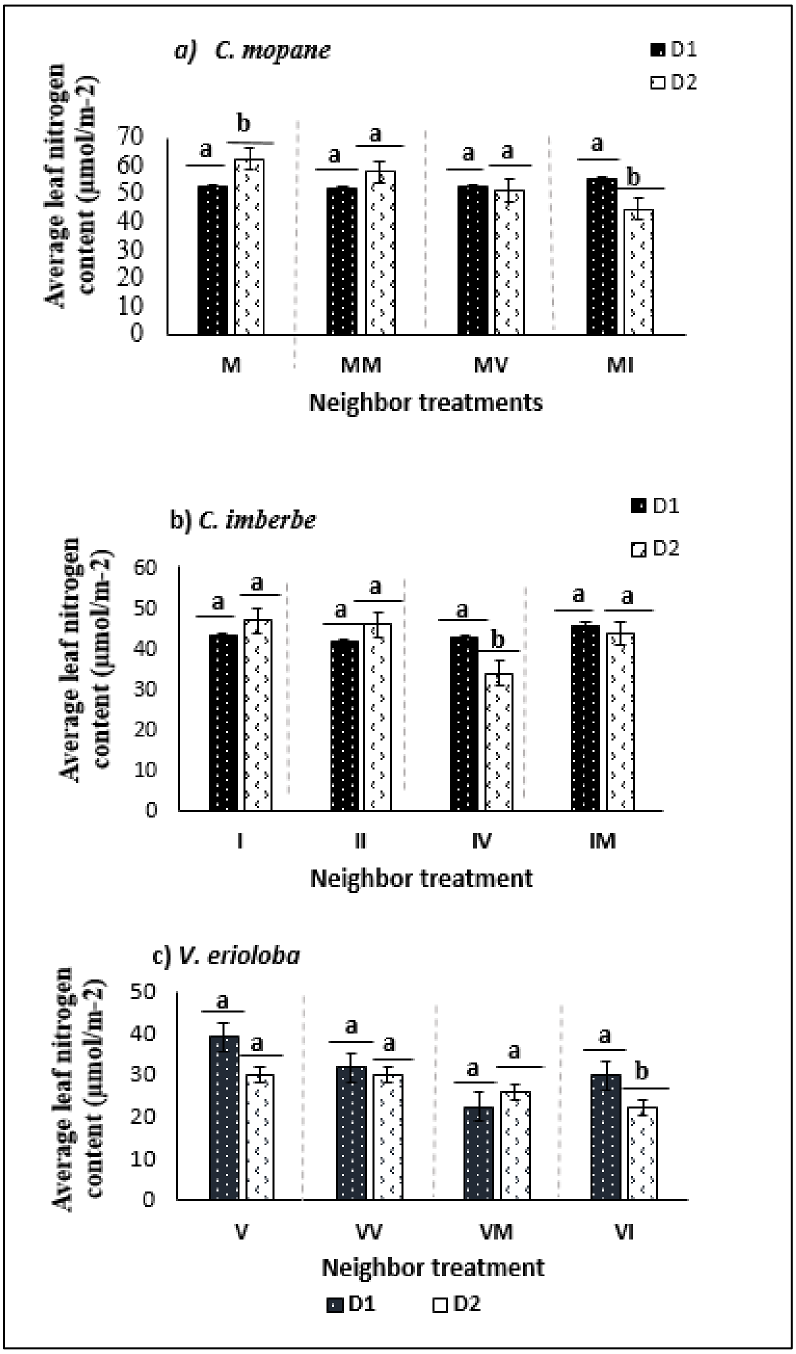

Figure 16 Average Leaf Nitrogen content (µmol m-2) of (a) (a) *C. mopane*-M, (b) *C. imberbe*-I, and (c) *V. erioloba*-V seedlings between single (M, I, V), conspecific (MM, II, VV) and heterospecific neighbors (MI, MV, IV, IM, VI, VM), under two distance treatments (D1-50cm and D2-1 m). The comparisons between distance treatments for each target species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.2.4 Leaf surface area

The GLM has further revealed that there was a significant difference in leaf surface area of *C. mopane* seedlings between distance treatments; when it was grown alone (F=7.6, df1, p<0.05) and when it was grown with *V. erioloba* (F=20, df1, p<0.001), but not when it was grown with its conspecific neighbors (F=2.3, df1, p>0.05) or with *C. imberbe* (F=4, df1, p>0.05). *C. mopane* seedlings had bigger leaves when they were grown as single individuals in a more spaced area of 1 m (F=5.2, df1, p<0.05), while the presence of heterospecific neighbors such as *V. erioloba* has decreased the leaf surface area of *C. mopane* seedlings under the wider distance treatment of 1 m (F=7.6, df1, p<0.05) (fig.4.10a). Additionally, there was a significant difference in leaf surface area of *C. imberbe* seedlings between distance treatments; when it was grown with its conspecific neighbors (F=10.8, df1, p<0.05), when it was grown with *C. mopane* (F=15.4, df1, p<0.001), and with *V. erioloba* (F=5.2, df1, p<0.05), but not when it was grown in the absence of neighbors (F=0.2, df1, p>0.05). The 1 m distance between seedlings increased the leaf surface area of *C. imberbe* when grown with neighbors (fig.4.10b). For *V. erioloba*, there was a significant difference in leaf surface area between distance treatments when it was grown with its conspecific neighbors (F=7.6, df1, p<0.05) and with *C. mopane* (F=4.8, df1, p<0.05), but not when it was grown alone (F=0.7, df1, p>0.05), or with *C. imberbe* (F=0.1, df1, p>0.05). The 0.5 m distance treatment increased the leaf surface area of *V. erioloba* when grown with its conspecific neighbors, whereas the 1 m distance treatment had a more positive influence when *V. erioloba* was grown with *C. mopane*.

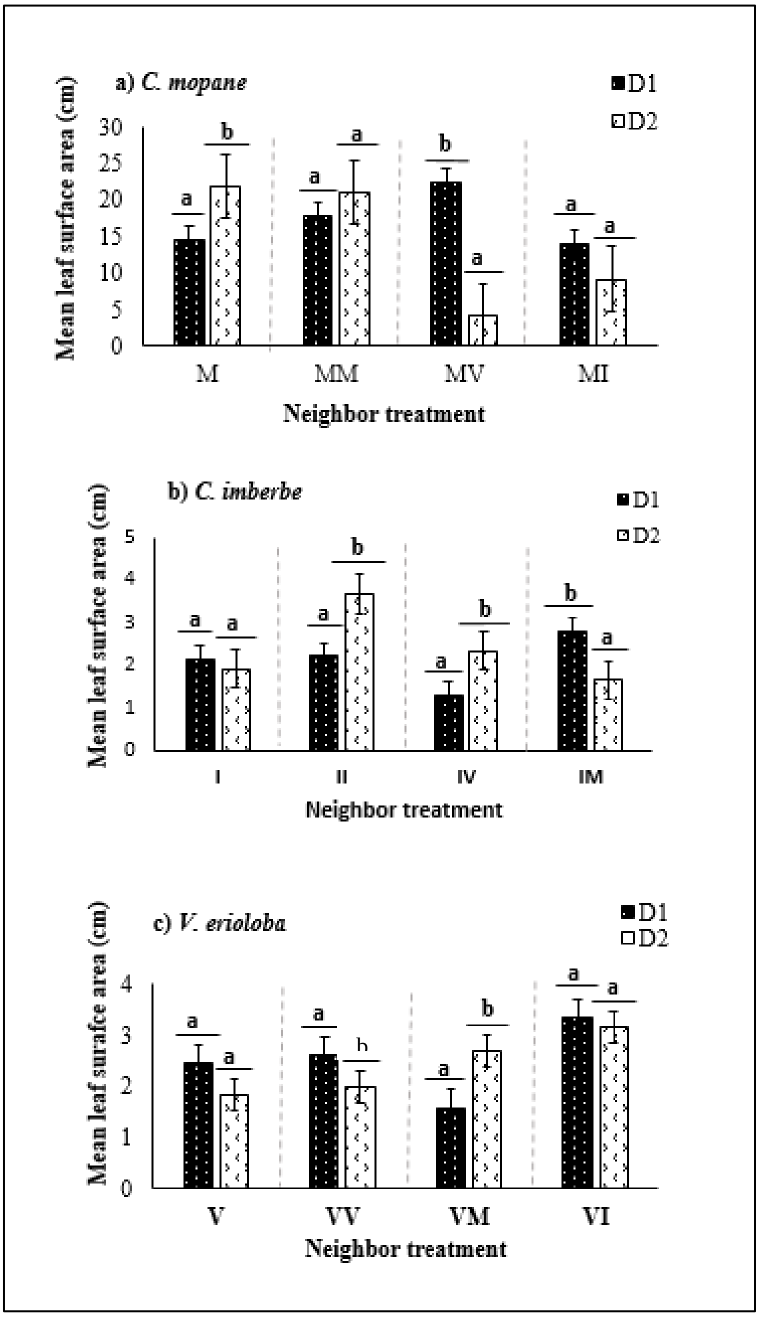

Figure 17 Average Leaf Surface area of (a) M (*C. mopane*), (b) I (*C. imberbe*), and (c) V(*V. erioloba*) seedlings between distance treatments when they were grown alone (M, I, V), with their conspecific (MM, II, VV), and heterospecific neighbors (MV, MI, IV, IM, VM, VI) in the field experiment. Single letters represent individual species, double letters conspecific neighbors, and mixed letters for heterospecific neighbors. The comparisons between distance treatments for each target species were within

neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences (p < 0.05).

4.3. The effect of fertilizer treatments on plant performance (greenhouse experiment)

4.3.1. Growth of seedlings

(a) Cumulative stem length

In the greenhouse experiment, the effect of fertilizer on the plant performances of target species was tested among neighbor combinations. A significant difference in cumulative stem length of *C. mopane* seedlings was observed between fertilizer treatments when it was growing alone (F=2.3, df1, p<0.05) and when grown with *V. erioloba* (F=13, df1, p<0.001). The addition of manure increased the cumulative stem length of *C. mopane* seedlings when grown without neighbors (F=4.2, df1, p<0.01), although growth was lower under manure-treated plots in the presence of *V. erioloba* (F=10, df1, p<0.001) (fig.4.11a). However, there was no significant difference in cumulative stem length between fertilizer treatments when *C. mopane* was grown with its conspecific neighbors (F=0.6, df1, p>0.05) or with *C. imberbe* (F=0.5, df1, p>0.05). In addition, there was a significant difference in cumulative stem length of *C. imberbe* seedlings between fertilizer treatments when they were grown with heterospecific neighbors: *C. mopane* (F=37.4, df1, p<0.001) and *V. erioloba* (F=6.4, df1, p<0.05), but not when it was grown alone (F=0.6, df1, p>0.05) or with its conspecific neighbors (F=0.001, df1, p>0.05). However, adding manure in the presence of heterospecific neighbors decreased the cumulative stem length of *C. imberbe* seedlings (fig.4.11b). Furthermore, there was no significant difference in cumulative stem length of *V. erioloba* between fertiliser treatments when it was grown alone (F=0.14, df1, p>0.05), with its conspecific neighbors (F=0.9, df3, p>0.05), with *C. mopane* (F=0.07, df1, p>0.05), and with *C. imberbe* (F=1.5, df1, p>0.05).

