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**THE PHYSIOLOGY OF SPROUTING AND ITS ECOLOGICAL IMPLICATIONS FOR
SAVANNA WOODLAND DYNAMICS IN THE NYLSVLEY NATURE RESERVE,
LIMPOPO PROVINCE, SOUTH AFRICA**

By

Maanda Hadzhi Ligavha-Mbelengwa (Student Number 8300491)

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Thesis submitted in fulfilment of the requirements for the degree of **Doctor of Philosophy**

In the

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DECLARATION

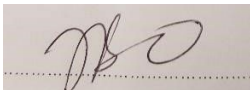
I, Maanda Hadzhi Ligavha-Mbelengwa, declare that the PhD thesis is submitted to the Faculty of Science, Engineering and Agriculture, University of Venda, fulfilling the requirements of Doctor of Philosophy. References cited in the writeup have been acknowledged. The statistician analysed the raw data in accordance with my instructions, and I provided the final results interpretation for report writing.



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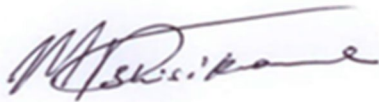
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Date

DEDICATION

I dedicate my work to relatives, for always encouraging me to put together work of this magnitude to completion.

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God is praised for His grace; I thank the Biological Sciences Department for permission to study. My supervisors, Professors O Ogola and MP Tshisikhawe are indeed thanked for supporting me fully throughout the whole journey of my PhD work. I also thank all the botany students who assisted me with data collection in the field. Nylsvley Nature Reserve management is thanked for permission to conduct my research in their reserve; their assistance is indeed appreciated.

ABSTRACT

Disturbance in its various forms is an integral component of any ecosystem, and it contributes significantly to the patterning of the vegetation. Many savanna plant species survive disturbance, such as cutting or clipping, through resprouting. Sprouting is important, particularly in situations where chances for the establishment of seedlings is rare. High disturbance intensity suppresses plant recovery, while low disturbance intensity stimulates plant regrowth. Disturbing plants frequently depletes stored carbohydrate reserves which are indispensable for regrowth, while disturbing plants less frequently allows plants space to accumulate root carbohydrate reserves. Savanna plants in game reserves are usually exposed to disturbance in the form of grazing, browsing, accidental fires, and competition. It is necessary to comprehend how savanna plant species respond to the disturbance for the sustenance of the life of the game in those ecosystems. This study assessed how savanna plants (i) respond to cutting, (ii) relate to bark thickness, stem diameter, and fire, and (iii) respond to release from competition.

Chapter 3 of the current thesis experimented on juveniles of the two savanna plant species, namely *Dichrostachys cinerea* (*D. cinerea*) and *Terminalia sericea* (*T. sericea*), and Chapter 4 experimented on seedlings and juveniles of the same two savanna plant species referred to in chapter 3. Juvenile individuals that were utilized for experimentation in chapter 3 were not the same as those utilized in Chapter 4. *Dichrostachys cinerea* (*D. cinerea*) and *Terminalia sericea* (*T. sericea*), were subjected to clipping. In one instance, a group of juvenile plants per species was cut seasonally during the first year of experimentation for the whole experimental period, while in another instance, seedlings

and juveniles were cut; the responses of plants were monitored and compared in both instances. Clipping of individual plant species monthly in the year simulated how seasons differentially affect plants' responses to cutting. The study was carried out for two and half years. The heights of cut plants were compared to establish how the plants responded to clipping. The heights of the plants were measured in both instances only towards the conclusion of the experiments. The bark thickness, and stem diameter of plants of different age groups were measured using Vernier callipers and diameter tapes, respectively. Gaps created between grass plants were measured pre- and post-removal of their potential competitors.

All the individual plant species that were clipped anyhow survived clipping throughout the experimental period. Winter-clipped plant species generally outgrew plants that were clipped in other seasons, probably due to ample carbohydrate root reserves during this season of the year. Juveniles grew faster than seedlings in terms of height when both were cut at the same time of the day, presumptively due to more carbohydrates in their roots than in those of the seedlings. More seedlings died than juveniles when both were exposed to the same fire intensity. We found root reserves affected differentially between seasons of the year. The bark thickness increased with plant age and height to about 50 cm in trunk circumference; thereafter, the relationship was inconsistent. Openings that resulted when grass plants competed for resources such as moisture became readily available for invasion by new plant species, mainly alien plants. Managed disturbance is thus important and necessary to maintain ecosystems in balance. Communities should thus be educated on how savanna ecosystems respond to disturbances at different seasons of the year to mitigate

situations where our savanna ecosystems could be converted into ecosystems that are not suitable for savanna games.

ABBREVIATIONS AND ACRONYMS

ANOVA	Analysis of Variance
IAPS	Alien Invasive Plant Species
NNR	Nylsvley Nature Reserve
SADC	Southern African Development Community
SPSS	Statistical Package for Social Sciences
TNC	Total Non-Structural Carbohydrates

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CHAPTER 1 OVERVIEW OF THE STUDY

1.1 INTRODUCTION

Disturbance can be defined as a physical process that brings a perturbation, to an ecosystem; it plays a pivotal role in changing natural vegetation. For example, the changes could be from grasslands to forests or savannas to bushes. The change in vegetative composition and the structure of vegetation depends on disturbance factors like season, disturbance type, and disturbance size amongst other factors. Any type of disturbance, for example, fire, may determine which functional groups prevail in the disturbance-prone ecosystems (Bond *et al.*, 2003). The disturbance may lead to the elimination of unwanted vegetation types, which would be replaced by "useful" ones, and *vice versa*; for example, shrublands and scrublands could be exterminated in favour of grasslands by frequent burning (Bond *et al.*, 2005; Uys *et al.*, 2004). In contrast, shrublands and scrublands could be promoted in what was originally savanna by suppressing fire for long periods (D'Odorico, Okin, and Bestelmeyer, 2012; O'connor, Puttick, and Hoffman 2014; Ward, 2005; Bond and van Wilgen, 1996).

Globally, tree-grass combinations have been impacted by the development of the human population and the extensive Anglo-European expansion (Scholes and Archer, 1997). Large-scale tree cutting for agriculture, timber, and fuel has resulted in degraded or anthropogenic savannas, and fragmented forests (Young and Solbrig, 1993). Moreover, herbaceous degradation has been brought about by livestock introduction amongst other factors (Miller and Wigand, 1994; Scholes and Archer, 1997).

Some areas that were once forests are now savannas, while areas that were once grasslands are now shrublands/woodlands with little or no grass biomass because of anthropogenic activities (Bond and Midgley, 2012; Scholes and Archer, 1997). Archer (1996) reported on the role of human activities as factors that contributed to the changes that we see today.

Savanna can be explained as a type of grassland, that is flat, with scattered and widely spaced trees (Higgins *et al.*, 2000), and is in between grasslands and forests (Bond and Midgley, 2012). This ecosystem is composed of plants of different age groups, such as seedlings, which are plants at their earliest stages of germination, saplings which are the young trees older than seedlings but younger than juveniles and generally with slender trunks, juveniles that are not yet at the reproductive stages older than saplings, and adults which are already at their reproductive stages.

Some of the trees that are commonly found distributed in the Nylsvley Nature Reserve savanna ecosystem are *Burkea africana*, *Dichrostachys cinerea*, *Terminalia sericea*, and *Vachellia karoo* (Figures 1.1 through 1.4), amongst others.



Figure 1.1: Nylsvley Nature Reserve sandy area with *Burkea africana*, *Terminalia sericea*, and some other bushy species scattered within the grasses.



Figure 1.2: Nylsvley Nature Reserve sandy area dominated by *Dichrostachys cinerea*.



Figure 1.3: Terminalia sericea in one of the sandy areas of Nylsvley Nature Reserve.



Figure 1.4: Nylsvley Nature Reserve with *Vachellia karoo* individuals densely populating a clayey waterlogged belt.

They are found in the tropics and subtropics, mainly in areas characterized by rainfall that ranges between 350 mm and 1800 mm per annum. High temperatures and wet and dry seasons are characteristics of such savannas (Sarmiento, 1992). The production of herbaceous biomass is impacted by the significant seasonal variations in rainfall in these places (Magandana *et al.*, 2020). Since ancient times, savanna habitats have been utilized in these areas for the production of cattle due to the comparatively good quantity of grass biomass they contain. But as cow production has expanded over time, savannas have seen an increase in woody plant density, or "bush encroachment" (Archer, 1997).

Savanna ecosystems are suitable for a variety of animals and are abundant in vegetation and wildlife. Many different types of species rely on the plants there as a source of nutrition and energy. Savanna ecosystems make up most nature reserves and parks (Bond and Midgley, 2005). According to Primack (1993), microbes assist in cleaning up the environment around pollination agents like insects and birds.

Disturbances like fire, storms, falling trees, pruning, branch fall, and herbivory cause the biomass of aboveground plants to be removed partially or entirely from all terrestrial ecosystems. After such disturbances, regenerating plants enable them to regain their height and leaf area. There are reports by some researchers on regenerating plants being the dominant pathway, which may have significant effects on the dynamics of vegetation of those communities (Bellingham and Sparrow, 2000; Loehle, 2000). Despite having been reported as an important component of the life history of plants in many plant biomes (Bond and Midgley, 2001; Vesk and Westoby, 2004), resprouting is nevertheless less included in routine plant strategy schemes (Westoby, 1998) for temperate forests (Loehle, 2000) and

Mediterranean woodlands (Pausas *et al.*, 2004). The existing information reported about woody plant resprouting is from fire-adapted systems, where species are categorized as capable of regrowing or producing seeds, with different ways of co-existed attributes (Pate *et al.*, 1990; Pausas *et al.*, 2004).

However, some systems with weaker disturbances are not affected by such a binary strategy as reported by Vesk and Westoboy (2004). It was suggested that an additional axis of strategy variation may exist and contribute to species diversity and coexistence (Dietze and Clark 2008). Salguero-Gómez (2018) did highlight that the regrowth behaviour of North American tree species was weakly correlated with other life-history trade-offs. The resprouting of woody angiosperm plants has also been reported by Del Tredici (2001), and regrowing is vegetation and disturbance-dependent. Bellingham and Sparrow (2000); Bond and Midgely (2001); Peterson and Reich (2001), and Del-Val and Crawley, 2005) reported that where aboveground plant parts are fatally destroyed resprouting is often seen occurring. They further indicated that this mode of regrowth provides a reliable alternative to recolonize and is a way to survive herbivory. Hoffmann and Solbrig (2003; Briggs *et al.* (2005), and LopezPintor *et al.* (2006) pointed out that shrub plants do undergo asexual regrowth following top kill if they lose more biomass. Drewa *et al.* (2002), Weyenberg *et al.* (2004), and Briggs *et al.* (2005) have observed top kill to result in clonal spread, particularly where disturbance regimes are altered, or where there is adequate supply of resources. Chapin *et al.* (1990), McCarron and Knapp (2003), and Keel *et al.* (2007) reported on the importance of carbohydrate storage capacity, relative growth rate, and photosynthetic rate being influential on regrowth. Following top death, roots or other surviving tissues store carbohydrates that are used to build new shoots (Bowen and Pate,

1993; Kruger and Reich, 1993; Cruz et al., 2002). According to Kabeya and Sakai (2005), plants that have greater whole-plant pools of stored carbohydrates or higher tissue concentrations are capable of resprouting their stem biomass.

Furthermore, bigger plants could be able to resprout from a larger bud bank (Bond and Midgley, 2001). It was found by other researchers that, previously undisturbed stems may produce greater biomass than stems of the same species that were previously disturbed because they contain more photosynthetic tissues (Kruger and Reich, 1993; Pena-Rojas et al., 2005).

Fires, herbivory, and other disturbance agents were noted by (Bond *et al.*, 2003; Dublin *et al.*, 1990; Scholes and Walker, 1993). (Dublin *et al.*, 1990; Scholes and Walker, 1993) to strongly affect changes in African savannas. In savanna ecosystems, juvenile trees need to outgrow the grass layer fire zone, no matter how long they are suppressed as seedlings if there is to be coexistence between trees and grasses. The long-term survival of trees as understory seedlings has been observed and reported widely. Meanut *et al.* (1990), and Bond and van Wilgen (1996) found that lignotuberous seedlings could persist in the grass layer for decades while making little or no growth above the ground. Similarly, lignotuberous seedlings with their established root systems have been reported to be distinctly advantaged over non-lignotuberous ones, which may establish themselves at the same time in the face of repeated multiple disturbances (Paula *et al.*, 2016). It is therefore likely that lignotuberous species would resist repeated disturbance while non-

lignotuberous species would lose life within a few numbers of similar disturbances that lignotuberous plant species are subjected to.

If juveniles of any tree species are not able to escape the fire “danger” zone but grow and develop to adulthood within the grass layer, they need to be fire-resistant. In a study, Rego *et al.* (2021) found dominant shrubs having their shoots destroyed by fire of low intensity; the stems of these species remained standing even after a severe burn, and the root crowns were found to grow prolifically following burning. Self-thinning of stems reduced the number of sprouts to between one and three per plant within a period of three years (Rego *et al.*, 2021). Canadell and Zedler (1995), and Canadell and Lopez-Soria (1998) reported on woody plants possessing swelling structures at the stem base, which are called lignotubers or burls.

Studies by Paula *et al.* (2016), and Moreno and Oechel (1991) suggested that lignotubers may be the source of new meristems that might be acting as regenospheres or bud banks. According to Canadell and Roda (1991) and Hilbert and Canadell (1995), these structures make up 80% of the biomass found below ground and 40% of the biomass found overall in plants. Mediterranean trees and shrubs are not the only ones that have a significant carbon investment in their lignotubers or burls (Canadell & Lopez-Soria, 1998). Whether lignotubers function as resource storage structures has never been proven but inferred indirectly from plant growth studies by Castell *et al.* (1994)), anatomical structure by Cruz *et al.* (2003), or tissue analysis of lignotuber nutrient and carbohydrate contents by

Montenegro *et al.* (2011). However, the role of lignotubers playing a greater role in the plant recovery process following disturbances was reported by Paula *et al.* (2016). Additionally, indirect quantitative findings on the usage of reserves of lignotuber in assisting with regrowth following disturbance were reported by Canadell and Lopez-Soria (1998).

Studies such as those by (Kays and Canham, 1991; Miller and Rose, 1992) suggested the importance of stored carbohydrates important source of carbon that supports regrowth. Contrary to that, Canadell and Lopez-Soria (1998) found substantial amounts of carbohydrate concentrations in dead plants killed by clippings. Interpretation following the observation of plants failing to exhaust carbohydrates following disturbance is that it is probably due to depletion of nitrogen and phosphorus, which limited the growth of the plant (Chapin *et al.*, 1990).

In a study of shrubs by Canadell and Lopez-Soria (1998) lignotuber resource nutrients were found heavily depleted after multiple clippings, and they concluded that lignotubers have a dual function of storing concealed buds as well as storing of non-structural carbohydrates, both of which would support regrowth following disturbance. This, perhaps, suggests that lignotuber's resources are large enough to support regrowth in the face of repeated disturbances.

In situations of multiple clipping of trees, savanna tree species are exhausted of bud bank or root carbohydrate reserves, whereas the opposite might be the case in situations of single clipping. A complete demise of tree species might result if such trees are depleted of root or lignotuber carbohydrate reserves; this may create gaps for the regeneration of other plant species. Such a scenario could drastically change vegetation composition and structure in a savanna ecosystem by enabling the invasion of the savannas by other original or non-original plant populations or communities.

Generally, competition could lead to the removal of some organisms from their original habitats or the outcompeting of one or more individuals by others; usually, organisms that are weak competitors during the strife lose the competition. In such interactive relationships between weak and strong competitors, some plant individuals, particularly those that are weak competitors, are outcompeted and removed from the system (Rees *et al.*, 2005). The spaces created following competitions usually become available for invasion by invasive alien plants (IAPS). Invasive alien plant species generally exploit spaces left behind by the outcompeted native plant species (Wang *et al.*, 2022). Invasive plant species are generalists who are quick to germinate, grow, and reproduce, and could therefore ultimately affect species composition and diversity in the reserve. Therefore, there is a need to understand how savanna grass plants interact with each other, and hence, find ways to reduce their invasion by IAPs.

1.2 PROBLEM STATEMENT

There is scanty knowledge on the invasiveness of one type of vegetation on the original vegetation's territory. Bush encroachment, which is just an invasion of indigenous trees, seems to depend on how quickly trees respond to injury, be it through burning, competition, overharvesting, or cutting. Tree responses to disturbance vary with species, seasons, sizes, and intensities. Moreover, different ecosystems may respond differently to similar disturbances. Knowledge of the type of vegetation one works with is thus necessary to avoid making misleading management decisions.

Knowledge of how savanna vegetation continues to resprout following cutting is necessary, and information thereof requires intensive pursuit to salvage it. Resprouting is an alternative to recolonization by seed following top-killing and is a mode of surviving following cutting. Such knowledge to reduce their invasion is necessary for their continuous usage and benefit to humans and animals. Game and nature reserves that animals rely on for their survival are mainly savannas, for example, Nylsvley Nature Reserve and Kruger National Park, amongst others. Countries like South Africa with protected savanna ecosystems in the form of reserves and national parks have their economies boosted by tourists who continuously visit them to appreciate both plants and the game thereof. How disturbances such as cutting affect savanna vegetation in reserves and parks requires investigation at different seasons of the year. If plants are top killed in the early and mid-growing season, they will have their growth reduced and may even die months or a few years following that. But plants that are top killed in the dormant season

do resprout following such experience. Some researchers have reported that top-killed plants do show greater mortality one year after treatment compared to those top-killed during the dormant periods (Robertson and Hmielowski, 2014; Hmieloski, Robertson, and Platt, 2014). The investigation covering all seasons continuously within a year, will provide a deep understanding of how wise management of savannas could be implemented.

1.3 HYPOTHESIS

Savanna plant species regrow or resprout irrespective of the season of the year in which they are disturbed. When they are cut savanna juvenile plant species should not struggle to regrow when so injured; their meristematic cells are stimulated to bring about resprouting following injury.

1.4 OBJECTIVES

The overall objective was to determine how savanna plant species respond to disturbance.

Specific follow:

1. investigate how resprout heights of two woody juveniles vary per species and season of cutting.
2. assess the response of savanna plants of different age groups to cutting.
3. assess cutting effects of the season on root sugar and starch concentration.
4. assess how root starch concentration and plant resprout height relate.
5. assess how root sugar concentration and plant resprout height relate.
6. establish the relationship between bark thickness and age group and how that relationship varies with species.

7. establish how stem diameter and age group relate, and how their relationship varies with species.
8. assess the effect of fire on plants of different age groups.
9. assess the potential interaction between conspecific nearest neighbour grass plants for soil moisture.
10. assess the grass species' xylem water potentials pre- and post-removal of their conspecific nearest neighbours.

