

Controlling woody plant encroachment in a southern African savanna

by

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Submitted in fulfilment of the academic requirements for the degree of

Doctor of Philosophy

School of Life Sciences

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Pietermaritzburg

South Africa

August 2021

ABSTRACT

Woody plant encroachment is considered one of the most extensive forms of degradation affecting savannas in arid and semi-arid ecosystems. Thus, reactive interventions such as chemical and mechanical controls, as well as fire application remains the norm in management of woody plant encroachment. I conducted a series of woody plant control experiments at the Agricultural Research Council's Roodeplaat experimental ranch, situated in Gauteng Province, South Africa. The first experiment was a tree-thinning study at two savanna sites that differ in soil texture and woody species. Site 1 was on previously cultivated clay-dominated soils characterized by severe soil erosion and was encroached by *Vachellia tortilis*. Site 2 has never been cultivated and was on sandy soils with several woody species. At each site, 24 30 m × 30 m plots separated by 5 m wide fire breaks were established. Trees were removed to the approximate equivalents of 0% (control-no removal), 10%, 20%, 50%, 75% and 100% (complete removal of trees), followed by herbicide application on half of the stumps for each plot. I also investigated the effectiveness of Tree Poppers® (weed wrench) as a low-cost mechanical control tool to physically uproot seedlings and saplings of woody plants. To examine the effectiveness of the Tree Popper®, I used eight dominant tree species that were grouped into three height classes (0-49 cm, 50-99 cm, 100-150 cm) of ten seedlings and saplings per species per height class. In addition, investigated the effects of five years of annual burning on vegetation dynamics in a *Vachellia karroo* woodland. To determine the effects of annual burning on vegetation dynamics, plots (0.25 ha) established in 2013 were used. These studies are summarized below:

(1) I determined the combined effects of tree species, tree thinning, stump diameter and herbicide application on resprouting patterns of woody plant species (*Dichrostachys cinerea*, *Ehretia crispa*, *E. rigida*, *Gymnosporia buxifolia*, *Pappea capensis*, *Searsia lancea*, *S. caffra*, *Vachellia karroo*, *V. nilotica*, *V. robusta*, *V. tortilis* and *Ziziphus mucronata*) that encroach study site 1. All the tree species in this study resprouted after cutting. Herbicide application significantly reduced the resprouting ability of *D. cinerea*, *E. rigida*, *V. robusta* and *Z. mucronata*. Tree removal positively influenced the resprouting ability and vigour of *E. crispa* only. The diameter of stumps was an important factor in determining resprouting ability, with shoot production decreasing with increasing stump diameter. The findings from this study

suggest that woody plants are more likely to resprout and survive as juveniles than as adults after cutting.

(2) I found no significant differences in the number of seedlings and saplings uprooted by Tree Popper[®]. However, there were significant differences in the number of juveniles uprooted using a Tree Popper[®] with a few individuals of *Vachellia* species uprooted. The effectiveness of the Tree Popper[®] may be due to differences in plant morphological structure, particularly the root system. The Tree Popper[®] is not an effective tool for controlling the *Vachellia* species used in this study. However, communal ranchers may mechanically control shallow-rooted tree seedlings with the Tree Popper[®] but not deep-rooted ones, specifically *Vachellia* species.

(3) In the tree thinning experiment, I determined the effects of different tree thinning-intensities on grass species-richness, composition, cover, β diversity, and soil fertility. I found that tree thinning did not have any significant effects on grass species-richness in either study site. However, we found a clear separation of different grass species among the treatments over the study period. Different levels of tree thinning increased the abundance of two dominant grass species (i.e. *Digitaria eriantha* and *Panicum maximum*) in both study sites, particularly in moderate (50%) and high removal (75% and 100%) treatments. However, the nitrophilous grass (i.e. *P. maximum*) will likely decline in abundance with time, particularly in the 100% thinning treatment because the ecological process that is responsible for N-fixation is no longer existent. Contrastingly, I found no evidence that tree thinning affects the amount of soil cover. In addition, tree thinning did not have a significant impact on soil fertility in either study site. I recommend maintaining a stand density of 50% in rangeland affected by woody plant encroachment. In this study, 50% thinning created an opportunity for different palatable grass species to increase in abundance, which may help to increase forage production.

(4) I determined the effects of different tree removal-intensities on grass production, tree-seedling establishment and growth, and the growth of the remaining large trees. In site 1, tree-removal treatments (i.e. 75 and 100%) significantly reduced grass biomass production after the first growing season, with no effect after the second season. In site 2, tree removal significantly increased grass biomass production. I found no significant effect of tree removal on tree seedling establishment in site 1. In site 2, tree removal had a significantly negative effect on overall tree seedling establishment. In both sites, there were no significant differences in tree seedling growth. Moderate (50%) to high (75%) removal of trees had a positive effect on the

growth of remaining large trees in both study sites. I found that increased and/or diminished grass biomass production plays a vital role on tree seedling recruitment. Reduced tree competition facilitates the growth of the remaining large trees. An implication of these findings is that regardless of the substantial costs of woody plant control, the recovery of key ecosystem services such as an increased forage production may not be realised. However, this may be system-specific. In other systems, the absence of management interventions such as tree removal may compromise provision of ecosystem services and ecosystem functioning.

(5) In the fire experiment, I investigated the effects of five years of annual burning on the density of young and adult *Vachellia karroo* plants. This study also aimed to investigate the effects of annual burning on tree growth (i.e. height, stem diameter and canopy size). The results supported the “fire-trap” paradigm by demonstrating substantially higher densities of young plants in the burned plots than in the unburned plots. In addition, the recruitment of young plants and saplings into adult trees was significantly higher in the unburned plots than in the burned plots. *V. karroo* populations substantially increased in growth (height and basal diameter) in the unburned plots. Different grass species changed in abundance in response to annual burning. However, I found no significant changes in grass species diversity and richness between the treatments. I found that the removal of the grass layer by fire and repeated topkill increased the number of young *V. karroo* individuals. Annual burning limited *V. karroo* juveniles and saplings from reaching an adult size class that may have detrimental effects on the herbaceous layer. I demonstrated that grass species composition is more prone to fire-induced changes than species diversity and richness in our study area. In conclusion, I show that managers of savanna rangelands may use annual burning to achieve specific vegetation structural objectives.

This thesis demonstrated that mechanical- and chemical -control, as well as fire application influences the structure and functioning of savannas. By creating gaps that promote grass production, these management practices may assist increase the economic viability of savanna ecosystems. However, despite the popular belief that reduced tree densities promote ecosystem functions, this thesis demonstrates that the impact of control techniques (especially tree thinning) on forage production vary across savanna sites. This thesis also shows that management with prescribed annual fire reduced woody plant encroachment across the 5-year study, suggesting that fire management can be beneficial and should be explored as a management method.

PREFACE

The research contained in this thesis was completed in the School of Life Sciences, College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa, under the supervision of Dr Zivanai Tsvuura. This thesis was co-supervised by Professor David Ward and Dr Julius Tjelele. The research was financially supported by the National Research Foundation and the Agricultural Research Council.

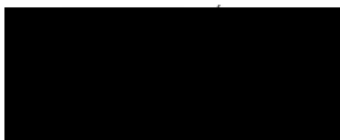
This thesis represents original work by the author and the contents of this work have not been submitted in any form to another university. Proper acknowledgement has been given where other people's work has been used.

The thesis was written as papers submitted or to be submitted for publication, except for Chapter 1 (Introduction) and Chapter 6 (Synthesis and future directions). As a result, the paper chapters were prepared according to the requirements of the particular journal to which they were submitted or published. Some information (especially the study area description) will inevitably be repeated. The key distinction is that acknowledgements are found in the acknowledgements section rather than in each chapter.

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DECLARATION 1: PLAGIARISM

I, Piet Monegi, student number: 217082169 declare that:

(i) the research reported in this thesis, except where otherwise indicated or acknowledged, is my original work;

(ii) this thesis has not been submitted in full or in part for any degree or examination to any other university;

(iii) this thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this thesis is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

(vii) this thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

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DECLARATION 2: PUBLICATIONS

Dr Tsvuura, Prof Ward, Dr Tjelele and Dr Ntuthuko Mkhize contributed helpful comments and suggestions to the manuscripts. The four paper chapters presented in this thesis were formatted according to the requirements of the particular journal to which they were submitted or published.

Publication 1 (chapter 2): Formatted for submission to *African Journal of Range and Forage Science*.

Monegi P, Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z. 2021. Chemical and mechanical control of woody plants on resprouting and seedling production in communal rangelands. Monegi P formulated the study, collected and analysed the data and prepared the manuscript. Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z contributed to experimental design, data analysis and manuscript preparation.

Publication 2 (chapter 3): Formatted for submission to *African Journal of Range and Forage Science*.

Monegi P, Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z. 2021. Short-term response of grass species richness, composition, β diversity and soil dynamics after tree thinning in a South African savanna. Monegi P formulated the study, collected and analysed the data and prepared the manuscript. Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z contributed to experimental design, data analysis and manuscript preparation.

Publication 3 (chapter 4): Submitted to the *Rangeland Journal* and formatted accordingly.

Monegi P, Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z. 2021. The impact of tree removal on grass biomass production, seedling recruitment and growth of woody species. Monegi P formulated the study, collected and analysed the data and prepared the manuscript. Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z contributed to experimental design, data analysis and manuscript preparation.

Publication (chapter 5) 4: Formatted for submission to the *African Journal of Ecology*.

Monegi P, Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z. 2021. Short-term effects of fire on vegetation dynamics in a *Vachellia karroo* woodland. Monegi P formulated the study, collected

and analysed the data and prepared the manuscript. Mkhize NR, Tjelele TJ, Ward D, and Tsvuura Z contributed to experimental design, data analysis and manuscript preparation.

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ACKNOWLEDGMENTS

No words can express how grateful I am to Prof Ward, Dr Tsvuura, Dr Tjelele and Dr N Mkhize for their leadership, patience, support, comments and suggestions throughout the study. Thanks Prof Ward and Dr Tsvuura for the timeous feedback and comments on the drafts. I would like to thank Dr Mkhize and Dr Tjelele for giving me an opportunity to work with them from when I was studying for my National Diploma. They have both shaped my science career and laid the groundwork for me to become an independent thinker. I have gained a lot of knowledge and experience from you. I would like to give a special acknowledgement to Dr Mkhize for his mentorship and support from the day we met to date. This PhD would not have been possible without the support that I received from him all these years. Thank you!

The financial support from the National Research Foundation and Agricultural Research Council (ARC) is gratefully appreciated. I thank the ARC (Animal Production) for providing research facilities.

Data collection would not have been possible if it was not for Humbelani Mavhunga, Tebogo Matlou, Michael Mkwala, Kabelo Bodiba, Ngoako Letsoalo, Lepuase Chiloane, Mante Mampuru, Michelle Monegi and Veronica Rakoena. Your assistance is highly appreciated.

Thank you to my friend Kabelo “Kassie” Molopo for taking his time after work to come and help with setting up the experiments. Your contribution is priceless! It will be impossible to express my gratitude to Nchaupa Rasekgokga and Nothando Ngcobo's assistance throughout this study. They assumed considerable responsibility for aspects of the project and gave everything they had to ensure its success. They both motivated me to keep at it during fieldwork. I hope they learned as much from me as I did from them. This PhD is not only mine, but theirs also.

Lastly, I would like to dedicate this PhD to my mother, Lentheng Monegi, and my siblings, Michelle Monegi, Emmanuel “Mavoo” Monegi and Ramokone Monegi. I cannot forget my friends Abia Mabothe, Tiisetso Phala, Bongani Mashele and Thapelo Masuku for their support and motivation throughout my studies. I thank you.

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Chapter 1: Introduction

1.1. Background

Savannas are ecosystems characterised by a continuous grass layer and a discontinuous layer of woody plants, are used for both livestock and game ranching (Moustakas et al. 2013). The coexistence of grasses and trees in savannas has attracted the attention of many researchers over the last decades (Walter 1939; Walker and Noy-Meir 1982; Jeltsch et al. 2000; Ward 2005; Ward et al. 2013). Changes in the relative proportion of trees and grasses may change the structure of savannas (Bond 2008). The changes in structure are regulated by several interacting factors such as herbivory, fire, soil moisture and nutrients (Frost et al. 1986). However, the manner in which these interacting factors influence savanna structure is not well understood (Bond 2008).

The two savanna life forms often compete for the same resources (e.g. nutrients and water) (Ward et al. 2013). For example, savannas receiving less than about 650 mm of rainfall per year (Sankaran et al. 2005) are classified as arid or semi-arid regions because soil moisture limits tree canopy closure, and trees and grasses strongly compete for water (D'Onofrio et al. 2014). Walter's (1939) two-layer hypothesis is often used to explain the codominance of the grasses and trees in savannas. The hypothesis suggests that grasses use water from the topsoil layers because of their shallow root system. In contrast, woody plants would use small amounts of the topsoil water but would have absolute access to subsoil water below the grass roots (Ward et al. 2013). In addition, nutrient availability can have profound effects on woody cover (Bond 2010). Studies suggest that soils with low nutrient availability limit tree cover in savannas because poor soil quality limits tree growth (Bond 2010). In contrast, other studies suggest that soils with high nutrient availability limit woody plant cover (Mills et al. 2013). When grasses are present, enhanced soil nutrients lead to water stress, which results in reduced growth of tree seedlings (Akıncı and Lösel 2012).

The majority of savanna ecosystems are found in drylands, which support about a third of the world's human population, many of whom rely on pastoralism and thus forage production for their livelihoods. (Maestre et al. 2016; Právělie 2016; Ribeiro et al. 2019). Savanna areas are long perceived as degraded ecosystems as a result of disturbances such as fire, herbivory and human activities such as fuel wood harvesting (Bond and Parr 2010; Parr et al. 2014;

Veldman et al. 2015; Ratnam et al. 2016). Savannas are by nature unstable because the ratio of trees-to-grasses is constantly fluctuating due to disturbances (Sankaran 2019). Disturbances prevent these ecosystems from achieving a stable state in the form of a grassland or a forest (Jeltsch et al. 2000).

1.2. Woody plant encroachment

In many areas of southern Africa woody plant densities have increased by 30-50% (Hudak and Wessman 2001; Ward 2005; Kraaij and Ward 2006). Given the widespread spread of woody plants into grasslands and savannas in southern Africa and worldwide (Hoffman and Ashwell 2001; Bond 2008; O'Connor et al. 2014; Archer et al. 2017; Skowno et al. 2017), there is a considerable decline in the agricultural potential of rangelands (Espach 2006; Börner et al. 2007). Although land degradation caused by woody plant encroachment is recognised under both communal and commercial systems (Lloyd et al. 2002), this problem is particularly acute for resource-constrained communities in southern Africa. The proliferation of woody plants in communal rangelands is often attributed to high livestock populations and the lack of conventional grazing management practices such as rotational grazing and resting, which diminishes grass cover. Diminished grass cover affords new spaces and resources for the development of woody plants (Archer et al. 2017).

Woody plant encroachment can drastically alter ecosystem services such as forage production for livestock and wildlife (Smit 2005). The encroachment of woody plant species has also been reported to increase the amount of bare soil surfaces and consequently declines in soil functions, which hinders the recovery of herbaceous plants (Eldridge et al. 2011). Woody plant encroachment has been ascribed to numerous mechanisms such as overgrazing by large herbivores, climate change and the suppression of fire that is used to control tree establishment in savanna ecosystems, and combinations of these factors (Ward 2005; Bond and Midgley 2012; Eldridge et al. 2013; Ding and Eldridge 2019). In addition, overgrazing by herbivores reduces both aboveground and belowground grass biomass, thereby reducing grass's ability to re-grow and to compete with woody plants for resources (Van Auken 2009). Herbaceous plants, particularly grasses, have the ability to compete with woody plants for resources, which suppresses woody plant establishment and growth (Kambatuku et al. 2011b, Ward and Esler 2011; Grellier et al. 2012; Vadigi and Ward 2013; Wakeling et al. 2015; Bhadouria et al. 2016; Morrison et al. 2018). However, the removal of the herbaceous layer through overgrazing

releases woody plants from competition and potentially enhances their growth (Walter 1939; Hoffman and Ashwell 2001). Heavy grazing also leads to reduced fuel load resulting in low fire intensity, which may render fire less effective in controlling woody plants (Hoffman and Ashwell 2001; Bond 2008). Thus, when overgrazing occurs with a concomitant reduction in fire frequency, the establishment and growth of woody plants are favoured and promoted (Van Auken 2009).

An increase in woody plant expansion has also been attributed to an increase in concentrations of atmospheric CO₂ (Ward et al. 2014; Stevens et al. 2017). Elevated atmospheric CO₂ concentration is expected to increase the proliferation of woody plants by promoting increased belowground carbon storage, resprouting ability and growth rates in tree saplings, which will enable woody plants to escape from the fire and herbivore-imposed traps (Hoffmann et al. 2000; Bond and Midgley 2012). In addition, predicted consequences of climate change such as fluctuating rainfall events, are expected to favour tree growth over grass growth (Kulmatiski and Beard 2013). Extended periods of increased annual rainfall may lead to encroachment (Fensham et al. 2005), particularly in arid and semi-arid savannas where woody cover is limited by rainfall (Sankaran et al. 2005). Increased rainfall leads to enhanced infiltration of water to deeper soil horizons (Walker and Noy-Meir 1982), which may increase tree growth rates (February et al. 2013). Therefore, changes in current and future climate have important implications for ecosystem processes, which results in changes in savanna structure, composition and function (Sankaran 2019).

1.3. Woody plant management in savannas

The different perspectives of land owners and users on woody plant encroachment pose a challenge for managing lands affected by this problem (Archer et al. 2017). Commercial cattle-ranch enterprises regard woody plant encroachment as a deterrent to livestock production. In contrast, rural communities in semi-arid rangelands prefer a bush-encroached state because they keep browsers such as goats, and thus see woody plants as an important source of forage and may favour increases in their abundance. In addition, rural communities may prefer encroached rangelands because they are dependent on woody plants for fuelwood (Shackleton et al. 2007; Twine et al. 2003; Inman et al. 2020). In conservation areas, ecologists have concerns that woody plant encroachment will negatively affect the biodiversity of savanna ecosystems (Archer et al. 2017).