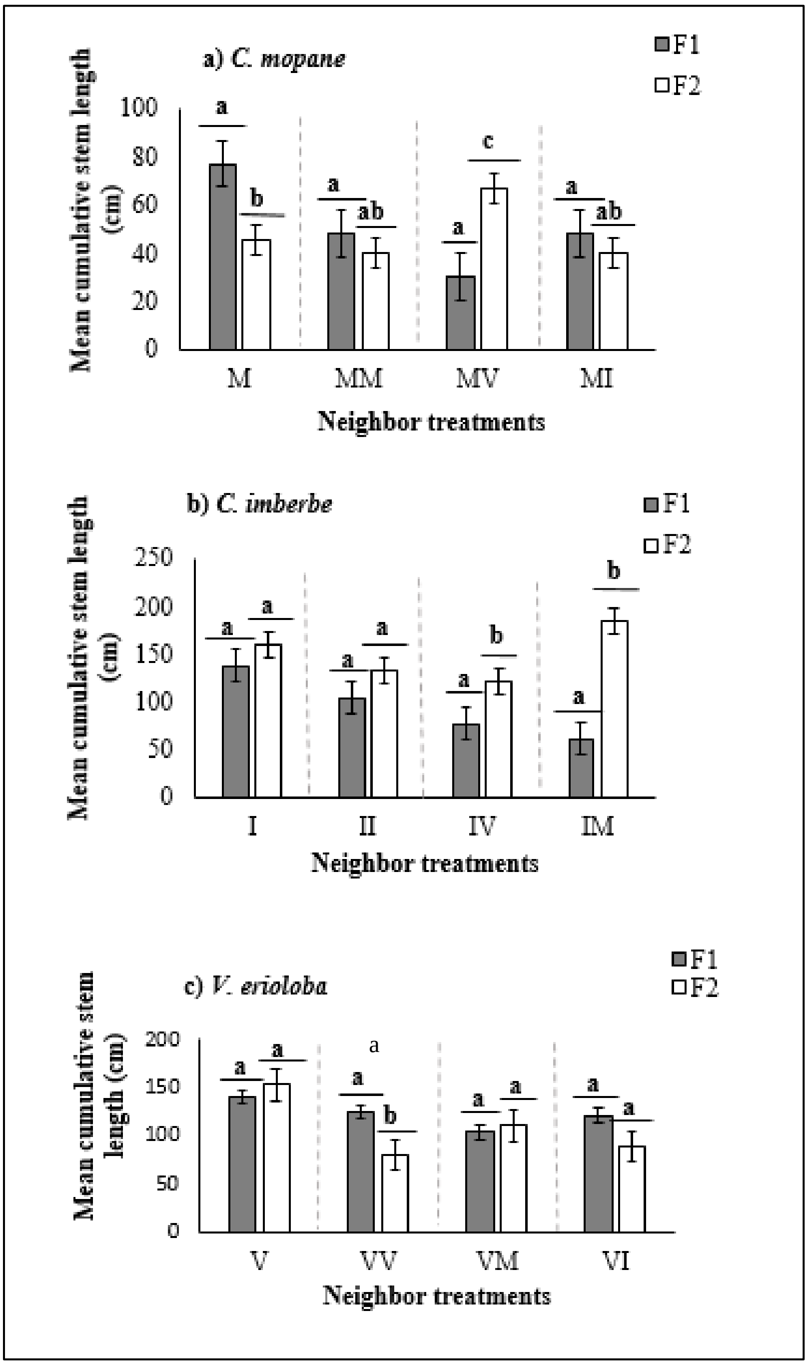

Figure 18 Average cumulative stem length (cm) of (a) M (*C. mopane*), (b) I (*C. imberbe*), and (c) V(*V. erioloba*) seedlings between fertilizer treatments (F1-With fertilizer and F2 –Without fertilizer) when they were grown alone (M, I, V), with their conspecific (MM, II, VV), and heterospecific neighbors (MV, MI, IV, IM, VM, VI),

in the greenhouse experiment. The comparisons between fertilizer treatments for each target species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

(b) **Estimated total biomass**

There was a significant difference in the total estimated biomass of *C. mopane* between fertilizer treatments when it was grown alone (F=8.1, df1, p<0.01), when it was grown with *V. erioloba* (F=23, df1, p<0.001), and with *C. imberbe* (F=1.4, df1, p<0.05), but not when it was grown with its conspecific neighbors (F=0.8, df1, p>0.05). Adding manure to the soil increased the seedling biomass of *C. mopane* when grown alone (F=7.8, df1, p<0.01) or with *C. imberbe* (F=2.3, df1, p<0.05) but seedling biomass decreased when manure was used in the presence of *V. erioloba* (F=13.4, df1, p<0.01) (fig.4.12a). Furthermore, there was a significant difference in the total estimated biomass of *C. imberbe* between fertilizer treatments when it was grown with *C. mopane* (F=4.8, df1, p<0.05), where the seedling biomass decreased when manure was added. However, there was no significant difference in the total estimated biomass of *C. mopane* seedlings when they were grown alone (F=0.1, df1, p>0.05), with conspecific neighbors (F=1.3, df1, p>0.05), or with *V. erioloba* (F=1.2, df1, p>0.05). Lastly, there was no significant difference in total estimated biomass of *V. erioloba* between fertilizer seedlings; when *V. erioloba* was grown alone (F=0.4, df1, p>0.05), with its conspecific neighbors (F=2.3, df1, p>0.05), with *C. mopane* (F=0.07, df1, p>0.05), and when it was grown with *C. imberbe* (F=1.57, df1, p>0.05).

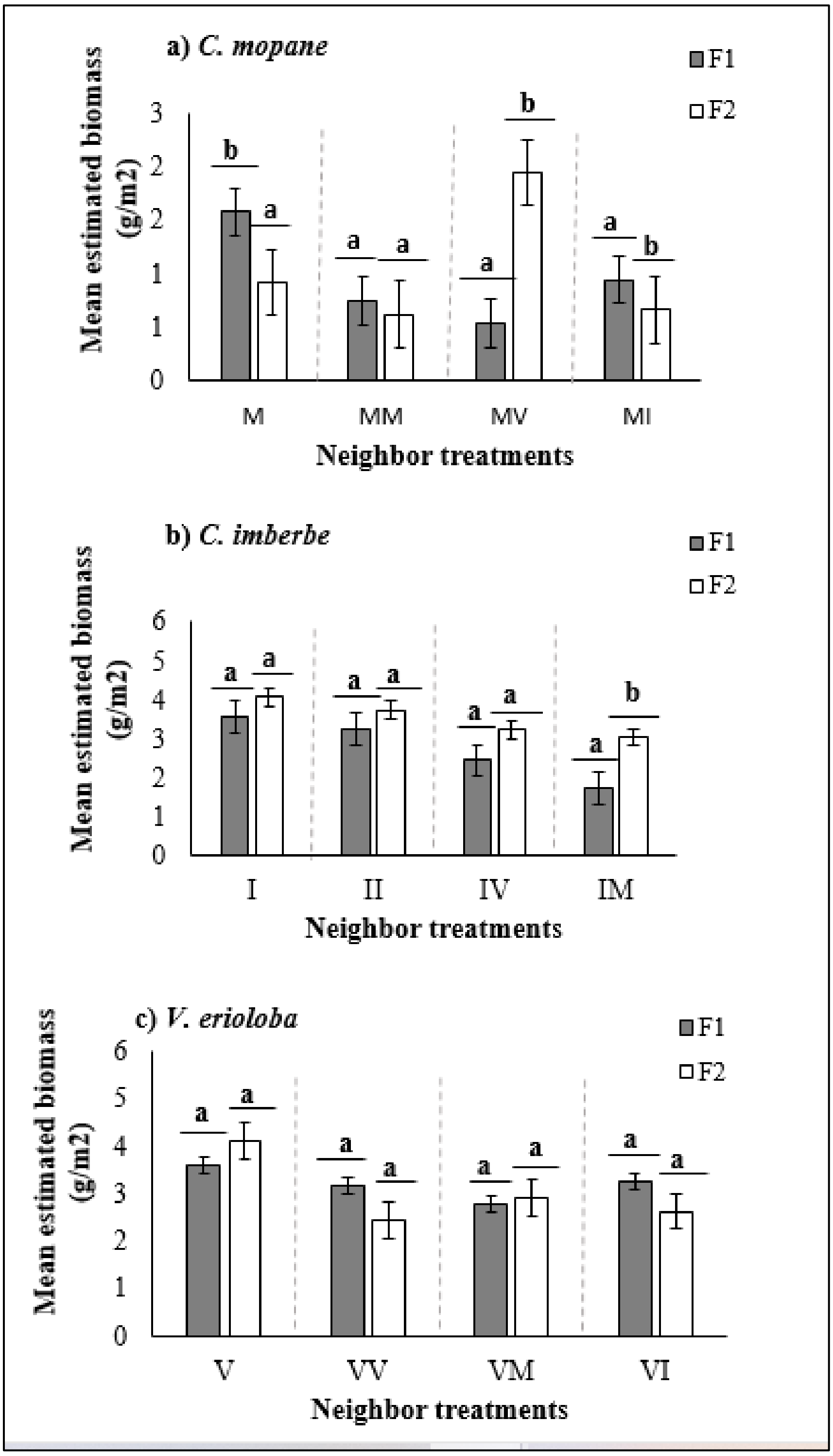

Figure 19 Mean total estimated biomass (g/m2) of study species; (a) M (*C. mopane*), (b) I (*C. imberbe*), and (c) V(*V. erioloba*) seedlings between fertilizer treatments (F1-With fertilizer and F2 –Without fertilizer) when they were grown alone (M, I, V), with their conspecific (MM, II, VV), and heterospecific neighbors (MV, MI, IV, IM, VM, VI), in the greenhouse experiment. The comparisons between fertilizer treatments for

each target species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.3.2 Seedling survival

There was a significant difference in seedling survival of *C. mopane* seedlings between fertilizer treatments when they were grown with heterospecific neighbors: *V. erioloba* (F=12.1, df1, p<0.01) and *C. imberbe* (F=0.9, df1, p<0.01), but not when they were grown alone (F=0.85, df1, p>0.05) or with their conspecific neighbors (F=1.6, df1, p>0.05). The addition of manure decreased the seedling survival of *C. mopane* in the presence of heterospecific neighbors; *V. erioloba* (F=7.9, df1, p<0.01) and *C. imberbe* (F=4.3, df1, p<0.001). There was also a significant difference in seedling survival of *C. imberbe* when it was grown alone (F=4.1, df1, p<0.001), with its conspecific neighbors (F=1.7, df1, p<0.01), with heterospecific *C. mopane* (F=5.9, df1, p<0.001) and *V. erioloba* (F=4.9, df1, p<0.05). Furthermore, there was a significant difference in seedling survival of *V. erioloba* seedlings between fertilizer treatments when they were grown with heterospecific neighbors; *C. mopane* (F=8.2, df1, p<0.001) and with *C. imberbe* (F=7, df1, p<0.001), but not when they were grown alone (F=1, df1, p>0.05) or with their conspecific neighbors (F=0.02, df1, p>0.05). The seedling survival was lower under the manure-treated plots when *V. erioloba* was grown with *C. mopane* (F=5.1, df1, p<0.05). However, survival increased in the presence of *C. imberbe* neighbors (F=4.9, df1, p<0.05) (fig.4.13c).