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CHAPTER 2 STUDY AREA AND SPECIES

2.1 DESCRIPTION OF THE STUDY AREA

The study was conducted in the Nylsvley Nature Reserve (NNR) (Figure 2.1) which is a savanna ecosystem that is in the upper catchment of the river Nyl (Greenfield *et al.*, 2012). It covers almost 20% of the floodplain. There are about 370 birds, of which over eighty thousand birds may be seen in the good rainy season. Roan antelope (*Hippotragus equinus*) and Tsetsebes (*Damaliscus lunatus*) are found in the reserve. There is a stand of wild rice, *Oryza longistaminata*, located in a wetland area of Nylsvley Nature Reserve.

The reserve is situated within the 3120 ha Nylsvley Provincial Nature Reserve (24° 39' S, 28° 42' E, 1080 m elevation), Limpopo Province, South Africa. It is characterised by a mean annual rainfall (56 years record) of 630±134 mm, of which 85% falls between November and April (Murungweni *et al.*, 2020). (Scholes and Walker, 1993) reported a mean annual temperature of about 19°C, with a mean annual range of 10.6°C and an absolute range between 38.5°C and -3.2°C. The vegetation is classified as mixed bushveld (Mucina and Rutherford, 2006). (Whitecross *et al.*, 2016) reported on the occurrence of *Burkea africana* on poor nutrient sandy soil. The area is currently grazed by animals such as impala (*Aepyceros melampus*), Cape hare (*Lepus capensis*), and was last used by cattle in 1977 (van Wilge, 2009). The area supports a semi-arid, dystrophic savanna (Huntley, 2023).

Nylsvley Nature Reserve is comprised of grasses, shrubs, and scattered trees (. The following are some of the grasses readily observable in the reserve: *Cynodon dactylon*, *Cymbopogon* sp., *Heteropogon muticans*, *Hyperrhenia hirta*, *Setaria sphacelata*, *Sporobolus africana*,

Themeda triandra, and *Fimbrostylus hispidula* (sedge), amongst others. The trees and shrubs commonly found at the reserve include *Vachellia karroo* (mainly dominant in the clayey waterlogged area of the reserve), *Vachellia tortilis* (mainly prevalent in the area that used to be residential for farm workers in the 1934 backwards), and *Burkea africana*, *Dombeya rotundifolia*, *Dichrostachys cinerea*, *Ochna pulchra*, *Peltiphorum africana*, and *Terminalia sericea*, which are found in sandy soil areas (Huntley, 2023; Whitecross *et al.*, 2016).

Reports from anecdotal information are that there were fires every 5 years (Whitecross *et al.*, 2016). Fire breaks were created in summer and autumn by clearing about 3m belts to separate reserve areas from the outside on an annual basis, and such assisted in preventing accidental fires from outside the reserve (Wilson and Witkowski, 2003). Different areas which are dominated by *Vachellia karroo*, *Burkea africana*, *Dichrostachys cinerea*, and *Terminalia sericea* occur within different burning blocks, therefore different sites have different fire histories (personal communication).



Figure 2.1: Map of Nylsvley Nature Reserve.

2.2 DESCRIPTION OF TWO MAIN SPECIES OF NYLSVLEY NATURE RESERVE CHOSEN FOR THE CURRENT STUDY

Two shrubs or tree plant species were selected for description in this study: Sicklebush (*Dichrostachys cinerea*) and Silver cluster leaf or Silver Terminalia (*Terminalia sericea*). The two tree species were dominant and had a relatively larger number of individuals than one would intend to sample in the study area.

2.2.1 *Dichrostachys cinerea* Wight et Arn

It is of the family *Mimosaceae* (Jayakumari *et al.*, 2011) and is a spiny, semi-deciduous to deciduous tree that can grow 7 m high it has an open crown with lateral dense shoots. It is only known as the sicklebush in South Africa, in the former Transvaal. It is an invader that takes advantage of open gaps; it grows and dominates in sandy soil areas in the NNR (Figure

2.2). The young stem is made of soft bark, and older branches are made up of dark grey-brown fissures, they have smooth spines formed from modified side shoots (Pedroso and Kaltschmitt, 2012). The flowers are typically in bicoloured cylindrical spikes (Pedroso and Kaltschmitt, 2012).

These plants are known to be among other encroaching species (Cloete, 2022). It is a native invasive woody shrub or tree which has been adversely found to affect native herbaceous species' plant vigour, basal cover, and species richness (Mudzengi *et al.*, 2014). Also, the litter cover of herbaceous species was reported negatively affected in sites invaded by *D. cinerea*. These observations were attributed to the fast growth, propagation, and propagule pressure that characterize *D. cinerea*, giving it a competitive advantage concerning the acquisition of light, nutrients, and other resources (Mudzengi *et al.*, 2014). *Dichrostachys cinerea* is considered medicinally significant by Mazimba *et al.* (2022) due to the discovery of alkaloids, flavonoids, tannins, and so on during the phytochemical screening. Additionally, *D. cinerea's* dichloromethane extracts (stem bark) and methanol extracts (whole stem) all showed encouraging in vitro antimalarial properties.



Figure 2.2: *Dichrostachys cinerea* on sandy area of NNR.

Dichrostachys cinerea has been reported to be useful as an antidiarrhoeal remedy and in the treatment of wounds, rheumatism, and renal pains (Aworet-Samseny *et al.*, 2011; Jayakumari *et al.*, 2011). In Côte d' Ivoire, its stem powder and stem bark are used for the treatment of asthma and chronic bronchitis. Some reports on *D. cinerea* showed antibacterial and antiviral effects (Aworet-Samseny *et al.*, 2011).

2.2.2 *Terminalia sericea* Burch. ex DC

It is a tree or shrub (Amri, 2010; Eldeen *et al.*, 2006) of about 6 to 9 m in height with leaves that are clustered at the endpoint of branches (Amri, 2010; Likoswe *et al.*, 2008). It is of the family Combretaceae (Katjiua and Ward, 2006); and is reported to be widely distributed in

tropical and warm temperate regions (Huntley, 2023; Moshi and Mbwambo, 2005). It is found in countries such as South Africa, Botswana, Lesotho, Swaziland, Zambia, Tanzania, and Malawi. About 200 tropical trees and shrubs belonging to the Combretaceae family of flowering plants are in the genus *Terminalia*. African traditional medicine has a long history of using *Terminalia sericea* Burch. ex DC., an important commercial, ornamental, and ethnomedicinal plant. It is a small to medium-sized deciduous tree that may be used for general lumber and furniture manufacture. It has an upright stem and a rounded to flattish crown (Fig. 2.3) (Van Wyk & van Wyk, 2013). The roots may be used as a dye, and the heartwood can be utilized to make walking sticks for the elderly, pestles, and domestic items like spoons and plates (Makhado *et al.*, 2009). It grows in sandy soil locations in South Africa, for example, in the NNR (Figure 2.3).



Figure 2.3: *Terminalia sericea* on sandy areas in Nylsvley Nature Reserve.

Terminalia sericea has a wide range of uses, including soil conservation, ornamentals, medicinal (Likoswe *et al.*, 2008), carvings, building materials, and tool handles (Amri, 2010). Also, it is a major contributor to browse for both domestic cattle and goats during the hot-dry season under heavy grazing systems (Katjiua and Ward, 2006). *Terminalia sericea* prevents soil erosion and improves sites by draining waterlogged soils and shading-out weeds (Amri, 2010). The wood, which is yellow and hard, provides useful, durable items such as carvings and fencing posts (Likoswe *et al.*, 2008). The aqueous and organic extracts from the leaves, roots, and bark of *T. sericea* have antimicrobial activity (Eldeen *et al.*, 2006; Fyhrquist *et al.*, 2006; Likoswe *et al.*, 2008; Mochizuki and Hasegawa, 2007). The leaves of *T. sericea* are used for treating stomach disorders like diarrhoea (Amri, 2010) and menorrhagia (Moshi and Mbwambo, 2005). A decoction of the dried roots of this plant wounds, and sexually transmitted diseases (Eldeen *et al.*, 2006), also it is reported to relieve colic.

There are reports that tuberculosis is treated using dried fruits (Eldeen *et al.*, 2006). *Terminalia sericea* has been linked to a wide range of pharmacological and ethno-therapeutic effects (Mongalo *et al.*, 2016). Additionally, they highlighted other research conducted by several teams of scientists, which demonstrated that it is a versatile medicinal plant mostly used to treat illnesses such as TB, skin rashes, diarrhoea, and STDs.

Numerous studies have extensively documented the pharmacological activities of the genus *Terminalia* (Moyo *et al.*, 2015), including its antibacterial, and antifungal, amongst others (Adiko *et al.*, 2013, Mann and Kuta, 2014, Rathinamoorthy and Thilangavathi, 2014).

2.3 CONCLUSIONS

Despite the two prevalent and important plant species selected for this study, Nylsvley Nature Reserve is a Ramsar site with a huge diversity of flora and fauna species. These two species amongst others are found to be prevalent in sandy soil areas, in the reserve. *Terminalia sericea* is also socio-ecologically useful, as some types of edible caterpillars are harvested from them by rural people for eating with porridge or relish and for selling them to generate income. Also, it reduces the rate of soil erosion. Notwithstanding its relatively small size compared to some known other reserves, NNR is necessary in conserving both flora and fauna.

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CHAPTER 3 THE RESPONSE OF SAVANNA JUVENILE *DICHOSTACHYS CINEREA* AND *TERMINALIA SERICEA* TO SINGLE CUTTING

ABSTRACT

Also, the investigation was conducted in the NNR savanna ecosystem. The study site is a savanna ecosystem, as described under materials and methods. The study focussed on two savanna woody juvenile species, namely *Dichrostachys cinerea* and *Terminalia sericea*. The juvenile plants were separated into groups of thirty-five, and each of the thirty groups was cut monthly to observe how they responded to cutting and how their resprout heights were affected by the season of cutting. It was found that these plants regrew following cutting in any month of the year and that their average resprout heights generally varied between seasons.

The average resprout heights of plants that were cut at different seasons are as follows: winter = 79.9 cm, autumn = 56.3 cm, spring = 51.6 cm, and summer = 18.3 cm. The winter season, therefore, proved to be a more favourable season to cut savanna woody plants for trying to prevent bush encroachment and keep plants as gullivers, while summer showed to be the least favourable season to cut these plants.

3.1 INTRODUCTION

Plants of different growth forms vary greatly in their recovery, growth, and development responses to tissue damage as reported by Van der Heyden and Stock (1996). Some studies by these same authors have reported increases in plant production following clipping. Stimulated resprouting following the clipping of trees is associated with increases in photosynthetic rates, probably because the response of woody plant species to defoliation is primarily thought to be determined by resource availability (Bryant *et al.*, 1991).

In wet forests, but not in dry forests, juveniles of shade-tolerant species often contain larger carbohydrate root stores than those of light-demanding species (Poorter *et al.*, 2010; Bond, 2008). Very few studies have compared the roles of carbohydrate root reserves for plant recovery and survival across species, despite alternative theoretical predictions that indicate that carbohydrate storage should improve plant life (Iwasa and Kubo, 1997; Kobe, 1997). In a study with tree seedlings by Myers and Kitajima (2007), they reported that species with more root carbohydrate reserves could survive defoliation.

Savanna juvenile plants are suggested to resprout and grow faster via their already established and functioning root systems, compared to those formed from their seedlings (Li *et al.*, 2013; Vesk, 2006; Zhu *et al.*, 2012). Resprouting is an effective regrowth response mechanism (Bond and Midgley, 2001; Lawes and Clarke, 2011). It is a key functional trait: how buds, protection and resources drive persistence after fire which allows the recovery and hence growth and development of original plant species in an area (Clarke *et al.*, 2013;

Vesk and Yen, 2019). Plant resprouting: how many sprouts and how deep? Flexible modelling of multi-species experimental disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 41, p.125497.); this aids in the maintenance of the status quo of biodiversity and thus minimizes the invasion by species that are foreign to the area. Resprouting is important where opportunities for seedling establishment are limited (Vesk and Westboy, 2004).

Furthermore, resprouting is thought to facilitate coexistence in a patch- or sessile dynamics framework (Bond and Parr, 2010; Vesk and Westboy, 2004). There may be internal factors that may freeze or decrease the rate of resprouting after disturbance (Martínková *et al.*, 2006). Plant intrinsic factors such as leaf sizes and shapes may not affect plant recovery, growth, and development following a single disturbance, but their effects may be manifested following multiple disturbances. How savanna woody juvenile plant regrowth is affected by single cutting at any season of the year is an aspect that is necessary to investigate and understand; the study is necessary to equip communities with knowledge on how to protect and maintain savanna plants.

The current chapter investigated how the resprout heights of two savanna woody tree juveniles, which are from a low-resource, environment-sandy, semi-arid area of Nylsvley Nature Reserve, vary per species and season of cutting. The resprout heights of juvenile woody plants in savanna ecosystems depend on the species and season of cutting. When these two woody plant species experience single-cutting at any time of the year, they do not die but regrow.

3.2 MATERIALS AND METHODS

3.2.1 Description of the study area

Nylsvley Nature Reserve (NNR) (Figure 2.1), is described in Chapter 2. The reserve is also home to Roan antelope (*Hippotragus equinus*) and Tsetsebes (*Damaliscus lunatus*). There is a stand of wild rice, *Oryza longistaminata*, located in a wetland area of Nylsvley Nature Reserve. The NNR is situated within the 3120 ha Nylsvley Provincial Nature Reserve (24°39' S, 28°42' E, 1080 m elevation), Limpopo Province.

3.2.2 Experimental sites

Two sites, one dominated by *Dichrostachys cinerea* (*D. cinerea*) (Figure 3.1) and the other dominated by *Terminalia sericea* (*T. sericea*) (Figure 3.2), plants were selected within the Nylsvley Nature Reserve (described in Chapter 2) and used for data collection.



Figure 3.1: Sandy area in the Nylsvley Nature Reserve dominated by *Dichrostachys cinerea* juveniles.



Figure 3.2: Sandy area in the Nylsvley Nature Reserve dominated by *Terminalia sericea* juveniles.

3.2.3 Experimental design

A group of 35 juvenile individuals of *D. cinerea* and 35 juvenile individuals of *T. sericea* (Figures 3.1 and 3.2) were randomly selected each month from March 2001 to November 2001, and then in January 2002 and February 2002, using the probability random sampling method (Taherdoost, 2016). Juvenile plants are young individuals that have not yet reached reproductive stages (explained in the introduction under Chapter One). This sampling method was chosen because it allows every item of the population to have an equal opportunity to be selected.

Data collection was carried out through flipping coins as follows: If the tail of a flipped coin happens to face up after flipping it, the researchers moved 4 meters to the east away from the initial standing point, a 4 m x 4 m square quadrat was constructed. If the tail of a flipped coin happens to face up after flipping it for the second time, the researchers moved 4 m to the west away from the center of the first square quadrat. A 4 m x 4 m square quadrat was then constructed. In an instance where the head of a flipped coin happens to face up in the third flip, the researchers moved 4 m to the west away from the center of the second 4 m x 4 m square quadrat. If the head of the flipped coin happens to face up in the fourth flip, the researchers moved 4 m to the north away from the center of the previous third 4 m x 4 m square quadrat. The same pattern was followed until all the 35 individuals of *Dichrostachys cinerea* and 35 individuals of *Terminalia sericea* were covered. A square quadrat was always constructed 4 m away from the centre of its preceding one, either towards the east, south, north, or west. The individuals of the same sizes and hence similar age groups were sampled within quadrats until 35 individuals of each of the two species were collected. This was to ascertain that only individuals of the same age were sampled.

Thirty-five individuals of *Dichrostachys cinerea* and 35 individuals of *Terminalia sericea* were each cut at 10 mm above the ground during each of the eleven months to observe how they were going to respond to cutting. Also, how their resprout heights interacted with the season of cutting was observed averaged per season. Their number of leaves was counted and averaged to obtain their mean. Standard errors were attached to numerical values on Tables 3.1 and 3.2. Analyses of the variance were drawn below under the Tables 3.1 and 3.2.

3.2.4 Data collection

Line transects and square quadrats methods were used to sample juvenile plants of both *D. cinerea* and *T. sericea*. *Dichrostachys cinerea* and *Terminalia sericea* plants were then cut in groups of 35 individuals during the four different seasons of the year from 2001 to 2002. The resprout heights for all cut juvenile individuals of both *D. cinerea* and *T. sericea* were then measured a year later, following cutting. The sizes of trees were not measured before they were cut. Rulers and tape measures were used to measure the resprout heights. Whether plant species, season, and the interaction between plant species and season affected the plant height of the resprouts was established.



Figure 3.3: Resprouting cut *Terminalia sericea* in the Nylsvley Nature Reserve.

3.2.5 Data analysis

The analyses were done in SPSS version 27. The ANOVA test procedure was used to test if the mean height and mean number of leaves varied by season. Since the height and number of leaves are expected to vary with species, a two-factor ANOVA with season and species as the factors was employed. The interaction effect of season and species was also included in the ANOVA model. Where the ANOVA procedure was $p < 0.05$, the Bonferroni ad hoc test was used for mean separation.

3.3 RESULTS

3.3.1 Resprout heights

All *Dichrostachys cinerea* and *Terminalia sericea* plants that were cut, irrespective of the month of cut, were resprouted by the end of the experimental period (Table 3.2). Average heights between plants of the two species were found to differ significantly at $p < 0.05$ (Table 3.1). Averaged across seasons, *T. sericea* resprouts were 24% (11.7 cm) taller compared to those of *D. cinerea* (Table 3.2). The average resprout heights were found to vary from season to season ($p < 0.05$), with winter average resprouts taller than those of other seasons and those of summer shorter than for the other three seasons (Tables 3.1 and 3.2).

In addition to the main effects of plant species and season of cutting, the interactive effect of plant species and season of cutting (P x S) on the height of resprouts was $p < 0.05$. The *T. sericea* resprouts were taller compared to the *D. cinerea* ones in all seasons except in autumn,

where no significant differences in the height of the two species were observed (Table 3.1 and Figure 3.4).

Table 3.1: Analysis of variance.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	30350	30350	236.727	<0.05
Season	3	311985	103995	811.145	<0.05
Species: Season	3	18046	6015	46.919	<0.05

Table 3.2: The mean number of resprout heights (cm) according to species and season of cutting. The alphabetical letters attached to the means indicate significant difference between the means according to the Bonferroni ad hoc test.