Livestock farming, which is the dominant land use in rangelands where woody plant encroachment occurs, is mostly dependent on grass production, which is frequently outcompeted by woody plants (Scholes and Archer 1997; Ward 2005; Maestre et al. 2017). Globally, government sponsored woody plant control programs have been implemented with the aim of rehabilitating previously economic rangelands that are now faced with economic problems induced by woody plant encroachment (Hamilton 2004; Ding and Eldridge 2019).

Research has shown that ecological effects conferred by woody plants differ, ranging from positive to negative or neutral based on land utilisation, type of species and density (Eldridge et al. 2011). For instance, woody plants at low densities have been demonstrated to have positive effects on the herbaceous layer, soils and ecological functions (Smit 2005; Chief et al. 2012). These positive effects of woody plants for forage production diminish at high densities (Riginos 2009). Therefore, when the objective is to increase or maintain herbaceous yields adequate for livestock and game farming, it is essential for land managers to manage the woody layer by controlling the density of mature trees and recruiting tree seedlings to sustain the economic viability of savannas (Smit 2005; Hare et al. 2020). In most parts of the world, chemical and mechanical control strategies as well as fire have been widely used to manage woody plant encroachment (Lett and Knapp 2005; Higgins et al. 2007; Archer et al. 2011; Archer and Predick 2014; Hoffmann et al. 2020). In North America these techniques are referred to as brush management, woody weed management in Australia and bush clearing in Africa (Hamilton et al. 2004; Paynter and Flanagan 2004; Noble and Walker 2006; Archer and Predick 2014).

Studies have demonstrated that the effects of tree removal differ within similar environmental conditions possibly because of the removal methods and/or plant species (Archer and Predick 2014; Archer et al. 2017; Daryanto et al. 2019). Ding and Eldridge (2019) reported that plant functional traits may influence ecosystem structure, which may change after tree removal and therefore influence ecological processes. Additionally, according to Ding and Eldridge (2019), few studies have evaluated the response of rangelands to tree removal/thinning among various woody species, raising the question of whether differences in plant traits influence the ecological or management outcomes of removal methods. The lack of this information impedes the ability of rangeland ecologists to suggest desirable management options and procedures that will meet the ecological and management goals that are related to woody plant removal (Ding and Eldridge 2019).

1.3.1. Tree thinning and fire application as woody plant control strategies

The threat posed by woody plant encroachment to the pastoral economy is frequently the driving force behind the control of encroachment by trees (Olson and Whitson 2002). Woody plant encroachment can cause a shift from an open savanna to closed woodlands (Eldridge et al. 2011), changing the ecological functions of the original savanna (Buitenwerf et al. 2012). When the encroachment of woody species alters ecosystem functions such as the herbaceous production, then the rehabilitation of such rangelands becomes a high priority. Rehabilitating degraded rangelands may be achievable by introducing other management regimes (e.g. mechanical and/or chemical control) in addition to the use of fire, owing to thresholds that ecosystems may cross (e.g. low fuel loads) during periods of fire suppression (Bassett et al. 2020). In such cases, successful rehabilitation may require structural interventions such as tree thinning (Smit 2004, 2005; 2014). Tree thinning involves a reduction in the number of trees in areas where woody plant encroachment has occurred (Smit 2005). Tree density reduction has been shown to have positive benefits in savannas such as an increase in grass production, which increases fuel loads (Smit 2005).

Annual or frequent fires are used to manage woody cover in savanna ecosystems (Bond 2008). In many savanna systems, fire is a common ecological process that affects the structure and composition of these ecosystems (Gordijn et al. 2012; Higgins et al. 2012; Forrestel et al. 2014). Woody plant species in these savannas have evolved life-history mechanisms that allow success in fire-prone environments (Higgins et al. 2012; Bond 2016). Frequent fires affect savanna structure by reducing tree densities and maintaining tree sizes at certain heights (Higgins et al. 2000, 2007), thereby reducing the recruitment of saplings into adult-sized woody plants that may have negative impacts on the herbaceous layer (Ward 2005). Reduced tree cover following frequent fires renders the savanna susceptible to burning and helps maintain them as open savannas (Lohmann et al. 2014). This leads to increased fuel loads for fires that could aid in maintaining low densities of woody plants (Bowles et al. 2017). In addition, frequent fires can also influence the diversity and composition of the herbaceous layer (Bassest et al. 2020). Fire removes the aboveground biomass of herbaceous species indiscriminately (Bond and Keeley 2005), which may shift its species composition.

The positive effects of woody plant control such as increased grass production have been reported to be relatively short-lived (Daryanto et al. 2019; Ding and Eldridge 2019), because many woody plants have the ability to resprout from the cut or broken stem after tree felling or burning (Bond and Midgley, 2001; Shackleton, 2001). Many empirical studies have

reported on the importance of resprouting as a persistence strategy across different habitats, from savannas (Shackleton 2000; Higgins et al. 2000; Clarke et al. 2013), forests (Dietze and Clarke 2008; Poorter et al. 2010) and deserts (Nano and Clarke 2011) to Mediterranean ecosystems (Verdú 2000; Keeley et al. 2012). Resprouting is a tolerance strategy that allows persistence at the plant level, enabling it to survive diverse disturbances such as tree cutting (Shackleton 2000; Nzunda et al. 2014). The resprouting ability of various woody plants is supported by the non-structural carbohydrate reserves stored in a well-developed, deep-root system (Vesk and Westoby 2004; Paula and Pausas 2006; Nzunda et al. 2014; Casals and Rios 2018). At the community level, the ability of woody plants to resprout after disturbance gives rise to biomes (e.g. savannas) that are resistant to disturbances (Vesk 2006), which may hinder the effectiveness of control methods such as mechanical removal of trees in the long term (Enloe et al. 2018). Thus, the ability of woody plants to resprout following cutting renders further treatments such as chemical application essential. Tree cutting followed by an immediate application of herbicides to the stump, has been reported to considerably reduce or prevent future resprouting in numerous woody plant species in various biomes globally (Burch and Zedaker 2003; Enloe et al. 2018; Young et al. 2017).

Increased nutrients, clumped seed dispersal and rainfall patchiness or a combination of them may increase woody plant regeneration, leading to aggregated patterns (Sankaran et al. 2005; Ward 2005; Kraaij and Ward 2006). Research has shown that one of the mechanisms among others that may lead to woody plant encroachment in savannas is the dispersal of woody tree seeds by herbivores (Tjelele et al. 2014; Tjelele et al. 2015a, b). Consequently, cost-effective strategies that may help control these seedlings are needed. For instance, it is generally more expensive to control mature savanna trees because this may require large amounts of resources (Eldridge and Ding 2020). However, it may be relatively cheaper to control these trees at their seedling stage. For example, Hale et al. (2020) showed that reintroductions of prairie dog colonies in North America has limited the proliferation of woody plants. Prairie dog colonies systematically fell tree saplings, which suppress woody plant growth thereby creating a “browse trap” that also contributes to a “fire trap” (Hale et al. 2020). Therefore, studies that test the efficiency of methods of controlling the proliferation of woody plants in savannas could aid in the development of appropriate control strategies. Mechanical tools such as Tree Poppers[®] may help control young trees in savanna rangelands. Tree Poppers[®] are hand-held mechanical tools that are designed to physically uproot tree seedlings. It is thus important to evaluate if Tree Poppers[®] may constitute a low-cost, potentially long-term, sustainable solution

for deterring woody plant encroachment and proliferation in savannas, particularly in resource-constrained communities.

1.4. Aims and objectives of the study

The overall aim of this study was to establish an optimal tree density (*sensu* Smit 2004, 2005) that will optimise forage production in two different systems that are situated in the same area. The effects of tree thinning have been reported in the literature (Archer and Predick 2014; Archer et al. 2017), however, these studies are often carried out in single locations, encroached by specific woody plants (e.g. Smit 2005; Ndhlovu et. 2016). Thus, it is of importance to study the effects of tree thinning on multiple locations that differ in tree species and soils because the impact of woody plant encroachment is species specific (Eldridge et al. 2011). In addition, this study aimed to evaluate the effects of five years of annual burning on grass and tree dynamics. A new approach is needed to understand and develop sustainable strategies aimed at controlling the spread of woody plant encroachment while promoting palatable grass production. Studying the effects of different techniques such as tree thinning and fire application on grass species composition, grass biomass, soil fertility and tree dynamics could help rehabilitate degraded rangelands.

The main objectives of this study were to:

- 1) determine the effects of mechanical clearing of woody plants and associated chemical application on the tree stumps on resprouting ability of the cut trees,
- 2) to determine the effectiveness of Tree Poppers® (hand-held mechanical tools) on uprooting seedlings of several woody species,
- 3) investigate the impact of reduction of tree density on grass species richness, composition and soil fertility,
- 4) determine the effects of tree thinning on the yields of herbaceous plants and on tree seedling dynamics and growth of remaining woody plants,
- 5) investigate the effects of fire on the composition and diversity of grasses, and tree growth patterns, and
- 6) explore guidelines and procedures to meet ecological and management objectives associated with tree thinning and fire application in bush-encroached rangelands.

1.5. Outline of the thesis and questions addressed

The thesis is comprised of six chapters. Chapter one introduces the study and includes a discussion on savannas, woody plant encroachment and management, ecological dynamics related to tree thinning and fire application and the theory underlying the study. Chapters two, three, four and five report data on different elements of the experimental study, whereas chapter six summarizes and integrates the results obtained in the preceding experimental chapters.

In chapter two, I investigated the effects of mechanical clearing of trees followed by chemical application of an herbicide on the tree stumps of woody plants on resprouting ability. In addition, I investigated the effectiveness of Tree Poppers[®] to mechanically uproot seedlings of different woody species. This chapter addressed the following questions: Does a higher density of trees reduce resprouting ability and vigour of felled trees? What are the effects of herbicide application on resprouting ability and vigour of cut trees of different species? Is tree stem size an important predictor of resprouting ability among different woody species? Are Tree Poppers[®] (hand-held mechanical equipment) effective in controlling juvenile woody plants in savannas?

In chapter three, I studied the effects of tree thinning on understory plant dynamics. I sought to address the following questions: What are the effects of different levels of tree thinning on grass species richness and composition? What is the impact of tree thinning on bare soil cover? How do different levels of tree thinning affect soil fertility?

Chapter four asks the following questions: What are the effects of tree thinning on grass biomass production? Does tree thinning enhance or deter tree seedling emergence and growth? Are canopy gaps established through tree thinning beneficial to the remaining mature trees in terms of growth?

Chapter five addresses the following questions: What is the impact of annual burning on the recruitment of tree seedlings? Can annual burning reduce the density of mature trees? What are the effects of annual burning on tree growth (i.e. basal diameter, height and canopy size)? What are the effects of annual burning on grass species composition and diversity?

Chapter six presents conclusions and provides future directions for all results obtained in the experimental chapters.

1.6. Study area

The study was performed at the Roodeplaat Experimental ranch (25°36'29"S, 28°2'08"E; 1182 m) of the Agricultural Research Council in Gauteng Province, South Africa (Figure 1.1). The ranch's natural vegetation component, which is used for livestock production and wildlife, covers over 2100 ha. The vegetation type of the ranch is classified as the Marikana Thornveld. The dominant woody plants of the ranch are *Vachellia* (previously *Acacia*) *karroo*, *Senegalia* (formerly *Acacia*) *caffra* (Mucina and Rutherford 2006). The ranch is also dominated by *Vachellia tortilis*, *Ziziphus mucronata* and *Euclea* tree species. The grass layer of the ranch is characterised by *Digitaria eriantha*, *Melinis repens*, *Panicum maximum*, *Setaria sphacelata* and *Sporobolus africanus*. *Eragrostis curvula*, *Themeda triandra*, and *Heteropogon contortus* are some of the important grasses found on the ranch (Van Rooyen 1983). The average annual precipitation is 687 mm, with the majority of it falling during the austral summer (November to March). The daily maximum temperature in summer ranges between 20-29 °C, while the minimum winter temperature can decrease to 2-16 °C. The soil types of the study area are described as Vertisols, Ferralsols and Luvisols. The study area is situated on the Roodeplaat Igneous Complex, which belongs to the Post-Waterberg Formation (Panagos et al. 1998). The Roodeplaat Igneous Complex is a unique ring-shaped structure with a diameter of approximately 16 km and is also referred to as the "Roodeplaat volcano" (Panagos et al. 1998).

On the farm, three sites that vary in grasses, tree species and soils were selected. The first study site (hereafter study site 1) was on clay-dominated soils characterized by severe soil degradation in the form of surface erosion (gully) and crust formations. Site 1 (25°36'10"S, 28°20'32"E; 1171 m) was under crop cultivation more than 20 years ago and is now encroached by a monospecific stand of *V. tortilis* at a mean density of 2 961 plants ha⁻¹ (formerly *Acacia tortilis*) (Kyalangalilwa et al. 2013). At the second study site (hereafter site 2) (25°36'06"S, 28°20'03"E; 1185 m) woody plant management programmes were not applied prior to the study. This resulted in closed canopy conditions at the onset of the experiment, with multiple woody plant species. Site 2 was on sandy soils and is encroached at a mean density of 4 065 plants ha⁻¹ by several woody species including *S. caffra*, *V. karroo*, *Vachellia* (formerly *Acacia*) *nilotica*, *Vachellia* (formerly *Acacia*) *robusta*, *V. tortilis* and *Z. mucronata*. Site 2 has never been cultivated and was not used for grazing. The study site has mainly been grazed and browsed by an unknown number of free ranging game species. The third study site (hereafter site 3) (25°35'45"S, 28°20'39"E; 1158 m) was in a *V. karroo* woodland on clay soils. Site 3 was also previously cultivated more than 20 years ago.

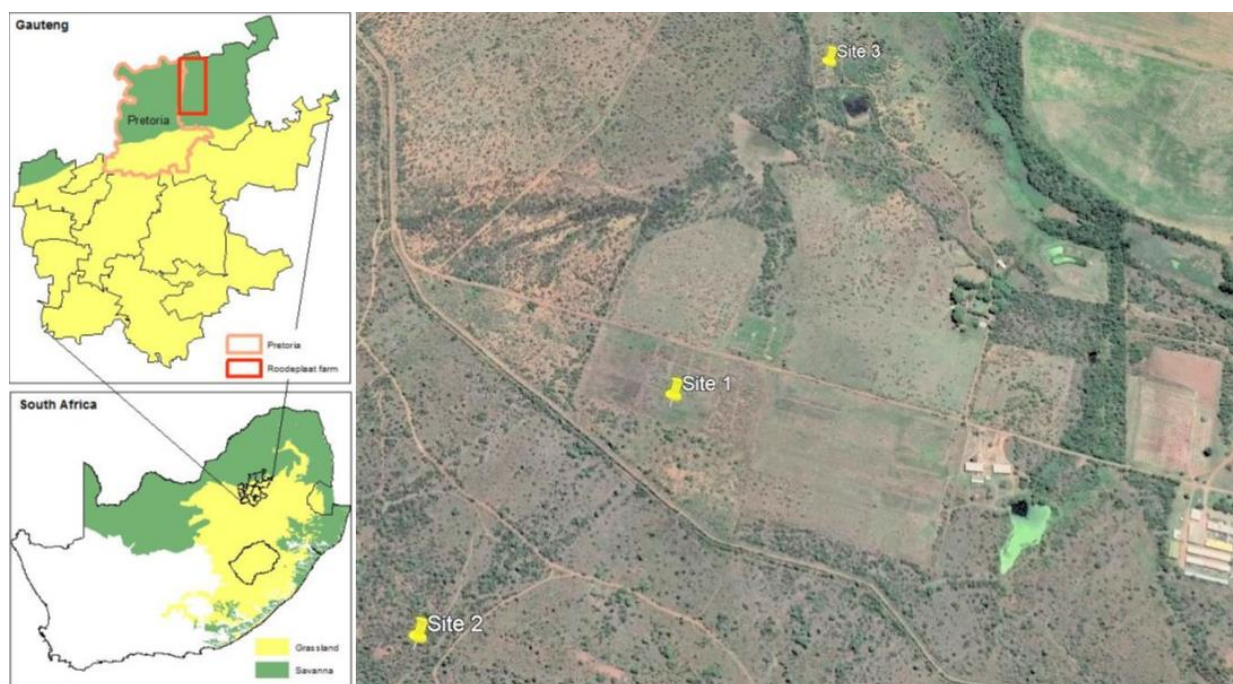


Figure 1.1. Map of South Africa showing the position of the Roodeplaat Farm in the Pretoria area of Gauteng Province. On the right is a Google Maps image of the farm.

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**Chapter 2: Chemical and mechanical control of woody plants on resprouting potential
and tree-seedling populations in savanna rangelands**

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Formatted for submission to *African Journal of Range and Forage Science*

Abstract

Communal rangelands in many African countries are suffering from woody plant encroachment. We sought to explore potential solutions for communal ranchers that would be cost-effective. We conducted two field experiments to determine (1) the effects of different tree removal treatments (10%, 20%, 50%, 75% and 100%), and herbicide application on resprouting ability and vigour of several woody plant species; and (2) the effectiveness of Tree Poppers[®] (weed wrench) as a low-cost mechanical control tool to physically uproot seedlings and saplings of woody species. In the first experiment, we examined 12 plant species from 20 plots (30 m x 30 m) each subjected to tree removal, followed by herbicide application on half of the stumps for each plot. In the second experiment, eight dominant tree species were grouped into three height classes (0-49 cm, 50-99 cm, 100-150 cm) of ten seedlings and saplings per species per height class. All the tree species in this study resprouted 9 mo after cutting. Herbicide application significantly reduced the resprouting ability of *Dichrostachys cinerea* (L.) Wight & Arn, *Ehretia rigida* (Thunb.) Druce, *Vachellia robusta* (Burch.) Kyalangalilwa & Boatwright and *Ziziphus mucronata* Willd. Tree removal positively influenced the resprouting ability and vigour of *Euclea crispa* (Thunb.) Gürke only. The diameter of stumps was an important factor in determining resprouting ability, with shoot production decreasing with increasing stump diameter. We found no significant differences in the number of seedlings and saplings uprooted by Tree Poppers[®] among the different size classes. There were significant differences in the number of juveniles uprooted using a weed wrench with a few individuals of *Vachellia* species uprooted. Woody plants are more likely to resprout and survive as juveniles than as adults after cutting. Communal ranchers may mechanically control shallow-rooted tree seedlings with a weed wrench but not deep-rooted ones, specifically *Vachellia* species.