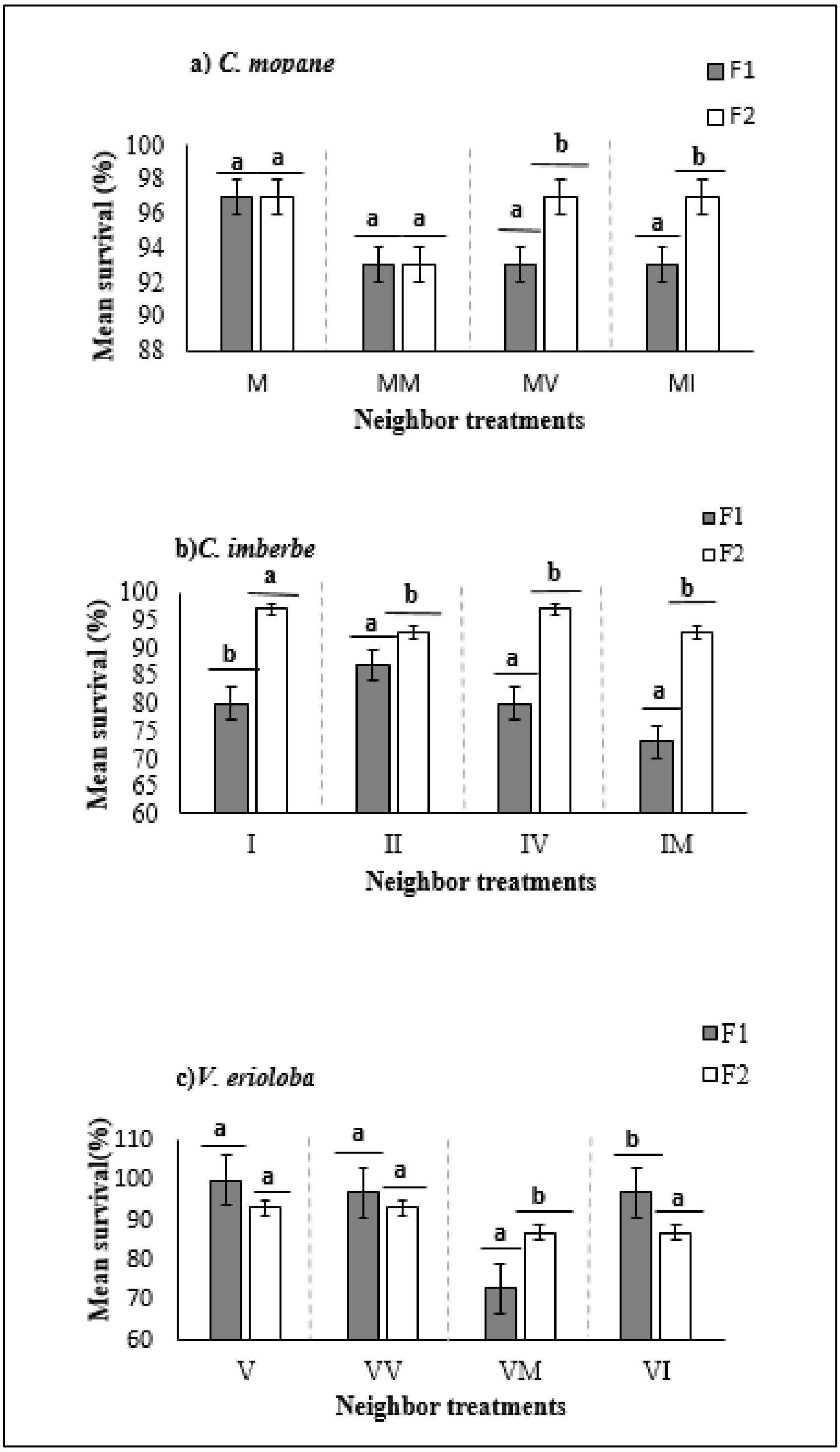

Figure 20 Mean percentage survival of study species; (a) M (*C. mopane*), (b) I (*C. imberbe*), and (c) V(*V. erioloba*) seedlings between fertilizer treatments (F1-With fertilizer and F2 –Without fertilizer) when they were grown alone (M, I, V), with their conspecific (MM, II, VV), and heterospecific neighbors (MV, MI, IV, IM, VM, VI), in the greenhouse experiment. The comparisons between fertilizer treatments for each

target species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.3.3 Leaf nitrogen content

The Generalized Linear Model (GLM) tests show that there was no significant difference in leaf nitrogen of *C. mopane* seedlings between fertilizer treatments when *C. mopane* was grown alone (F=0, df1, p>0.05), with conspecific neighbors (F=0.6, df1, p>0.05), with *C. imberbe* (F=2.4, df1, p>0.05) and *V. erioloba* (F=0.4, df1, p>0.05). However, there was a significant difference in leaf nitrogen content of *C. imberbe* between fertilizer treatments; when grown alone (F=5.4, df1, p<0.05) and when it was grown with *C. mopane* (F=6.9, df1, p<0.05), but not when it was grown with its conspecific neighbors (F=1.7, df1, p>0.05) or with *V. erioloba* (F=0.2, df1, p>0.05). The addition of manure increased the leaf nitrogen content of *C. imberbe* seedlings for all neighbor treatments (fig. 4.14). In addition, there was also a significant difference in leaf nitrogen content of *V. erioloba* between fertilizer treatments; when it was grown alone (F=4.6, df1, p<0.05), but not when it was grown with its conspecific neighbors (F=0.16, df1, p>0.05), with *C. mopane* (F=1.5, df1, p>0.05), or with *C. imberbe* (F=0.38, df1, p>0.05).

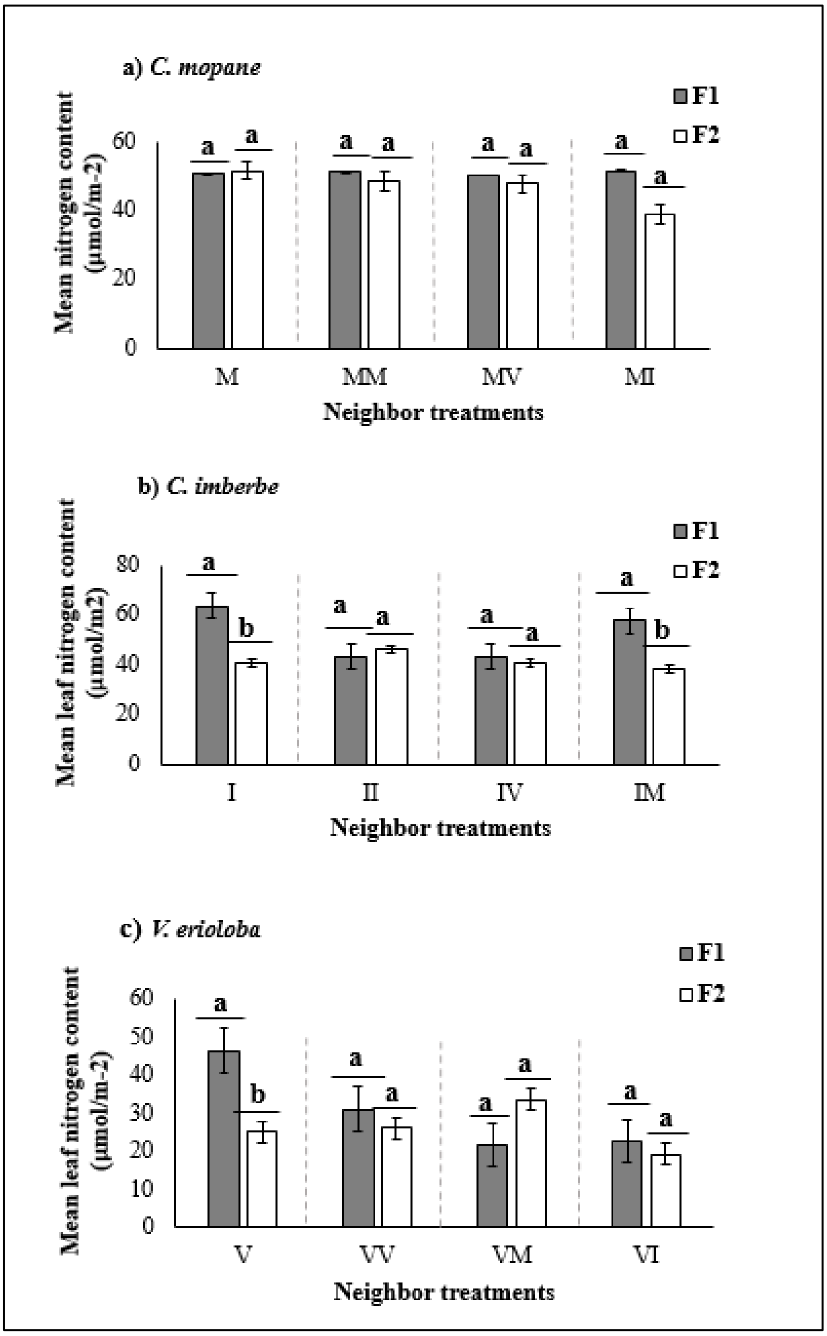

Figure 21 Average Leaf Nitrogen content (µmol/m-2) of (a) M (*C. mopane*), (b) I (*C. imberbe*), and (c) V(*V. erioloba*) seedlings between fertilizer treatments (F1-With fertilizer and F2 –Without fertilizer) when they were grown alone (M, I, V), with their conspecific (MM, II, VV), and heterospecific neighbors (MV, MI, IV, IM, VM, VI), in the greenhouse experiment. The comparisons between fertilizer treatments for each target species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.3.4 Leaf surface area

There was a significant difference in the leaf surface area of *C. mopane* seedlings between fertilizer treatments when they were grown with their conspecific neighbors (F=5.5, df1, p<0.05) or with *V. erioloba* (F=3.9. df1, p<0.05). The addition of manure positively influenced the leaf surface area of *C. mopane* in the presence of other conspecific seedling neighbors (F=9.2, df1, p<0.05), whereas it had reduced leaf area when grown with *V. erioloba* (fig. 4.15a). However, there was no significant difference in the leaf surface area of *C. mopane* seedlings when grown alone (F=0.3, df1, p>0.05) or with *C. imberbe* (F=5.9, df1, p>0.05). Furthermore, there was a significant difference in the leaf surface area of *C. imberbe* between fertilizer treatments; when *C. imberbe* was grown alone (F=8, df1, p<0.001), when it was grown with its conspecific neighbors (F=9.4, df1, p<0.05), when it was grown with *C. mopane* (F=6.9, df1, p<0.05), and with *V. erioloba* (F=23.4, df1, p<0.05). Moreover, there was a significant difference in the leaf surface area of *V. erioloba* between fertilizer treatments when it was grown alone (F=9.2, df1, p<0.05) and when it was grown with its conspecific neighbors (F=17.5, df1, p<0.001), but not when grown with *C. mopane* (F=0.3, df1, p>0.05), and with *C. imberbe* (F=2.2, df1, p>0.05). The addition of manure to the soil has increased seedling leaf surface area of *V. erioloba* when grown alone (F=7.5, df1, p<0.01) or with its conspecific neighbors (F=13, df1, p<0.05) (fig. 4.15c).