Treatments	Mean resprouts heights (cm)
Plant Species	
<i>Dichrostachys cinerea</i>	49.6(0.89)b
<i>Terminalia sericea</i>	61.3(1.23)a
Season	
Autumn	56.3(0.731)c
Winter	79.9(0.731)d
Spring	51.6(0.731)a
Summer	23.4(0.895)b

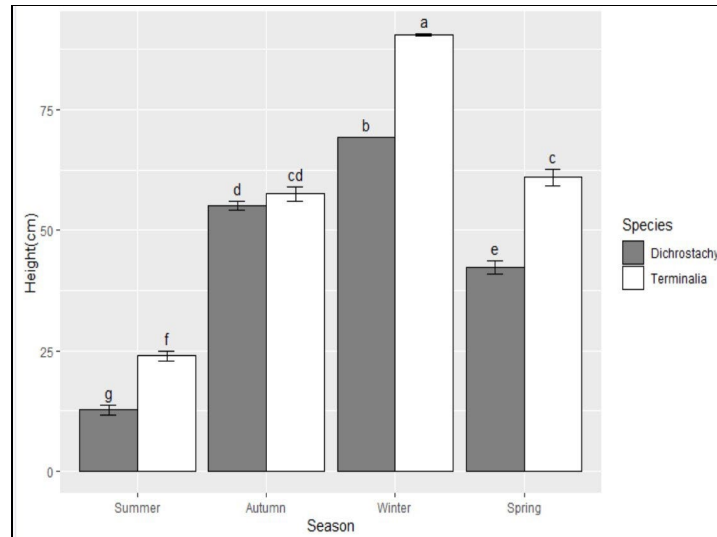


Figure 3.4: Mean resprouts heights of the two species, *Dichrostachys cinerea* and *Terminalia sericea* according to seasons of clipping which are autumn, winter, spring, and summer of 2001. Error bars are not visible in other cases because they are very narrow; significance can be assessed from alphabetical letters provided on graphs.

3.3.2 Resprouts number of leaves

The resprouts of all *Dichrostachys cinerea* and *Terminalia sericea* plant individuals that were cut produced leaves during the experimental period, throughout all seasons of cut (Table 3.4 and Figure 3.5). The average resprout leaves were found to vary from season to season ($p < 0.05$). The number of resprouting leaves of the winter-cut plants was 16 (12%) and (32) 27% more than those cut in autumn and spring, respectively (Table 3.4). The number of resprout leaves from the summer-cut plants was fewer than those from the rest of the seasons, with the resprout leaves from the winter-cut plants being more than 1-fold (87,1) larger than the summer ones (Table 3.4). The average number of leaves between plants of the two species was found to differ significantly at the significance level of $p < 0.05$. Averaged across seasons, the number of *T. sericea* resprout leaves was 4 (3.4%) less than that of *D. cinerea* (Tables 3.3 and 3.4).

In addition to the main effects of plant species and season of cutting, the interactive effect of plant species and season of cutting (P x S) on the resprout leaves was also significant (Table 3.3). The *T. sericea* resprouts produced fewer leaves compared to the *D. cinerea* ones in all seasons except in winter, where their resprouts produced more leaves than those of the *D. cinerea* resprouts (Figure 3.5).

Table 3.3: Analysis of variance.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	4124	4124	11.627	<0.05
Season	3	787600	262533	740.175	<0.05
Species: Season	3	27712	9237	26.043	<0.05

Table 3.4: The mean number of resprouts leaves according to species and season of cutting. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni ad hoc test.

Treatments	Mean resprouts leaves
Plant species	
<i>Dichrostachys cinerea</i>	123(0.898)a
<i>Terminalia sericea</i>	119(0.898)b
Season	
Autumn	134(1.216)c
Winter	150(1.216)d
Spring	118(1.216)a
Summer	62.9(1.489)b

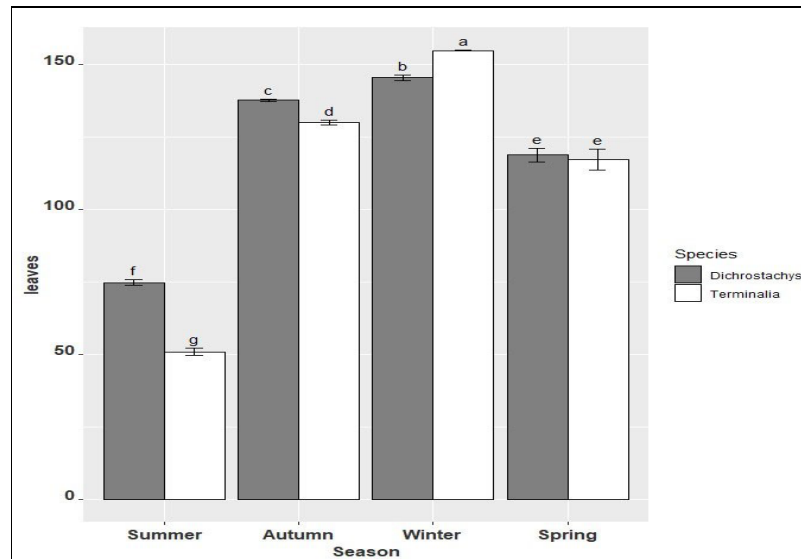


Figure 3.5: Mean resprouts leaves of the two species, *Dichrostachys cinerea* and *Terminalia sericea* according to seasons of clipping which are autumn, winter, spring, and summer of 2001. Error bars are not visible in other cases because they are very narrow; significance can be assessed from letter's provided on graphs.

3.4 DISCUSSION

Plants decreased in their vigour for both recovery and growth, but all cut plant individuals survived their whole experimentation period of 12 months for each group of 35 juvenile individuals. The survival and growth of almost all the individuals observable till the end of the experimental period is an indication that cutting these plants does not lead to their demise. The variation in the average seasonal plant resprout heights observed to the conclusion of the experimental period indicates that survival and growth of plants vary at different seasons. The average heights of resprouts obtained during harvesting varied with the seasons, with plants cut in winter being taller than those cut in other seasons. The dominance of average winter resprout plant heights compared to those that were cut in the other three seasons is presumptively due to the storage of large quantities of carbohydrate reserves in that season.

Canadell and Lopez (1998) have presumptively reported on the relationship between below-ground non-structural carbohydrate (NC) concentration and the regrowth of the above-ground parts of plants. Plants, however, may fail to regenerate irrespective of the large quantities of total non-structural carbohydrates (TNC) that plants may store in their roots if they do not contain buds (Van der Heyden and Stock, 1996; Cruz and Moreno, 2001).

If the presumption that plants that are cut in winter contain large quantities of reserve carbohydrates is true, they could therefore regrow and maintain themselves for a relatively longer period than those cut in the other seasons before they start to rely on recent photosynthates. It is thus prudent to consider cutting savanna plants in winter as compared to other seasons. The other two seasons, namely spring and autumn, may not necessarily be unfavourable seasons for cutting savanna plants, as relatively taller plant resprouts than those of summer were produced. Summer is a season when plants would probably have a shortage of root non-structural carbon supply, as such would have been used for regrowth (Hoch, Richer and Korner, 2003), and accordingly performed less than during all other seasons in terms of plant resprout heights.

Notwithstanding summer being the season that produced shorter plant resprouts than the other three seasons, the savanna plants that the current study investigated could be cut in all four seasons without causing fatalities. The trend of recovery shown by the species investigated will be surety to the maintenance of the savanna nature of Nylsvley Nature Reserve; it may thus be difficult for the alien species to invade Nylsvley Nature Reserve.

Authors such as Cruz and Moreno (2001) reported on seasonal differences in the vigour of resprouting and interpreted them as due to seasonal variation in the TNC reserves. -The resprouts are thus the result of bud break, and this implies that the regrowth of cut plants relies mainly on the availability and breaking of buds to grow. The significant interaction between season and plant species proved that there is variation in the genetic make-up and behavioural patterns of different plant species despite them surviving and growing in the same ecosystem.

The seasonal single cutting of the savanna plants in the current study did not result in a total kill of the plants, which suggests that less frequent cutting of savanna plants at any time of the year could never cause the demise of savanna ecosystems. Some studies have reported on disturbance of plants by clipping or cutting to have less direct mortality (Cruz *et al.*, 2002; Cruz *et al.*, Perez and Moreno, 2003), while studies that were conducted on shrub species where plants were top killed had those plants sprouting (Briggs *et al.*, 2002; Hoffmann and Solbrig, 2003; Briggs *et al.*, 2005; Lett and Knapp, 2005; Lopez-Pintor *et al.*, 2006; Cohen *et al.*, 2009; Caltry *et al.*, 2013; Andruk, 2014).

Inter-species seasonal variation in terms of average number of leaves could be due to the differences in their leaf morphologies. The leaves of *Dichrostachys cinerea* (*D. cinerea*) are compound and narrow in nature, while those of *Terminalia sericea* (*T. sericea*) are simple and broad. The lower number of leaves of *Dichrostachys cinerea* in winter compared to those of *T. sericea* is probably because they dry early in winter and are hence shed before those of

Terminalia sericea. The revelation from this study that plants resprout heights of *T. sericea* proved taller than those of *D. cinerea* throughout all seasons is probably manifesting that broad leaves of *T. sericea* are photosynthetically more efficient than those of *D. cinerea*; they brought about faster and taller growth of *T. sericea* resprouts than what compound and narrow leaves of *D. cinerea* achieved. Leaves are always necessary for photosynthesis and hence carbohydrates production (Atkin *et al.*, 2006); it should therefore be commonplace to observe broad leaves of *T. sericea* performing better than those of *D. cinerea*.

3.5 CONCLUSION

The response of two plant species, which are *Dichrostachys cinerea*, and *Terminalia sericea* in terms of increase in heights was found to be influenced by the season of disturbance, with plants that were cut in winter regenerating very well compared with those that were cut during other months of the year. The average plant resprout heights of plants that were cut in winter months were found to have grown taller than those of plants that were cut in other months of the year. It is therefore more favourable to disturb savanna plants during the winter months than during other months of the year. The average plant resprout heights, and the average number of leaves depend on the interaction between species and the season of cut. There were differences in the responses of species to the seasons of cut. Interestingly observed was that irrespective of the average number of leaves of the two species, *Terminalia sericea* performed better than *D. cinerea* in all seasons in terms of plant resprout heights. The pattern of recovery shown by the species investigated may be beneficial to Nylsvley Nature Reserve and perhaps to other savanna ecosystems in South Africa.

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CHAPTER 4 THE RESPONSE OF SAVANNA PLANTS OF DIFFERENT AGE GROUPS TO CUTTING

ABSTRACT

The current investigation was also conducted at NNR which is located between Mookgophong and Modimolle. The study site is a savanna ecosystem, as described in Chapter Two. The study focussed on two savanna woody species, namely, *Dichrostachys cinerea* (35 saplings individuals plus 35 juveniles) and *Terminalia sericea* (35 saplings plus 35 juveniles). Each of the thirty-five (35) groups was cut at the same time monthly during the year to observe how they responded to cutting and how their resprout heights compared. For a season, readings of three months were added and averaged, for example, May, June, and July for Winter, and August, September, and October for Spring, etc). Harvesting was done a year later following cutting. If a group of plants are cut this year in Winter, they would be harvested twelve months later in the following year. It was found that these plants regrew following cutting and that their average resprouts heights generally varied between age groups. The average resprout heights of plants of the two different ages that were cut is as follows: saplings = 121 cm and juveniles = 151 cm. Saplings' average heights showed that they grow slower than those of juveniles, but that may not necessarily be interpreted to imply that the two different age groups do not recover to maturity when cut.

4.1 INTRODUCTION

Disturbance is defined as a change in ecosystem structure caused by factors external to the hierarchical level of the system of interest (Brawn *et al.*, 2001; Myster, 2003). When a large tree falls in a mature forest, it creates a hole that allows light to reach the forest floor with ease. This type of disturbance allows light-loving plants to grow in spots that would otherwise be too shaded for them. Earlier, according to Turner *et al.* (2003) a disturbance is any discrete event in time that modifies resources, substrate availability, population structure, or the physical environment. Disturbances, in all their manifestations, have the fundamental effect of destroying the primacy of the primary stem and the hierarchical relationships that govern the formation of a tree form (Hobbs, Schimel, Owensby and Ojima, 1991; Hobbs, 1993).

Some trees resprout when damaged; it was reported that buds that are closest to the point of damage, show the most vigorous growth, which is suspected to be an indication that basal sprouting is generally an induced response (Smith *et al.*, 1997; Pommerening and Murphy, 2004; Sayer *et al.*, 2004; Smith *et al.*, 2013). Some reports are that there is variation in resprouting during plant development because the number of buds increases with plant age, the availability of stored nutrients, as well as meristematic activity, and secondary thickening (De Tredici, 2001; Martínková *et al.*, 2004; Matula *et al.*, 2019). Martínková *et al.* (2004) observed that resprouting from axillary buds is faster and, in terms of energy cost, more advantageous than resprouting from root buds, which suggests that the ability to resprout is related to life history, stage of plant development, and plant age.

Trees at their earlier stages of development are therefore more susceptible to destruction following disturbance than trees at their later stages of development (Paciorek *et al.*, 2000,). Also, the ability to resprout is related to the interplay between the disturbance regime (characterized by disturbance severity, timing, and frequency) and plant traits, such as the amount of stored reserves, bud bank size, and bud protection (Clarke *et al.*, 2013; Charles-Dominique *et al.*, 2015; Klimešová *et al.*, 2018). Plants of different growth forms, such as shrubs and perennials, were found to survive and cope under disturbances such as drought and herbivory due to their belowground bud bank and carbohydrate storage (Martínková *et al.*, 2020; Bombo *et al.*, 2022). The importance of bud banks is paramount (Charles-Dominique *et al.*, 2015), though, although plant species do require nutrients to survive under different forms of disturbances (Canadell and Zedler, 1995; Bellingham and Sparrow, 2000; Klimeš, 2007; Pausas and Keeley, 2014).

Roots are important sinks for stored carbon in resprouting plants (Cruz *et al.*, 2003) and offer more surface area for water and nutrient uptake (Konstantinidis *et al.*, 2006); hence, seedlings are likely to be less effective in terms of resprouting than saplings, juveniles, and adults, partly because of their smaller root systems (Campbell and Holdo, 2017). Plants rely on underground root-stored, total non-structural carbohydrates (TNC) for regrowth of above-ground parts during the early stages of resprouting (Cruz *et al.*, 2003); therefore, this implies a need for a greater root system to store a relatively maximum amount of TNC.

Despite the importance of savanna ecosystems socio-economically, simultaneous comparative studies on the response of savanna plants of different age groups to cutting have, to my knowledge, not been conducted to date. At what age group would it be prudent to clip savanna plants and have them recover? It is necessary to establish and understand. Knowledge on how plants respond to cutting would be informative on the cautious management of savanna ecosystems. The current study is, therefore, necessary to disclose information on how wise humans should interact with savanna ecosystems.

The main hypothesis tested was that the resprouting, after cutting, of savanna plants would vary with age and plant species. The specific hypotheses were: Plant height and number of leaves of savanna plants resprouts vary with age. There is genotypic variation in the plant height and number of leaves of savanna plants.

The main objective of the study was to determine the effect of age and savanna plant species on cutting. The specific objectives were to determine the effect of (1) age on plant height and number of leaves of savanna plant resprouts; (2) plant species on plant height and number of leaves of savanna plant resprouts.

4.2 MATERIALS AND METHODS

4.2.1 Experimental sites

Two sites were selected within the Nylsvley Nature Reserve (described in Chapter 2), one dominated by *Terminalia sericea* (*T. sericea*) saplings and juveniles (Figure 4.1) and the other dominated by *Dichrostachys cinerea* (*D. cinerea*) saplings and juveniles (Figure 4.2), were used for data collection.

4.2.2 Experimental design

A group of 35 saplings and 35 juvenile plants of *D. cinerea* and 35 saplings and 35 juvenile plants of *T. sericea* (Figures 4.1 and 4.2) were randomly selected from about 500 m x 500 m rectangular sites using the probability random sampling method (Taherdoost, 2016). This sampling method was chosen because it allows every item in the population to have an equal chance of being included in the sample. Data collectors took turns in flipping coins as follows: If the head of a flipped coin happened to face up after flipping it, the researchers moved 2 meters to the east away from the initial standing point, and a 4 m x 4 m square quadrat was constructed. If the head of a flipped coin happens to face up after flipping it for the second time, the researchers moved 4 m to the south away from the center of the first square quadrat. A 4 m x 4 m square quadrat was then constructed. In an instance where the tail of a flipped coin happens to face up in the third flip, the researchers moved 4 m to the west away from the center of the second 4 m x 4 m square quadrat. If the head of the flipped coin happens to face up in the fourth flip, the researchers moved 4 m to the north away from the center of the previous third 4 m x 4 m square quadrat. The same pattern was followed

until all the 35 sapling individuals and 35 juvenile individuals of *Dichrostachys cinerea* and 35 sapling individuals and 35 juvenile individuals of *Terminalia sericea* were covered. A square quadrat was always constructed 4 m away from the center of its preceding one, either towards the east, south, north, or west. The individuals of the same sizes and hence similar age groups were sampled within quadrats until 35 individuals of each of the two species were collected. This was to ascertain that only individuals of the same age were sampled.

Thirty-five individuals of *Dichrostachys cinerea* and 35 individuals of *Terminalia sericea* were each cut at 10 mm above the ground during each of the eleven months referred to above to observe how they were going to respond to cutting. Their heights were averaged per age group to obtain their means and similarly, the number of their leaves was counted and averaged to obtain their means as per age group. Standard errors were attached to numerical values and analyses of variance were indicated in Tables 4.1 and 4.2.

4.2.3 Data collection

Line transects and square quadrats methods were used to sample saplings (saplings which are the young trees older than seedlings but younger than juveniles and generally with slender trunks – see introduction under Chapter one) and juvenile plants of both *D. cinerea* and *T. sericea* (Buckland *et al.*, 2007). *Dichrostachys cinerea* and *Terminalia sericea* plants were then cut into groups of 35 individuals from 2001 to 2002. The resprout heights for all cut saplings and juvenile individuals of both *D. cinerea* and *T. sericea* were then measured

a year later, following cutting. Rulers and tape measures were used to measure the resprout heights. Whether plant species, age group, and plant species and age group interacted was established.



Figure 4.1: A vegetation mixed stand dominated by saplings and juveniles of *D. cinerea* and *T. sericea*.

4.2.4 Data analysis

Analyses were done using SPSS version 27. The ANOVA test was employed to test if the mean height and mean number of leaves varied. Since the height and number of leaves are expected to vary with species, a two-factor ANOVA with age group and species as the factors was employed. The interaction effect of age groups and species was also included in the ANOVA model. Where the ANOVA procedure showed $p < 0.05$, the Bonferroni ad hoc test was used for mean separation.



Figure 4.2: One of the two groups of data collectors using a measuring tape to construct quadrats, with one member locating a sapling for cutting.



Figure 4.3: A group of data collectors with one member sawing a sapling of *D. cinerea*.



Figure 4.4: One member of a group of data collectors sawing a juvenile of *T. sericea*.



Figure 4.5: A member of data collectors demonstrating how resprouts sizes were estimated using a 30 cm ruler.