Keywords: picloram; savanna; stem diameter; tree cutting; weed wrench; woody plant encroachment.

2.1. Introduction

Woody plant encroachment is considered one of the most extensive forms of degradation affecting savanna rangelands in arid and semi-arid areas globally (Hoffman and Ashwell 2001; Ward 2005; Bond 2008; O'Connor et al. 2014). In Africa, woody plant encroachment reduces the amount of grazing land for ranchers (Vetter 2013). In South Africa, nearly 6 million ha of communal rangelands are negatively affected (Shackleton et al. 2001; Hoffman and Ashwell 2001).

Woody plant encroachment can drastically reduce forage production for livestock and wildlife animals (Smit 2005; Ward 2005; Ward et al. 2014). To properly manage and sustain the economic viability of savanna rangelands affected by woody plant encroachment, it is important to encourage the ecological benefits of woody plants in terms of nitrogen fixation by leguminous trees (Mureva et al. 2018) and the improvement of hydraulic lift while limiting their encroachment (Smit 2005; Magda et al. 2009; Eldridge et al. 2013; Mureva and Ward 2016; Marquart et al. 2019).

Effective rangeland management can be achieved by developing appropriate strategies that can help increase or maintain grass production adequate for livestock- and game-ranching (Smit 2004; Harmse et al. 2016). One strategy for optimizing the availability of grass and maintaining the ecological benefits conferred by woody plants is by reducing the tree density (also termed *tree thinning*), which involves a reduction in the number of trees in areas where woody plant encroachment has occurred (Smit 2005). Tree density reduction has been shown to have positive benefits in savannas such as an increase in grass production and reducing soil erosion (Smit 2005; Ndhlovu et al. 2016). Globally, brush management techniques may include mechanical control methods such as shredding or roller chopping to remove most of the woody layer (Smit 2005; Archer 2010; Eldridge and Ding 2020). These methods are widely used in developed countries such as the United States of America and Australia (Eldridge and Ding 2020). In southern Africa, resource-constrained communal ranchers cannot normally afford to implement these methods. Given that the problem of woody plant encroachment is particularly acute in communal rangelands (Mograbi et al. 2015), alternative low-cost strategies that are effective, less complex and that can control the growth and survival of young trees in small-scale rangeland systems are needed. Mechanical tools such as Tree Poppers® may help control young trees in communal rangelands (see <https://treepopper.co.za>). Tree Poppers® are hand-held mechanical tools that are designed to physically uproot tree seedlings. Tree Poppers® work in a similar way to weed wrenches that are normally used in North America by nature

conservation groups and land management agencies to control young trees (see e.g. <https://www.theuprooter.com>). The use of Tree Poppers® in savanna rangelands for mechanical woody-plant control has not previously been recorded in southern Africa.

A problem that is widely understood is that mechanical-control methods are limited by the abilities of many trees to resprout after disturbances (Neke et al. 2006; Mwavu and Witkowski 2008; Poorter et al. 2010; Moyo et al. 2015; Pausas and Keeley 2017). Many empirical studies have demonstrated the importance of resprouting as a persistence strategy across different habitats, from savannas (Shackleton 2000; Higgins et al. 2000; Clarke et al. 2013), forests (Dietze and Clarke, 2008; Poorter et al., 2010) and deserts (Nano and Clarke, 2011) to Mediterranean ecosystems (Verdú 2000; Keeley et al. 2012). Woody plants have been reported to regenerate from the cut or broken stem as well as through seedling recruitment (Zimmerman et al. 1994; Lamont and Markey 1995; Bond and Midgley 2001; Shackleton 2001). Resprouting is a mechanism that allows individual plants to regenerate after the elimination of the above-ground biomass and persist in ecosystems with recurrent disturbances (Bond and Midgley 2001; Del Tredici 2001; Ickes et al. 2003; Vesk 2006; Nzunda et al. 2014; Pausas and Keeley 2014). The resprouting ability of various woody plants is supported by the non-structural carbohydrate reserves stored in a well-developed, deep-root system (Vesk and Westoby 2004; Paula and Pausas 2006; Nzunda et al. 2014; Casals and Rios 2018). Additionally, gap formation through high intensities of tree removal may reduce stump shading by the remaining trees (Casals and Rios 2018), which may consequently result in an increase in resprouting ability and vigour (Shultz et al. 2009; Casals and Rios 2018). Resprouting vigour depends on the allocation of belowground stored reserves and the capacity to acquire new resources through photosynthesis (Vesk and Westoby 2004; Casals and Rios 2018), which may be enhanced by high intensities of tree removal. Regardless, shoots produced by the cut stumps are undesirable because they have the ability to regrow into mature trees with multiple stems that may have negative competitive effects for resources on grasses (Shackleton 2000; Nano and Clarke 2010). To prevent tree stumps from regenerating after tree cutting, the cut stumps are frequently treated with chemical herbicides (Burch and Zedaker 2003; Ansley and Castellano 2006; Enloe et al. 2018). However, poverty-stricken communal ranchers may be unable to afford such herbicides, so we sought to determine whether they could use other, less-expensive means.

In general, the larger the stump, the greater the belowground resources that the plant has to support resprouting (Neke et al. 2006). However, there is considerable variance in this

relationship; some authors have found the opposite pattern (Keeley 2006) and some have found no relationship (Nzunda et al. 2008; Mostacedo et al. 2009). These results suggest that the effects of stump diameter on resprouting ability may be species-specific, and may be related to the development of the root systems of the species (Wigley et al. 2019; Zhou et al. 2020). Differences in root systems among tree species may subsequently influence resprouting patterns and the efficacy of control methods.

Here we examined the resprouting patterns of 12 dominant woody plant species at Roodeplaat ranch in Gauteng Province of South Africa. We applied mechanical tree removal and herbicides to determine which of these two factors were most important for controlling woody plant encroachment. We sought to determine the combined effects of tree species, removal treatments, stump diameter, and herbicide application on resprouting patterns of the study species. Further, we investigated the effectiveness of Tree Poppers[®] to mechanically uproot tree seedlings and saplings of eight dominant species in the study area. To achieve these aims, we conducted two field experiments and made the following predictions: (1) A higher density of trees in low-removal treatments will result in reduced resprouting ability and vigour due to stump shading by the remaining trees; (2) Herbicide application will result in reduced or no growth from cut stumps regardless of the species; (3) There will be a positive correlation between resprouting ability and stump diameter because larger trees should have greater storage of below-ground resources (Nzunda et al., 2008); (4) The effectiveness of Tree Poppers[®] is likely to be negatively affected by seedling height and be greater for shallow-rooted trees.

2.2. Materials and Methods

2.2.1. Study Area

The study was conducted at the Roodeplaat experimental farm of the Agricultural Research Council (25°36'29"S, 28°2'08"E) in Gauteng Province, South Africa. The farm is about 2100 ha, which is mostly used for livestock and game production. The vegetation type of the farm is Marikana Thornveld (Mucina and Rutherford 2006). *Vachellia* (formerly *Acacia*) *karroo* and *Senegalia* (formerly *Acacia*) *caffra* (Kyalangalilwa et al. 2013), are among the major dominant woody plants on the farm. Other dominant woody plants includes *Euclea species*, *Vachellia* (formerly *Acacia*) *tortilis* and *Ziziphus mucronata*. Coates-Palgrave's (2002) nomenclature for tree species was followed. The grass component of the site is characterised by *Digitaria eriantha*, *Eragrostis curvula*, *Heteropogon contortus*, *Melinis repens*, *Panicum maximum*, *Setaria sphacelata*, *Sporobolus africanus* and *Themeda triandra*. We used van Oudtshoorn's

(2006) nomenclature for grass species. The study area is a mesic savanna with a mean annual rainfall of 687 mm, which largely falls between November and March. The minimum temperature during the winter season ranges between 2-16°C and maximum summer temperature ranges between 20-29°C. The study area is located on the Roodeplaat Igneous Complex (Panagos et al. 1998). The study was conducted on sandy soils (67% sand; 16% silt; 17% clay). Although the study was not conducted in a communal area, tree species examined in this study are common in many communal savanna rangelands in South Africa.

2.2.2. Research Design

The study was carried out in two sites within the ranch. The first study site consisted of 20 plots of 30 m x 30 m each subjected to different intensities of tree removal. Tree densities were determined by doing a direct count of all trees in each plot. Trees were removed in October 2018 to the approximate equivalents of 10%, 20%, 50%, 75% and 100% (total clearing of the tree density) per plot, following Smit (2005). The plots were close to each other and were separated by 5-m wide fire breaks. Tree removal treatments were replicated four times and allocated randomly. Trees were cut with a chainsaw and any accumulated sawdust or debris was removed from the cut stumps. All trees were cut at a height of 0.25 m (Shackleton 2000; Moyo et al. 2015). The herbicide used contains picloram as its active ingredient (Teague and Killilea 1990; Burch and Zedaker 2003). This herbicide is a water-soluble systemic herbicide with residual activity that acts through roots and cut surfaces of woody plants (Teague and Killilea 1990). The herbicide was applied at a concentration of 6 mL L⁻¹ of water (Browser Herbicide®, Arysta Lifesciences). Tree stumps were treated with herbicide within 15 min after felling during the growing season. A knapsack sprayer (Spraying Systems TG-1, Delavan CE 1) with a single solid-cone nozzle was used for herbicide application.

The combined effects of tree species, removal treatments, stump diameter, and herbicide application on the resprouting ability were examined on the following woody species that encroach study site 1: *Dichrostachys cinerea*, *Euclea crispa*, *Ehretia rigida*, *Gymnosporia buxifolia*, *Pappea capensis*, *Searsia lancea*, *Senegalia caffra*, *Vachellia karroo*, *V. nilotica*, *V. robusta*, *V. tortilis* and *Ziziphus mucronata*. To determine the regrowth patterns for each resprouting stump the following variables were measured in each plot 9 months after tree felling towards the end July 2019: (1) total number of resprouting shoots per stump, (2) number of leaves on the leader (longest) shoot, (3) shoot length of the leader shoot and (4) shoot diameter

of the leader shoot, measured at the base of the shoot. Shoot production was calculated as the number of shoots produced per unit area of stump (Moyo et al. 2015).

In study site 2, we assessed the effectiveness of Tree Poppers® (Fig. 2.1) to mechanically uproot woody seedlings and saplings of eight dominant species during the wet season (February 2019) (viz. *D. cinerea*, *E. crispa*, *E. rigida*, *G. buxifolia*, *V. karroo*, *V. nilotica*, *V. tortilis* and *Z. mucronata*). We used plant height to differentiate between seedlings and saplings (i.e., trees taller than 1 m were considered saplings). Individual plants were grouped into three height classes (i.e., 0-49 cm; 50-99 cm; 100-150 cm) of 10 tree seedlings per species per height class. In the study area, there were no *D. cinerea* and *V. nilotica* saplings of the third height class (i.e., 100-150 cm). Tree seedlings and saplings that were uprooted by the Tree Poppers® were recorded as successfully removed and those that were either not removed or broke at the bottom of the stem were recorded as *unsuccessful*. A single person of 70 kg body weight carried out the removal of tree seedlings and saplings.

The effectiveness of the Tree Poppers® mechanical tool may depend on soil moisture (Treepopper, 2019). We conducted the Tree Poppers® experiment during the wet season in February 2019. To determine the soil water content of the study area, eight soil samples at were collected to a depth of 0.3 m, weighed and oven-dried at 60 C for 72 h. Soil moisture content was calculated as moisture content m (moisture) [%] = $100 \times (\text{weight wet} - \text{weight dry}) / \text{weight dry}$ (Fatma et al. 2018). Soil samples collected while assessing the Tree Poppers® had a moisture content of $16.6 \pm 1.6\%$ (mean \pm 1 SE).

2.2.3. Data Analysis

Prior to analysis, shoot production data were log₁₀-transformed to ensure a normal distribution of residuals. We used multivariate analysis of covariance (MANCOVA) to test the effects of tree species, stump diameter, herbicide application and tree removal treatments on the resprouting ability and vigour of the study plants. Shoot production, number of leaves, shoot length and shoot diameter were the dependent variables, with stump diameter as a covariate. MANCOVA was used to reduce Type 1 error that may be caused by testing multiple dependent variables on the same subjects. We used the Wilks' Lambda test statistic to investigate the effect of treatments (species, herbicide application and tree removal) on resprouting parameters. When the MANCOVA was significant, we used univariate ANOVA to identify factors that contributed to the significant MANCOVA, followed by a Bonferroni *post hoc* test among groups of each factor. We used linear regression to determine the relationship between

resprouting ability of the trees and stump diameter. A two-factor ANOVA was used to determine whether there were significant effects of tree species and tree height on the number of juvenile plants uprooted by the Tree Popper®. The number of juveniles uprooted were the dependent variables while the plant species and height class were the independent variables. A Bonferroni *post hoc* test was applied for pairwise comparisons of the mean number of juveniles uprooted by Tree Poppers®. IBM SPSS for Windows v. 26 (IBM SPSS 2019) was used for all data analysis.

2.3. Results

There was a significant interaction between tree species and tree-removal treatments (Wilks' $\lambda = 0.714$; $F = 1.846$; $P < 0.001$) and the interaction between tree species and herbicide application (Wilks' $\lambda = 0.963$; $F = 2.200$; $P < 0.004$). We found a significant effect of tree removal on resprouting patterns (Wilks' $\lambda = 0.971$; $F = 1.705$; $P < 0.039$) (Fig. 2.2). A Bonferroni *post hoc* test revealed that tree removal had a significant effect on the resprouting patterns of *E. crispa* only. We found that shoot diameter ($P = 0.001$) and shoot production ($P = 0.004$) of *E. crispa* were inconsistently affected by the removal treatments. We found significant effects of stump diameter on resprouting patterns of 10 of the 12 study species (Wilks' $\lambda = 0.885$; $F = 29.383$; $P < 0.001$). There was no significant effect of stump diameter on resprouting for *E. rigida* ($P = 0.276$) and *V. karroo* ($P = 0.181$). Furthermore, we observed a significant negative relationship between stump diameter and shoot production on all the study species, except for *E. rigida* where there was no clear pattern (Fig. 2.3).

We found a significant effect of herbicide application on resprouting patterns of five of the 12 study species (Wilks' $\lambda = 0.819$; $F = 50.798$; $P < 0.001$) (Table 2.1). Significant effects of herbicide application were found on *E. rigida*, *V. robusta*, *V. tortilis* and *Z. mucronata* ($P < 0.05$). A marginally significant effect ($P < 0.058$) of herbicide application was found for *D. cinerea* (Table 2.1). Tree stumps treated with herbicide had a mean mortality of 79.1% compared to the control (untreated) mean of 13.89%.

We found significant differences in the number of juveniles removed using the Tree Poppers® ($P < 0.05$) among species, with a higher number of juveniles removed for *E. crispa*, *E. rigida*, *G. buxifolia* and *Z. mucronata* than for *D. cinerea*, *V. karroo*, *V. nilotica* and *V. tortilis* (Fig. 2.4). Although a substantial number of *D. cinerea* juveniles were uprooted, a Bonferroni *post hoc* test showed no significant differences between *D. cinerea* and the *Vachellia* species.

Also, we found no significant differences in the number of seedlings removed among the height classes regardless of the tree species ($P > 0.05$) (Table 2.2).

2.4. Discussion

Tree removal

After brush management, tree regeneration is a major potential problem encountered by resource-constrained communal ranchers (Hoffman and Ashwell 2001; Moyo et al. 2015). All the tree species in this study resprouted following cutting, demonstrating their ability to regenerate from the damaged tissues. Our results are consistent with the results obtained by similar studies demonstrating woody plants' abilities to resprout after disturbances (Shackleton 2001; Bond and Midgley 2001; Mwavu and Witkowski 2008; Sands and Abrams 2009). The ability of woody plants to resprout after disturbance may be attributed to the stored resources (Clarke et al. 2013; Nzunda et al. 2014). The current study results suggest that trees examined in this study have the ability to regenerate after cutting and thus further stump treatments may be required to successfully control the plants to ensure long-term reduction of woody populations. Reduced tree populations will improve forage production. This may, however, pose a challenge for communal ranchers who seldom have access to sufficient funds to finance control of woody plants. Thus, controlling woody plants by uprooting them at the seedling stage may be a viable option for communal ranchers.

Different intensities of tree-removal applied in this study were not important determinants of resprouting ability (shoot production) and vigour (shoot length and shoot diameter) of 11 of the 12 species examined. This may be attributed to the distribution pattern of woody plants in savanna rangelands (Mureva and Ward 2016). Competition for resources (particularly soil moisture) among savanna trees usually results in reduced plant densities and sizes, and leads to a more regular pattern of tree distribution (Pillay and Ward 2012). Density of the remaining trees in the low tree removal-treatments may have not been sufficient to suppress resprouting. However, we observed that certain tree stumps that were under or in close proximity to the remaining trees showed a relatively low production of shoots and leaves regardless of species. Shading by the remaining trees may reduce resprouting of individual stumps due to limited light availability because many savanna trees are shade-intolerant (Gordon et al. 2006; Hoffmann et al. 2012). For example, Casals and Rios (2018) reported that

stump shading limits resprouting vigour of *Buxus sempervirens* (forest tree) as a result of tree-removal. Nevertheless, we found that tree removal had a significant effect on the resprouting ability and vigour of *E. crispa*. However, the results did not show a clear pattern. For example, resprouting ability and vigour were significantly higher from 20% and 50% removal than in other treatments. These results were not consistent with our prediction that resprouting ability and vigour will be significantly lower in the low removal-treatments (10% and 20%). Thus, the effects of tree removal on *Euclea crispa* suggest possible influence by undetermined factors outside the scope of our study.