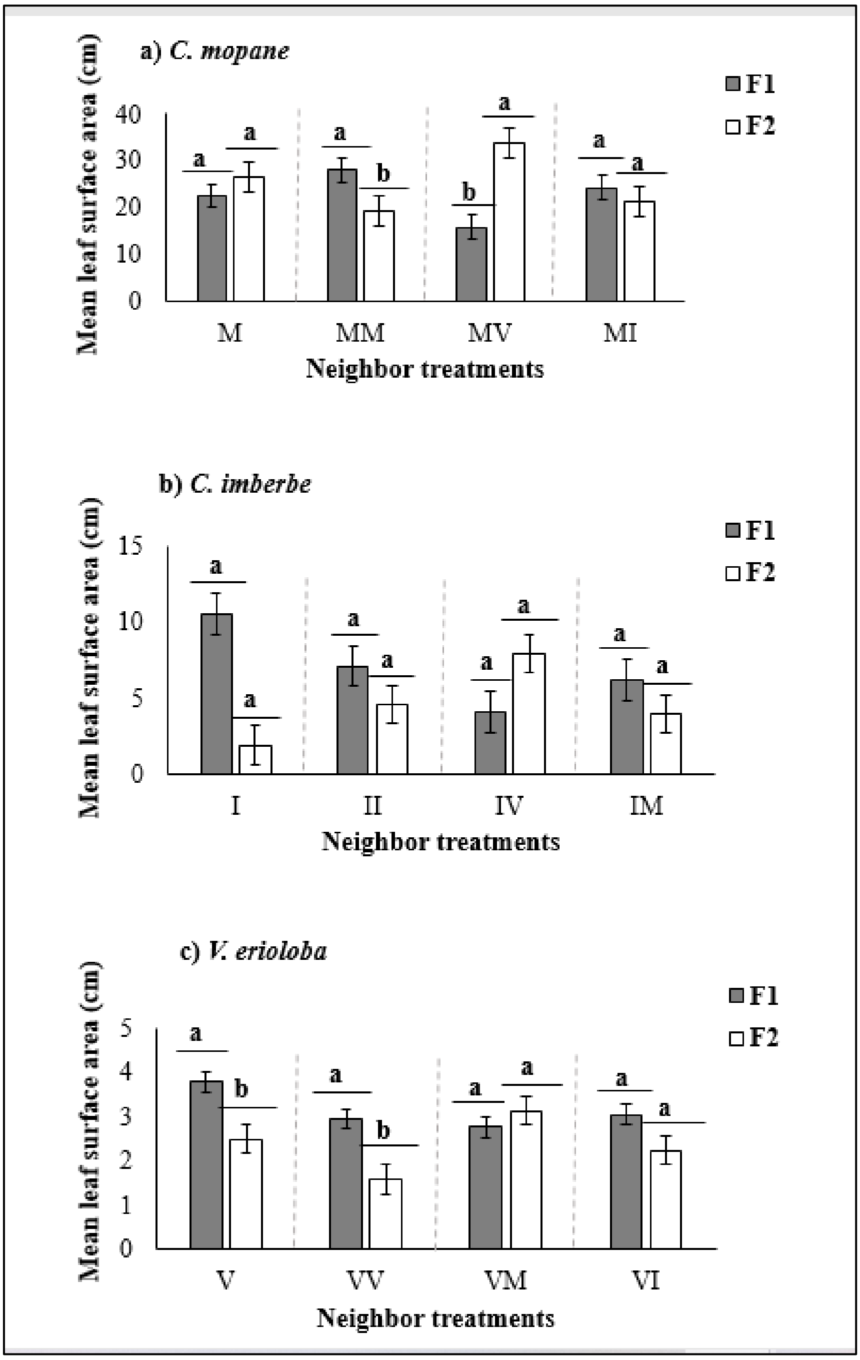

Figure 22 Average Leaf surface area (cm2) of (a) M (*C. mopane*), (b) I (*C. imberbe*), and (c) V(*V. erioloba*) seedlings between fertilizer treatments (F1-With fertilizer and F2 –Without fertilizer) when they were grown alone (M, I, V), with their conspecific (MM, II, VV), and heterospecific neighbors (MV, MI, IV, IM, VM, VI), in the greenhouse experiment. The comparisons between fertilizer treatments for each target

species were within neighbor combinations, separated by the faded lines. Different letters on the bars (e.g. a, b, c) indicate significant differences ($p < 0.05$).

4.4 Seedling recruitment

Species richness of self-recruited woody seedlings was higher in the presence of *C. mopane*, followed by *C. imberbe*. Particularly, more species were recorded around *C. mopane* when it was grown alone (6 species) and with conspecific neighbors (4 species) (Fig. 4.16). In contrast, the presence of *V. erioloba* showed a negative correlation with the species richness of recruited seedlings. Furthermore, the highest recruitment of native species occurred at a spacing treatment of 1 m between target species (fig.4. 17). This distance appears to provide an optimal balance between proximity to potential facilitative neighbors and reduced competition. Moreover, among self-recruited plants, *Vachellia* and *Terminalia* species outperformed adjacent target species in terms of height and cumulative stem length. The most abundant recruited species recorded was *C. mopane* in all distance treatments. Other self-recruited species included *Boscia foetida, Terminalia pruinoides, Ziziphus mucronata, Euphorbia sp*., and *Acacia sp.*

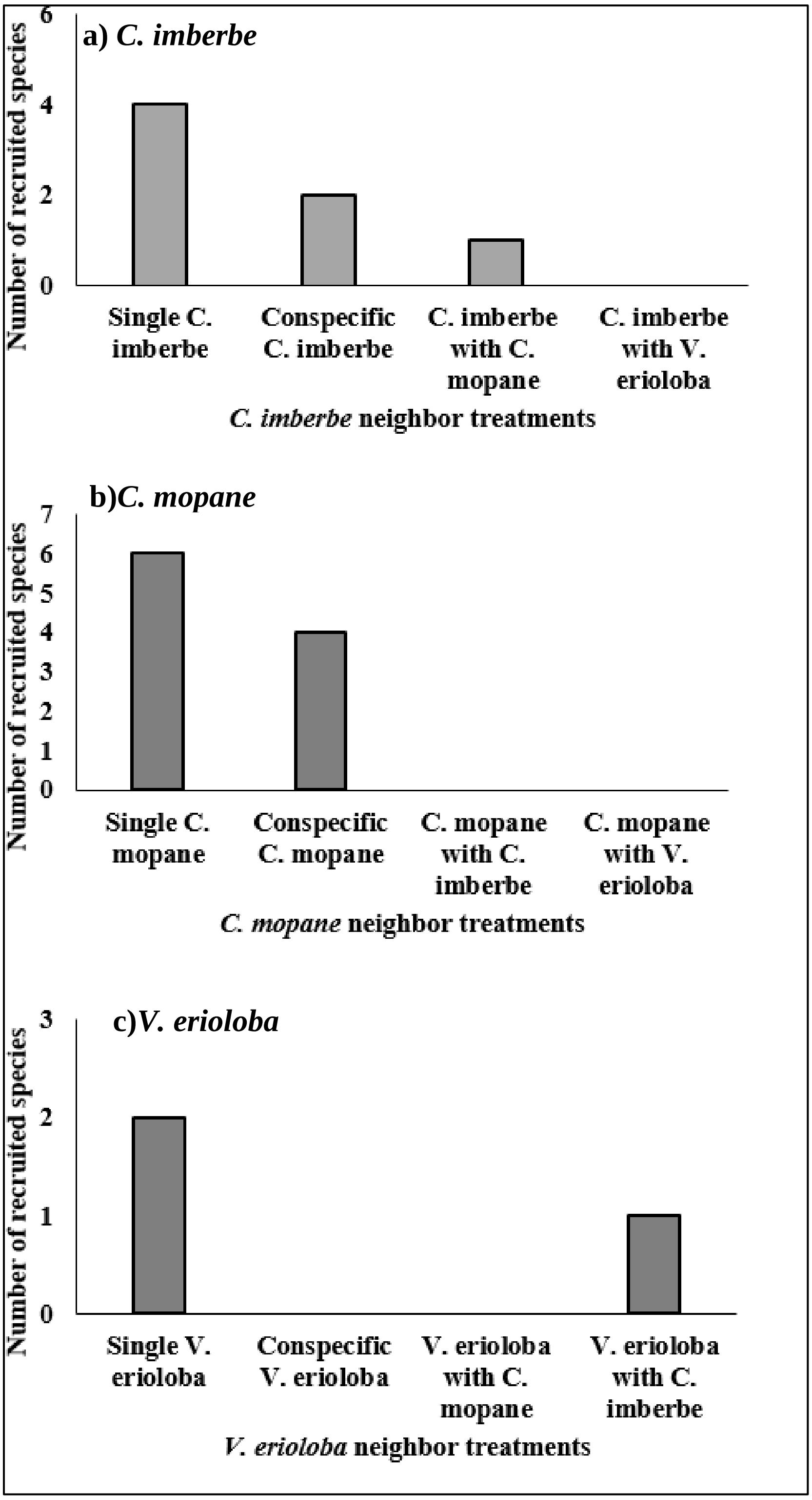

Figure 23 Number of different species recruited around the target species (a)*C. mopane,* (b) *C. imberbe*, (c) *V. erioloba*, between different neighbor treatments (single individuals, conspecific and heterospecific neighbors) in the field experiment.

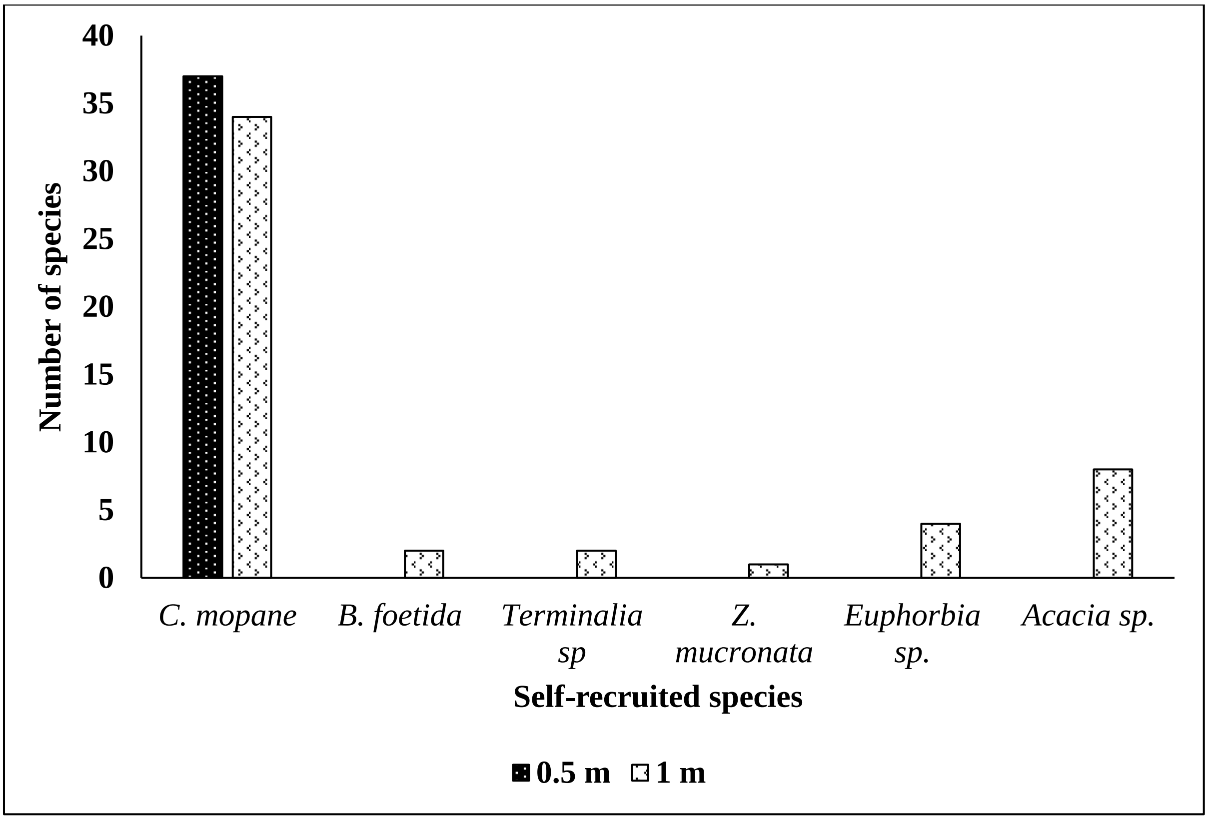

Figure 24 Species richness of self-recruited seedlings across distance treatments (0.5 m amd 1 m), in the field experiment.

5: DISCUSSION

5.1 The effect of neighbor treatments on the growth of target species (field experiment).

5.1.1. Seedling growth (cumulative stem length and estimated biomass)

The insignificant differences in growth, in terms of cumulative stem length and estimated biomass, between *C. mopane* and *V. erioloba* under varying neighbor treatments at distances of both 0.5 m and 1 m; suggests that the presence of neighboring seedlings did not significantly impact the growth of these target species compared to when they were grown alone. In acccordance to the ecological theory, plants in savanna ecosystems often compete vigorously for resources such as nutrients, space, and water (Ludwig et al., 2004). Competition can influence seedlings by altering resource availability or increasing susceptibility to stressors like diseases or herbivory (Champeau et al., 2013). However, this was a different case with *C. mopane* and *V. erioloba*.