Figure 4.6: An illustration of how the heights of resprouts were estimated.

4.3 RESULTS

4.3.1 Resprout heights

The average resprout heights were found to vary between plant age groups ($p < 0.05$), with juveniles' average resprout heights being taller than and significantly different from those of the saplings (Tables 4.1 and 4.2). From Table 4.1, we can also see that the average resprout heights varied between the two plant species ($p < 0.05$). *Terminalia sericea* average resprout height was significantly taller than that of *Dichrostachys cinerea* (Table 4.2). The interaction between age group and species was however significant ($p < 0.05$). Among the juvenile plants, *Terminalia sericea* had a higher mean resprout height compared to *Dichrostachys cinerea* for saplings there was no significant difference in the mean resprout heights of the two species (Figure 4.7).

Table 4.1: Analysis of variance

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	10940	10940	21.7192	<0.05
Age	1	67658	67658	134.3269	<0.05
Species: Age	1	1484	1484	2.9453	<0.05

Table 4.2: The mean number of resprouts heights (cm) according to species and age group. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni ad hoc test.

Treatments	Mean resprouts heights (cm)
Plant Species	
<i>Dichrostachys cineria</i>	130(1.87)b
<i>Terminalia sericea</i>	142(2.34)a
Age group	
Juvenile	151(1.76)a
Sapling	121(1.91)b

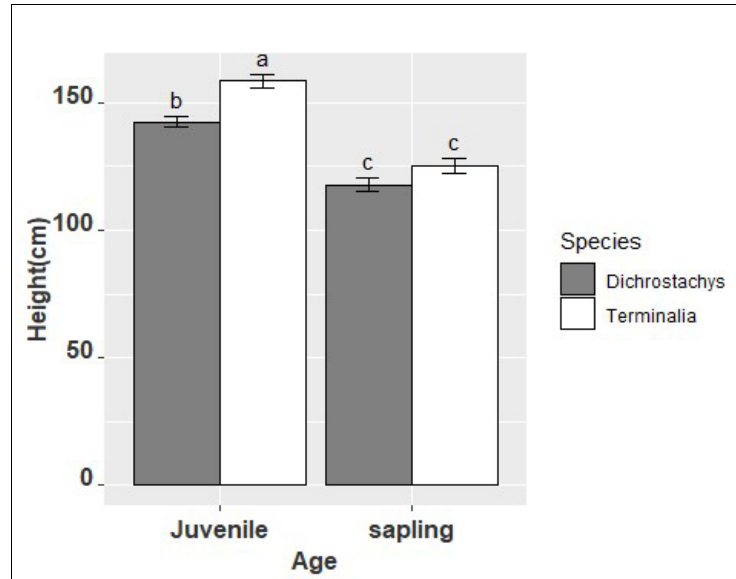


Figure 4.7: Mean resprouts heights of the two species, *Dichrostachys cinerea* and *Terminalia sericea* according to species and age groups. Error bars are not visible in other cases because they are very narrow; significance can be assessed from alphabetical letters provided on graphs.

4.3.2 Resprouts number of leaves

The average resprout leaves were found to vary from one age group to another (p -value <0.05). Juvenile plants average resprout leaves significantly exceeded those of saplings (Tables 4.3 and 4.4). Also, the average number of leaves between plants of the two species differed significantly at $p < 0.05$, irrespective of age groups (Tables 4.3 and 4.4). Averaged across age groups *Dichrostachys cinerea* had a higher number of resprout leaves compared to *Terminalia sericea*. The interactions between species and age groups were not significant (Table 4.4 and Figure 4.8).

Table 4.3: Analysis of variance

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	139905	139905	19.6910	<0.05
Age	1	5968054	5968054	839.9799	<0.05
Species: Age	1	2015	2015	0.2836	NS

Table 4.4: The mean number of resprouts leaves according to species and age group. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni ad hoc test.

Treatments	Mean plant resprouts leaves
Plant Species	
<i>Dichrostachys cinerea</i>	563(12.9)a
<i>Terminalia sericea</i>	521(12.5)b
Age group	
Juvenile	678(8.39)a
Sapling	405(4.84)b

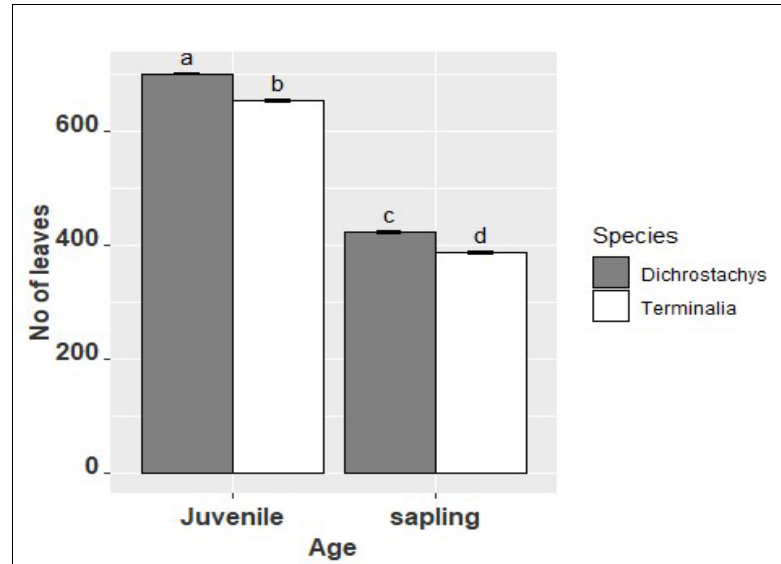


Figure 4.8: Mean leaves numbers of the two species, *Dichrostachys cinerea*, and *Terminalia sericea* according to species and age group. Error bars are not visible in other cases because they are very narrow; significance can be assessed from alphabetical letters provided on graphs.

4.4 DISCUSSION

Both saplings and juveniles that were cut responded by producing resprouts of heights that differed significantly by the end of the experimental period, which showed that plant age had effects on how plants regrew following cutting. The production of more leaves by juvenile plants of the two species than their saplings is an indication that age groups affect plant production. Also, the two different plant species were found to vary in terms of resprout height increase and production of resprout leaves, which might imply that there is genotypic variation in plant height and number of leaves for these two savanna plants. It was interesting to find that *T. sericea* plants on average produced taller resprouts with fewer leaves than *D. cinerea* which produced shorter resprouts with more leaves.

Terminalia sericea is a tree species, as opposed to *Dichrostachys cinerea*, which is a shrub species (Belay and Moe, 2015; Martens *et al.*, 2000; Randle *et al.*, 2018). On the other hand, some plants are generally found to grow faster than others due to the different adaptations they have. The main elements that influence plant development are light, nutrients, and water. Every species of plant has specific needs for the conditions in which it grows. Certain plants develop more quickly than others. Additionally, the space requirements of the plants vary. Sometimes, differing light and moisture circumstances lead two plants of the same species to grow differently, but this might also be due to the variations in individual plants. The fact that the two species vary genetically may not be ruled out because they differ in height. The leaves of *T. sericea* are morphologically simple, while those of *D. cinerea* are compound; hence, there are more leaves for the latter species than for the former species.

The differences in the average resprout heights of saplings and juveniles, with those of the saplings shorter than those of the juveniles, were not unusual. Both two age groups were still at their developmental stages, with juveniles expected to perform better than saplings in terms of growth. The growth and development of saplings and juveniles, as interpreted from their heights, might be confirmation that juvenile resprouts grow and develop faster than those of saplings. Also, it might be a revelation that juveniles respond better to cutting than saplings.

There are several reports on young plants possessing lignotubers, or burls, at stem bases, and these structures are described as sources of new meristems that serve as bud banks (Charles-Dominique *et al.*, 2015), and are hence, important in plant recovery (; Canadell *et al.*, 1991; Moreno and Oechel, 1991; Canadell and Zedler, 1995; Canadell and Lopez-Soria, 1998; Cruz *et al.*, 2003). It is believed that these structures at plant stem bases play a role in plant recovery until individual plants form new leaves to photosynthesize and sustain themselves (Charles-Dominique *et al.*, 2015). A study by Pausas *et al.*, (2018) has reported on the importance of lignotubers during the early stages of development of plants, which brings about an increase in the number and size of resprouts following the establishment of the individuals. The resprouting of the plants that were cut and their subsequent growth and development could be linked to the presence of lignotubers even though this was not investigated. Tredici (2001) reported on some plants that were found to retain the ability to sprout from the collar into adulthood.

Other studies have found that lignotubers enhance seedlings' ability to survive perturbations such as grazing, or fire. This persistence has been reported to be partly due to the reserve carbohydrates stored in the lignotuber (Bond and Midgley 2001; Walters *et al.*, 2005 and Zwicke *et al.*, 2015). It was reported by Bond and Midgley (2001) that later in the life of a plant, the lignotuber appears to lose the ability to ensure the development of new basal sprouts. The recovery of saplings and juveniles in this study is probably due to root-stored reserves, which supplied carbohydrates for plant regeneration (Cruz *et al.*, 2003; Herben *et al.*, 2016; Klimešová *et al.*, 2018). The continuous growth and development of the resprouts of cut plants through to the end of the experiment continued unhindered, as the plants were

themselves probably self-sustaining naturally through the process of photosynthesis. Plant disturbances, therefore, need to be carried out after having accumulated enough knowledge of their biology.

4.5 CONCLUSION

Disturbance in the form of cutting has an impact on plant recovery, growth, and development of plants of different age groups. It is thus necessary to consider plant age as the cutting of plants is carried out. Cut plants of different age groups showed that the average resprout heights of saplings increased at a slower rate than those of juveniles. The average resprout heights of saplings were shorter than those of juveniles by end of the experimental period.

Also, plant production in terms of the number of leaves differed from one age group to the next with saplings producing less than juveniles at the end of the experimental period. The differences between plant species average resprout heights and the average number of leaves produced indicate that genetic make-up varies from species to species and affects how species grow and develop. The current study revealed the importance of considering plant age groups and species types during a disturbance in the form of clipping. Also, the consideration might be relevant when applying other forms of disturbances in the control and management of vegetation ecosystems.

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CHAPTER 5 THE EFFECTS OF SEASON OF CUTTING ON ROOT SUGAR AND STARCH CONCENTRATIONS AND HOW RESPROUT HEIGHTS DEPEND ON SUGAR AND STARCH CONCENTRATIONS

ABSTRACT

The study looked at the effects of the season of cutting on root sugars and starch contents. The effects of the season of cutting aboveground plant parts on root starch and sugar reserves were assessed. Also, the relationship between root starch, and sugar reserves, and plant height of resprouts was assessed. The starch and sugar concentrations of the roots of individual plants of *Dichrostachys cinerea* and *Terminalia sericea* were measured. The glucose standard curves 0.05g/50 ml (glucose/distilled water) of stock solution were prepared. Glucose standards in the range of 0-80 $\mu\text{g/ml}$ were also read at 490 nm to generate a standard curve.

The pellets from the sugar extraction were retained and dried. Ten millilitres of 3.6% hydrochloric acid were added to hydrolyse the starch, and the tubes were put in the water bath, where they were boiled for 3 hours, and thereafter centrifuged. Samples were prepared for spectrophotometer analysis for the sugars.

There were some effects of sugar on plant height established, but no clear relationship between starch and plant height was found. The results of the current study showed that sugar is more important for plant height increase than starch; starch is first hydrolysed to sugar and thus becomes readily available for plant recovery as such. Both sugar and starch are important for plant growth and development during all seasons of the year.

5.1 INTRODUCTION

The assimilates of photosynthesis are stored in the stems and roots in various forms, for example, sugars and starch. When environmental stresses decrease photosynthetic rates, these stored carbohydrates are re-mobilized and used in respiration (Sala *et al.*, 2011). Studies by Hoch *et al.* (2003), Wurth *et al.* (2005), Palacio *et al.* (2007), Sala *et al.* (2012), Richardson *et al.* (2013) have attributed seasonal variation in resprouting vigour to fluctuations in carbohydrate reserves. Roots of younger clipped trees have lower concentrations of starch than those of older clipped trees, and the carbohydrate concentration in both the stumps and roots was found to increase with age (Zhang *et al.*, 2020).

It has been reported that underground organs such as lignotubers, rhizomes, and bulbs are structures of plants that are known to store food reserves from which new shoots regenerate after the aboveground parts are destroyed (Hernández *et al.*, 2011; Paula and Pausas, 2011; Moreira *et al.*, 2012; Vilagrosa *et al.*, 2014; Zeppel *et al.*, 2015). In a study of two Mediterranean shrubs, it was found by (Canadell and Lopez-Soria, 1998) that lignotuber resources such as starch and sugar got heavily depleted after multiple clippings. Lignotubers have been described as organs that are sources of buds (Moreno and Oechel, 1991) or regenosphere (Meney *et al.*, 1997; Canadell and Lopez-Soria, 1998).

Previous studies show that the seasonal trend of sprouting vigour is associated with the seasonal fluctuation of carbohydrates (Sala *et al.*, 2012; Richardson *et al.*, 2013). However, information on how cutting plants, seasonally or multiple times in a season, affects the

amount of plant root reserves is scarce. Present knowledge on whether more reserves are extracted and depleted if plants are cut multiple times during any season is implied rather than based on empirical evidence. For example, the investigation of whether reserves that are stored in the lignotubers of two Mediterranean shrubs, *Arbutus unedo*, and *Erica arborea*, were significantly mobilized to support the demands of regrowth and respiration after clipping the plant tops at different frequencies was simply inferred by noticing some of the plant species dying following clipping (Canadell and Lopez-Soria, 1998).

Plant species that are clipped at different seasons could therefore differ in resprout heights. Individuals that are cut in winter could produce resprouts taller than those of plants that are cut in other seasons. Plants that are cut in winter could contain more root starch and sugar reserves than plants that are cut in other seasons (Landhäusser and Lieffers, 2003; Regier *et al.*, 2010). Plants re-absorb carbohydrates and nutrients from the leaves into roots as they lose leaves in winter, while in other seasons some carbohydrates and nutrients remain aboveground and get lost with the aboveground parts when they are cut (Burch, 1997). It was hypothesized that the season of cutting would affect the height of resprouts by affecting starch and sugar root reserves. Therefore, the study assessed (i) the effects of the season of cutting aboveground plant parts on root starch and sugar reserves and (ii) the relationship between root starch and sugar reserves, and plant height of resprouts.

5.2 MATERIALS AND METHODS

5.2.1 Experimental sites

Two sites, one dominated by *Dichrostachys cinerea* (*D. cinerea*) Wight et Arn (Figure 5.1) plants and the other dominated by *Terminalia sericea* (*T. sericea*) Burch ex Dc. (Figure 5.2) plants, were selected within the Nylsvley Nature Reserve (described in Chapter 2) and used for data collection.



Figure 5.1: Sandy area in the Nylsvley Nature Reserve dominated by *Dichrostachys cinerea* juveniles.



Figure 5.2: Sandy area in the Nylsvley Nature Reserve dominated by *Terminalia sericea* juveniles.

5.2.2 Experimental design

A group of 40 juvenile (juveniles are individuals of plants of ages older than saplings but younger than adults and have not yet reached reproductive stages) plants of *D. cinerea* Wight et Arn and *T. sericea* Burch ex Dc. was randomly selected each month from March to November 2001 and then in January and February 2002, using the probability random sampling method (Taherdoost, 2016). This sampling method was chosen because it allows every item in the population to have an equal chance of being included in the sample. Data collectors took turns flipping coins as follows: If the tail of a flipped coins happened to face up after flipping it, the researchers moved 2 meters to the west away from the initial standing point, and a 4 m x 4 m square quadrat was constructed. If the tail of a flipped coin happens to face up after flipping it for the second time, the researchers moved 4 m to the west away from the center of the first square quadrat. A 4 m x 4 m square quadrat was then constructed. In an instance where the tail of a flipped coin happens to face up in the third flip, the researchers moved 4 m to the east away from the center of the second 4 m x 4 m square

quadrat. If the head of the flipped coin happens to face up in the fourth flip, the researchers moved 4 m to the south away from the center of the previous third 4 m x 4 m square quadrat.

The same pattern was followed until 40 individuals of *Dichrostachys cinerea* and 40 individuals of *Terminalia sericea* were covered. A quadrat that was constructed was always 4 meters away from the centre of the preceding one, either towards the east, south, north, or west. The individuals of the same age group (that is of the same morphology) were sampled within each quadrat until 40 individuals were collected. This was to ascertain that only individuals of the same age group were sampled. Each of the forty individuals of the two plant species was selected one by one (Figure 5.3) and cut (Figure 5.4) at 10 mm above the ground during each of the eleven months referred to above to observe how they were going to respond to cutting. Also, how starch and sugar interacted with the season of cutting was observed.



Figure 5.3: One of the two groups of data collectors using a measuring tape to construct quadrats with another member locating individuals for cutting.



Figure 5.4: A member of data collectors preparing to saw an individual *Dichrostachys cinerea* from one of the quadrats.

5.2.3 Data collection

Line transects and square quadrats methods were used to sample juvenile plants of both *D. cinerea* and *T. sericea* (Buckland *et al.*, 2007). *Dichrostachys cinerea* and *Terminalia sericea* plants were then cut in groups of 40 individuals during the four different seasons of the year from 2001 to 2002. The resprout heights for all cut juvenile individuals of both *D. cinerea* and *T. sericea* were then measured a year later, following cutting. Rulers and tape measures were used to measure the resprout heights. Whether plant species, season, and the interaction between plant species and season affected starch and sugar concentrations was established.

The relationship between starch and sugar and plant resprout height was presented and described.



Figure 5.5: A member of data collectors sawing an individual of *Terminalia sericea* from one of the quadrats.

Forty similar sized juvenile individuals of *Dichrostachys cinerea* and 40 similar sized juvenile individuals of *Terminalia sericea* were clipped on a seasonal basis as follows: autumn (February, March, and April), winter (May, June, and July), spring (August, September, and October), and summer (November, December, and January). Each of the cut individuals was allowed one year to recover before they were dug; that is, those cut in summer year 2000 were dug in the summer in the year 2001, those cut in autumn in the year 2000 were dug in the autumn in the year 2001, and those cut in winter of year 2000 were dug in the winter in the year 2001. The trend proceeded in a similar pattern for all the groups.

The dug roots were oven-dried at 100°C for 1 hour immediately after digging. After one hour of oven-drying, the temperature was lowered to 70°C for another hour (Zhou *et al.*, 2020). The purpose of oven-drying the roots was to lessen the enzyme activity effects on the roots. Such enzyme action leads to starch or carbohydrates interconversions as follows: sucrose reduced to sugars (Narra *et al.*, 2004; Zhou *et al.*, 2020). Roots were ground to powder after drying them using the grinding machine.