We predicted that larger stumps would show a higher resprouting ability than smaller stumps. However, we found that shoot production decreased with increasing stump diameter of the study plants, except for *Ehretia rigida*. Similar studies have demonstrated that the effectiveness of resprouting differs according to tree age, which is usually measured by stem diameter at the time of disturbances (Bellingham and Sparrow 2000, 2009; del Tredici 2001; Keeley 2006; Dietze and Clarke 2008; Sands and Abrams 2009). For example, several studies (e.g., Keely 2006; Mwavu and Witkowski 2008; Sands and Abrams 2009) reported that tree species resprout as juveniles and lose their ability to resprout when they reach the adult stage. Additionally, models developed by Gould et al. (2007) to predict resprouting ability among oaks in the central Appalachians in Pennsylvania (USA) show that white oak *Quercus alba* trees rapidly lost their resprouting abilities with increasing stem diameter. The causes of this resprouting pattern in woody species are unclear, but are often assumed to arise from a combination of genetic, physiological and related anatomical changes that occur with stage of tree development (del Tredici 2001; Waters et al. 2010; Clarke et al. 2013).

Waters et al. (2010) suggested that the resprouting ability of woody plants as influenced by plant age is related to bud senescence. Thick bark in older trees may inhibit resprouting abilities through hindering bud emergence (Clarke et al. 2013; Charles-Dominique et al. 2015). In systems that experience disturbances such as frequent fires (e.g., study site 1), trees avoid such disturbances by growing tall and developing a thicker bark (Vesk and Westoby 2004; Vesk 2006; Higgins et al. 2000; Bond 2008; Burrows et al. 2008). Where faster growth allows trees to escape damage by disturbances such as frequent fires, then resprouting ability may decline with increasing size (Vesk 2006).

The tendency of young trees to be better resprouters than older trees is reported to be an effective adaptive strategy against frequent fires (Keeley et al. 2012; Pausas and Keeley 2017). Shackleton (2001) demonstrated that larger stems take longer to respond to the initial cutting,

but once recovered have the capacity to regrow at a rate faster than that of smaller stems. Shackleton's (2001) study (39 mo) lasted longer than our study (9 mo). This may possibly explain why the results from his study and ours differed.

Chemical Control

Herbicide application significantly reduced the resprouting abilities of *D. cinerea*, *E. rigida*, *V. robusta*, and *Z. mucronata*. Although herbicide application significantly reduced shoot length and leaf production of *V. tortilis*, it did not affect the resprouting ability (i.e. shoot production) and diameter of the leader shoot of this species (Table 2). Furthermore, herbicide application had no significant effect on the resprouting ability of seven species tested (*E. crispa*, *G. buxifolia*, *P. capensis*, *S. lancea*, *V. caffra*, *V. karroo* and *V. nilotica*), inconsistent with our prediction that herbicide application will significantly reduce the resprouting ability of all cut stumps regardless of species. A possible reason for the inconsistency of the effects of herbicide application across species may be attributed to the equal concentration of picloram applied to the cut stumps and time of application for each plant species. Elsewhere, Enloe et al. (2015) found that the herbicide triclopyr amine applied at a 25% v/v (i.e. (volume of solute/volume of solution) x 100) concentration was not effective for *Triadica sebifera* control, an invasive woody species invading the south-eastern United States. However, in the same study, Enloe et al. (2015) found that the same amount of triclopyr amine was effective in controlling *Ligustrum sinense*, which invades the same area. Their results also showed that reducing the recommended concentrations of two herbicides (i.e. glyphosate and triclopyr amine) by 50% was effective for controlling *L. sinense*. Reducing herbicide inputs into the environment is a desirable goal for land users globally (Enloe et al. 2018), and particularly for resource-poor communal ranchers. Thus, testing the amount of picloram needed to kill certain woody species may be of importance for land users in southern African savannas. This will inform land managers on optimal concentrations of picloram to use on certain species. Moreover, the seasonal timing of herbicide application on cut stumps has been reported to influence subsequent resprouting of woody plants (Badalamenti et al. 2015; Enloe et al. 2016, 2018). In our study, trees were cut and treated with herbicide during the wet season. However, Enloe et al. (2018) demonstrated that woody plants are controlled better with herbicides during autumn (fall) when woody plants are not actively growing. Additionally, Burch and Zedaker (2003) showed that using mixtures of several herbicides provide better control than using single herbicides because different

herbicides have different physiological pathways and modes of action. Future studies should focus on testing the optimal concentrations and time (wet or dry season) of application of different herbicides needed to kill the tree stumps of the species we examined.

Mechanical Control

Our prediction that weed wrenches such as Tree Poppers® may be an effective mechanical tool to control woody plant seedlings and saplings was partially supported by our results. We also predicted that the effectiveness of the Tree Poppers® would differ among different plant species due to differences in rooting systems. The majority of *Vachellia* trees, regardless of species, were either not successfully uprooted or broke at the base of the stem. This is because many *Vachellia* species have a long taproot to access underground water (Ward and Esler 2011; Kambatuku et al. 2013). This kind of root system makes it difficult to uproot seedlings of these species. In cases where the seedlings broke at the bottom of the stem, supplemental chemical treatments would be necessary to completely control the plant. However, we found no significant differences in the number of uprooted *Vachellia* and *D. cinerea* juveniles. We ascribe this to the absence of taller *D. cinerea* plants (i.e. 100-150 cm) in the study area and note that plant height was not an important factor in determining the effectiveness of the Tree Poppers®. Regardless, the Tree Popper® harvesting tool was effective in controlling the *D. cinerea* seedlings (Table 3), which is among the major woody plant encroachers in southern African savannas (Kraaij and Ward 2006; O'Connor et al. 2014). Wakeling and Bond (2007) have shown that *D. cinerea* reproduces vegetatively by means of root suckering, which means that the roots of this species are often close to the surface. Moreover, the Tree Popper® harvesting tool was effective in uprooting tree seedlings of shallow-rooted *E. crispa*, *E. rigida*, *G. buxifolia* and *Z. mucronata*. This is due to the differences in root depths between the aforementioned species and the *Vachellia* species. Our results suggest that communal ranchers may mechanically control shallow-rooted tree seedlings with Tree Poppers® but not deep-rooted species such as those in the *Vachellia* genus.

2.5. Conclusions and Management Implications

Our findings provide evidence that woody species in our study area are capable of resprouting after cutting. However, different levels of tree removal were not a major determinant of resprouting success in this study. The effects of herbicides in preventing tree stumps from

resprouting are species-specific. Stump diameter was the most important factor affecting resprouting capabilities of the study plants. Woody plants species from the study area are more likely to resprout and survive disturbances as juveniles than as adults.

Although the Tree Popper[®] was not effective in controlling the *Vachellia* species that are responsible for much of the woody plant encroachment in southern Africa (Hoffman and Ashwell 2001), it was adequate for control of *D. cinerea*, another major encroacher in the region. The results provided a scientific basis for deciding whether Tree Poppers[®] are viable rehabilitation tools for managing tree seedlings in the study area. Further development of hand-held tools may revolutionize mechanical bush-control measures, particularly in developing countries with limited economic resources. This information may better inform land managers regarding more effective approaches to inform communal ranchers regarding control of young trees that can encroach savannas.

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1288 Table 2.1. The effect of herbicide application on mean of each of number of leaves, shoot
 1289 diameter (cm), length of the leader shoot (longest shoot) (cm) and shoot production of 12 tree
 1290 species. Significant differences of the ANOVA results are denoted with an *. Species names
 1291 are *Dichrostachys cinerea* (n = 72), *Euclea crispa* (n = 151), *Ehretia rigida* (n = 100),
 1292 *Gymnosporia buxifolia* (n = 82), *Pappea capensis* (n = 35), *Searsia lancea* (n = 42), *Senegalia*
 1293 *caffra* (n = 40), *Vachellia karroo* (n = 55), *V. nilotica* (n = 70), *V. robusta* (n = 201), *V. tortilis*
 1294 (n= 47) and *Ziziphus mucronata* (n = 140).

Species	Treatment	Significance of Wilks' λ in MANCOVA (<i>p</i> value)	Number of leaves (mean \pm SE)	Diameter of the leader shoot (mean \pm SE)	Length of the leader shoot (mean \pm SE)	Shoot production (mean \pm SE)
<i>D. cinerea</i>	Herbicide	0.058	0 \pm 0	0.03 \pm 0.01	6.20 \pm 3.13	13.5 \pm 0.8
	Control		5.29 \pm 2.83 *	0.49 \pm 0.07	68.03 \pm 9.39	193.3 \pm 32.6 *
<i>E. crispa</i>	Herbicide	0.225	0.77 \pm 0.88	0.03 \pm 0.01	3.79 \pm 1.44	25.32 \pm 10.67
	Control		46.24 \pm 6.42	0.31 \pm 0.04	37.60 \pm 3.61	204.44 \pm 29.79
<i>E. rigida</i>	Herbicide	0.001	1.32 \pm 0.64	0.04 \pm 0.01	4.81 \pm 3.22	20.6 \pm 9.2
	Control		20.63 \pm 4.02 *	0.75 \pm 0.07 *	65.85 \pm 5.93 *	317.9 \pm 29.6 *
<i>G. buxifolia</i>	Herbicide	0.138	0.52 \pm 0.35	0.05 \pm 0.02	2.35 \pm 1.03	9.0 \pm 3.7
	Control		8.34 \pm 2.14	0.33 \pm 0.05	22.76 \pm 3.34	149.8 \pm 42.4
<i>P. capensis</i>	Herbicide	0.099	5.17 \pm 1.82	0.08 \pm 0.02	6.54 \pm 2.58	44.5 \pm 21.8
	Control		16.38 \pm 4.55	0.37 \pm 0.09	119.66 \pm 87.26	156.2 \pm 37.8
<i>S. lancea</i>	Herbicide	0.347	11.68 \pm 7.18	0.12 \pm 0.06	9.64 \pm 4.89	114.7 \pm 100.1
	Control		90.75 \pm 23.48	2.81 \pm 1.82	89.00 \pm 9.71	194.9 \pm 28.5
<i>V. caffra</i>	Herbicide	0.122	10.37 \pm 3.91	0.21 \pm 0.07	3.70 \pm 10.06	28.1 \pm 9.7
	Control		57.06 \pm 16.04	0.45 \pm 0.08	62.29 \pm 10.19	134.3 \pm 36.9

<i>V. karroo</i>	Herbicide		0.78 ± 0.63	0.01 ± 0.01	1.89 ± 1.36	10.1 ± 6.2
	Control	0.158	5.72 ± 2.54	0.35 ± 0.07	42.22 ± 4.68	221.7 ± 85.3
<i>V. nilotica</i>	Herbicide		2.87 ± 2.17	0.04 ± 0.03	2.09 ± 1.23	3.9 ± 2.9
	Control	0.083	42.31 ± 9.30	0.36 ± 0.05	42.28 ± 5.45	130.1 ± 29.5
<i>V. robusta</i>	Herbicide		3.63 ± 1.08	0.09 ± 0.02	5.84 ± 1.15	6.8 ± 1.7
	Control	0.004	21.15 ± 4.29	$0.42 \pm 0.04 *$	$39.64 \pm 3.08 *$	$155.7 \pm 15.2 *$
<i>V. tortilis</i>	Herbicide		14.96 ± 4.88	0.15 ± 0.05	17.67 ± 4.75	98.6 ± 48.2
	Control	0.038	$78.94 \pm 13.52 *$	0.65 ± 0.12	$61.94 \pm 6.67 *$	212.9 ± 63.5
<i>Z. mucronata</i>	Herbicide		3.83 ± 1.66	0.07 ± 0.02	7.02 ± 2.44	4.3 ± 1.5
	Control	0.001	$118.30 \pm 13.17 *$	$1.05 \pm 0.08 *$	$104.92 \pm 5.89 *$	$192.4 \pm 26.8 *$

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1314 Table 2.2. Proportion of tree seedlings and saplings successfully uprooted with Tree Poppers®
 1315 per height class among woody plant species.

Height class (cm)	<i>D.</i> <i>cinerea</i>	<i>E.</i> <i>crispa</i>	<i>E.</i> <i>rigida</i>	<i>G.</i> <i>buxifolia</i>	<i>V.</i> <i>karroo</i>	<i>V.</i> <i>nilotica</i>	<i>V.</i> <i>tortilis</i>	<i>Z.</i> <i>mucronata</i>
0 – 49	1	0.9	0.9	0.9	0	0.3	0.1	0.9
50 – 99	0.8	1	1	1	0.2	0	0	1
100 – 150	–	1	1	0.9	0.3	–	0	1

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1342 Figure 2.1. Shows the Tree Popper[®] harvesting tool or weed wrench (Pictures by
1343 Treepopper.co.za).

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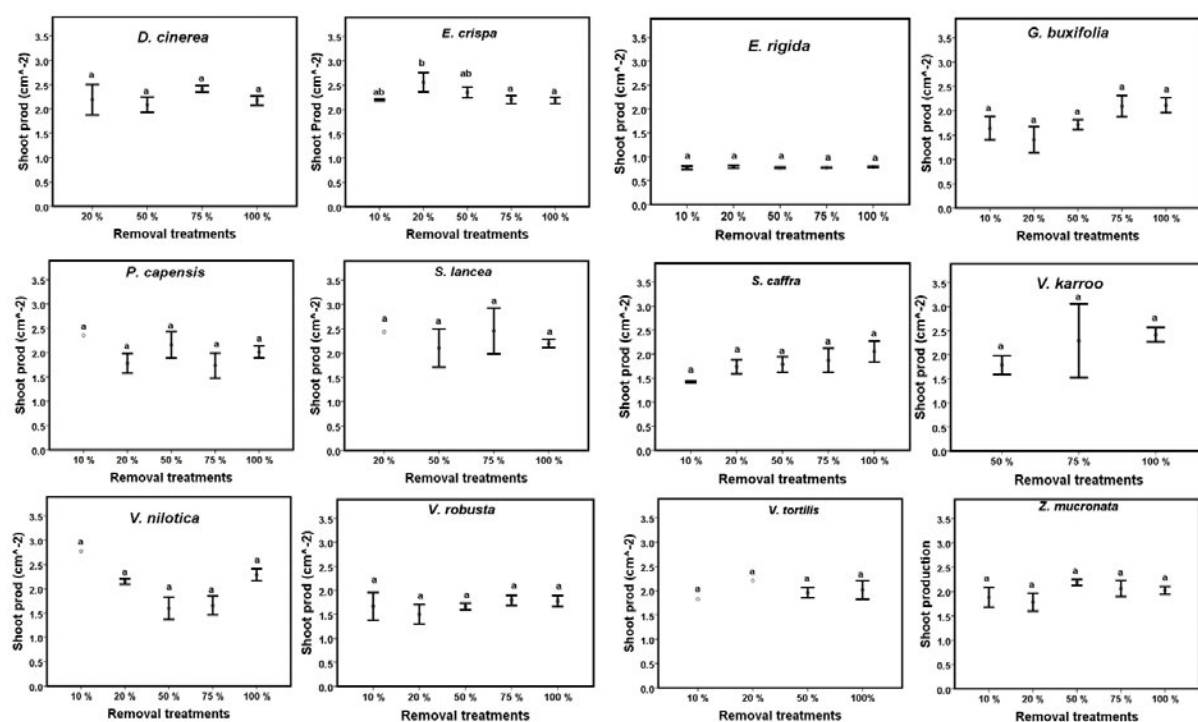


Figure 2.2. Mean shoot production (± 1 S.E.) of *D. cinerea*, *E. crispa*, *E. rigida*, *G. buxifolia*, *P. capensis*, *S. lancea*, *V. caffra*, *V. karroo*, *V. nilotica*, *V. robusta*, *V. tortilis* and *Z. mucronata* stumps at different removal treatments (100 % removal = total clearing of tree biomass). Different superscript letters represent significant differences based on a Bonferroni *post hoc* test.

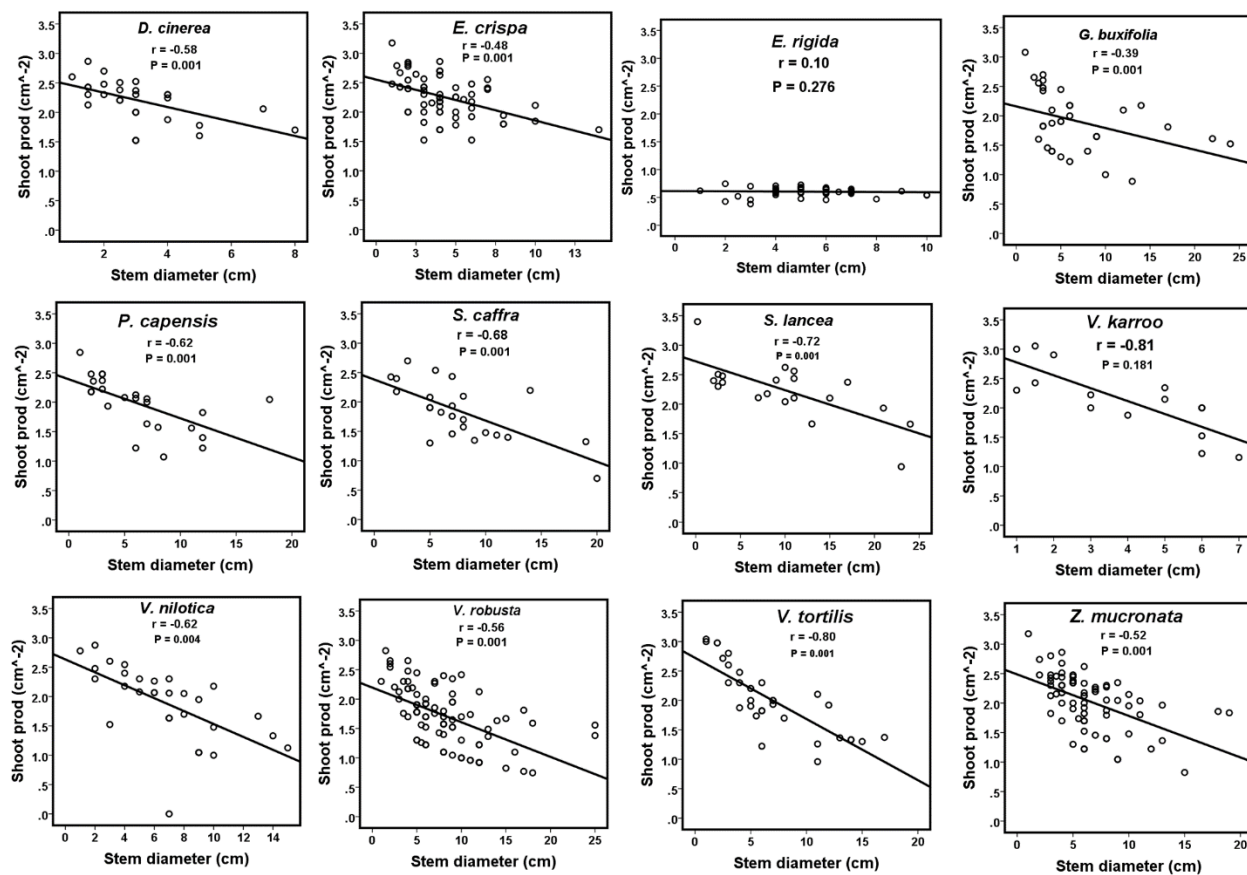


Figure 2.3. The relationship between stump diameter and new shoot production of *D. cinerea*, *E. crispa*, *E. rigida*, *G. buxifolia*, *P. capensis*, *S. lancea*, *V. caffra*, *V. karroo*, *V. nilotica*, *V. robusta*, *V. tortilis* and *Z. mucronata*.