Firstly, it is possible that *C. mopane* and *V. erioloba* employ efficient resource allocation strategies that minimize direct competition. These strategies could include differences in root depth or nutrient uptake patterns that allow them to access resources without significant overlap with neighboring plants (Ndjiondjop et al., 2016). Alternatively, these species may have influenced soil microbial communities in ways that enhance nutrient availability or alter soil conditions, thereby mitigating competitive pressures (Chen et al., 2018). In addition, the concept of compensatory growth may apply to this finding. A compensatory growth is defined as the ability of plants to offset the negative impacts of competition or damage by increasing growth rates or allocating resources differently (Li, 2021). This might have occurred between neighbor treatments of *C. mopane* and *V. erioloba,* allowing them to maintain similar growth rates across different treatments. Furthermore, according to Krug (2017), *C. mopane, C. imberbe,* and *V. erioloba* species are drought-resistant, and they are adapted to nutrient-poor soils, and therefore they can obtain minerals from the soil using their adaptive nutrient uptake strategies. Since these species can effectively obtain nutrients from their surroundings, neighboring plants that could potentially provide additional or reduce nutrients may not have a significant impact on their growth.

However, the results indicated an increase in cumulative stem length and estimated biomass of *C. imberbe* seedlings when they were grown with *V. erioloba* under the 1 m distance treatment. According to the facilitation theory, one species might profit from the presence or activity of its neighbors (Zélé et al., 2018), which could explain the growth performance of *C. imberbe* in the presence of *V. erioloba*. The findings suggest the possibility of a facilitative interaction between the species (*V. erioloba* and *C. imberbe*), meaning that the presence of *V. erioloba* may promote the growth of *C. imberbe*'s seedlings. In addition, there may have been reduced competition and more resources available (Bernhardt et al., 2020), which is responsible for the increase in cumulative stem length, similarly influencing the overall growth of *C. imberbe* when it was grown with *V. erioloba*.

5.1.2. Seedling survivorship

The significant differences in *C. mopane, C. imberbe,* and *V. erioloba*'s seedling survival among neighbor treatments, emphasize how crucial resource availability and inter-plant competition are to seedling viability in their early growth stages. As cited in Hortal et al., (2017), seedlings will likely compete with greater intensity for resources such as water and nutrients when planted close to one another. There was a decrease in seedling survival with the presence of neighbors for all target species under both 0.5 m and 1 m distance treatments, especially in the presence of *V. erioloba*. According to Mwangi et al., (2015), neighbors are capable of changing the soil microbial communities, which may adversely affect the survival of some species. Plant-plant interactions could involve mechanisms such as root exudation, where plants release substances into the soil that can influence neighbor seedlings' establishment (i.e., Koza et al., 2022). Therefore, alteration of soil communities by neighbors may result in an overall reduction in the availability of essential nutrients, reducing seedling survival.

However, there were no significant differences in seedling survival of *C. mopane* among neighbors when a 1 m distance between neighbors was used. This can be explained by the fact that the intensity of competition between neighbor seedlings decreases when seedlings are planted apart, making more space and resources accessible to each plant (i.e. Yin, et. al, 2023). It also implies that the effect of inter-plant competition on seedling survival of *C. mopane* decreases with increasing distance. According to Jiang, Cadotte and Jin (2022), seedling survival can be influenced by various factors, including short-term biotic interactions and longer-term abiotic conditions. Therefore, the response of *C. mopane* seedlings to the presence of neighboring seedlings may differ from that of *C. imberbe* and *V. erioloba*, indicating species-specific responses to interspecific interactions. In addition, the presence of neighbors may have influenced seedling survival indirectly by mediating trait variation, contributing to species-specific variation in traits with the species-specific variation in seedling survival (Jiang et al., 2022).

5.1.3. Leaf Nitrogen content

Overall results shows that there was a significant difference in leaf nitrogen content of *C. mopane*, *C. imberbe*, and *V. erioloba* seedlings among neighbor treatments. The results could be attributed to factors such as competition between neighbors, species-specific responses, resource partitioning and allocation, species variations, and root structures (Zhou et al, 2020). For *C. mopane*, the leaf nitrogen content was significantly different between conspecific neighbors when it was grown with *C. imberbe* or with *V. erioloba*; when a 1 m distance between seedlings was used. Growing *C. mopane* seedlings without neighbors may allow them to get most of the nutrients available in the soil, including nitrogen. Compared to seedlings growing with neighbors, those growing alone might be able to absorb more nitrogen from the soil, leading to increased leaf nitrogen content (Zhang et al., 2022). According to Qiao et al (2024), some heterospecific neighbors can form symbiotic relationships with neighboring plants (i.e. *C. mopane* seedlings and *V. erioloba*) that may improve the soil's nutrient availability, leading to increased leaf nitrogen contents (Qiao, et al., 2024). It is possible that when *C. mopane* was grown with *V. erioloba*, which is a nitrogen-fixing species, it could have enhanced positive interactions.

Furthermore, there was no significant difference in leaf nitrogen content of *C. imberbe* seedlings among neighbor treatments (zero neighbors, conspecific and heterospecific neighbors. To reduce competition for nitrogen with neighboring seedlings, *C. imberbe* may have implemented an efficient allocation of resources (i.e. Xuan, Chaohe, and

Dafeng, 2020). This can result in similar nitrogen content across the neighboring treatments. Another possibility is the fact that one of the target neighbor species (*V. erioloba*) can fix atmospheric nitrogen, which could contribute to the consistent leaf nitrogen content of *C. imberbe*, regardless of neighbor treatments. In addition to direct effects on nutrient availability, different plant species may have different abilities to efficiently obtain and use nitrogen from the soil (Ronald et al., 2012). For example, when *V. erioloba* seedlings were surrounded by heterospecific neighbors, their leaf nitrogen content decreased, possibly due to increased competition.

While *V. erioloba* is a nitrogen-fixing species that can increase soil nitrogen availability for the benefit of both itself and its neighbors, the results indicated that *C. mopane* seedlings had the highest leaf nitrogen content across all neighbor treatments. Various studies (e.g., Ward et al., 2000; Mlambo et al., 2012; Ben-Shahar, 2002) have confirmed that *C. mopane* can have higher leaf nitrogen than many other species. This may be because mopane trees have a higher capacity for nitrogen usage than *V. erioloba* (Mlambo, Nyathi, and Mapaure, 2005). As a result, mopane trees may be better at obtaining nitrogen from the soil than *V. erioloba*, or they allocate most of their nitrogen to the leaves to maximize production and build structural proteins. Mopane trees have tough, leathery leaves that may last longer than the softer leaves of *Vachellia erioloba*. Longer-lived leaves might collect and keep more nitrogen over time, leading to higher overall nitrogen levels when measured (Reich et al., 1998). According to Takashima, Hikosaka, and Hirose (2004), “there may be a trade-off in nitrogen partitioning between components pertaining to productivity (photosynthetic proteins) and those pertaining to persistence (structural proteins) of different species”. This trade-off may result in the convergence of leaf traits, where species with a longer leaf life span have a greater leaf mass per area (e.g., *C. mopane*), regardless of the environment (Takashima et al., 2004). This was confirmed by Krug (2017) that *C. mopane's* green leaves are very high in proteins, as well as the dry leaves can retain about 40% of their original leaf proteins.

Another point is that the target species have different root structures, where some roots may release substances that affect soil nitrogen, or even root traits that improve nutrient absorption (McNear, 2013). The root interactions between neighbor seedlings could also influence nutrient acquisition, hence the plant's above-ground growth and development. Furthermore, Makhado et al., (2018) stated that *C. mopane* trees have developed specialized root systems that allow them to access deeper soil, where nitrogen availability might be higher. In summary, the patterns observed in leaf nitrogen content among the three species may not only be attributed to interspecific competition or spacing, but also to functional traits such as nitrogen fixation in *Vachellia erioloba*, protein-rich, long-lived foliage in *C. mopane*, and root morphological adaptations that influence soil nitrogen uptake. These biological mechanisms help explain why *C. mopane* maintained higher nitrogen levels across treatments and why interactions with *V. erioloba* did not always result in the expected facilitative gains for its neighbors.

5.1.4 Surface leaf area

The presence of conspecific and heterospecific neighbors significantly impacted the leaf surface area of *C. mopane, C. imberbe* and *V. erioloba* seedlings. Plant neighbors can influence the leaf surface area of other plants through competition (Korpelainen and Sack, 2013). According to Pickett and Barker (2010), neighboring plants may have slower growth and development as a result of competing with neighboring plants for resources. Plants may allocate more nutrients to lateral growth, including leaf development, in the absence of neighbors because they have greater access to resources (Pickett and Barker, 2010).

In particular, *C. mopane* seedlings had larger leaves when they were grown with *V. erioloba* under 0.5 m distance treatment, and *C. mopane* had bigger leaves when it was growing alone or with its conspecific neighbors under 1 m distance treatment. This could suggest a complex interaction of competition, resource availability, and facilitation among these species' neighbors (Zélé, 2018). Although *C. mopane* has big leaves, they can still reduce their leaf surface area by folding the two sides together and preventing water loss (Krug, 2017). Conversely, *C. mopane* displayed bigger leaves when growing alone or with conspecific neighbors. Facilitative interactions between individuals of the same species might have promoted better growth conditions for *C. mopane* seedlings. *C. imberbe* was observed to have bigger leaves when grown with *C. mopane* or with neighbors of the same species.

For *V. erioloba*, bigger leaves were observed when *V. erioloba* was grown with *C. imberbe* under both 0.5 m and 1 m distance treatments. Plants grown together can benefit each other using mechanisms like the exchange of nutrients, allelopathy, or facilitation (Zélé et al., 2018). The presence of *C. imberbe* neighbors could enhance the nutrient availability for *V. erioloba* seedlings if there are any mutualistic relationships between them, leading to larger leaves. Furthermore, it was observed in the study experiment that *C. imberbe* grew taller with branching stems spread out, unlike *V. erioloba,* which lies on the ground lower than *C. imberbe*. In this case, *C.*

imberbe can shade the *V. erioloba* seedlings beneath, slightly affecting their exposure to light. As a result, the seedlings may respond physiologically to this change in light conditions by developing larger leaves to adjust to reduced light levels (Li, Liang, and Liu, 2022).

5.2 The effect of distance treatment between seedlings on the performance of target species (field experiment)

5.2.1 Seedling growth (cumulative stem length and estimated biomass)

The distance between seedlings can influence plant growth (Xu et al., 2023). Significant differences in cumulative stem length and biomass of *C. mopane* seedlings between distance treatments when grown with conspecific neighbors or *V. erioloba* suggest varying neighbor interactions. Growth was generally higher at the wider 1 m spacing, possibly due to reduced competition for resources (Callaway, 2007). When grown with *V. erioloba*, favorable interactions may have occurred (Goldberg et al., 1999), whereas intraspecific competition when grown alone or with conspecifics likely intensified due to overlapping resource demands. The lack of difference when grown with *C. imberbe* could imply minimal competitive overlap between the species due to different space requirements and tolerances.

Similarly, *C. imberbe* seedlings showed greater growth under wider spacing, particularly when grown alone, with *C. mopane*, or with *V. erioloba*. These results are consistent with findings that neighbors in close proximity experience more competitive stress than those spaced farther apart (Forrester , 2013; Bhandari et al., 2021). Wider distances may allow woody species to expand their root systems and reduce belowground competition (Wang et al., 2010). The sensitivity of *C. imberbe* to

V. erioloba suggests possible competition for shared resources. For *V. erioloba*, seedling growth was also greater under wider spacing when grown alone, with *C. imberbe*, or with conspecifics. This may be attributed to reduced resource competition at wider distances (Canham et al., 2004). The species' biomass responses appear to be species-specific, showing that *V. erioloba* has high stress tolerance but is particularly sensitive to conspecific density, as reflected in the significant difference under that treatment (Telford et al., 2023).