5.2.4 Extraction of starch and soluble sugar

The extraction of sugars and starch was carried out as described by Hermiati *et al.* (2023). In brief, plant powder of 0.1 g was weighed out and extracted using 10 ml of 80/20 (v/v) ethanol/water mixture (sugars). Eighty percent ethanol was then added to the 0.1 g of ground root powder, and samples were immediately incubated at 0°C for 72 hours. Samples were centrifuged and supernatants diluted to 25 ml with ethanol. To prepare the samples for spectrophotometer analysis, 0.5 ml of the diluted supernatant was added to 1 ml 28% phenol, 5 ml 98% H₂SO₄ and 0.5 ml distilled water. Tubes were vortexed and allowed to stand for 15 minutes. Samples were read at OD 490 nm. The glucose standard curves 0.05g/50 ml (glucose/distilled water) of stock solution was prepared. Glucose standards in the range of 0 - 80 μ g/ml were also read at 490 nm to generate a standard curve.

The pellets from the sugar extraction were retained and dried. Ten millilitres of 3.6% hydrochloric acid were added to hydrolyse the starch, and the tubes were put in the water

bath, where they were boiled for 3 hours and thereafter centrifuged. Samples were prepared for spectrophotometer analysis of the sugars.

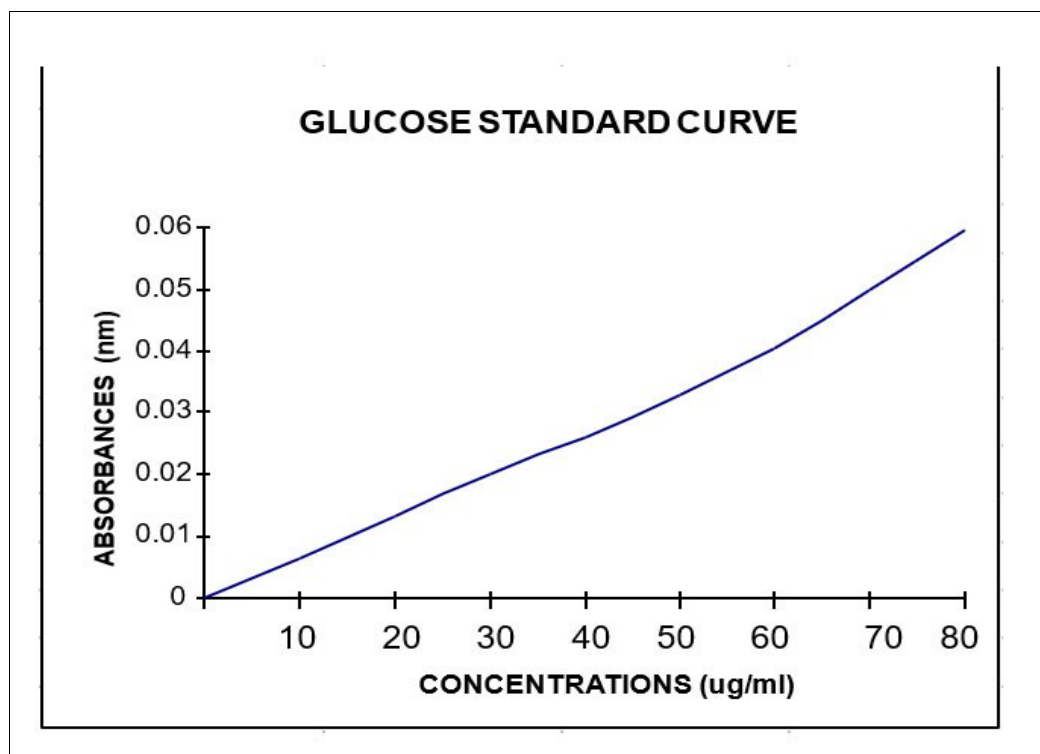


Figure 5.6: The glucose standard curve.

Figure 5.6 was used to determine the concentration of both the sugar and the starch. The prepared sample solutions were diluted by measuring out 1 ml of the prepared solution for spectrophotometer analysis and diluted with 9 ml of ethanol (i.e., 10 times dilution).

5.2.5 Data analysis

Analyses were done in SPSS version 27. The ANOVA procedure was employed to test if the mean sugar concentration and mean starch varied by season. Since the sugar starch

concentrations are expected to vary with species, a two-factor ANOVA with season and species as the factors was employed. The interaction effect of season and species was also included in the ANOVA model. Where the ANOVA procedure showed $p < 0.05$, the Bonferroni ad hoc test was used for mean separation.

For each season and species combination, simple linear regression models were used to investigate the nature of the relationship between plant sugar and plant height as well as that between plant starch and height. Scatter plots depicting the equation of the line of best fit, the R value for the regression line and the p -value for testing the significance of the relationship were drawn in each case.

5.3 RESULTS

5.3.1 Starch

Starch concentrations varied with seasons ($p < 0.05$). The root starch concentrations from the spring-clipped plants were 45.6% (29.4 $\mu\text{g/ml}$), 101.1% (46.2 $\mu\text{g/ml}$), and 262.5% (25.9 $\mu\text{g/ml}$) higher than those clipped in autumn, winter, and summer respectively (Table 5.2). Root starch concentration from the summer-clipped plants was less than those from the rest of the seasons, with root starch concentration from the spring-clipped plants being more than 3-fold (77.7 $\mu\text{g/ml}$) greater than the summer ones (Tables 5.1 and 5.2). Averaged across seasons, *Terminalia. sericea* exhibited 250% (56.2 $\mu\text{g/ml}$) greater concentration of starch than *D. cinerea*.

Additional to the main effects of plant species and season of clipping, the interactive effects of plant species and season of clipping (PxS) on the root starch concentration were also significant (Table 5.2). The *T. sericea* root starch concentrations were greater compared to the *D. cinerea* ones in all seasons except in summer, where no significant difference in the root starch concentrations of the two species was observed (Figure 5.7). Also, the spring-clipped *T. sericea* and autumn-clipped *D. sericea* plants produced more and less root starch concentration, respectively (Figure 5.7).

Table 5.1: Analysis of variance.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	130713	130713	4308.15	<0.05
Age	3	32483	10828	356.87	<0.05
Species: Age	3	9496	3165	104.33	<0.05

Table 5.2: Mean root starch concentration according to species and season of clipping. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni ad hoc test. Error bars are displayed on bar graphs.

Treatments	Mean starch concentrations ($\mu\text{g/ml}$)
Plant Species	
<i>Dichrostachys cinerea</i>	22.5(0.235)b
<i>Terminalia sericea</i>	78.7(0.235)a
Season	
Autumn	64.5(0.406)b
Winter	46.7(0.287)c
Spring	93.9(0.406)a
Summer	25.9(0.287)d

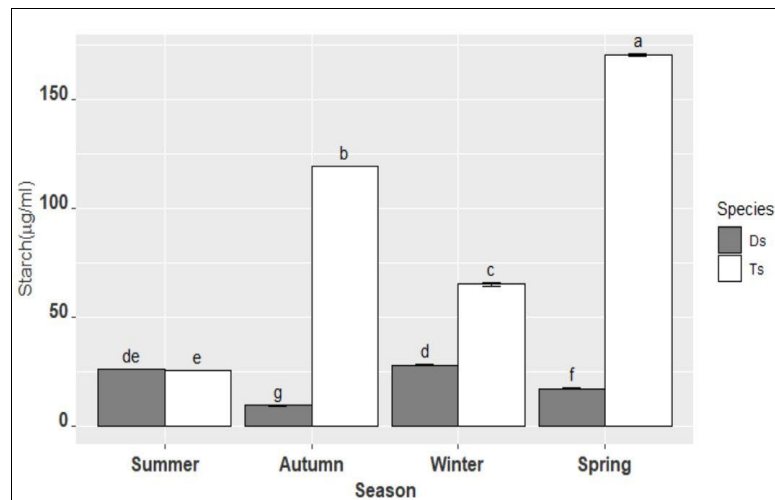


Figure 5.7: Mean root starch concentrations of the two species, *Dichrostachys cinerea* and *Terminalia sericea* according to seasons of clipping. Error bars are not visible in other cases because they are very narrow; significance can be assessed from letters provided on graphs.

5.3.2 Sugar

Plant species (P), season (S), and the interaction between plant species and season affected sugar concentrations (Table 5.4). Averaged across seasons, the root sugar concentration in *T. sericea* was 220% (46.7) higher than that of *D. cinerea*. Root sugar concentrations from the spring-clipped plants were 6.6% (3.7), 101.3% (30.1), and 30% (13.8) greater than those clipped in autumn, winter, and summer, respectively (Table 5.4). Root sugar concentrations from the winter-clipped plants were lower than the rest of the seasons, with root sugar concentrations from the spring-clipped plants being more than 2-fold (59.4) greater than the winter ones (Table 5.4).

In addition to the main effects of plant species and season of clipping, the interactive effects of plant species and season of clipping (PxS) on the root sugar concentrations were also significant (Table 5.4). The *T. sericea* root sugar concentrations were higher compared to the *D. cinerea* ones in all seasons (Figure 5.8). Also, the autumn and spring clipped *T. sericea* plants produced more root sugar concentration, but the difference was greater in the autumn, while less root sugar concentration was produced in the winter by *D. cinerea* (Figure 5.8). There was a lower difference in sugar concentration between *T. sericea* and *D. cinerea* in winter (Figure 5.8). There was no difference in sugar concentration in *Terminalia sericea* in spring and autumn (Figure 5.8).

Table 5.3: Analysis of variance

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	189619	189619	28694.0	<0.05
Age	3	132659	44220	6691	<0.05
Species: Age	3	194787	64929	9825.4	<0.05

Table 5.4: Mean root sugar concentration according to species and season of clipping. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni ad hoc test. Error bars are displayed on bar graphs.

Treatments	Plant sugar concentrations (µg/ml)
Plant Species	
<i>Dichrostachys cineria</i>	21.2(0.503)b
<i>Terminalia sericea</i>	67.9(0.503)a
Season	
Autumn	56.1(5.48)b
Winter	29.7(1.83)d
Spring	59.8(4.03)a
Summer	46.0(2.92)c

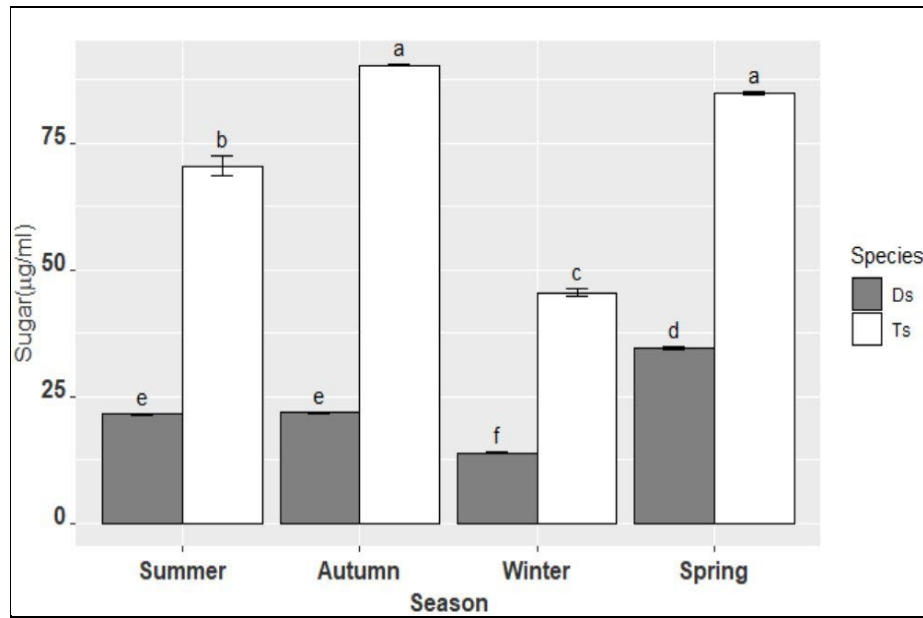


Figure 5.8: Mean root sugar concentrations of the two species, *Dichrostachys cinerea* and *Terminalia sericea* according to seasons of clipping. Error bars are not visible in other cases because they are very narrow; significance can be assessed from letters provided on graphs.

5.3.3 The relationship between plant sugar and plant height

The plant heights of the resprouts of *Dichrostachys cinerea* had a negative relationship ($R = 0.5$; $p < 0.05$) with the root sugar concentration in winter (Figure 5.9c). The relationship was such that a one-unit increase in sugar concentration corresponded to a 0.288 cm decrease in height on average.

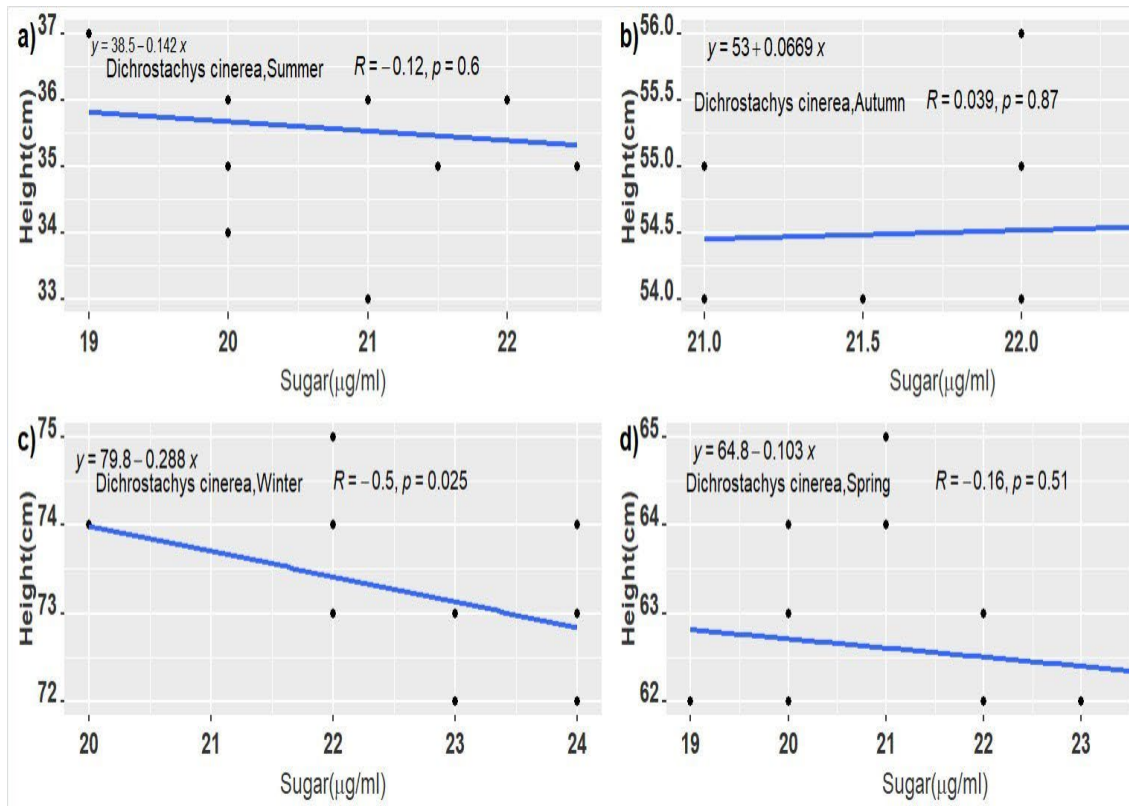


Figure 5.9: The relationship between root sugar concentration and resprout height of *Dichrostachys cinerea* in (a) summer, (b) autumn, (c) winter, and (d) spring.

In contrast to *Dichrostachys cinerea*, the relationship between root sugar concentration and resprout heights in *Terminalia sericea* was positive in autumn ($R = 0.51$; $p < 0.05$), negative in summer ($R = -0.55$; $p < 0.05$), and non-significant in the other two seasons. For summer, a one unit increase in root sugar concentration corresponded to a 0.526 cm decrease in height on average (Figure 5.10a). For autumn, a unit increase in root sugar concentration corresponded to a 0.437 increase in height on average (Figure 5.10b).

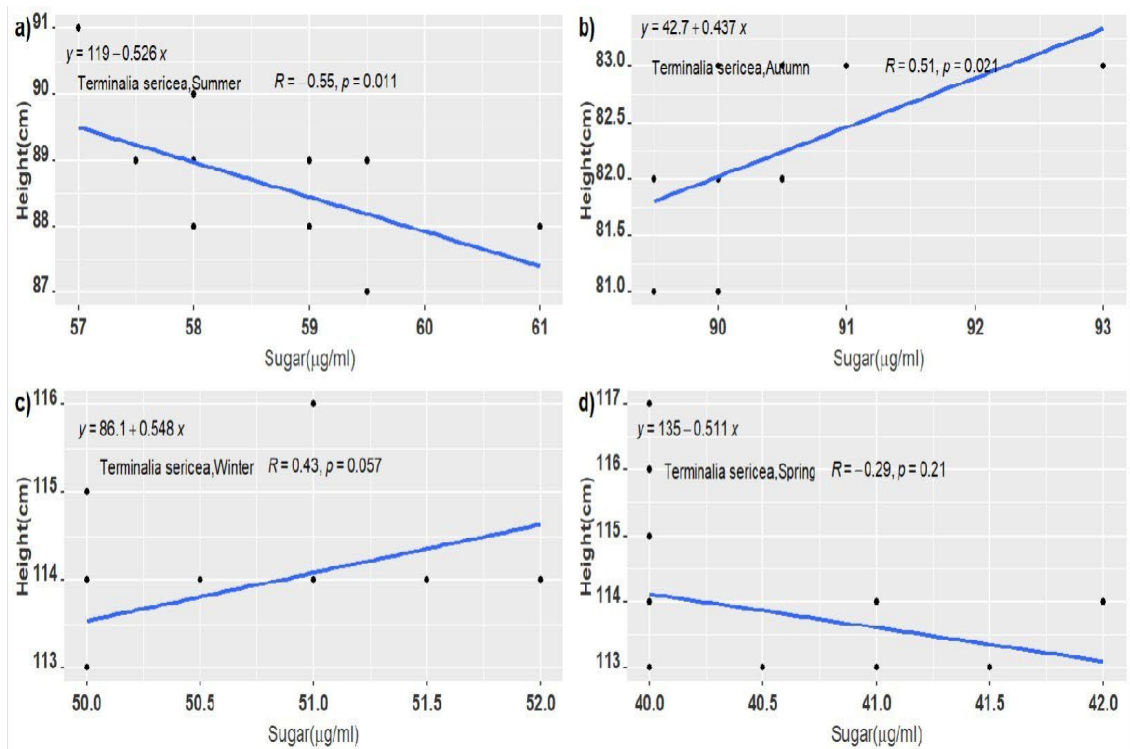


Figure 5.10: The relationship between root sugar concentration and resprout height of *Terminalia sericea* in (a) summer, (b) autumn, (c) winter, and (d) spring.