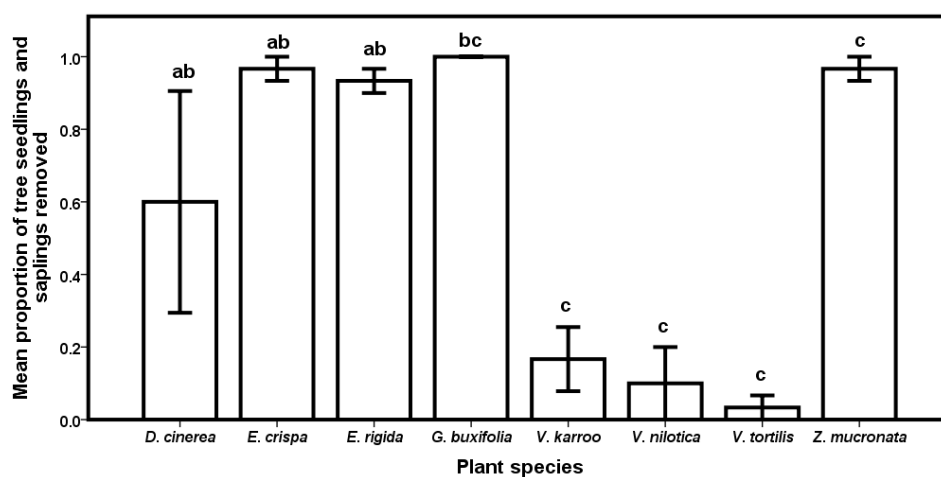


Figure 2.4. Mean proportion of tree seedlings and saplings (i.e. *Vachellia karroo*, *V. nilotica*, *V. tortilis*, *Dichrostachys cinerea*, *Euclea crispa*, *Ehretia rigida*, *Gymnosporia buxifolia* and *Ziziphus mucronata*) successfully removed (± 1 S.E.) using Tree Poppers[®]. Different superscript letters represent significant differences based on a Bonferroni *post hoc* test.

Chapter 3: Short-term response of grass species richness, composition, β diversity and soil dynamics after tree thinning in a South African savanna

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Formatted for submission to *African Journal of Range and Forage Science*

Abstract

In savannas, woody plant encroachment negatively affects ecosystem services such as forage production and thus, reactive interventions such as tree thinning are commonly applied. We conducted a field experiment in two study sites with 24 plots (30 m x 30 m) in each site to determine the effects of different tree thinning-intensities (0%, 10%, 20%, 50%, 75% and 100% tree removal), on grass species-richness, composition, cover, β diversity, and soil fertility and cover. We found that tree thinning did not have significant effects on grass species-richness in either study site. In site 1, β diversity results showed no treatment effects on compositional change between thinned plots and the control (no thinning). However, in site 2, β diversity results demonstrated moderate compositional change between thinned plots and the control plots. Different levels of tree thinning increased the abundance of two dominant grass species, *Digitaria eriantha* and *Panicum maximum* in both study sites, particularly in moderate (50%) and high removal (75% and 100%) treatments. However, the nitrophilous *P. maximum* will likely decline in abundance over time, particularly in the 100% tree thinning treatment because N-fixation from trees will no longer exist because of the lack of woody plants. Contrastingly, we found no evidence that tree thinning alters soil cover. In addition, different levels of tree thinning did not have a significant impact on soil fertility in either study site. The 50% tree thinning created an opportunity for different palatable grass species to increase in abundance, which may be important for forage production that may support livestock and wild herbivores in savannas. Maintaining a certain density of woody plants in rangelands affected by woody plant encroachment will help maintain the ecological benefits conferred by woody plants on the herbaceous layer, soil enrichment and provision of browse.

Keywords: communal rangelands, rehabilitation, soil erosion, tree clearing, woody plant encroachment

3.1. Introduction

In savanna rangelands, the imbalance in the coexistence of trees and grasses caused by woody plant encroachment negatively affects ecosystem services such as forage production (Ward 2005, Riginos et al. 2009; Schleicher et al. 2011). Thus, reactive interventions such as tree thinning remains are normally applied (Smit 2005, Smit 14; Ndhlovu et al. 2016a; Ding and Eldridge 2019). Tree-thinning (also termed *brush management*) has been widely employed to improve the quality of forage production and maintain the economic viability of rangelands that are affected by woody plant encroachment (Smit 2005; Ndhlovu et al. 2016a). Tree thinning often involves clearing the total tree-biomass (Ludwig and Tongway 2002; Smit 2005; Ndhlovu et al. 2016a). Although woody-plant clearing leads to a significant increase of the herbaceous layer (Ludwig and Tongway 2002), in low-input agro-ecosystems where irrigation and fertilisation are not applied, complete thinning of all trees could negatively affect rangeland productivity, particularly in the long term (Sangha et al. 2005; Smit 2014).

Studies of woody plant encroachment have shown their ecological effects on rangeland productivity (Ludwig et al. 2003; Smit 2005; Kambatuku et al. 2013; Marquart et al. 2019). Woody plants are able to take up deeper water resources to the surface through their deep root systems by means of a process called hydraulic lift (Ludwig et al. 2003; Schleicher et al. 2011; Kambatuku et al. 2013; Ward et al. 2013; Marquart et al. 2019). This in turn allows grasses, which generally have shorter root systems, to access more water, which positively influences their growth and persistence, especially in water-limited agro-ecosystems (Ludwig and Dawson 2003). In addition, at low densities woody plants have been reported to protect the top soil layer from erosion by improving vegetation cover (Marquart et al. 2019), which promotes rainfall infiltration and reduces runoff (Herrick et al. 2005; Ndhlovu et al. 2016). Moreover, many savanna leguminous trees are able to fix atmospheric nitrogen in symbiosis with their *Rhizobium* bacteria (Cramer et al. 2007; Kambatuku et al. 2013). This nitrogen also becomes available to the grasses, which in turn, may positively influence grass production and grass species composition (Smit 2005). For example, certain nitrophilous grasses such as *Panicum maximum*, grow well under leguminous trees (Bosch and Van Wyk 1970; Smit 2005). Similarly, other grass species may be lost in the presence of woody plants, particularly the shade-intolerant species (Ndhlovu et al. 2016b). Consequently, tree thinning may influence grass species richness, composition and diversity (Dodson and Peterson 2010). The canopy gaps created through tree thinning are expected to lead to an increase in species richness and abundance of different grass species due to reduced competition for water, nutrients and light availability

(Savadogo et al. 2008; Bassett et al. 2020). It is thus important to test how understory communities and individual grass species react to tree thinning.

Despite the ecological benefits conferred by leguminous trees, woody plant encroachment is regarded as an indication of rangeland degradation (Ward 2005; O'Connor et al. 2014; Archer et al. 2017) and has the potential to threaten the social and ecological viability of livestock and game farming (Archer and Predick 2014). However, at low densities, woody plants have been reported to have positive effects on herbaceous plant production and soil cover (Smit 2005; Marquart et al. 2019). In this study, we evaluated the effects of different tree thinning-intensities on grass species richness, composition, and soil fertility and soil cover at two savanna sites that differ in soil texture and woody species at Roodeplaat ranch in the Gauteng Province of South Africa. The predictions were:

- 1) Grass-species richness will increase with increasing intensity of tree-thinning because thinning may increase the abundance of previously suppressed grasses;
- 2) Grass species that are adapted to nutrient-enriched sub-canopies and neighbourhoods of the trees will decrease in abundance with increasing tree-thinning intensities;
- 3) Total clearing of trees will have a negative effect on soil fertility in both study sites because biological nitrogen fixation and soil nutrient accumulation are no longer operational;
- 4) The thinning treatments will reduce the amount of bare soil because the removal of woody plants is expected to increase herbaceous biomass and cover.

3.2. Materials and methods

3.2.1. Study area

The study was carried out at Roodeplaat Experimental Farm (25°36'29"S, 28°2'08"E) which is situated in the north of Gauteng Province, South Africa. Roodeplaat farm is a 2100 ha farm of the Agricultural Research Council (ARC), and it is used for livestock and wildlife production. The vegetation of this area is described as the Marikana Thornveld (Mucina and Rutherford 2006) and is dominated by several woody plants, which include *Euclea* species, *Vachellia* (previously *Acacia*) *karroo*, *Senegalia* (formerly *Acacia*) *caffra*, *Vachellia* (previously *Acacia*) *tortilis* (Kyalangalilwa et al. 2013) and *Ziziphus mucronata*. We used Coates-Palgrave's (2002) nomenclature for tree species. The grass layer consists of *Digitaria eriantha*, *Melinis repens*, *Panicum maximum*, *Setaria sphacelata*, and *Sporobolus africanus*. *Eragrostis curvula*, *Themeda triandra*, and *Heteropogon contortus* are some of the important grasses found on the ranch (Van Rooyen 1983). van Oudtshoorn's (2006) nomenclature is followed for grass species.

The farm receives annual precipitation of 687 mm with most of it falling during summer (November to March). The maximum daily temperature of the area in summer ranges between 20-29 °C, while the minimum winter temperature can decrease to 2-16 °C. The most common soil types of the study area are Ferralsols, Luvisols, and Vertisols. The study area is situated on the Roodeplaat Igneous Complex, which belongs to the Post-Waterberg Formation (Panagos et al. 1998). The Roodeplaat Igneous Complex is a unique ring-shaped structure with a diameter of approximately 16 km and is also referred to as the “Roodeplaat volcano” (Panagos et al. 1998). Rainfall and temperature data for the study area was received from an accredited Agricultural Research Council’s Institute for Soil, Climate and Water (Figs. 3.1 and 3.2).

3.2.2. Study design

The study was conducted in two sites that vary in grasses, tree species and soils within the same ranch from October 2018 to April 2020 over two growing seasons. The first study site (hereafter study site 1) was on clay-dominated soils (sand 38%; silt 17%; clay 45%) characterized by severe soil degradation in the form of surface erosion and crust formations. The study site had a closed canopy woodland dominated by *V. tortilis*. The second study site (hereafter study site two) was on sand-dominated soils (67% sand; 16% silt; 17% clay) with several common woody species (*Dichrostachys cinerea*, *Euclea crispa*, *Ehretia rigida*, *Gymnosporia buxifolia*, *Pappea capensis*, *Searsia lancea*, *Senegalia caffra*, *V. karroo*, *Vachellia* (formerly *Acacia*) *nilotica*, *V. robusta*, *V. tortilis* and *Ziziphus mucronata*).

At each site, we set up 24 plots of 30 m × 30 m each subjected to different intensities of tree thinning. Tree thinning-treatments were replicated four times and allocated randomly to the plots. Trees were removed to the approximate equivalents of 0% (control-no removal), 10%, 20%, 50%, 75% and 100% (total clearing of the tree biomass), following Smit (2005). The plots were fenced to restrict grazing/browsing by livestock. Grass species richness and composition were determined using the nearest-plant species method described by Hardy and Tainton (1993). Because the size of our plots was relatively small (i.e. 30 m x 30 m), the nearest species and basal strikes were estimated along a 25 m line transect in each plot. At 1-m intervals, a metal rod was dropped and any herbaceous species on which the rod struck (basal strikes) was identified. When the distance to the nearest plant was ≥ 30 cm from the marked step point, “bare ground” was recorded. This technique has been reported to be sufficient to obtain reliable results (Tefera et al. 2010). Percentage bare ground was calculated following Herrick et al. (2005). Grass species richness was calculated by summing the total number of plant

species in each plot. Pielou's Evenness Index was used to calculate grass species evenness. β diversity was calculated using Sørensen index between each pair of treatments (control vs thinning treatments), using the formula $C_s = 2j/(a + b)$, where “j” is the number of species shared between two treatments and “a” and b are the numbers of species unique to each treatment. The herbaceous surveys were conducted before tree thinning and at the end of two growing seasons during the experimental period.

To assess the effects of tree thinning on soil properties (pH, organic carbon), five soil samples at 5 cm depth were collected from each plot, 5 m from each corner and one from the centre of each plot. The soil samples from each plot were mixed together to obtain one composite sample. The soil organic carbon was determined using the Walkley-Black method (Walkley and Black 1934). Soil pH (H₂O) was determined using a pH meter in a 1:5 soil:water suspension. We determined soil fertility by growing radish, *Raphanus sativus*. *Raphanus sativus* has no known preference for a specific soil type and is considered a reliable bioassay (Olsvig-Whittaker and Morris 1982; Ward et al. 1998). Three soil samples collected 5 m from each corner of the plot and from the centre were used. The three soils were collected 2 m apart and mixed together to form one sample and a total of five soil samples per plot. Prior to planting, radish seeds were germinated in growth chambers. The germination tests used circular plastic petri dishes (9 cm in diameter) containing one disc of filter paper and 5 ml of distilled water. The germination chamber was kept at a temperature of 20-30 °C with 16 h of dark period and 8 h of light period. Germinated seeds were then transplanted into seedling trays and grown for 4 weeks. Radish plant material including below ground storage organs were harvested and oven dried at 70°C for 72 h and weighed to calculate the dry-matter yield. The differences in plant dry material were used to determine the variations of soil quality among the treatments.

3.2.3. Data analysis

Prior to analysis, data were square-root transformed to ensure a normal distribution of residuals. We used multivariate analysis of covariance (MANCOVA) to test the effects of tree thinning on grass species-richness. MANCOVA was used to reduce Type 1 error caused by testing multiple dependent variables on the same subjects. Grass species-richness recorded in the first and second growing seasons were considered the dependent variables. Grass species richness recorded before treatment application was used as a covariate. MANOVA was applied to test the effects of the tree thinning treatments on soil pH and organic carbon, which were the dependent variables. We used the Wilks' Lambda test statistic to investigate the effect of the

thinning treatments on grass species-richness and soil parameters. When the MANCOVA was significant, we used ANOVA for significant differences, followed by a Bonferroni *post hoc* test among groups. One-way ANOVA was applied to test for significant differences in soil fertility as indexed by the soil assay based on radish biomass. IBM SPSS for Windows v. 26 (IBM SPSS 2019) was used for all data analysis.

Canonical correspondence analysis was used to determine the effects of tree thinning on grass species composition. Species composition analyses were performed using XLSTAT software (version 2020.5, Addinsoft, New York, USA).

3.3. Results

Values of β diversity of grasses for study sites 1 and 2 are presented in Fig. 3.3. Tree thinning had no significant effect on grass species-richness in either site (Wilks' $\lambda = 0.451$; $F = 0.931$; $p > 0.539$ for site 1 and Wilks' $\lambda = 0.753$; $F = 0.332$; $p > 0.990$ for site 2.). Values for grass species richness and evenness are presented in table 3.1. There was a significant association between different grass species and the thinning treatments in both sites during the two growing seasons ($\chi^2 = 3435$, $p < 0.001$ and $\chi^2 = 4278$, $p < 0.001$, respectively) (Figs. 3.4 and 3.5). In site 1, tree thinning had a substantial effect on *Digitaria eriantha* and *Sporobolus africanus*, with the former increasing in abundance in cleared plots (100%) and the latter in the 50% removal treatment (Fig. 3.6). In site 2, *Heteropogon contortus* (the most dominant grass species before treatment application) decreased in abundance in all treatments, with the most decreases observed in 75% and 100% thinning treatments. Moderate (50%) and high intensities (75% and 100%) of tree thinning increased the abundance of palatable grasses (i.e. *D. eriantha* and *Panicum maximum*) in site 2 (Fig. 3.7).

We found no significant differences in bare soil area among treatments in sites 1 and 2 (Wilks' $\lambda = 0.523$; $F = 1.225$; $p > 0.313$ and Wilks' $\lambda = 0.687$; $F = 0.662$; $p > 0.750$, respectively) (Table 3.2). There were no significant differences in soil organic matter and pH among the different thinning treatments in site 1 (Wilks' $\lambda = 0.585$; $F = 1.044$; $p > 0.429$ and site 2 (Wilks' $\lambda = 0.688$; $F = 0.700$; $p > 0.717$). Additionally, we found no significant differences in soil fertility among thinning treatments as indexed by the soil assay (radish biomass) in sites 1 and 2 ($F = 0.898$; $p > 0.485$ and $F = 0.975$; $p > 0.436$, respectively) (Table 3.3).