5.2.2 Seedling survival

The absence of significant differences in *C. mopane* seedling survival between distance treatments suggests that site conditions such as water, soil nutrients, and quality were adequate for seedling establishment, regardless of spacing. *C. mopane*'s ability to tolerate resource competition (Makhado et al, 2014) may also explain this outcome. The species is known to grow naturally in dense aggregates (<0.6 m) without clear differences in survival compared to widely spaced individuals, indicating crowding tolerance (Makhado et al., 2018).

For *C. imberbe*, survival varied significantly with distance when grown alone and with *V. erioloba*. Reduced competition when grown alone likely contributed to better survival (Craine and Dybzinski, 2013). In contrast, proximity to *V. erioloba* may have intensified resource competition, lowering survival at closer spacing. Although *C. imberbe* showed higher survival at 0.5 m, this may also reflect stress-induced mortality at narrow spacing due to intensified belowground competition (Jevon et al., 2020).

V. erioloba's influence may extend beyond resource competition. It is known to engage in allelopathic interactions, releasing secondary metabolites like phenolics and alkaloids that suppress neighboring plant growth (Grime and Jeffrey, 1995; Ward and Trollope, 2000; Kong et al., 2024). Such mechanisms may reduce *C. imberbe*'s survival near *V. erioloba*. Resource partitioning could also be a factor, where distinct species draw from different resource pools, affecting survival outcomes depending on distance (Bouchard et al., 2022). Similarly, *V. erioloba*’s survival was significantly influenced by spacing when grown alone or with heterospecific neighbors. In these cases, competitive interactions varied by species and spacing, highlighting the importance of species-specific responses (Åkesson et al., 2021). However, when grown with conspecifics, survival remained consistent, possibly due to shared growth patterns and resource needs.

5.2.3 Leaf nitrogen content

The significant differences in leaf nitrogen content observed for *C. mopane* between distance treatments when grown alone or with *C. imberbe* suggest that spatial arrangements can strongly influence nutrient uptake and foliar traits. In conditions where seedlings were spaced further apart (1 m), the likely reduction in below-ground competition allowed greater access to soil nutrients and water, contributing to elevated nitrogen accumulation in leaves (Jevon et al., 2020). These findings are consistent with the understanding that close plant proximity intensifies competition for limited resources, potentially suppressing nutrient acquisition efficiency. Moreover, the presence of heterospecific neighbors, such as *C. imberbe*, may further affect nutrient uptake through species-specific root interactions and partitioning mechanisms (Khan et al., 2022). Given that leaves are highly sensitive to environmental conditions, variation in leaf nitrogen content can serve as an important indicator of a species' adaptive strategy to spatial competition (Westoby and Wright, 2006).

For *C. imberbe,* a significant difference in leaf nitrogen content was only evident when the species was grown with *V. erioloba*, highlighting the potential importance of interspecific interactions. In contrast, spacing had no discernible effect when *C. imberbe* was grown alone or with other neighbors. This pattern indicates that nutrient uptake and distribution may be more strongly influenced by specific neighbor identity than by spacing alone, especially when involving dominant or functionally competitive species like *V. erioloba*. On another hand, several root-related physiological mechanisms may underlie these patterns. According to Huangfu, Hui, and Hu (2023), nutrient acquisition strategies in plants often involve modifications in root architecture, secretion of exudates, and symbiotic associations with mycorrhizal fungi. These adaptations enable plants to exploit different soil nutrient pools, often with species-specific costs and benefits. The observed influence of *V. erioloba* on nitrogen dynamics could be explained by the release of root exudates that alter microbial community composition and subsequently affect nitrogen cycling processes (Scarlett et al., 2021).

Furthermore, *V. erioloba* is a known nitrogen fixer and an ecologically dominant species capable of outcompeting neighbors for essential nutrients (Prayag et al, 2020; Kambatuku et al, 2013). Despite this competitive advantage, it consistently displayed lower leaf nitrogen content compared to *C. mopane* and *C. imberbe*. This counterintuitive result may reflect differential nitrogen allocation patterns. As suggested by Grossnickle and MacDonald (2018), some woody species allocate more nitrogen to below-ground structures such as roots, particularly under competitive conditions, to enhance nutrient foraging capacity. Zayed et al. (2023) further assert that nitrogen allocation toward root systems can significantly increase nutrient uptake potential, albeit at the expense of foliar nitrogen content.

Finally, *V. erioloba* also displayed a significant variation in leaf nitrogen content between distance treatments when grown alone and with *C. imberbe*, but not with conspecific neighbors or *C. mopane*. This outcome suggests that interspecific interactions and spacing jointly influence nitrogen dynamics. According to Morgan and Connolly (2013), under nutrient-limited conditions, plants often respond by altering their root architecture either increasing surface area or elongating roots to access distant nutrient sources. It is therefore plausible that wider spacing (1 m) enabled *V. erioloba* seedlings to expand their root systems and access greater volumes of nutrient-rich soil, resulting in higher leaf nitrogen levels than under more crowded conditions.

5.2.4 Leaf surface area

Variation in leaf size has important implications for plant responses to environmental change (Wang et al., 2019). Leaf surface area affects thermal regulation and water loss, which can differ significantly even among co-occurring species (Wright et al., 2017). In this study, significant differences in the leaf surface area of *C. mopane* were observed between distance treatments when grown alone and when paired with *V. erioloba*. Under competitive conditions, plants may adapt their leaf morphology to optimize resource capture (Reich, 2018). As *C. mopane* adjusted to closer spacing (0.5 m), it may have developed larger leaves to enhance light interception and outcompete neighboring *V. erioloba* seedlings. This trait plasticity could be linked to below-ground interactions, such as root competition or facilitation, influencing resource acquisition and allocation (Bell et al., 2021). Additionally, *V. erioloba* may have facilitated nutrient uptake, indirectly supporting increased leaf development in *C. mopane*.

Significant differences in *C. imberbe* leaf surface area were also observed between distance treatments when grown with conspecifics and with *C. mopane*. At closer spacing, competition likely triggered vertical growth strategies, resulting in smaller leaves; a common response to crowding stress (Wright et al., 2017). In drier environments, such as the study site, limited water availability under narrow spacing may further constrain leaf size (Basal et al., 2005; Sack and Holbrook, 2006). However, in contrast, *C. imberbe* seedlings grown with *V. erioloba* at 0.5 m displayed larger leaves, suggesting a facilitative interaction that may have reduced competition and enhanced growth.

For *V. erioloba*, a significant difference in leaf surface area was found between distance treatments under conspecific conditions. Larger leaves were recorded at the 1 m spacing, supporting the notion that reduced competition allows for more resource allocation to leaf expansion. However, as a drought-adapted species with inherently smaller leaves, *V. erioloba*'s leaf area is likely more constrained by its ecological strategy to minimize water loss than by neighbor spacing alone. This functional adaptation may explain its less pronounced response in leaf area across treatments.

5.3 The effect of fertiliser treatments on the performance of target species (greenhouse experiment)

5.3.1 Seedling growth (cumulative stem length and estimated biomass)

The results revealed significant differences in the cumulative stem length of *C. mopane* between fertilizer treatments, particularly when seedlings were grown alone or with *V. erioloba*. This suggests that manure positively influences *C. mopane* growth, especially in the absence of interspecific competition. Previous studies have shown that the addition of nitrogen and phosphorus nutrients present in manure can enhance the growth of *C. mopane* (Zhang, 2017). However, when grown with *V. erioloba*, the growth benefits from manure were reduced, likely due to below-ground competition. *V. erioloba* is known for its efficient nutrient uptake strategies, including competition for nitrogen (Ward et al., 2000), which may hinder *C. mopane*'s ability to fully utilize added nutrients under mixed plantings.

These outcomes are consistent with the understanding that plant responses to fertilization are influenced by both species-specific traits and environmental context (Davies, 2001; Liu et al., 2016). Manure also alters soil pH, microbial communities, and resource availability (Feng et al., 2024), which may have amplified benefits for *C. mopane* when grown alone but not under competitive conditions. For *C. imberbe,* significant differences in stem length were only observed when seedlings were grown with heterospecific neighbors (*C. mopane* or *V. erioloba*), suggesting that interspecific interactions influenced the effectiveness of manure treatments. This aligns with Bueno et al, (2019), who highlighted how nutrient competition dynamics in mixed plantings can shape species-specific growth outcomes.

In contrast, no significant differences in *V. erioloba* stem length were observed across fertilizer treatments. As a nitrogen-fixing species, *V. erioloba* forms symbiotic associations with rhizobia that allow it to fix atmospheric nitrogen (Schwember et al., 2019), reducing its dependence on external nutrient sources. This likely explains its stable growth response regardless of manure application.

Manure, as an organic fertilizer, plays a critical role in enhancing seedling health and biomass accumulation. It improves soil structure, water retention, and nutrient uptake (Liu et al., 2020;). The slow-release nature of manure ensures prolonged nutrient availability, supporting sustained seedling development (Kumar, 2012). In its absence, soils may be nutrient-deficient, resulting in reduced seedling vigor and biomass accumulation (Davies, 2001).

5.3.2 Seedling survivorship

Manure addition can influence seedling establishment either positively or negatively, depending on plant interactions and soil conditions (Shackelford et al., 2021). In this study, *C. mopane* seedlings showed significantly lower survival under manure treatment when grown with heterospecific neighbors (*V. erioloba* and *C. imberbe*), suggesting that nutrient enrichment intensified competitive interactions. Interestingly, *C. mopane* showed better survival without manure, indicating a potential competitive advantage under nutrient-limited conditions. This aligns with Browne et al. (2022), who found that seedling mortality may increase with higher soil nutrient content, especially nitrogen and phosphorus. While manure typically enhances soil fertility (Henuk and Dingle, 2003), excessive nitrogen levels may lead to nutrient imbalance and physiological stress in seedlings (Zayed et al, 2023). The higher survival of *C. mopane* in the control treatment, particularly when grown alone, supports the idea that manure-induced nutrient stress may have undermined performance in mixed-species settings.

For *C. imberbe*, survival was significantly affected by fertilizer treatments across all neighbor levels, with consistently higher survival in the absence of manure. The negative impact of manure was most apparent when *C. imberbe* was grown alone, but a significant interaction between neighbor presence and fertilizer suggests that interspecific competition also contributed to reduced survival. In mixed planting treatment, manure may exacerbate competition for nutrients, limiting *C. imberbe*'s ability to establish (Russo et al., 2019). These findings suggest that *C. imberbe* may be less tolerant of elevated nutrient levels, or slower to capitalize on nutrient enrichment compared to its neighbors.

Furthermore, *V. erioloba* seedling survival was significantly influenced by manure treatments only when grown with heterospecific neighbors. No significant differences were observed when seedlings were grown alone or with conspecifics, indicating that *V. erioloba* may rely less on external nutrient sources due to its nitrogen-fixing ability (Schwember et al., 2019). However, in heterospecific combinations, the improved nutrient availability from manure may have altered rhizosphere interactions, potentially promoting mutualistic associations that improved survival (Tamme et al., 2010). Still, excessive nutrient enrichment can negatively impact seedling establishment, particularly when nutrient uptake by conspecifics is limited, resulting in harmful nutrient accumulation (Khan et al., 2023).