The relationship between starch concentration in the roots and plant heights of the resprouts in the two species was not significant in all the seasons (Figures 5.11 and 5.12). Their data were therefore not accounted for.

5.3.4 The relationship between starch and height.

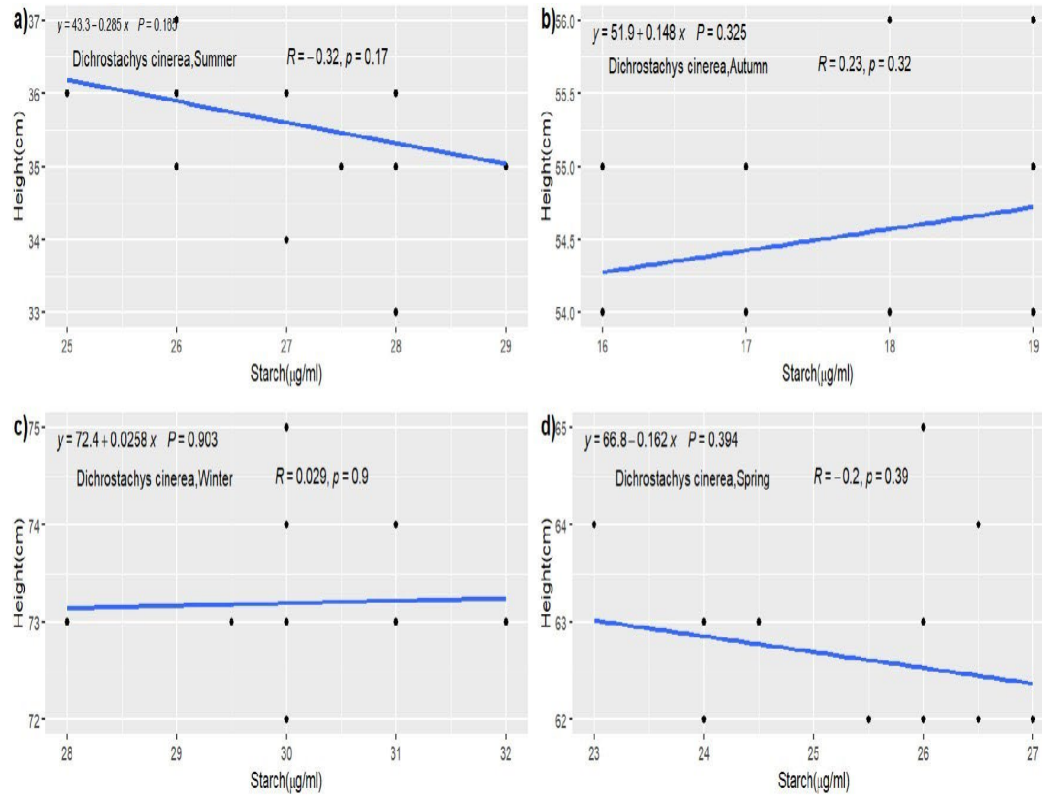


Figure 5.11: The relationship between root starch concentration and resprout height of *Dichrostachys cinerea* in (a) summer, (b) autumn, (c) winter, and (d) spring.

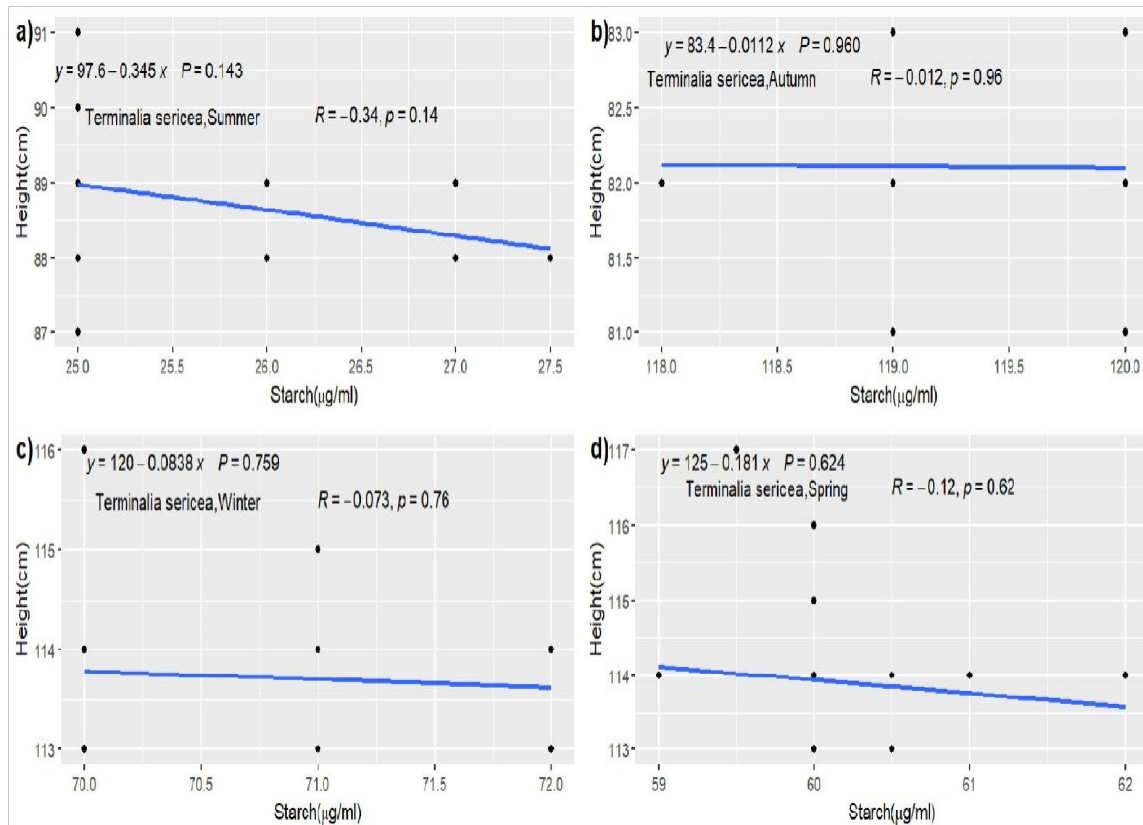


Figure 5.12: The relationship between root starch concentration and resprout height of *Terminalia sericea* in (a) summer, (b) autumn, (c) winter, and (d) spring.

5.4 DISCUSSION

The varying degrees of reliance of plants for their initial regeneration and further growth from root sugar and root starch reserves have been reported previously (Canadell and Lopez-Soria, 1998). de Figueiroa *et al.* (2006) found that plants that were clipped in the dry season had higher and similar survival rates, irrespective of the species or clipping treatment. The current study revealed that trees do store root starch and sugar reserves in all seasons of the year (Figures 5.7 and 5.8). These reserves are necessary for survival and resprouting following injury (Regier *et al.*, 2010). The storage of these reserves varied with the seasons, which is probably an indication that plant species requirements do differ with season. For

example, plants need to survive in winter and fuel bud flush and shoot growth in spring until leaves are formed to support the plant through the process of photosynthesis (Regier *et al.*, 2010). Kalke and Dawson (2005) reported on the importance of starch and sugars in the survival of plants following stress.

The trend observed in the current study with variation in root starch and sugar reserve storage, with *Dichrostachys cinerea* generally having much lower starch concentrations. There were observations of the differences in the root diameters/shapes of the two species, (Nakanyala, 2020, Nakanyala and Hipondoka, 2020, Rankin, 2017) with *D. cinerea* generally containing significantly fewer storage reserves than *T. sericea*; this is a reflection that root reserve storage differs from species to species. The lower root starch and sugar reserves of *D. cinerea* than those of *T. sericea* might be an indication that the requirements of these reserves by the two species differ with the former species using more than the latter for recovery from perturbations. Winter did not appear to be a very favourable season to clip the two species in terms of the relative amounts of root starch and sugar reserves, more seemed to have been extracted for their survival in winter and bud flush and shoot growth in early summer. On the other hand, the observed greater storage of starch and sugar by *Terminalia sericea* than by *Dichrostachys cinerea* might be ascribed to the observed root structures of the two species, with one of *Terminalia sericea* being lignotuberous and that of *Dichrostachys cinerea* being nonlignotuberous.

The increase in root sugar concentration in winter, which corresponded with a decrease in the average plant resprout heights in *Dichrostachys cinerea* might imply that root sugar concentration increases at certain seasons may not necessarily always have a positive relationship with resprout height; instead, carbon allocation may have been geared towards the roots and other plant structures. Also, plants naturally allocate carbohydrate reserves to roots from aboveground parts. The allocation of root sugar reserves in *Terminalia sericea* in autumn might imply that it has a positive relationship with resprout height formation besides other plant structures. Autumn is the time of year when plants are still allocating below ground reserves to above ground structures. In summer, plants might allocate more sugar to root in *Terminalia sericea* than to resprout height formation because summer could be a time when not yet enough is accumulated belowground to supply resprout height formation. Also, plants might increase their root sugar reserves by adding to what is not enough to allocate to other parts of their structures. Carbon supply for regrowth few weeks of resprouting depends on stored, non-structural carbohydrates in the belowground organs (Cruz *et al.*, 2003).

Seasonal variations in the vigour of resprouting of plant species have been interpreted to result from the differences in non-structural carbohydrates reserves, which vary seasonally (Cruz and Moreno, 2001). Current data do not support hypotheses "I expected to find a positive relationship between starch/sugar concentrations and resprout vigour but the results were confusing and inconclusive". Expectations were not fulfilled I think because of how data were collected, there was no cutting of plants before starting with data collection for comparison of pre- clipping and post-clipping plants. Also, concentrations were used, not

total stored reserves, and resprout heights from a pre-clip without knowing the stored reserves the plant had available when they were clipped, only after it was clipped.

The current study has shown both positive and negative relationships between sugar and starch concentration of species and resprout heights formed. For instance, in only one instance, an increase in sugar concentration resulted in an increase in resprout heights formed for one species, and in another instance, we observed a decrease in resprout heights. This study did not reveal the indispensability of root starch and sugar reserves for the continued survival of savanna plant species, regardless of the season of disturbance. The level and extent of requirements for these root reserves would generally vary from plant species to plant species.

For example, a study by Figueiredo *et al.* (2012) in the Caatinga region found the effects of cutting practices varying among species. They found plants that were cut in the dry season sprouting better than those cut in the other seasons. A study by Klimes (2007) found that some species have higher mortality rates when cut in the wet season than when cut in other seasons of the year. The variation in the effects of cutting practices on how plant species respond is probably species-specific as species are genetically different. Also, plant species-response to cutting could depend on where cutting practices are done. My data suggest that starch/sugar concentrations in the plant roots could be important in explaining these differences.

5.5 CONCLUSION

Plant species did respond differently to cutting in the current study when they were clipped at different seasons of the year. Generally, *T. sericea* showed a greater amount of starch than that of *D. cinerea*; it was only in the summer that root starch concentrations did not differ. Root starch concentration was not found to improve significantly for all four seasons for *D. cinerea*, while for autumn and spring, *T. sericea* showed greater improvement in the accumulation of the amount of root starch concentration. There was a negative relationship between root sugar concentration and plant resprout heights of *D. cinerea* in winter. In contrast, a positive relationship was observed between root sugar concentration for *T. sericea* and their resprout heights in the autumn while a negative relationship between root sugar concentration and their resprout heights was observed in the summer. The cutting of plants at different seasons particularly summer and winter, results in a more negative effect on their root starch content than those cut in autumn and spring, but that is species-dependant. In contrast, the cutting of plants at all seasons results in some improvement in their root sugar concentration but that also shows that it is species-dependent. The current study showed that root starch and root sugar accumulation and concentration following the cutting of aboveground parts is generally species-dependent.

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CHAPTER 6 THE EFFECT OF FIRE ON DICHROSTACHYS CINEREA AND TERMINALIA SERICEA OF DIFFERENT AGE GROUPS AND THE RELATIONSHIP BETWEEN THEIR BARK THICKNESS AND STEM DIAMETERS

ABSTRACT

The bark is important as a protective mechanism and also for the storage of water and sugars. The response of bark to harvesting is in various ways, such as bark recovery growth and agony shoot development, which is largely species-dependent. The current study investigated the relationship between bark thickness and age group and how that relationship varies with species, as well as the relationship between stem diameter and age group and how that relationship varies with species. Also, the effect of fire on plants of different age groups was assessed.

Bark thicknesses and stem diameters of plants of the three different age groups, namely seedlings, juveniles, and adults, were measured using vernier callipers and rulers where necessary. Meter rods were used to measure the heights of plants of different age groups to ascertain that plants of the same age group were put in the same cohort. One of the Nylsvley Nature Reserve areas was burned to observe how the two plant species, *Dichrostachys cinerea* and *Terminalia sericea* of three different age groups, responded to being destroyed by fire. Seedlings and juveniles were found to possess thinner barks and stems than adult plants, which were found to be thicker. Seedlings and juveniles were found to be less protected from fire; in other words, few adults were killed by fire. Adult plants are more tolerant to fire; probably due to their thick barks, than seedlings and juveniles, which possess

thin barks. This suggests that possession of thick barks is advantageous as plants are protected from destruction.

6.1 INTRODUCTION

Regardless of their makeup, tissues outside the vascular cambium are referred to as bark (Delvaux *et al.*, 2009). Williams *et al.* (2007), for instance, defined bark as an aggregate of secondary phloem, cortex, and periderm. The meristematic cell layer that drives periderm growth is known as the phellogen. Phellem or cork refers to cells that develop outward, while phelloderm refers to cells that grow inward from that point. The inner bark is made up of living tissue known as phloem. It is also known as non-collapsed secondary phloem (Delvaux *et al.*, 2009). According to Williams *et al.* (2007), bark thickness varied across species depending on the tree's location and site characteristics.

Ring barking usually leads to tree death due to the long time taken before bark recovery to close the wound (Delvaux *et al.*, 2010). As defined by Moore (2013), ring barking is a circumferential incision performed around a tree's trunk that instantly affects the transfer of materials in the phloem tissues by removing a band of tissue that contains cork and cork cambium, phloem tissues, and the cambium. Transport of simpler compounds dissolved in phloem sap, as well as complex chemical molecules like sugars, amino acids, and hormones, is impacted by the loss of phloem tissues (Moore, 2013). Moreover, Chungu *et al.* (2007) found that bark removal resulted in extensive fungal and insect infestations, which accelerated wood deterioration.

Different species react differently to the harvesting of bark; examples include the production of agony shoots, which are vegetative shoots that sprout around a wound in response to wounding; these responses are primarily species-dependent (Delvaux *et al.*, 2009). When the cambium glides across the wound surface, closure is most effective. The wound could never heal if the cambium rolled inward to produce a callus. To prevent pathogens from spreading and protect vascular, storage, and meristematic tissues, the tree forms boundaries within the wound that was present at the time of wounding during the initial phase following bark harvesting (Delvaux *et al.*, 2010).

Bark harvesting often leaves the tree severely wounded, especially if all of the bark is taken off. The livelihoods of the people who depend on valued medicinal plant species are also negatively impacted by non-sustainable bark harvesting (Delvaux *et al.*, 2010). The bark is collected more often as a result of the growth of bark harvesters and merchants and the ensuing increased competitiveness, which frequently results in trees being ring-barked (Chungu *et al.*, 2007). The Southern African Development Community (SADC) region's current tree bark harvesting techniques for medicinal purposes have killed out numerous forest tree species, resulting in a significant loss of biodiversity (Chungu *et al.*, 2007). However, the properties of the bark, particularly bark thickness, play a role in the survival of trees (Gignoux *et al.*, 1997). Other studies reported that the bark thickness sizes of tropical savanna plant species reveal their resistance to fire (Hengst and Dawson, 1994; Pinard and Huffmann, 1997, and Lawes *et al.*, 2011). It was reported that bark thickness determines the degree of heat insulation and protection of vital tissues in the stem and has a role as a defensive trait (Pausas, 2015).

Hedge *et al.* (1998) reported on the direct proportion between bark thickness and girth size and that it is in more disturbed habitats where plant species possess thicker barks than those in less disturbed sites. Similarly, Fasola *et al.* (2014) observed a direct correlation between bark thickness and the girths of plant species. Accordingly, plant bark thickness and girth sizes should increase with plant age, and older plants are better resilient to burning than younger ones. All aboveground parts of seedlings of *Dichrostachys cinerea* and *Terminalia sericea* will be killed by fire because they are at a tender age, while juveniles and adults will survive the fire. The objectives follow, to assess (1) how bark thickness and age group relate, and how that relationship varies with species; (2) how the stem diameter relates with age group, and how relationship varies with species; and (3) the effect of fire on plants of different age groups.

6.2 METHODS AND MATERIALS

6.2.1 Experimental sites

Two sites, one dominated by *Dichrostachys cinerea* (*D. cinerea*) (Figure 6.1) and the other dominated by *Terminalia sericea* (*T. sericea*) (Figure 6.2) plants were selected within the Nylsvley Nature Reserve (described in Chapter 2) and used for data collection.



Figure 6.1: Sandy area in the Nylsvley Nature Reserve dominated by *Dichrostachys cinerea* juveniles.



Figure 6.2: Sandy area in the Nylsvley Nature Reserve dominated by *Terminalia sericea* juveniles.

6.2.2 Experimental design

Fourty seedlings, 40 juveniles, and 40 adult plants of *D. cinerea* and *T. sericea* were randomly selectcted towards the end of August 2013 using the probability random sampling method (Taherdoost, 2016) from the study site. The study site burned accidentally on the 19 September 2013 (personal communication; Whitecross, Witkowski, Archibald, 2016). The amount of grass biomass could therefore not be determined. The focus of the three days of the fire by rangers, managers and the farmers surrounding Nylsvley Nature Reserve (NNR) was only to attempt to put down the wildfire (personal communication). (Taherdoost, 2016)'s probability random sampling method was chosen because it allows every item in the population to have an equal chance of being included in the sample. A quadrat that was constructed was always two meters away from the centre of the preceding one, either towards the east, south, north, and west.

6.2.3 Data collection

Fourty seedlings, 40 juveniles and 40 adults of both *D. cinerea* and *T. sericea* were selected from the study site. Data collectors took turns flipping coins from the centres of 4 m x 4 m constructed quadrats until all individuals for each of *Dichrostachys cinerea* and *Terminalia sericea* were covered. Line transects and square quadrats methods were used (Buckland *et al.*, 2007) to sample the seedlings, juveniles, and adults of both *D. cinerea* and *T. sericea* that were cut before the wild accidental fire. The selected plants were sawn towards the end of August 2013 to measure their bark thicknesses, and their stem diameters Measurements of the bark thicknesses and stem diameters were carried out on the same day immediately following plant cutting. The observation of how the cut plants interacted with the wild accidental fire was carried out in November 2014.