3.4. Discussion

Woody plant encroachment can greatly influence the species richness and composition of herbaceous plants particularly grasses, and soil functions (Archer and Predick 2014; Ding and Eldridge 2019; Bassett et al. 2020). Studies have reported that woody vegetation thinning may create canopy gaps that can either result in increased grass species diversity or create unfavourable thermal conditions that may favour growth of drought-tolerant grass species due to competition for resources (Casado et al. 2004; Savadogo et al. 2008; Angassa et al. 2012). Although it was difficult to single out particular species that were consistently associated with thinning treatments at either site this study demonstrated that the abundance of dominant grass species changed in response to different levels of tree thinning. However, we found no significant differences in grass species richness among the treatments in either study site. Grass species evenness also showed no change as result of tree thinning in either site. In addition, tree thinning was not an important determinant of soil fertility and cover in either study site, but see site 1 (Table 3.2).

3.4.1. The impact of tree thinning on β diversity and grass species richness

We expected thinned treatment plots to change in grass species composition compared to the control treatment. In site 1, values of β diversity showed no indication of treatment effects on compositional change between thinned plots and the control. However, in site 2, β diversity results demonstrated moderate compositional change between thinned plots and the control (no thinning). The emergence and disappearance of certain grass species after the two growing seasons in site 2 could explain the species turnover. The findings from site 2 suggest that tree thinning may cause a change in grass species composition after treatment application. These findings were consistent with Dodson and Peterson (2010) who demonstrated that tree thinning leads to a change in herbaceous species composition relative to the control. These results showed that thinned plots may change in grass species composition compared to the control plots, although this may be site specific. Regardless, the results from both study sites were not consistent with the prediction that increases in tree thinning will result in a significant increase in grass species richness. This is because grass species richness significantly decreases in rangelands affected by woody plant encroachment (Mogashoa et al. 2021). Thus, the duration of this study may have not been sufficient to cause substantial changes in grass species richness. However, the results from our study are consistent with the results obtained in Burkina Faso, West Africa by Savadogo et al. (2008) who reported negligible effects of tree thinning on grass

species-richness in a mesic savanna. Our study findings suggest that grass species richness in these savannas is resistant to thinning imposed changes and/or the duration of the study was insufficient to cause significant changes.

3.4.2. The impact of tree thinning on the abundance of grass species

It is established that substantial effects of tree thinning on the herbaceous recovery are observed after 2 years (Lett and Knapp 2005; Archer and Predick 2014). This may explain an increase in abundance of different grass species in this study post thinning. In both study sites, the thinning treatments were associated with an increase in abundance of different grass species, while no thinning (control) had limited impact. In site 1, clear effects of tree thinning were observed on the abundance of two dominant grasses, *Digitaria eriantha* and *Sporobolus africanus* after the two growing seasons. The abundance of *D. eriantha* was not affected in other treatments (0%, 10%, 20%, 50%, and 75%) but significantly increased in cleared plots (i.e. 100% removal treatment). On the other hand, *S. africanus* substantially declined in abundance in all treatments but increased in the 50% thinning treatment. An increase in abundance of *D. eriantha* in cleared plots may be attributed to the substantial reduction of tree competition following clearing, particularly for soil moisture. Although tree thinning showed a substantial effect on the abundance of *S. africanus* in site 1, the causes of these effects were not clear. *S. africanus* has been identified as an indicator species of rangeland degradation (Mansour et al. 2012). We expected *S. africanus* to remain high in abundance in the control and low thinning (i.e. 10%) plots only. This is because encroached rangelands are a sign of degradation (Ward 2005; Okin et al., 2006), and tree thinning is expected to restore the rangeland (Smit 2005; Ding and Eldridge 2019). Thus, the increased abundance of *S. africanus* in 50% thinning only suggest possible influences by undetermined factors.

In site 2, moderate (50%) and high intensities of tree thinning (75% and 100%) positively affected the abundance of *Panicum maximum*. These results contradicted the expectation that grasses such as *P. maximum* that normally prefer to grow under tree canopies will reduce in abundance, particularly in 75% and 100% thinning treatments. Additionally, there was a substantial increase in abundance of *D. eriantha* in the 50% thinning treatment. The abundance of *Heteropogon contortus*, the most dominant grass species prior to tree thinning in site 2 substantially reduced in all treatments with the lowest reductions observed in 75% and 100% thinning compared to other treatments. An increase in abundance of *P. maximum* in 50% thinning treatment may be attributed to the ability of this species to colonize fertile islands

created by N-fixing tree species (Smit 2005). The results from site 2 are consistent with Smit (2005) who reported an increase in abundance of *P. maximum* under trees and between canopies after tree thinning. Moreover, an increase in abundance of *D. eriantha* suggests that 50% thinning in site 2 may have created an opportunity for different palatable grass species to increase in abundance, which may be important for ecosystem services such as forage production that may support livestock and wild herbivores in savannas (van Oudtshoorn (2006).

The majority of the dominant woody plants in site 2, such as *D. cinerea*, *S. caffra* and *Vachellia* spp. are nitrogen-fixing legumes (Schulze et al. 1991). Consequently, 75% thinning and complete removal of the total tree biomass (100%) may have created favourable conditions for *P. maximum* to increase in abundance because of the significant reduction of competition from trees. Also, *P. maximum* tends to be highly competitive (Smith et al. 2013), and therefore, the decline in abundance of other grass species observed in 75% and 100% thinning treatments may be due to increased competition among the grasses. However, because *P. maximum* performs better in nitrogen-rich soils, it will likely decline in abundance with time in 75% and 100% thinning treatments. This is because post-clearing effects on soil fertility and its effects on the herbaceous layer have been reported to be transient as they are a legacy of ecological processes that are no longer existent (Kaur et al. 2007; Ndhlovu et al. 2016a, b).

The results from both study sites demonstrated that tree thinning has both positive and negative effects on the abundance of different grass species. Our results are consistent with Ndhlovu et al. (2016b) who showed that clearing *Prosopis* trees that are invasive species in South Africa (Bromilow 1995), positively and negatively influenced the abundance of different grass species. Additionally, our results agree with Smit and Rethman (1999) who demonstrated that tree thinning increases the abundance of different grass species, particularly pioneer grasses in a *Colophospermum mopane* savanna in South Africa. The results from both of our study sites demonstrated that changes in the composition of the grass species may have been stimulated by a reduction in competition from woody plants or through recruitment of new species from the seedbank (Mndela et al. 2019; Bassett et al. 2020). Many studies have indicated that woody plants suffer from competition from grasses (e.g. Kraaij and Ward 2006; Riginos et al. 2009; Tjelele et al. 2015; Grellier et al. 2012; Vadigi and Ward 2013); here we showed that the reverse was also possible.

3.4.3. The effect of tree thinning on plant cover and soil fertility

Woody plant encroachment has been reported to results in the desertification of rangelands by increasing bare soil areas (Eldridge et al. 2011). As a result, we expected moderate (50%) and high intensities (75 and 100%) of thinning of the woody vegetation to reduce percentage bare soil area because tree thinning is expected to increase grass biomass production and cover (Smit and Rethman 1999; Smit 2005; Ndhlovu et al. 2016a). In both study sites, we did not find any significant differences in percentage bare soil area among the thinning treatments. However, see the results from site 1. Our results are consistent with the results of Ding and Eldridge's (2019) meta-analysis where they found no evidence that tree thinning changes bare soil cover. The results from both study sites demonstrated that tree thinning did not have any effect on soil cover. In addition, tree thinning may in turn reduce soil erosion because an increase in abundance of different grass species is expected to protect the soil layer from erosion (Berendse et al. 2015).

Research has demonstrated that tree clearing (complete removal of trees) may negatively affect soil properties related to fertility (Sangha et al. 2005; Abbasi et al. 2010). We expected changes in soil organic carbon, pH and fertility in cleared plots compared to other treatments in the present study. Our results were not consistent with this expectation. We related this to the short study period (two growing seasons). Studies on tree clearing have shown that soil properties relating to soil fertility may take longer (between five and seven years) to change (Sangha et al. 2005; Kaur et al. 2007). Although high intensities of tree thinning did not have any negative effects on soil fertility in either study site, this may change over time (Kaur et al. 2007). The lack of a significant reduction in soil fertility in high-thinning treatments (particularly complete removal of trees) in this study may be due to the temporary legacy of nitrogen fixation and nutrient accumulation by woody plants (Ward et al. 1998; Ward and Ngairorue 2000; Sangha et al. 2005). Nonetheless, our results are consistent with Kaur et al. (2007) and Ndhlovu et al. (2016a, b) who demonstrated that soil fertility remains adequate for herbaceous production after clearing woody plants. These findings suggest that properties related to soil fertility in either site are resistant to tree thinning-induced changes.

3.5. Conclusions

We showed that thinning of encroaching trees may change grass species composition but not species richness, although this may be site-specific. Most importantly, tree thinning was not associated with negative effects on the abundance of palatable grass species in either study site.

For instance, *D. eriantha* and *P. maximum*, which are highly palatable grasses, were positively associated with the thinning treatments in the two sites. However, we found no evidence that tree thinning reduces the amount of bare soil through increased herbaceous cover in either site. In addition, different levels of tree thinning did not have a significant impact on soil fertility. This study provides insight into effects of tree thinning on grass vegetation and soil functions. Long-term studies should test the effects of different levels of tree thinning on palatable grass production and soil fertility, which is relevant for informing land managers regarding effective bush control methods that would result in increased economic viability of savanna rangelands.

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 1929 *African Journal of Range and Forage Science* 22: 101-105.
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1931 Table 3.1 Grass species richness and evenness in study sites 1 and 2 during the study period.

1932 Values inside brackets represent grass species evenness.

Site and period	Treatments					
	0%	10%	20%	50%	75%	100%
Site 1						
Before tree removal	13 ± 2 (0.8)	11 ± 3.2 (0.7)	12 ± 1.9 (0.8)	12 ± 1.8 (0.8)	13 ± 1.1 (0.9)	11 ± 2.2 (0.8)
First season	12 ± 2.1 (0.8)	9 ± 3.6 (0.8)	11 ± 1.2 (0.9)	10 ± 1.6 (0.9)	12 ± 2.1 (0.8)	10 ± 1.6 (0.9)
Second season	10 ± 2.5 (0.9)	10 ± 2.4 (0.9)	12 ± 1.8 (0.8)	14 ± 2.4 (0.8)	11 ± 2.1 (0.8)	9 ± 4.7 (0.6)
Site 2						
Before tree removal	13 ± 1.9 (0.9)	12 ± 3.6 (0.7)	12 ± 2.2 (0.8)	11 ± 2.6 (0.8)	12 ± 1.9 (0.9)	13 ± 2.5 (0.8)
First season	14 ± 2.1 (0.8)	17 ± 1.4 (0.8)	17 ± 1.5 (0.8)	15 ± 1.2 (0.9)	13 ± 2.1 (0.8)	17 ± 1.8 (0.8)
Second season	9 ± 2.6 (0.9)	13 ± 3.1 (0.7)	13 ± 2.1 (0.8)	11 ± 2.8 (0.8)	13 ± 2.0 (0.9)	14 ± 2.9 (0.8)
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1952 Table 3.2. Percentage bare area in study sites 1 and 2 at Roodeplaat during the study period.

Site and period	Treatments					
	0%	10%	20%	50%	75%	100%
Site 1						
Before tree removal	20	25	32	34	39	39
First season	0	22	25	35	23	37
Second season	8	10	11	22	18	27
Site 2						
Before tree removal	6	8	12	18	3	3
First season	3	6	4	9	6	3
Second season	6	5	1	5	3	1

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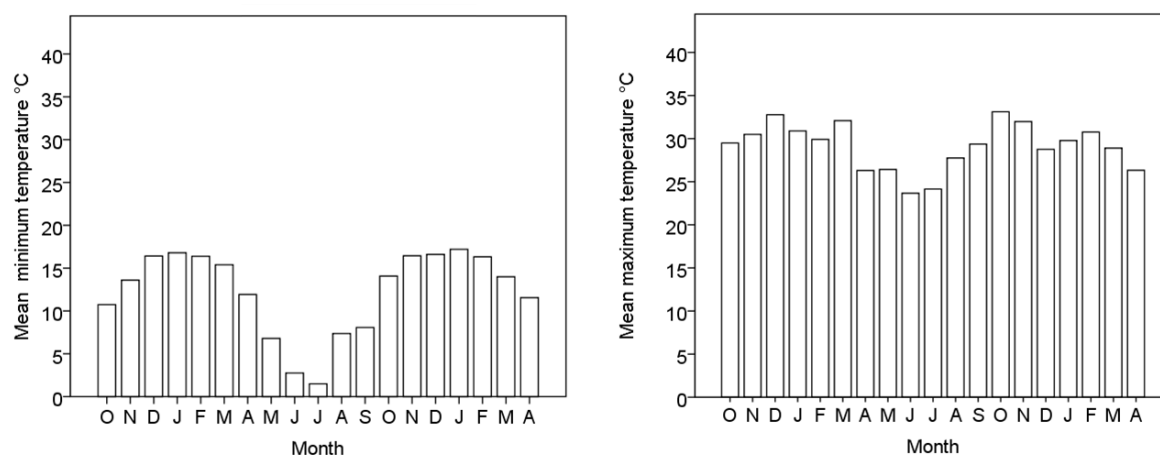
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1974 Table 3.3 Mean (± 1 S.E.) soil parameters measured for study sites 1 and 2.

Soil parameters	Treatments					
	0%	10%	20%	50%	75%	100%
Site 1						
Soil pH (H ₂ O)	7.2 \pm 0.36	7.1 \pm 0.19	7.0 \pm 0.27	6.6 \pm 0.45	7.2 \pm 0.24	6.8 \pm 0.19
Soil organic carbon (%)	1.5 \pm 0.20	1.6 \pm 0.07	1.5 \pm 0.11	2.0 \pm 0.20	1.6 \pm 0.14	1.6 \pm 0.07
Bioassay biomass (g)	0.53 \pm 0.05	0.59 \pm 0.03	0.60 \pm 0.04	0.64.1 \pm 0.03	0.60 \pm 0.02	0.60 \pm 0.04
Site 2						
Soil pH (H ₂ O)	6.5 \pm 0.09	6.2 \pm 0.09	6.4 \pm 0.15	6.5 \pm 0.17	6.3 \pm 0.10	6.5 \pm 0.14
Soil organic carbon (%)	3.0 \pm 0.34	2.6 \pm 0.27	2.6 \pm 0.27	3.4 \pm 0.46	2.5 \pm 0.44	3.0 \pm 0.44
Bioassay biomass (g)	0.26 \pm 0.21	0.23 \pm 0.03	0.30 \pm 0.3	0.28 \pm 0.03	0.26 \pm 0.04	0.32 \pm 0.04
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1993 Fig. 3.1. Mean monthly temperatures (°C) recorded at the Roodeplaat farm during the
 1994 experimental period (2018/2019, 2019/2020).

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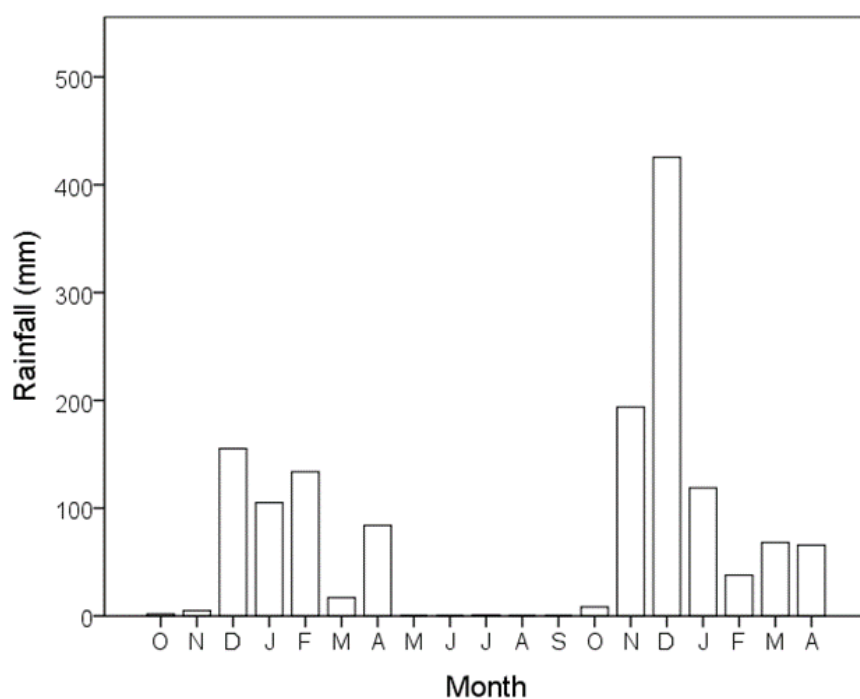


Fig. 3.2. Monthly total-rainfall recorded at Roodeplaat experimental farm during the two growing seasons (October-April) of the experimental period (2018/2019, 2019/2020).

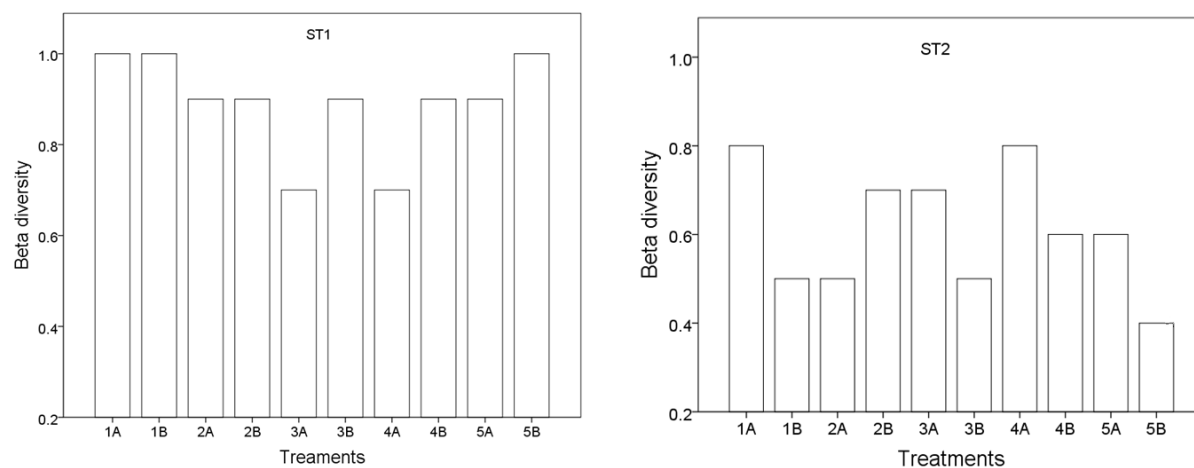


Fig. 3.3. Values of β diversity (based on Sørensen's index) between thinning treatments and the control over the study period (A = first growing season; B = second growing season) in site 1 (ST1) and site 2 (ST2). Key to treatments: 1, 10%; 2, 20%; 3, 50%; 4, 75%; 5, 100%.