5.3.3 Leaf nitrogen content

The results indicated that *C. mopane* seedlings showed no significant difference in leaf nitrogen content between fertilizer treatments across all neighbor levels. Whether grown alone or with *C. imberbe*, *V. erioloba*, or conspecifics, leaf nitrogen levels remained consistent, suggesting that factors beyond fertilizer application such as microbial symbiosis may play a more substantial role in nitrogen uptake. This finding contrasts with Pretorius et al. (2011), who reported increased leaf nitrogen in fertilized *C. mopane* trees. However, root-associated mutualisms may explain the limited fertilizer response. *C. mopane* is a legume known to thrive in nitrogen-poor soils, potentially due to associations with nitrogen-fixing endophytic bacteria inhabiting specialized coralloid-like lateral roots (Jordaan et al., 2000; Burbano et al., 2015). Such microbial interactions likely enable nitrogen acquisition independent of soil enrichment, thus masking the effects of manure treatments. Moreover, interactions with *V. erioloba*, another nitrogen-fixing species, may have further enhanced *C. mopane*'s nitrogen economy through facilitative effects. As Reid et al. (2024) noted, integrating nitrogen-fixing and non-fixing species in restoration improves nitrogen use efficiency, which may also reduce dependence on exogenous inputs.

In contrast, *C. imberbe* displayed significant differences in leaf nitrogen content between fertilizer treatments when grown alone and with *C. mopane*, but not with conspecifics or *V. erioloba*. Manure application increased leaf nitrogen levels across treatments, likely due to improved nutrient availability through gradual release

(Kumar, 2012). Differences in nutrient partitioning strategies in mixed-species arrangements (Saurav and Maharjan, 2023) may also have contributed to the variation. While *C. imberbe* responded positively to manure, the underlying mechanisms remain underexplored and warrant further investigation. For *V. erioloba*, no significant differences in leaf nitrogen content were found across fertilizer treatments at any neighbor level. As a leguminous nitrogen-fixer, *V. erioloba* forms symbiotic associations with rhizobia, enabling it to access atmospheric nitrogen (Lindström and Mousavi, 2020). This inherent ability likely minimized its dependence on external nitrogen inputs. Additionally, neighbor-induced resource competition may have masked any indirect fertilizer effects on leaf nitrogen content.

5.3.4 Surface leaf area

Surface leaf area plays a crucial role in photosynthetic capacity and overall plant fitness, directly influencing growth potential (Falster et al., 2018). In this study, *C. mopane* seedlings displayed significantly larger leaf surface areas under manure treatment when grown with conspecific neighbors. This suggests that organic fertilization enhanced resource availability, promoting leaf expansion within conspecific groupings. However, no significant differences were observed when *C. mopane* was grown with heterospecific neighbors, implying that neighbor identity and associated interactions may modulate nutrient response. These results align with Liu et al. (2012), who reported that species such as *C. mopane* display rapid growth and larger leaf development in fertile soils but are constrained in nutrient-poor environments.

For *C. imberbe*, significant differences in leaf surface area between fertilizer treatments were observed across neighbor combinations, particularly in the presence of heterospecifics. This finding suggests a strong interactive effect between manure and interspecific competition. Manure likely enhanced nutrient availability, and its combination with neighbor interactions may have led to synergistic effects on leaf morphology (Kichamu-Wachira et al., 2023). The complexity of these outcomes emphasizes the role of both biotic (neighboring species) and abiotic (fertilizer) factors in shaping leaf trait responses.

V. erioloba seedlings also showed significantly increased leaf surface area under manure treatment when grown with conspecifics. This indicates that nutrient enrichment may support foliar development when intraspecific interactions are present. However, when grown alone or with heterospecifics, manure had a limited impact, likely due to *V. erioloba*'s conservative growth strategy and adaptation to low-resource environments (Krug, 2017). With its naturally reduced leaf area; a trait that minimizes water loss in arid ecosystems, *V. erioloba* may display limited plasticity in response to external nutrient inputs (Davies, 2001; Liu et al., 2012).

5.4 Seedling recruitment

Seedling recruitment is fundamental for the regeneration and persistence of woody plant communities in degraded ecosystems. In this study, species richness of self-recruited seedlings was higher in the presence of *C. mopane*, particularly when it was grown alone or with conspecific neighbors. This supports the notion that certain woody species can act as facilitators by modifying microclimatic conditions or enhancing soil nutrient availability, thereby creating favorable niches for other species (Pringle et al., 2012).

In addition, the presence of *C. mopane* appears to enhance such facilitative effects, potentially due to its canopy structure, leaf litter, or microbial associations. In contrast, the presence of *V. erioloba* was associated with lower species richness and abundance of recruited seedlings, suggesting a competitive influence. This aligns with findings from arid ecosystems where dominant species can suppress recruitment of others through intense resource competition (Schwinning and Sala, 2004). In addition, distance treatments also played a critical role in shaping recruitment dynamics. The wider 1-meter spacing between target seedlings was associated with the highest richness and abundance of self-recruited species. This spacing may balance facilitation and competition, reflecting natural spatial patterns that support species coexistence (Pugnaire et al., 2004). In denser plots (0.5 m spacing), intense below- and above-ground competition likely limited germination and establishment.

Seedling recruitment is also influenced by other ecological factors, such as dispersal, dormancy, and germination capacity. The frequent occurrence of *C. mopane* as a recruited species across both spacing treatments could reflect its rapid germination and high survival rate under local conditions (Inman, 2020). Particularly, some recruited species such as *Terminalia sp*. and *Vachellia sp* surpassed target seedlings in height and stem length, likely due to inherent drought resilience and efficient resource uptake (Vadigi and Ward, 2013). Although statistical comparisons were limited by uneven recruitment patterns and small sample sizes, a multivariate PCA effectively illustrated associations between neighbor identities, spacing, and the composition of recruited species.

6: CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study investigated the influence of seedling neighbors (conspecific and heterospecific), distance between seedlings, and organic fertilizer treatment on the early performance of three woody species; *Combretum imberbe*, *Colophospermum mopane*, and *Vachellia erioloba*, within a restoration context in the semi-arid Kunene Region, Namibia. The study contributes valuable insights into plant-plant interactions, spatial planting strategies, and early recruitment dynamics for woody species restoration in dryland ecosystems.

Combretum imberbe demonstrated improved growth performance, particularly in terms of cumulative stem length and leaf surface area, when grown with conspecific neighbors under wider spacing (1 m). Fertilizer application improved its leaf nitrogen content and leaf size, especially when grown alone or with *C. mopane*, but reduced survival overall,suggesting that manure addition may not be beneficial during the early establishment phase. Recruitment around *C. imberbe* was moderate, indicating that while it may not strongly facilitate other species, it performs well when given space and minimal competition.

Colophospermum mopane consistently showed strong performance across multiple parameters. It had the highest recruitment rates of self-seeded species when grown alone or with conspecific neighbors, suggesting facilitative traits. Growth and biomass accumulation were significantly higher under 1 m spacing, and although manure improved certain traits like leaf size, its presence in combination with neighbors reduced survival. *C. mopane* showed resilience and self-reliance, likely due to its capacity to access deep soil nutrients and harbor beneficial root microbiota, making it a key species for initiating woody cover in degraded systems.

Vachellia erioloba had a strong influence on neighboring seedlings, often reducing their growth, survival, and nitrogen uptake. Despite its ability to fix atmospheric nitrogen, *V. erioloba* did not significantly benefit from manure addition and demonstrated lower recruitment potential. While it grew better at wider spacing, its presence often coincided with decreased seedling recruitment, possibly due to its competitive dominance and allelopathic potential. This suggests that *V. erioloba* may be more suitable for monoculture or boundary planting in restoration areas where high diversity is not a priority.

6.2 Recommendations

The target species are recommended for restoration due to their excellent performance (growth and survival) under different conditions. They have proved to have the potential to restore a degraded area. Based on the study findings, it is recommended that *C. mopane* be prioritized as a foundational species in restoration programs in semi-arid ecosystems, particularly when the goal is to enhance recruitment and natural regeneration. Its robust performance under both isolated and conspecific conditions, especially at a wider spacing of 1 meter, makes it a suitable candidate for initiating revegetation efforts. Fertilizer may be used cautiously with *C. mopane* when planted alone, but should be avoided in competitive settings as it reduces survival.

For *C. imberbe*, planting at wider spacing (1 m) is recommended, especially in combination with other species such as *C. mopane*. Its survival and growth may be compromised by fertilizer in early stages, thus manure application should be limited or deferred. However, *C. imberbe* is a valuable species due to its growth potential and response to spacing, making it ideal for mixed-species restoration strategies where structural diversity is desired. While *V. erioloba* should be incorporated selectively into restoration trials, preferably at low densities or along margins of restoration plots. Due to its competitive nature and suppressive effect on recruitment, it is less suitable for central or dense interplanting schemes where facilitation is a priority. Fertilizer application does not improve its performance, and in some cases, may exacerbate interspecific competition. Given its adaptations to harsh conditions, *V. erioloba* may be best used in drier, nutrient-poor zones or as a nurse species for very specific facilitative arrangements.

Furthermore, the use of manure in restoration should be tailored based on species combinations and planting objectives. While it can enhance leaf traits in certain species, its negative effect on survival particularly in competitive conditions, indicates the need for cautious application. Slow-release organic amendments or soil microbial enhancers could be explored in future trials to achieve more balanced nutrient availability.

The study further recommends that a monitoring period of at least >2 years be instituted post-planting to assess long-term growth trends, species-specific interactions, and seedling recruitment patterns. Monitoring should ideally occur twice per year, during the peak of the rainy season and at the end of the dry season, to capture performance variation under different climatic conditions. Additional research integrating soil microbial analysis, root architecture studies, and water-use efficiency is also advised to better understand the underlying mechanisms driving facilitation and competition in woody plant restoration.

Moreover, future research could delve deeper into understanding the mechanisms underlying neighbor interactions and nutrient dynamics in savannah ecosystems. Exploring genetic diversity within target species and its implications for adaptation and resilience could also further refine restoration approaches. Additionally, integrating advanced modelling techniques to predict species interactions under changing environmental conditions would advance our ability to forecast and manage restoration outcomes effectively.

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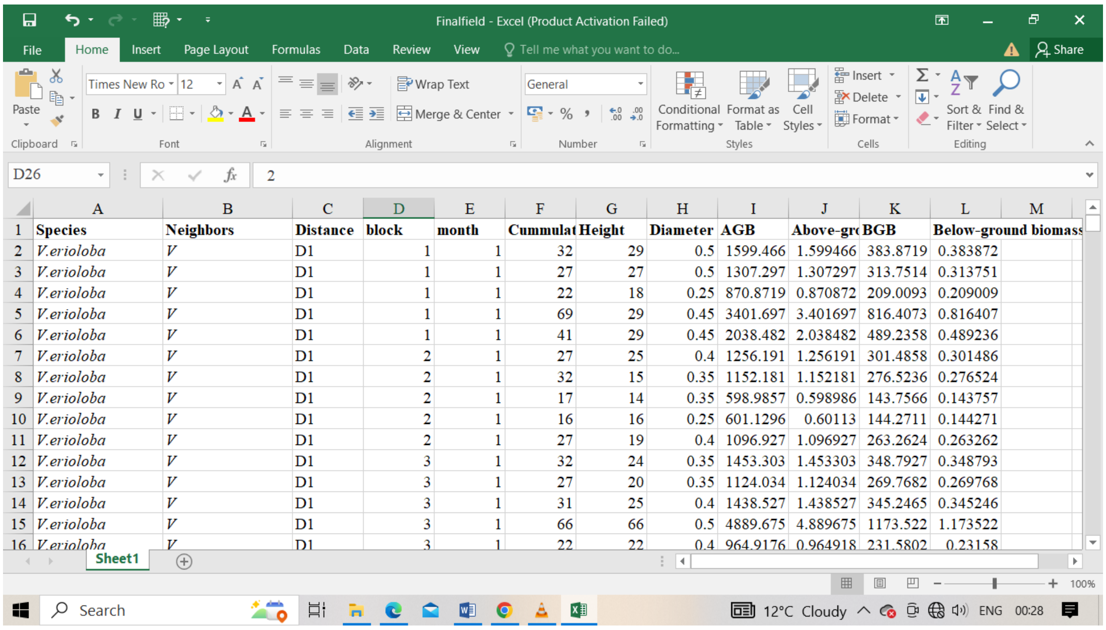
APPENDICES