6.2.4 Data analysis

Analyses were done in SPSS version 27. The ANOVA test procedure was employed to test if the mean bark thickness and stem diameter varied with age and species. Since the bark thickness and stem diameter are expected to vary with species and age group, a two-factor ANOVA with age group and species as the factors was employed. The interaction effect of age group and species was also included in the ANOVA model. Where the ANOVA procedure showed $p < 0.05$, the Bonferroni ad hoc test was used for mean separation.

6.3 RESULTS

6.3.1 Stem diameter

Plant species (P), age group (A), affected stem diameter (Table 6.1). Averaged across species, *T. sericea* stem diameter was 103% (5.54 cm) taller compared to that of *D. cinerea* (Table 6.2). The stem diameters of the adult plants were 206% (11.98 cm) and 1970% (16, 94 cm) thicker than those of juveniles, and seedlings respectively (Table 6.2). In addition to the main effects of plant species and age group, the interactive effect of plant species and age group (PxA) on the stem diameter was also significant (Table 6.1). The difference in mean stem diameter is more apparent in older plants compared to younger ones (Figure 6.3).

Table 6.1: Table of Analysis of variance.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	2000.4	200.4	5241.9	<0.05
Age	2	13461.7	6730.8	17638.1	<0.05
Species: Age	2	1325.4	662.7	1736.6	<0.05

Table 6.2: Mean stem diameters of the two trees species, *D. cinerea* and *T. sericea* according to species and age groups. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni adhoc test. Error bars are displayed on bar graphs (Figure 6.3).

Treatments	Mean stem diameter (cm)
Plant Species	
<i>Dichrostachys cinerea</i>	5.36(0.430)b
<i>Terminalia sericea</i>	10.9(0.822)a
Age group	
Adult	17.8(0.625)a
Juvenile	5.82(0.235)b
Seedling	0.730(0.041)c

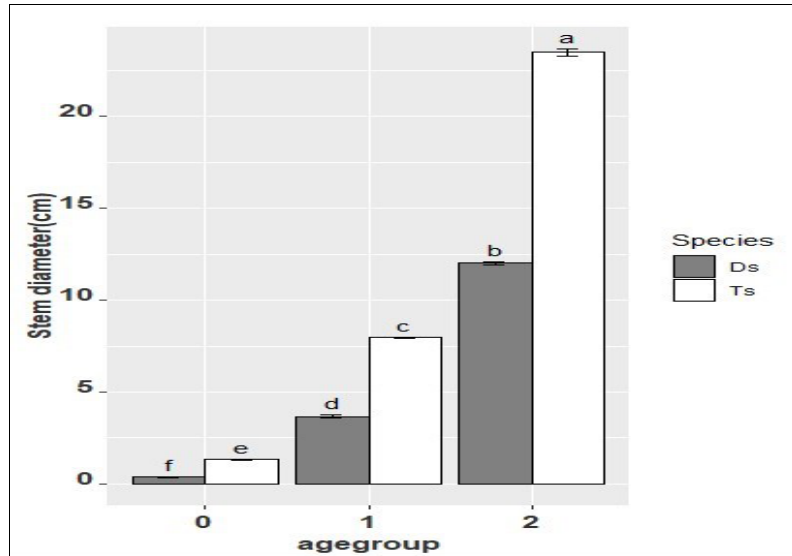


Figure 6.3: Mean stem diameters of the two tree species, *D. cinerea*, and *T. sericea* according to the interaction of species and age group. Error bars are not visible in other cases because they are very narrow; significance can be assessed from letters provided on graphs.

6.3.2 Bark Thickness.

Plant species (P), age group (A), affected bark thicknesses (Table 6.4). Averaged across species, *T. sericea* bark thickness was 68% (0.26 cm) thicker compared to that of *D. cinerea* (Table 6.4). The bark thickness of from the adult plants was 194% (0.70 cm) and 783% (0.94 cm) thicker than that of juveniles and seedlings, respectively (Table 6.4). In addition to the main effects of plant species and age group, the interactive effect of plant species and age group (PxA) on the bark thickness was also significant (Table 6.4). Again, the difference in bark thickness between *Terminalia* and *D. cinerea* becomes more apparent as plant age increases.

Table 6.3: Analysis of variance.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F value	P value
Species	1	4.866	4.8656	390.333	<0.05
Age	2	41.756	20.8778	1674.901	<0.05
Species: Age	2	1.304	0.6519	52.301	<0.05

Table 6.4: Mean bark thicknesses of the two trees species, *D. cinerea* and *T. sericea* according to species and age groups. The alphabetical letters attached to the means indicate significant differences between the means according to Bonferroni adhoc test. Error bars are displayed on bar graphs (Figure 6.4).

Treatments	Bark thickness (cm)
Plant Species	
<i>Dichrostachys cinerea</i>	0.38(0.0292)b
<i>Terminalia sericea</i>	0.64(0.0427)a
Age group	
Adult	1.06(0.0310)a
Juvenile	0.36(0.0124)b
Seedling	0.12(0.0105)c

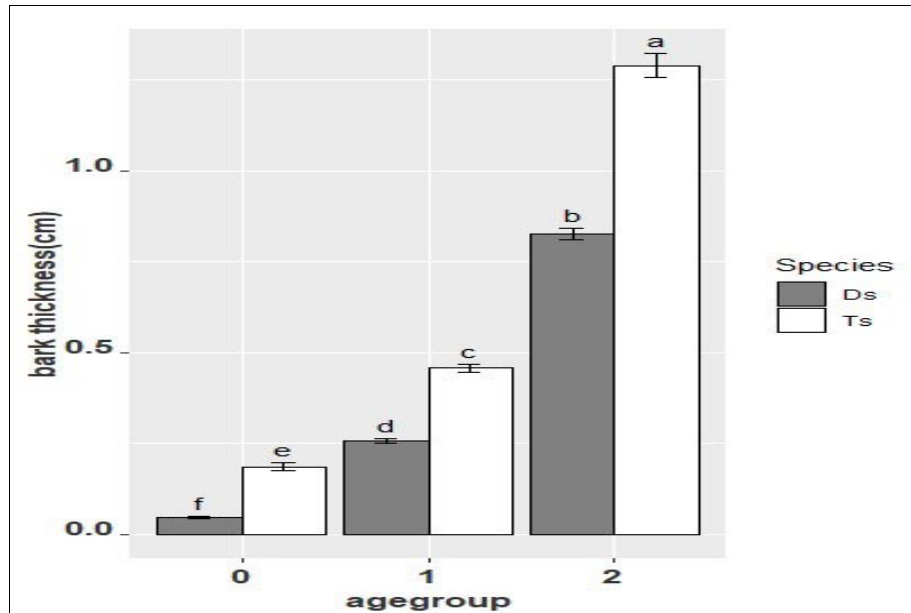


Figure 6.4: Mean bark thickness of the two tree species, *D. cinerea* and *T. sericea* according to the interaction of species and age group. Error bars are not visible in other cases because they are very narrow; significance can be assessed from letters provided on graphs.

6.3.3 The response of plants of different age groups to fire.

Exposure to fire killed all the seedlings and juveniles of *Dichrostachys cinerea*, and all adults were spared (Table 6.5). For *Terminalia sericea* 0% of the seedlings survived, 7.5% of the juveniles survived, and 77.5% of the adults survived (Table 6.5), suggesting that the rate of survival increased with age group. The test of equality of proportions shows that the proportions of survivors significantly differ according to age groups (Chi-square = 71.984, df = 2, $P < 0.05$).

Table 6.5: Responses of two tree species, *D. cinerea* and *T. sericea* of Nylsvley Nature Reserve in November 2014 which were burned by fire in September 2013.

	Number	Dichrostachys cinerea		Terminalia sericea	
		Survived	Died	Survived	Died
Seedlings	40	0 (0%)	40 (100%)	0 (0%)	40 (100%)
Juveniles	40	0 (0%)	40 (100%)	3 (7.5%)	37 (92.5%)
Adults	40	40 (100%)	0 (100%)	31 (77.5%)	9 (22.5%)

6.4 DISCUSSION

The formation of stem diameters and bark thicknesses of varying sizes by plants of different age groups observed in the current study is a reflection that as plants of different species and sizes grow, they expand at different rates. Both plants of the two species were found to grow and expand differently throughout the experimental period, which indicates that individual plants of different species generally differ in their growth and development. The variation in the average plant stem diameters and bark thicknesses observed in the final stages of the experimental period indicates that the development and expansion of plant structures vary with different plant species and their ages. The direct proportionality between plant species

age groups and their stem diameters and bark thicknesses implies that both plants would better survive fire as they grow into adulthood.

Most previous work on bark ecology reported that bark plays an important role as a protective structure of the stem (Pane *et al.*, 2010; Rosell *et al.*, 2013). Several studies showed that trees ‘escape’ the effects of ground fires by protecting their stems with thick bark (Gignoux, Clobert and Menaut 1997; Hegde, Chandran, and Gadgil 1998; Michaletz and Johnson 2007; Nefabas and Gambiza 2007; Lawes *et al.*, 2011). Adult plants of both *Dichrostachys cinerea* and *Terminalia sericea* are therefore better protected from fire destruction than younger plants, as they were found to possess thicker barks than other age groups. However, there is contention that epicormic resprouting plants in fire-prone habitats, especially savanna, acquire absolute thick bark at an early age (Hoffmann, Orthen and Do Nascimento, 2003; and Hoffmann and Solbrig, 2003).

The bark thickness is a defensive trait that is easy to measure. It is correlated with other stem traits, which are still poorly understood (Poorter *et al.*, 2014). Despite the importance of thick bark in protecting trees against fire damage, some trees have relatively thick barks with inner barks to store water (Scholz *et al.*, 2007; Poorter *et al.*, 2014; Rosell and Olson, 2014). Results of this current study found that more seedlings and juveniles are destroyed by fire, which might be implication that adults are better protected from injuries because of their possession of thicker barks. Bark thickness has been reported to determine the degree of heat insulation and protection of vital tissues in the stem (Pausas, 2014). The differences in the

extent of tolerance to fire by plants of different age groups are important to prevent the decimation of all plants of different age groups in instances of fire of high intensities.

Where there could be varying patterns of bark thicknesses and stem diameter expansions from tree species to tree species, this could be attributable to variation in species genetic make-up and hence differences in the rate at which species or components thereof develop. Also, microhabitat heterogeneity might affect within and between species development. Savanna plants in the current study are growing in open sites at Nylsvley Nature Reserve and were found to produce thicker barks from seedling to adulthood stages, and this observation is in agreement with Williams *et al.* (2007).

Moore (2013) reported on the interference of the transport of sugars, amino acids, and hormones dissolved in the phloem in situations where the phloem is tempered with. Tree wood boring and infestation of tree stems would be more impactful to seedlings and juveniles than to adults, which would thus cause more injury and hence more death to young plants than to adults. Young plants could therefore be readily found infested by wood-boring insects, as the plants are still at a tender age of building up the bark rather than at the adulthood stage. Adults are thus found to be more tolerant to disturbances such as fire and wood boring, among other disturbance factors. There are reports by Canadell and Lopez-Soria (1998) on the importance of thick bark as a protective cover for savanna trees against disturbance, or injury such as fire. This study revealed the importance of savanna plant species bark thicknesses as plants grow older, with adult plants better protected from injuries than younger plants. A disturbance might completely decimate the whole vegetation in

ecosystems unless such species are reseederers or resprouters. For example, if the disturbance type could be insect borers, plant species with thick barks may be less affected than those with thin barks and hence survive better in such a form of disturbance. Many individuals of *Dichrostachys cinerea* and *Terminalia sericea* were destroyed by fire when they were at their seedling and juvenile stages rather than at adulthood stages, which suggests that plant species survival rates are directly proportional to age group. Adult plants had thicker barks than seedling and juvenile plants, which might therefore imply that resilience to disturbance is positively correlated to bark thickness and age group.

6.5 CONCLUSION

The bark thickness of savanna plants is important in the protection of plants against damages that may be brought about by various forms of disturbances. In situations where plants possess thin barks, they are more easily damaged and hence killed by disturbances such as fire than when they possess thick barks. *Dichrostachys cinerea* and *Terminalia sericea* plants at a young age, such as seedlings and juveniles, are less protected from damage by disturbances than adults. The current study revealed a direct relationship between bark thickness and stem diameters, with young plants possessing thin barks and thin stem diameters and adult plants having thick barks and thick stem diameters.

The fire that burned in the Nylsvley Nature Reserve in September 2013 destroyed all seedlings and all juveniles of *Dichrostachys cinerea*, and almost all juveniles of *Terminalia sericea* were destroyed, while almost all adults of *Terminalia sericea* were spared. It was encouraging, though, to notice that seedling and juvenile savanna plants, which had all their

aboveground parts destroyed by fire, recovered from below-ground organs after months of dormancy. It is therefore prudent to attempt to have a better understanding of the ecology of fires in savannas to assist in the knowledge of the type and intensity of fires that need to be applied so that biodiversity can be continuously maintained.

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CHAPTER 7 PLANT COMPETITION

ABSTRACT

Plant competition usually leads to the displacement of some of their own or different plant species from their original habitats. It is the weak competitors that get displaced during interactive relationships between the competing plant individuals. The gaps that are left behind by the outcompeted plants may be occupied by native plant species which were never occupants of the created gaps, or by alien invasive plant species (IAPS). Grass/plant population compositions get completely changed once infested by plant species that are foreigners in the gaps created through competition. In instances where gaps are created to be occupied by invasive alien plant species, the problem is that vegetation composition changes may be huge. Invasive plant species are generalists who are quick to germinate, grow, and reproduce, and could therefore ultimately affect species composition and diversity in the reserve. Therefore, the study investigated how savanna grass plants compete for moisture between each other, with the possibility that open spaces created through competition could facilitate invasion by IAPs.

A group (Group A) of 34 grass plants of each of the species *Digitaria eriantha* (*D. eriantha*), *Sporobolus africanus* (*Sporobolus africanus*), and *Themeda triandra* (*T. triandra*) were randomly selected from the three sites. The grass tiller xylem water potentials of the 34 grass plants of each of the grass species were measured in August 2012. For each group within a species, data collectors took turns flipping coins from centres of 2 m x 2 m constructed

quadrats until 34 individuals for each of *D. eriantha*, *S. africanus*, and *T. triandra* were covered. Similarly, 34 pairs of the three grass plants were again measured two months later, in October 2012, to compare pre- and post-removal grass tiller xylem water potentials. For each species, another group (Group B) of 34 plants was also selected. For each group within a species, data collectors took turns flipping coins from the centres of 2 m x 2 m constructed quadrats until 34 individuals for each of *D. eriantha*, *S. africanus*, and *T. triandra* were covered. This sampling method was chosen because it allows every item in the population to have an equal chance of being included in the sample.

At the beginning, the xylem water potential of group A and B plants was obtained. This was done for each species. Immediately after measuring the xylem water potentials, two nearest neighbours of group A plants were removed. Therefore, group A was the treatment, and group B was the control. After a month, the xylem water potentials of both the treatment and control groups were determined. Significant intraspecific competition was established among all three species. The study concluded that there appears to be minimal distances between grass plants in ecosystems such as Nylsvley Nature Reserve.

7.1 INTRODUCTION

Competition, one of the most evasive and contentious subjects in ecology (Stoll and Prati, 2001; Silletti *et al.*, 2003; Smith and Knapp, 2003), is defined as any negative impact of two or more organisms for the same limited resource (Holden and Cahill Jr, 2024). However, competition can be clearly explained by defining its two aspects, which are intensity and importance. Intensity is the harm that competition causes to an organism's well-being, while importance is the relative degree to which competition causes the overall decrease in the life of an organism to below its optimal condition (Reynolds and Rajaniemi, 2007). Authors such as Reynolds and Rajaniemi, (2007) and Hart *et al.*, (2018) reported that the intensity and importance depend on the type of the species and where the species are located.

The most widely employed technique in attempting to detect competition within and between plants is referred to as nearest neighbour analysis (Yodzis, 2013); the sizes of two pair members of plants versus their interplant distances measured (Schenk and Mahall, 2002 and Schenk *et al.*, 2003). This technique is continuously employed, directly and indirectly, in plant competition studies (Cahill Jr, 2003; Gordon *et al.*, 2003; Kluse and Diaz, 2005; Buisson *et al.*, 2008; Flory and Clay, 2009). Competition manifests itself as follows:

- (a) There should be a positive correlation between the distance of the two neighbouring plants and the sum of their sizes (Schenk and Mahall, 2002).
- (b) There could be lower limit where no other plant may colonizer between the two neighbouring plants.

Competition for soil moisture amongst other factors, plays a crucial role in patterning vegetation composition in ecosystems. For example, increased nutrients such as nitrogen availability in terrestrial ecosystems have large impacts on the structure and function of some ecosystems (Harpole *et al.*, 2007), while water is one of the resources that is commonly known to be indispensable throughout the lifetime of organisms.

Also, rainfall is reported to strongly control grassland ecosystem processes (Bond, 2016; Potts *et al.*, 2006). Grassland ecosystems, for example, in California, receive a limited water supply with a favourable amount of rainfall experienced in winter, while drought conditions occur in summer when optimal temperatures for growth occur (Harpole *et al.*, 2007). Limitations of resources such as water and nutrients, amongst others, could result in the demise of some plant species within plant communities. Moreover, some reports suggest that the establishment of invasive species in new environments may facilitate the occupation of those areas by non-native species (Simberloff and Von Holle, 1999), resulting in a long-term serious negative impact on pristine ecosystems that could cause a complete change in the plant species composition (Hooper *et al.*, 2005).

Some studies that investigated competition for either moisture or nutrients and employed removal experiments to establish the reactions of plant individuals released of stress found that the removal of neighbouring individual(s) relieved remaining individuals of competition (Fransen and De Kroon, 2001; Silletti *et al.*, 2004; Kluse and Diaz, 2005; Wilson, 2007). Such relief was followed by an increase in the stem xylem water potential (Silletti *et al.*, 2004; Kluse and Diaz, 2005; Wilson, 2007) and an improvement in the production of above-ground materials such as the number of leaves (Kluse and Diaz, 2005). In contrast, clearing

of neighbours could result in the taking over of spaces created by foreign plant species not original to the sites (Vitousek *et al.*, 1997; Parker *et al.*, 1999; Mack *et al.*, 2000; Ehrenfeld, 2010; Andreu and Vila, 2011).

Generally, competition could lead to the removal of some organisms from their original habitats or the outcompeting of one or more individuals by others; usually, organisms that are weak competitors during the strife lose the competition. In such interactive relationships between weak and strong competitors, some plant individuals, particularly those that are weak competitors, are outcompeted and removed from the system (Rees *et al.*, 2005). The spaces created following competitions usually become available for invasion by IAPS. Invasive alien plant species generally exploit spaces left behind by the outcompeted native plant species (Wang *et al.*, 2022). Invasive plant species are generalists who are quick to germinate, grow, and reproduce, and could therefore ultimately affect species composition and diversity in the reserve. Therefore, there is a need to understand how savanna grass plants interact with each other, and hence, find ways to reduce their invasion by IAPs.