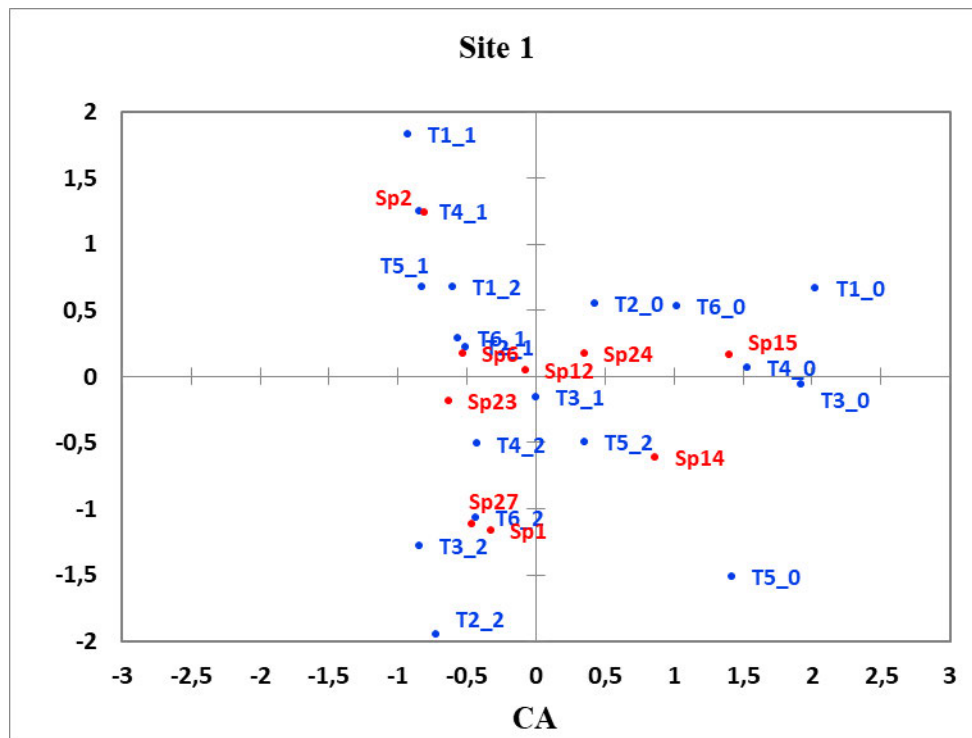


Fig. 3.4. Correspondence analysis (CA) scatterplot showing grass species assemblages in different thinning treatments during the study period in study site 1. Key to treatments: T1, 0%; T2, 10%; T3, 20%; T4, 50%; T5, 75%; T6, 100%. The numbers 0, 1 and 2 on the treatments represents grass species assemblages before treatment application and, after the first and second growing seasons post tree thinning. Key to species: SP1, *Aristida adscensionis*; SP 2, *Aristida bipartita*; SP6, *Bothriochloa insculpta*; SP12, *Digitaria eriantha*; SP13, *Eragrostis curvula*; SP14, *Eragrostis chloromelas*; SP23, *Setaria sphacelata* var. *torta*; SP24; *Sporobolus africanus* SP27, *Urochloa mossambicensis*.

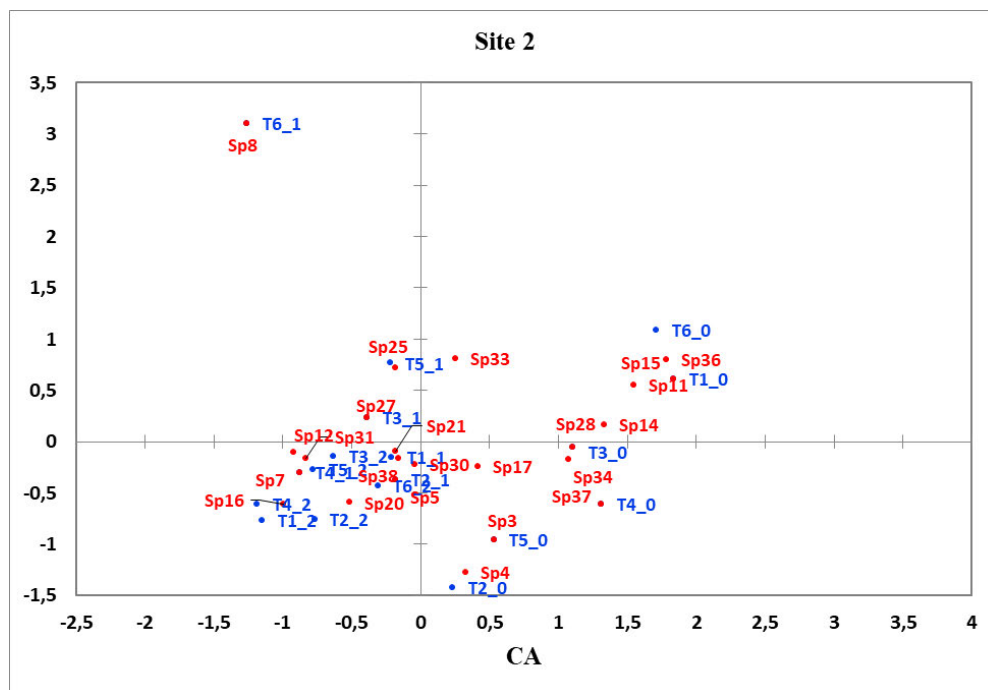


Fig. 3.5. Correspondence analysis (CA) scatterplot showing grass species assemblages in the tree thinning treatments during the study period in study site 2. The numbers 0, 1 and 2 on the treatments represents grass species assemblages before treatment application and, after the first and second growing seasons post tree thinning. Key to treatments: T1, 0%; T2, 10%, T3, 20%; T4, 50%; T5, 75%; T6, 100%. The numbers 0, 1 and 2 on the treatments represent grass species assemblages before treatment application, first and second growing seasons after tree thinning, respectively. Key to species: SP3, *Aristida congesta* subsp. *Barbicollis*; SP4, *Aristida congesta* subsp. *congesta*; SP5, *Aristida junciformis*; SP7, *Brachiaria serrata*; SP8, *Cenchrus ciliaris*; SP11, *Cenchrus ciliaris*; SP12, *Digitaria eriantha*; SP, *Eragrostis chloromelas*; SP15, *Eragrostis curvula*; SP16, *Eragrostis racemosa*; SP17, *Heteropogon contortus*; SP20, *Melinis repens*; SP21, *Panicum maximum*; SP25, *Themeda triandra*, SP27, *Urochloa mossambicensis*; SP28, *Andropogon chinensis*; SP30, *Cymbopogon pospischilii*; SP31, *Enneapogon cenchroides*; SP33, *Eragrostis gummiflua*; SP34, *Eragrostis rigidior*; SP36, *Schmidtia kalihariensis*; SP37, *Schmidtia pappophoroides*; SP39, *Setaria sphacelata* var. *sericea*.

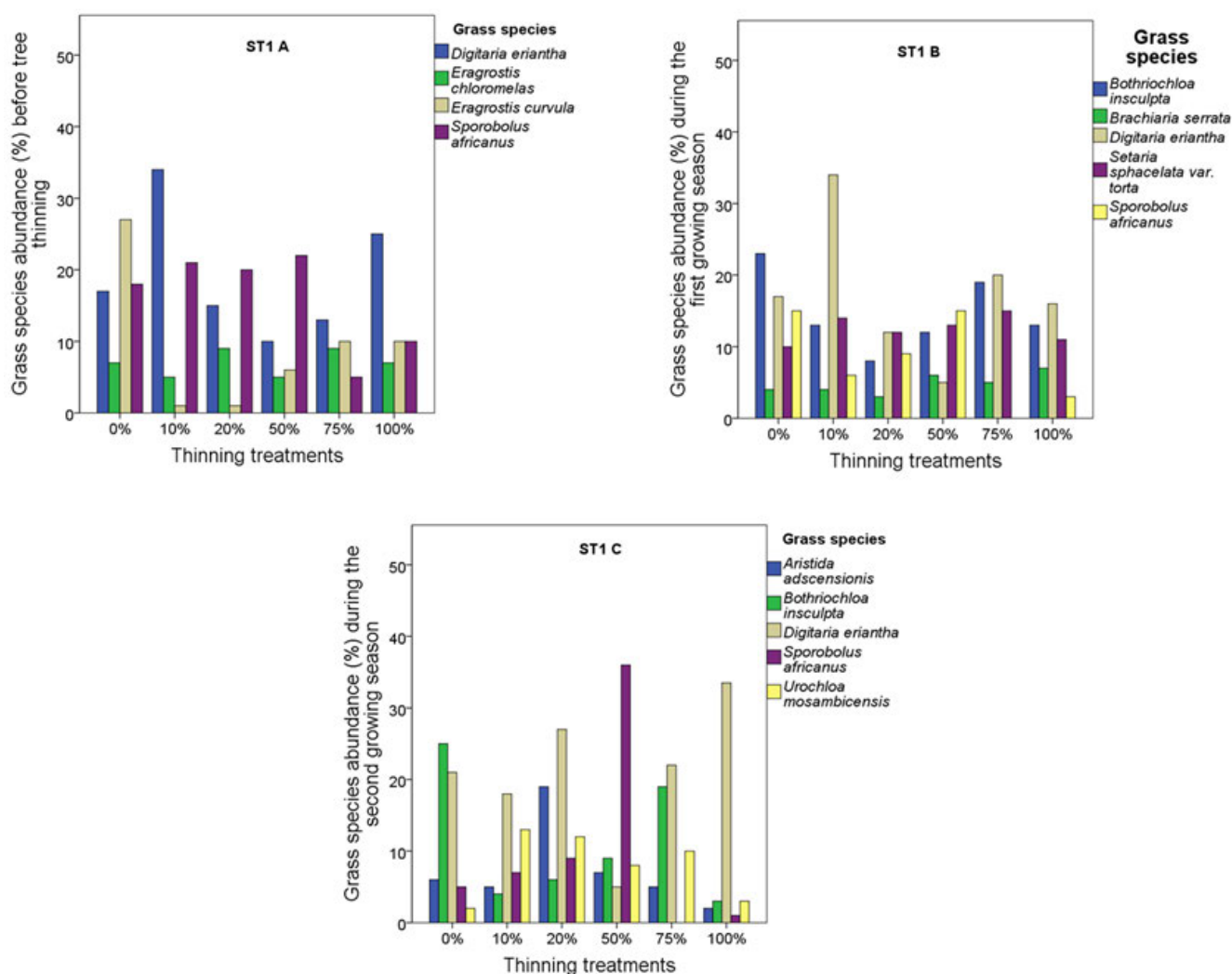


Fig. 3.6. Grass species abundance (%) from study site 1 before and after tree thinning. The letters embedded in the figures represent collection period (A = before tree thinning (September 2018); B = during first growing season (March 2019); C = during the second growing season (March 2020)).

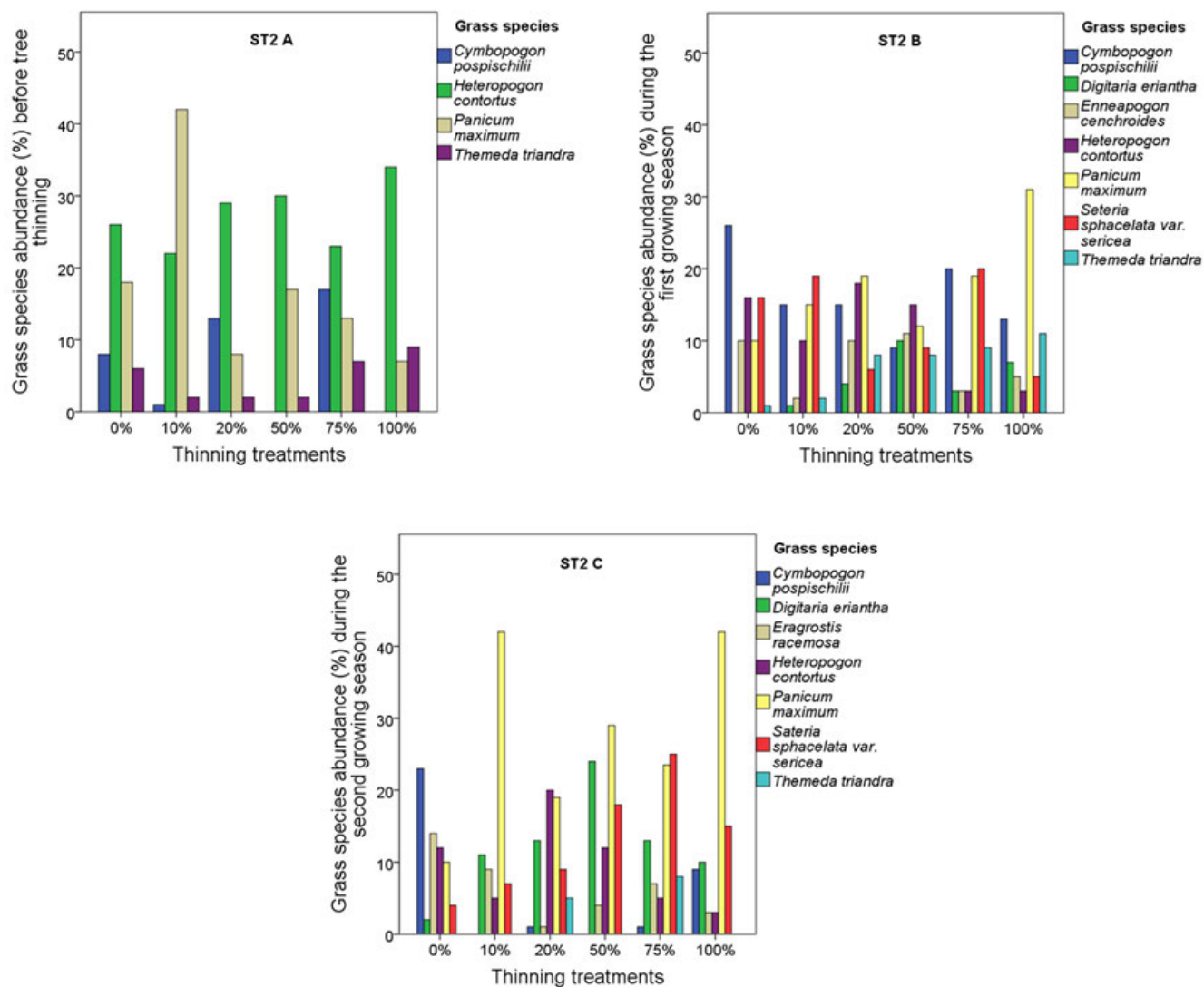


Fig. 3.7. Grass species abundance (%) from study site 2 before and after tree thinning. The letters embedded in the figures represent collection period (A = before tree thinning (September 2018); B = during first growing season (March 2019); C = during the second growing season (March 2020).

**Chapter 4: The impact of tree removal on grass biomass production, tree seedling
recruitment and growth of woody species**

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Submitted to the *Rangeland Journal* and formatted accordingly

Abstract

The removal of trees in rangelands can create gaps and lead to increased grass production that could suppress tree seedling recruitment and growth. However, gaps can also enhance the growth of remaining trees. We conducted a field experiment at two savanna sites with different soil texture and woody species. We used 24 plots (30 m × 30 m) at each site to determine the effect of tree removal-intensities (0%, 10%, 20%, 50%, 75% and 100%) on grass production, tree-seedling establishment and growth, and growth of the remaining large trees. Site 1 was on previously cultivated severely-eroded clay-dominated soils, encroached by a monospecific stand of *Vachellia tortilis*. Site 2 had never been cultivated, and was on sandy soils with several woody species. At site 1, 75 and 100% tree removal significantly reduced standing grass biomass towards the end of the first growing season, with no differences towards the end of the second season. At site 2, tree removal significantly increased grass biomass. There was no significant effect of tree removal on tree seedling establishment at site 1. At site 2, tree removal had a significantly negative effect on overall tree seedling establishment. At both sites, there were no significant differences in tree seedling growth. Moderate (50%) to high (75%) removal of trees had a positive effect on the growth of remaining large trees at both study sites. We found that increased and/or diminished grass biomass plays a vital role in tree seedling recruitment. Reduced tree competition facilitates growth of remaining large trees. An implication of these findings is that, regardless of the substantial costs of woody plant control, the recovery of key ecosystem services such as an increased forage production may not be realised. However, we recognize that this may be system-specific. In other systems, the absence of management interventions such as tree removal may compromise provision of ecosystem services and ecosystem functioning.