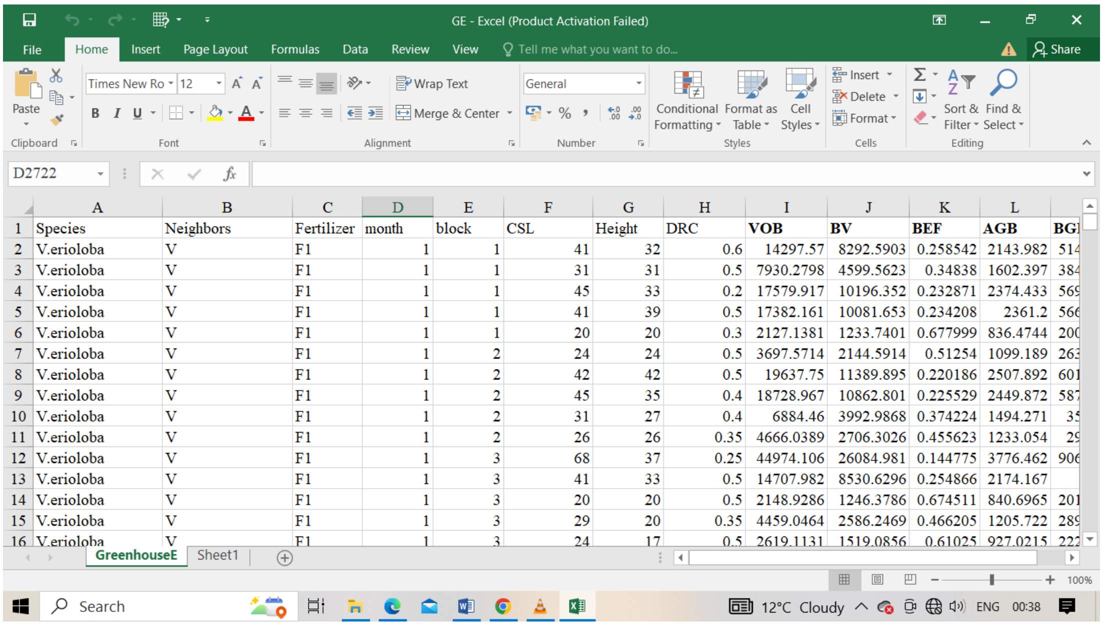
Appendix 1: The raw data used for analysis collected from the field experiment



D26 = 2

	A	B	C	D	E	F	G	H	I	J	K	L
1	**Species**	**Neighbors**	**Distance**	**block**	**month**	**Cummulat**	**Height**	**Diameter**	**AGB**	**Above-gr**	**BGB**	**Below-ground biomass**
2	*V.erioloba*	*V*	D1	1	1	32	29	0.5	1599.466	1.599466	383.8719	0.383872
3	*V.erioloba*	*V*	D1	1	1	27	27	0.5	1307.297	1.307297	313.7514	0.313751
4	*V.erioloba*	*V*	D1	1	1	22	18	0.25	870.8719	0.870872	209.0093	0.209009
5	*V.erioloba*	*V*	D1	1	1	69	29	0.45	3401.697	3.401697	816.4073	0.816407
6	*V.erioloba*	*V*	D1	1	1	41	29	0.45	2038.482	2.038482	489.2358	0.489236
7	*V.erioloba*	*V*	D1	2	1	27	25	0.4	1256.191	1.256191	301.4858	0.301486
8	*V.erioloba*	*V*	D1	2	1	32	15	0.35	1152.181	1.152181	276.5236	0.276524
9	*V.erioloba*	*V*	D1	2	1	17	14	0.35	598.9857	0.598986	143.7566	0.143757
10	*V.erioloba*	*V*	D1	2	1	16	16	0.25	601.1296	0.60113	144.2711	0.144271
11	*V.erioloba*	*V*	D1	2	1	27	19	0.4	1096.927	1.096927	263.2624	0.263262
12	*V.erioloba*	*V*	D1	3	1	32	24	0.35	1453.303	1.453303	348.7927	0.348793
13	*V.erioloba*	*V*	D1	3	1	27	20	0.35	1124.034	1.124034	269.7682	0.269768
14	*V.erioloba*	*V*	D1	3	1	31	25	0.4	1438.527	1.438527	345.2465	0.345246
15	*V.erioloba*	*V*	D1	3	1	66	66	0.5	4889.675	4.889675	1173.522	1.173522
16	*V.erioloba*	*V*	D1	3	1	22	22	0.4	964.9176	0.964918	231.5802	0.23158

Appendix 2: The raw data used for analysis collected from the greenhouse experiment



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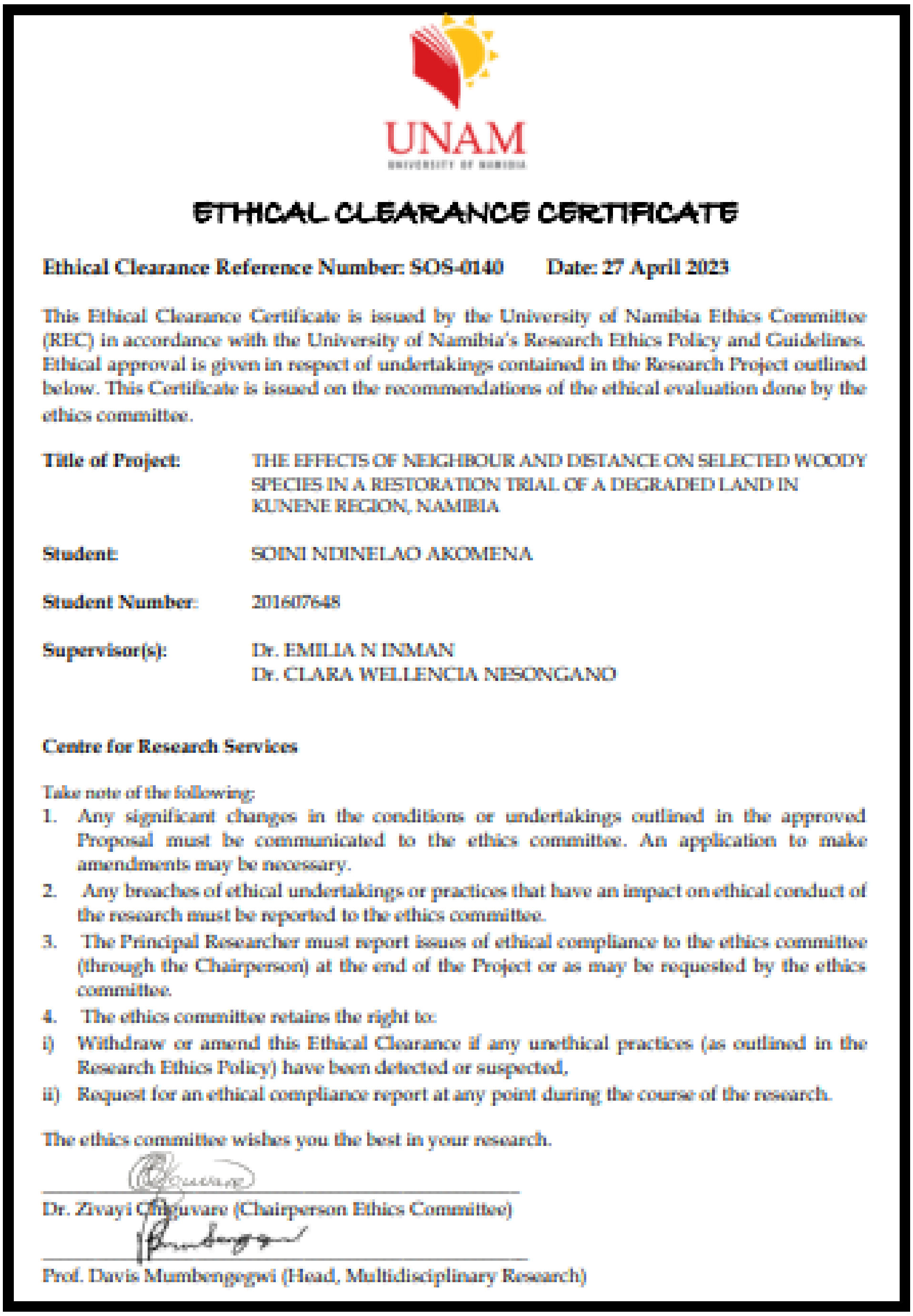
	A	B	C	D	E	F	G	H	I	J	K	L	
1	Species	Neighbors	Fertilizer	month	block	CSL	Height	DRC	**VOB**	**BV**	**BEF**	**AGB**	**BG**
2	V.erioloba	V	F1	1	1	41	32	0.6	14297.57	8292.5903	0.258542	2143.982	514
3	V.erioloba	V	F1	1	1	31	31	0.5	7930.2798	4599.5623	0.34838	1602.397	384
4	V.erioloba	V	F1	1	1	45	33	0.2	17579.917	10196.352	0.232871	2374.433	569
5	V.erioloba	V	F1	1	1	41	39	0.5	17382.161	10081.653	0.234208	2361.2	566
6	V.erioloba	V	F1	1	1	20	20	0.3	2127.1381	1233.7401	0.677999	836.4744	200
7	V.erioloba	V	F1	1	2	24	24	0.5	3697.5714	2144.5914	0.51254	1099.189	263
8	V.erioloba	V	F1	1	2	42	42	0.5	19637.75	11389.895	0.220186	2507.892	601
9	V.erioloba	V	F1	1	2	45	35	0.4	18728.967	10862.801	0.225529	2449.872	587
10	V.erioloba	V	F1	1	2	31	27	0.4	6884.46	3992.9868	0.374224	1494.271	35
11	V.erioloba	V	F1	1	2	26	26	0.35	4666.0389	2706.3026	0.455623	1233.054	29
12	V.erioloba	V	F1	1	3	68	37	0.25	44974.106	26084.981	0.144775	3776.462	906
13	V.erioloba	V	F1	1	3	41	33	0.5	14707.982	8530.6296	0.254866	2174.167	
14	V.erioloba	V	F1	1	3	20	20	0.5	2148.9286	1246.3786	0.674511	840.6965	201
15	V.erioloba	V	F1	1	3	29	20	0.35	4459.0464	2586.2469	0.466205	1205.722	289
16	V.erioloba	V	F1	1	3	24	17	0.5	2619.1131	1519.0856	0.61025	927.0215	222

Appendix 3: Ethical clearance certificate



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ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: SOS-0140 **Date: 27 April 2023**

This Ethical Clearance Certificate is issued by the University of Namibia Ethics Committee (REC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the ethics committee.

Title of Project:	THE EFFECTS OF NEIGHBOUR AND DISTANCE ON SELECTED WOODY SPECIES IN A RESTORATION TRIAL OF A DEGRADED LAND IN KUNENE REGION, NAMIBIA
Student:	SOINI NDINELAO AKOMENA
Student Number:	201607648
Supervisor(s):	Dr. EMILIA N INMAN Dr. CLARA WELLENCIA NESONGANO

Centre for Research Services

Take note of the following:

1. Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the ethics committee. An application to make amendments may be necessary.
2. Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the ethics committee.
3. The Principal Researcher must report issues of ethical compliance to the ethics committee (through the Chairperson) at the end of the Project or as may be requested by the ethics committee.
4. The ethics committee retains the right to:

i) Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,
ii) Request for an ethical compliance report at any point during the course of the research.

The ethics committee wishes you the best in your research.

Dr. Zivayi Chiguvare (Chairperson Ethics Committee)

Prof. Davis Mumbengegwi (Head, Multidisciplinary Research)