The grass plants that we studied are *Digitaria eriantha* (*D. eriantha*), *Sporobolus africanus* (*S. africanus*), and *Themeda triandra* (*T. triandra*) in the Nylsvley Nature Reserve (NNR), as they are prevalent and were found to be preferred by grazing animals in the reserve. These three grass species under the current study in the reserve co-occur but are gradually separating from each other, leaving some open gaps between them. Some of these resulting inter-plant developing spaces are invaded by shrubs and grasses foreign from those that were originally there. Original grass species, particularly one or all the three under study, would

eventually lose their prominence, probably because of potential competition between each other. Such interaction between these grass plants will result in invasion by plants that are not original to the area, and hence a change in the structure and abundance of these grasses that appear favourable to the grazers in the reserve.

Grass plants in the NNR compete for soil moisture. The competition between the grass plants would eventually affect plant composition and diversity. The main objective of this study was to investigate competition between neighbouring grass plants. Specifically, the objectives were to (1) assess the potential interaction between conspecific nearest neighbour grass plants for soil moisture, and (2) assess the grass species' xylem water potentials pre- and post-removal of their conspecific nearest neighbours.

7.2 METHODS AND MATERIALS

7.2.1 Experimental sites

Three 200 m x 200 m sites, one dominated by *Digitaria eriantha* (*D. eriantha*), and others by *Sporobolus africanus* (*S. africanus*) and *Themeda triandra* (*T. triandra*) grass plants (Figures 7.1, 7.2, and 7.3 respectively), were selected within Nylsvley Nature Reserve for data collection.

7.2.2 Description of the species

Digitaria eriantha (*D. eriantha*) Steud

It is known as digit or Pongola grass (Figure 7.1). It is perennial and sometimes stoloniferous or tufted. It grows a dense tussock with extended stolons that are covered with or without hairs. Each grass is erect or ascending, reaching about 35 cm. The lowest basal leaf sheaths are densely hairy or very rarely smooth. The leaf blades are typically 5-60 cm long, 2-14 mm wide, and may be either hairy or smooth. Each inflorescence typically has six or seven spicate branches, each of which carries numerous flowers. These spikelets are usually 2-4 mm long, where the lower glume is long like the spikelet and the upper glumes are where the lemma is situated (covered with 1 mm long hairs) (Oudtshoorn, 1999; Fish, 2015).



Figure 7.1: *Digitaria eriantha* Steud

Sporobolus africanus (*S. africanus*) (Poir.) Robyns & Tournay

It is a fast-growing, tufted, rhizomatous perennial grass, growing from 280 – 1 500 mm high (Figure 7.2). Its roots are fibrous. The leaf blade is 200–400 × 1–4 mm; blade rolled in the bud, slender, stiff. Leaves are reasonably strong and difficult to break, leaf sheaths are hairless and slightly compressed. The dark, slightly green inflorescence is a dense, elongated, almost spikelike panicle. Branches are not whorled, relatively short, rigid, and the central axis is usually visible. The panicle is 100–350 mm long and 10–40 mm wide, with a pointed tip. Spikelets 2.0–2.8 mm long, with unequal outer glumes closely arranged along the panicle branches; lower glume 1/4– 1/2 long as spikelet, broadly oblong, apex obtuse, nerveless; upper glume 1/2 the spikelet length, narrowly ovate, apex acute; lemma ovate-elliptic, apex acute, grain ellipsoid, 1.1–1.2 mm long; anther 0.8–1.0 mm long. Seed are brown, sublobular, and tiny, about 1 mm diameter. It flowers from autumn to early summer, from April to October (Van Oudtshoorn 1999; Fish, 2015).



Figure 7.2: *Sporobolus africanus* (Poir.) Robyns & Tournay

Themeda triandra (*T. triandra*) Forssk

It is a very hardy, evergreen, tall, tufted grass with foliage in many shades of green that turns reddish when older (Figure 7.3). The pendulous, purple-red flower spikes are most attractive from September to June. Another lovely aspect of this grass are the seeds that sprout up afterwards. This grass is an indicator of healthy climax grassland in the natural world. This ubiquitous grass comes in a broad range of sizes; the high-altitude grasses are substantially shorter than the coastal variant. It is available in all of South Africa's provinces. *Themeda triandra* is a perennial tussock-forming grass widespread in Africa, Australia, Asia, and the Pacific. In Australia, it is commonly known as kangaroo grass, and in East Africa and South Africa, it is known as red grass, red oat grass, or rooigras in Afrikaans. The colour is also much more intense on the shorter grasses. The Marsh and Common Hottentot Skipper butterflies graze on this plant as their host. *Themeda triandra* gives the garden movement as it softly sways in the wind. Like other grasses, they should be burned once every five years if feasible, and they should also be chopped back once a year. Their sizes vary from 0.5 to 1m (Van Oudtshoorn, 1999; Fish, 2015).



Figure 7.3: *Themeda triandra* Forssk

7.2.3 Experimental design

A group (Group A) of 34 grass plants of each of the species *D. eriantha*, *S. africanus*, and *T. triandra* (Figures 7.1, 7.2, and 7.3) were randomly selected from the three sites in September 2012 using the probability random sampling method (Taherdoost, 2016). This sampling method was chosen because it allows the selection of each member of the population to be sampled. For each species, another group (Group B) of 34 plants was also selected. For each group within a species, data collectors took turns flipping coins from the centres of 2 m x 2 m constructed quadrats until 34 individuals for each of *D. eriantha*, *S. africanus*, and *T. triandra* were covered. Group A plants had their two neighbours in each of the three species removed, while Group B plants were left intact after pre-pressure bombing and Group A were treatments, and Group B were control plants.

7.2.4 Data collection

Line transects and square quadrats methods were used to sample plants from each group of the 34 randomly selected plants of *D. eriantha*, *S. africanus*, and *T. triandra* grass plants (Buckland *et al.*, 2007). The tiller xylem water potentials of the 34 pairs of *Digitaria eriantha*, *S. africanus*, and *T. triandra* plants were measured using a pressure chamber, as shown in Figure 7.4. Measurements were carried out three days following the other in the afternoons of September 2012. The xylem water potentials of four tillers per individual of pairs were measured, and the average thereof was taken in each case. The clearing of two grass individuals from all individuals of all group A plant species following the determination of pre-clearing xylem water potential was carried out (Figure 7.5). Tiller xylem water potentials of the same 34 groups of each A and B for the three grass species were again measured two months later, on 12 November 2012 to compare pre- and post-removal grass tiller xylem water potentials.

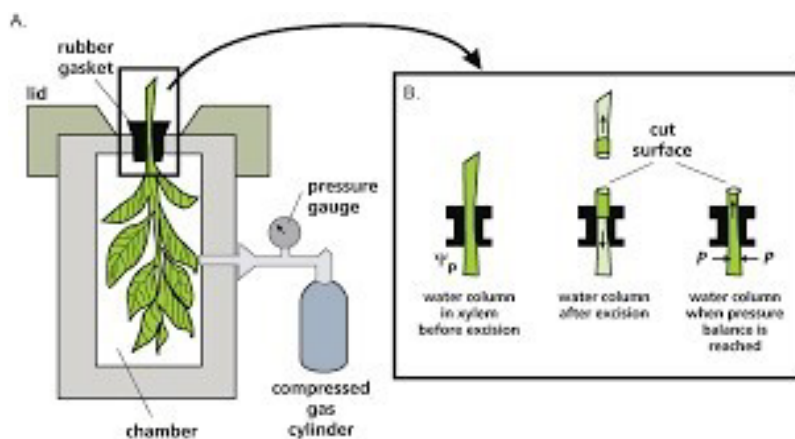


Figure 7.4: Pressure Chamber for measuring tiller xylem water potentials (adapted from Lambers, H., Chapin, F.S. and Pons, T.L., 2008, page 186).



Figure 7.5: Clearing of stand to observe the effects of inter-plant gaps on plant composition.

Hibiscus cannabinus plants invaded gaps between the grasses, as observed during the study (Figure 7.6)



Figure 7.6: Observation and assessment of the extent of invasion by *Hibiscus cannabinus* within intergrass plants gaps.

7.2.5 Data analysis

SPSS version 27 was used to analyse the results. For each species, independent sample t-tests were used to compare the mean xylem water potential of the treated and controls before and following the clearing of nearest neighbour plants. Mean numbers of grass tillers for the treated and controls before and following isolation neighbours were also compared using independent sample t-tests.

7.3 RESULTS

There was no difference in xylem plant water between the two groups for each of the three plant species before the treatments were imposed (Table 7.1). In contrast, the removal of the neighbouring plants increased the xylem plant water potential of all three grass species (Table 7.1). For *Digitaria eriantha*, pre-removal, the mean grass tiller xylem water potentials for the experimental ($M = -10.24$) and control groups ($M = -10.50$) ($p > 0.05$), hence no significant difference. For the same species, post-removal, the experimental group ($M = -2.79$) had a higher ($p < 0.05$) mean grass tiller xylem water potential as compared to the control group ($M = -10.15$).

For *Sporobolus africanus*, pre-removal, the mean grass tiller xylem water potential for the experimental ($M = -9.53$) and control group ($M = -8.38$) ($p > 0.05$), hence no difference. For the same species, post-removal, the experimental group ($M = -2.56$) had a higher ($p < 0.05$) mean grass tiller xylem water potential as compared to the control group ($M = -9.38$). For *Themeda trianda*, pre-removal, the mean grass tiller xylem water potential for the experimental ($M = -10.74$) and control groups ($M = -10.56$) ($p > 0.05$), this implies no

significant difference. For the same species, post-removal, the experimental group (M = -3.44) had a higher ($p < 0.05$), mean grass tiller xylem water potential as compared to the control group (M = -10.26).

Table 7.1: Means and standard errors (in brackets) of the grass tiller xylem water potentials for the treated and control before and after neighbours were removed. Units are in Pascal (Pa or kg/s/m²).

Species	Stage	N	Mean (Group A)	Mean (Group B)	P-value
<i>Digitaria eriantha</i>	preremoval	34	-10.50 ^a (±0.35)	-10.24 ^a (±0.37)	Ns
<i>Digitaria eriantha</i>	postremoval	34	-10.15 ^a (±0.330)	-2.79 ^b (±0.18)	S
<i>Sporobolus africanus</i>	preremoval	34	-8.38 ^a (0±.17)	-9.53 ^a (±0.27)	Ns
<i>Sporobolus africanus</i>	postremoval	34	-9.38 ^a 0±.27)	-2.56 ^b ±0.16)	S
<i>Themeda triandra</i>	preremoval	34	-10.56 ^a (±0.34)	-10.74 ^a (±0.32)	Ns
<i>Themeda triandra</i>	postremoval	34	-10.26 ^a (±0.31)	-3.44 ^b (±0.13)	S

There was some difference in mean grass tiller numbers between the two groups for each of the three plant species before the treatments were imposed (Table 7.2). In contrast, the removal of the neighbouring plants increased mean grass tiller numbers significantly for all three grass species (Table 7.2). For *Digitaria eriantha*, pre-removal, the mean grass tiller numbers for the experimental (M= 4.71) and control groups (M = 4.65) ($p > 0.05$). For the same species, post-removal, the experimental group (M= 16.29) had higher ($p < 0.05$) mean grass tiller numbers as compared to the control group (M = 8.35).

For *Sporobolus africanus*, pre-removal, the mean grass tiller numbers for the experimental (M = 4.68) and control groups (M = 4.47) ($p > 0.05$). For the same species, post-removal, the experimental group (M = 15.12) had higher ($p < 0.05$), mean grass tiller numbers as compared to the control group (M = 8.03).

For *Themeda trianda*, pre-removal, the mean grass tillers for the experimental (M = 7.21) and control groups (M = 7.85) ($p > 0.05$). For the same species, post-removal, the experimental group (M = 17.21) had higher ($p < 0.05$) mean grass tiller numbers as compared to the control group (M = 8.71).

Table 7.2: Means and standard errors (in brackets) of the grass tiller numbers for the treated and controls before and after neighbours were cleared. Units are in Pascal (Pa or kg/s/m²)

Species	Stage	N	Mean (Group A)	Mean (Group B)	P-value
<i>Digitaria eriantha</i>	preremoval	34	4.65 ^a (±0.240)	4.71 ^a (±0.143)	Ns
<i>Digitaria eriantha</i>	postremoval	34	8.35 ^a (±0.211)	16.29 ^b (±0.213)	S
<i>Sporobolus africanus</i>	preremoval	34	4.47 ^a (±0.240)	4.68 ^a (±0.201)	Ns
<i>Sporobolus africanus</i>	postremoval	34	8.03 ^a (±0.155)	15.12 ^b (±0.506)	
<i>Themeda triandra</i>	pre-removal	34	7.85 ^a (±0.212)	7.21 ^a (±0.256)	
<i>Themeda triandra</i>	postremoval	34	8.71 ^a (±0.177)	17.21 ^b (±0.202)	



Figure 7.7: Observed invasion following the isolation of some plants from the stand.



Figure 7.8: Observed extent of invasion by ephemerals following gap creation.

7.4 DISCUSSION

There is no difference in xylem plant water potentials between the two groups (Groups A and B) for each of the three plant species, *Digitaria eriantha*, *Sporobolus africanus*, and *Themeda triandra* grasses, before the treatments were imposed. As contrasted to the significant differences in xylem plant water potentials after the treatments were imposed, the removal of two nearest neighbours allowed the remaining individuals of the treated group access to extra moisture which could have been utilized by isolated plants. Some difference in mean grass tiller numbers between the two groups (A and B) for each of the three plant species before the treatments were imposed, in contrast with a significant increase in mean grass tiller numbers after the removal of the neighbouring plants for all three grass species, implied that removal of the nearest neighbouring plants allowed the remaining individuals of the treated group access to extra soil moisture which was available for the isolated plants.

Whether the investigated pairs of grass individuals competed significantly for soil moisture was verified by comparing their grass tiller xylem water potentials and grass tiller number differences before and after one group of the individuals were isolated from two nearest neighbour individuals by using a student t-test. Significant grass tiller xylem water potentials and grass tiller number differences between plants closely neighboured by others and those isolated by nearest neighbour plants indicate that this implies that plants that are sparsely distributed may compete less and hence produce better.

Despite positive improvements in plant productivity following a reduction in the isolation of neighbour plants, gaps created between individual plants through plant competitive

interactions or any other form of clearing of neighbouring plants resulted in the invasion of gaps created by either alien or indigenous plant species. A sparse invasion that was observed on some sections of Nylsvley Nature Reserve (NNR) by species such as *Hibiscus cannabifolius* where there were open spaces between grasses, probably due to clearing, might signal that a serious invasion could occur if more spaces are created. Such could be possible if inter- or intra-plant competition occurs in the reserve. So far, the invasion of NNR is mainly caused by herbaceous plants that seem less threatening to the status of savanna vegetation. The dominant plants that were seen infesting the reserve were mainly shrubs and ephemerals (Figures 7.7 and 7.8).

Notwithstanding minor invasions of the NNR by alien invaders such as *Hibiscus cannabifolius*, as the infestations were still in the early stages of establishment, this observation might imply that savanna ecosystems may be susceptible to invasion by foreign plants in the long term if not well understood and hence properly managed. Savannas are susceptible to invasion and competition; therefore, there is a need for further research to continue to understand how they operate as well as to understand the dynamics of these ecosystems. Management must be based on a solid scientific base structure that allows us to adapt and respond quickly to an ever-changing system (Scogings, 2004).

7.5 CONCLUSION

One of the key mechanisms influencing the patterning of plant communities in ecosystems is competition amongst plants for moisture; this competition probably influences species diversity. Competition could affect the number of species in each region, hence preventing the cooccurrence of highly identical species. However, competition will eventually drive specialization and divergence, increasing species diversity (Pfennig & Pfennig, 2010). Both parties suffer from competition since, in the absence of the other species, some would have better rates of survival and reproduction. Plants could be found to change in the way they are distributed depending on the intensity and importance of competition in ecosystems. Plant composition and diversity could easily be changed from one standing to the next. Also, the amount of resources might be depleted due to plant species competition. Plant productivity is usually influenced by the extent of competition in ecosystems. Distributions of species, population dynamics, community organization, food webs, and social dominance hierarchies are all influenced by how organisms compete. Over time, behavioural and physical adaptations resulting from competitive encounters influence a species' evolutionary trajectory. It lessens overall dynamic stability, keeps population imbalances at bay, and aids in regulating ecological interactions.

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CHAPTER 8 GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATION

8.1 DISCUSSION

Disturbance, whether natural, anthropogenic, or in any other form, is a phenomenon we will always live with, and in some instances, it is good while in others, it is not necessary to apply to manage ecosystems. The aftermath of disturbances such as clipping and burning, among others, may be advantageous or disadvantageous depending on factors such as timing, frequency, intensity, size, and season of disturbance. For instance, when savanna vegetation was disturbed in winter, it generally tended to respond more positively than when disturbed in other seasons of the year. The summer season showed to be a less favourable season to disturb savanna plants compared to the other three seasons. Both savanna individual plant species, irrespective of age groups, were negatively affected by cutting, fire, and clearing for some time in terms of months. Plants of all age groups regenerate when disturbed, but at different times and rates, with adults showing more resilience to disturbances than all the other age groups.

The response of savanna plants following injury, such as cutting, was seen to rely on the availability and hence mobilization of root sugar and starch reserves. The availability of these reserves is important for the regrowth of injured plants and the maintenance of their primary leaves before plants can start to photosynthesize.

Bark thicknesses and stem diameters are structures of plants that play important roles in protecting woody plants against injury by disturbances such as fire. Plants with thicker barks are better protected from injury than those with thinner barks. Savanna seedlings and

juveniles were destroyed by fire in 2013 and 2014, while adults did not succumb to the same fire. The results of the study showed the importance of the outer bark as a structure that plays a greater role in protecting the plants against injury, and hence, death.

Plant soil moisture was shown to be one indispensable resource without which life may never be possible. The current study revealed strong competition between grass plants, with weak competing members of the grass pairs outcompeted by strong ones. The outcompeting of some members of the pairs in the reserve resulted in the opening of gaps that became available to some species that were originally in the areas and some that were never in the study areas before; the new-comer invaders were either native or alien. How long Nylsvley Nature Reserve would be safe from serious invasion and, hence, change in its plant species composition and distributional patterns following competition requires long-term investigation and the season of disturbance. For instance, when savanna vegetation was disturbed in winter, it generally tended to respond more positively than when disturbed in other seasons of the year. The summer season showed to be a less favourable season to disturb savanna plants compared to the other three seasons. Both savanna individual plant species, irrespective of age groups, were negatively affected by cutting, fire, and clearing for some time in terms of months. Plants of all age groups regenerate when disturbed, but at different times and rates, with adults showing more resilience to disturbances than all the other age groups.

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