Keywords: Grass competition; Restoration; Soil erosion; Tree competition; Woody plant encroachment

4.1. Introduction

Interactions among mature trees play a significant role in structuring savannas (Meyer *et al.* 2007; Sea and Hanan 2012; Schleicher *et al.* 2011a, b). While these interactions can either reduce or facilitate woody plant encroachment (Meyer *et al.* 2008; Pillay and Ward 2012), in savanna rangelands (Jeltsch *et al.* 2000) such interactions may lead to woody plant encroachment. Given the negative effects of woody plant encroachment on pastoral productivity, ecologists and land users have often considered tree removal (also termed *tree thinning*) as a management option (Smit 2005; Brudvig *et al.* 2011; Ndhlovu *et al.* 2016). High tree densities in savannas may negatively affect tree growth due to competition among woody species (Kambatuku *et al.* 2011a; Pillay and Ward 2012, 2014) and is associated with a reduction in the size of one or more neighbours (Meyer *et al.* 2007). However, the removal of some trees may result in substantial increase in size of remaining individuals (Smit 2001; Shackleton 2002; Back *et al.* 2009; Brudvig *et al.* 2011; Schleicher *et al.* 2011a, b). Moreover, increased woody plant size can also benefit rangelands by increasing understory grass and forb biomass because of increased water availability and/or nutrient contents below the tree canopy area (Treydte *et al.* 2008; Schleicher *et al.* 2011b).

In savannas, large trees have been reported to limit tree seedling establishment by outcompeting seedlings for resources (Loth *et al.* 2005; Brudvig and Asbjornsen 2009), so tree removal can promote tree seedling establishment and growth (Kambatuku *et al.* 2011a; Smit 2014). Tree removal in rangelands can open the canopy while maintaining a pool of recruits to replace large, older trees when they die (Schnitzer *et al.* 2001; Sapkota and Odén 2009; Smit 2014). However, gaps created by tree removal can increase grass production (Smit 2005; Sagar *et al.* 2012), which negatively affects tree seedling germination, survival and growth (Kambatuku *et al.* 2011b, Ward and Esler 2011; Grellier *et al.* 2012; Vadigi and Ward 2013; Wakeling *et al.* 2015; Bhadouria *et al.* 2016; Morrison *et al.* 2018). Increased grass biomass is expected to reduce tree seedling establishment similarly to tree establishment. Evidence suggests *Vachellia* seeds do not germinate under *Vachellia* trees (Loth *et al.* 2005). The suppressive effect of grass competition has also been reported to affect larger trees (Riginos 2009). Regardless, there is considerable variance in this relationship; some studies have found that grasses facilitate tree seedling survival and growth (Duncan and Chapman 2003; Anthelme and Michalet 2009; Tomlinson *et al.* 2019), whereas others have found non-significant effects of grasses on tree seedling performance (Scariot *et al.* 2008).

The effects of tree removal can differ within similar environments (Archer and Predick 2014), with site-specific drivers such as plant species and soils perhaps responsible for these variations (Ding and Eldridge 2019). Few studies have compared the response of rangelands to removal of different tree species, which leaves open whether differences in species traits influence the ecological or management outcomes of removal (Ding and Eldridge 2019). For example, multi-specific stands usually have a higher total ecosystem productivity and tree density compared with monospecific stands (Pretzsch 2014) because monospecific stands are often associated with more intense self-thinning, resulting in lower tree density (Pretzsch 2014). Mixed tree species may also improve resource use compared with monospecific stands by improving resource supply and capture (Forrester 2015). In addition, plant traits may be an important determinant of the outcome of tree removal (Ding and Eldridge 2019). For example, woody species such as *Vachellia tortilis* enhance water infiltration and soil nutrients inside their canopies rather than outside the canopies (Ludwig *et al.* 2003; Abdallah *et al.* 2008). This suggest that canopy gaps created through tree removal may not be beneficial in increasing overall herbaceous biomass production in a *V. tortilis* monospecific stand.

Soil texture may also affect plant growth. Soil texture alters water intake rate, storage and aeration (Rodriguez-Iturbe and Porporato 2004). Studies have shown that sand-dominated soils allow for rapid infiltration and permeability of soil water (Laio *et al.* 2006). In clay-dominated soils, infiltration which increase run-off or waterlogging (Knapp *et al.* 2008). Since water extraction is more difficult from clayey than sandy soils, particularly when soil moisture content is low (Fensham *et al.* 2015), soil texture could alter tree and grass physiological responses to soil moisture variability, aggravating water stress. Thus, differences in plant species and soil texture could be important determinants of ecological services after tree removal.

In this study, we evaluated the effects of different intensities of tree-removal on grass biomass, tree seedling establishment and growth, and the growth of the remaining large trees at Roodeplaat farm, Gauteng Province, South Africa. We tested the following predictions:

- (1) Grass biomass will increase with increasing tree removal because of reduced competition from woody plants; and
- (2) Increased grass biomass after tree removal will reduce tree seedling establishment;
- (3) Reduced tree competition through moderate (50%) and high (75%, 100%) tree removal will significantly increase the growth (stem diameter, height and canopy size) of tree seedlings and growth of the remaining trees.

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2210 **4.2. Materials and methods**2211 4.2.1. *Study area*

2212 The study was conducted at Roodeplaat Experimental Farm (25°36'29"S, 28°2'08"E) which is
 2213 situated in the north of Gauteng Province, South Africa. Roodeplaat farm is a 2100 ha farm of
 2214 the Agricultural Research Council (ARC), and it is used for livestock production and wildlife.
 2215 The vegetation of this area is described as the Marikana Thornveld (Mucina and Rutherford
 2216 2006) and dominated by woody plants, which include *Vachellia* (previously *Acacia*) *karroo*,
 2217 *Senegalia* (formerly *Acacia*) *caffra*, *Vachellia tortilis* (Kyalangalilwa *et al.* 2013), *Ziziphus*
 2218 *mucronata*, and some *Euclea* tree species. We used Coates-Palgrave (2002)'s nomenclature for
 2219 tree species. The grass layer consists of *Digitaria eriantha*, *Melinis repens*, *Panicum maximum*,
 2220 *Setaria sphacelata*, and *Sporobolus africanus*. *Eragrostis curvula*, *Themeda triandra* and
 2221 *Heteropogon contortus* are some of the important grasses found on the ranch (Van Rooyen
 2222 1983). van Oudtshoorn (2006)'s nomenclature is used for grass species. The area receives
 2223 annual precipitation of 687 mm with most of it falling during summer (November to March).
 2224 The maximum daily temperature of the area in summer ranges between 20-29 °C, while the
 2225 minimum winter temperature can decrease to 2-16 °C. The most common soil types of the study
 2226 area are Ferralsols, Luvisols, and Vertisols. The study area is situated on the Roodeplaat
 2227 Igneous Complex, which belongs to the Post-Waterberg Formation (Panagos *et al.* 1998).

2228 The study was conducted in two sites within the same farm. The first study site
 2229 (hereafter site 1) was on clay-dominated soils (38% sand; 17% silt; 45% clay) characterized by
 2230 severe soil degradation in the form of surface erosion and crust formations. Site 1 was under
 2231 crop cultivation more than 20 years ago and is now encroached by a monospecific stand of *V.*
 2232 *tortilis*. Site 1 was encroached at a mean density of 2 961 plants ha⁻¹. The second study site
 2233 (hereafter site 2) was on sandy soils (67% sand; 16% silt; 17% clay) with several woody species
 2234 (*Dichrostachys cinerea* (L.) Wight & Arn, *S. caffra* (Thunb.) P.J.H. Hurter & Mabb, *V. karroo*
 2235 (Hayne) Banfi & Galasso, *V. nilotica* (L.) P.J.H. Hurter & Mabb, *V. robusta* (Burch.)
 2236 Kyalangalilwa & Boatwright, *V. tortilis* (Forssk.) Galasso & Banfi and *Ziziphus mucronata*
 2237 (Willd.). Site 2 has never been cultivated and was encroached at a mean density of 4 065 plants
 2238 ha⁻¹. Site 2 was characterised by a virtually low grass cover and, was grazed and browsed by
 2239 an unknown number of game species. The experimental sites were fenced to exclude herbivores
 2240 from the area during the study duration. Rainfall and temperature data for the study area was

received from an accredited Agricultural Research Council's Institute for Soil, Climate and Water (Figs. 4.1 and 4.2). The present study lasted for 18 months (October 2018 to April 2020).

4.2.2. Study design

At each site, 24 plots of 30 m × 30 m were established and subjected to different intensities of tree removal. Tree removal treatments were replicated four times and allocated randomly to the plots. Trees were cut with a chainsaw to the approximate equivalents of 0% (control-no removal), 10%, 20%, 50%, 75% and 100% (complete removal of trees, Smit (2005)) in October 2018 at the beginning of the wet season. Grass biomass was assessed using five randomly-placed 50 cm × 50 cm quadrats in each plot, with all of the grass samples within the quadrats harvested regardless of species. Grass samples were collected towards the end of the wet season of each year (in March). Harvested grass material was oven dried at 70°C for 72 h and dry-matter yield calculated.

The effects of tree removal on seedling establishment were determined through a direct count of all tree seedlings in each plot before treatments were applied and at the end of the study period in April 2020. To investigate the effects of tree removal on the growth of tree seedlings and large trees at site 1, five seedlings and five large trees of *V. tortilis* from each plot were randomly marked and monitored for growth over two growing seasons. At site 2, seven tree species (*D. cinerea*, *S. caffra*, *V. karroo*, *V. nilotica*, *V. robusta*, *V. tortilis* and *Z. mucronata*) were randomly marked (i.e. two seedlings and two large trees per species per plot) and monitored for growth. At site 2, four plants (i.e. two seedlings and two large trees) per species per plot were used. Tree seedlings were defined as pre-reproductive trees < 1 m in height.

Tree and seedling growth were measured by recording height, canopy area (maximum and perpendicular lengths) and stem diameter. Seedling stem diameter was measured at the base of the stem; tree diameter was re-measured at a permanently marked point to minimize error. Four healthy shoots were randomly selected on each tree, permanently marked, and monitored for growth (length). The shoots included shoots from both the upper and lower canopy (Smit 2001). Only live trees were measured. Tree measurements were made on trees >2 m in height. Measurements were recorded at the beginning and end of the study. Tree and seedling canopy sizes were calculated using an ellipse function ($C = ab\pi / 4.0$), where "a" = long axis and "b" = perpendicular short axis of the canopy (Smith and Grant 1986). Plant growth rate was calculated

using: Relative growth rate (RGR) = $(\ln W_2 - \ln W_1) / (t_2 - t_1)$, where W_1 and W_2 refer to log-transformed plant measurements at times t_1 and t_2 (Hoffmann and Poorter 2002).

4.2.3. Data analysis

Prior to analysis, data were \log_{10} transformed to conform to ANOVA test assumptions. We used multivariate analysis of covariance (MANCOVA) to test the effects of tree removal on grass biomass production, where grass biomass recorded after the first and the second growing seasons were considered the dependent variables. Grass biomass and tree density recorded before tree removal were used as covariates. We used MANCOVA to reduce Type 1 error caused by testing multiple dependent variables. Wilks' Lambda test statistic was used to investigate the effect of the removal treatments on the measured parameters. For significant MANCOVA results, we used univariate ANOVA to test which tree-removal levels differed significantly from the others. ANCOVA was used to test the effects of tree removal on seedling establishment, where the number of seedlings after tree removal was considered the dependent variable. The number of seedlings recorded before tree removal was used as a covariate. Tree and seedling stem-diameter, height and canopy area (growth rates) were analysed using MANOVA. To determine the effects of the tree removal on tree canopy shoot-growth, we used one-way ANOVA. A Bonferroni *post hoc* test was applied for pairwise comparisons among the removal treatments. Data from the two sites were analysed separately. IBM SPSS for Windows v. 26 (IBM SPSS 2019) was used for data analysis.

4.3. Results

There were significant differences in grass biomass among tree-removal treatments at study site 1 (Wilks' $\lambda = 0.330$; $F = 2.223$; $p < 0.044$) (Fig. 4.3). ANOVA results showed that grass biomass was significantly different among treatments during the first growing season only at site 1 ($F = 5.357$; $p = 0.004$). A Bonferroni *post hoc* test revealed that the control plots had a higher recorded grass biomass than at 75% and 100% (complete removal) removal treatments. In addition, the grasses *Digitaria eriantha* (Steud.) and *Sporobolus africanus* (Poir.) Robyns & Tournay dominated site 1. At site 2, tree removal significantly increased grass-biomass at the end of the first and second growing seasons (Wilks' $\lambda = 0.067$; $F = 8.624$; $p < 0.001$). Grass biomass increased in the plots totally cleared of trees in the first growing season at site 2 ($F = 14.280$; $p = 0.001$). Towards the end of the second growing-season, grass biomass was greater than the previous season across all treatments, with substantial increases at 50%, 75% and 100%

removal ($F = 7.713$; $p = 0.001$). Grass biomass largely consisted of *Panicum maximum* and *Setaria sphacelata* var. *sericea* (Stapf) Clayton in the cleared plots at site 2. No significant differences in tree seedling establishment were recorded among treatment levels at sites 1 ($p > 0.05$) and 2 ($p > 0.05$) before tree removal. Tree removal level did not affect tree seedling establishment at site 1 ($p > 0.05$). At site 2, tree removal level significantly reduced mean tree seedling establishment ($p < 0.05$), with greatest reductions at 50%, 75% and 100% removal (Fig. 4.4). Mean seedling recruitment (i.e. number of trees) after tree removal was significantly different between the 50-100% removed and the 0-20% removed at site 2. However, at both sites, there were no significant differences in seedling growth among treatment levels (Wilks' $\lambda = 0.809$; $F = 1.406$; $p = 0.410$ and Wilks' $\lambda = 0.878$; $F = 1.374$; $p = 0.156$ for sites 1 and 2, respectively). Significant differences were recorded in mean large tree growth among treatments at site 1 (Wilks' $\lambda = 0.377$; $F = 8.956$; $p < 0.001$) (Fig. 4.5). A Bonferroni *post hoc* test indicated that only trees in the 75% removal treatment significantly increased in stem diameter, height and canopy area compared with other treatments. Large tree canopy-area results were supported by results for shoot growth which showed that size (i.e. length) of canopy shoots in the 75% removal treatment increased significantly more following tree removal than trees in other treatment levels ($p = 0.001$). Large trees in the 50% removal treatment showed a greater increase in canopy area and height than the control (no removal). We also recorded a significant increase in large tree height at site 2 in the 50% and 75% removal treatments (Wilks' $\lambda = 0.410$; $F = 14.594$; $p < 0.001$), but no treatments differences for canopy area ($p = 0.639$). A significant difference was only recorded in large tree height only. At site 2, growth in stem diameter was not significantly affected by tree-removal level ($p = 0.147$ and $p = 0.639$, respectively). The canopy-area results were supported by the canopy shoot-growth results that showed no significant differences among removal treatments ($p = 0.856$).

4.4. Discussion

4.4.1. The impact of tree removal on grass production

Diminished grass biomass production during the first growing season in the 75% and 100% removal treatments in site 1 can be attributed to the ability of *Vachellia tortilis* to facilitate herbaceous biomass under their canopies (Yadeta *et al.* 2018; Abdallah *et al.* 2008). For example, Yadeta *et al.* (2018) demonstrated that herbaceous biomass increases under *V. tortilis* canopies rather than in open spaces. Other studies have demonstrated that tree removal may have contrasting effects on herbaceous production (Archer and Predick 2014; Ding and

Eldridge 2019). Literature syntheses by Archer and Predick (2014) based on North American studies indicated that only 64% of the papers emerging from their work reported an increase in herbaceous biomass following tree removal. The results from site 1 were consistent with Beale (1973) who recorded substantial declines in grass yield with low tree densities. In addition, the results from site 1 were consistent with Alleghetti *et al.* (1997) who reported negligible effects of tree removal on herbaceous cover. The results from site 1 after the first growing season suggest that high intensities of tree removal may further diminish the grass layer, particularly during low rainfall seasons. Additionally, the results from site 1 suggest that success of bush encroachment control through tree removal may also depend on soil texture. For instance, Smit (2005) reported a recovery of the herbaceous layer after tree removal in eroded sand-dominated soils, a result consistent with findings from site 2 (sand-dominated soils).

The results from site 2 were consistent with results from similar studies showing that grass biomass increases as a result of tree removal (Brockway *et al.* 2002; Smit 2005, 2014; Lett and Knapp 2005; Angassa *et al.* 2012; Ndhlovu *et al.* 2016). It is established that substantial effects of tree removal on the herbaceous production are observed after 2 years (Lett and Knapp 2005; Archer and Predick 2014). This may explain the significant increase of grass biomass production in cleared plots only in site 2 in the second growing season. Increases in grass biomass depend on annual rainfall (Archer and Predick 2014). In the study area, rainfall was higher during the second growing season than during the first growing season. Thus, the results from site 2 may have been driven by increased rainfall availability. Importantly, the results from site 2 were supported by Ludwig and Tongway (2002) who reported that tree removal in a *Eucalyptus* savanna in Queensland (Australia) increased grass production. Also, Smit (2005, 2014) showed that the removal of some trees positively affected the herbaceous layer in a *Colophospermum mopane* savanna in South Africa, a result consistent with those of Angassa *et al.* (2012). The results from study site 2 suggest that tree removal may help rehabilitate the herbaceous layer in rangelands affected by woody plant encroachment. For some sites, this may need to be accompanied by seed replenishment. However, we did not measure the size and composition of the soil seed bank in order to determine whether the lower biomass of site 1 may have been driven by a depauperate soil seed bank.

Additionally, high rainfall is known to promote grass production in savanna rangelands. In study site 2, grass biomass production was relatively low after tree removal during the first growing season (low rainfall) across all treatments except for plots that were cleared of all trees. However, during the second growing season (high rainfall) (see Fig. 4.2), grass biomass

increased in all treatments, with greater increases observed in moderate- (50%) and high- (75 and 100%) removal treatments. These results suggest that the interaction between tree removal and high rainfall availability may positively affect the herbaceous layer and improve the rangelands, although this may depend on the system. For example, Smit (2005) reported the suppression of the herbaceous layer by *C. mopane* even under high rainfall availability.

4.4.2. The effects of tree removal on tree-seedling establishment and growth

The lack of significant differences in growth response of the tree seedlings could be attributed to the negative and positive responses of the herbaceous layer after tree removal in the study sites. In site 1, diminished grass production across all treatments may have provided seedlings with an equal opportunity for growth, resulting in the lack of substantial differences in seedling growth among the treatments (Grellier *et al.* 2012; Vadigi and Ward 2014). In site 2, grass production increased across all the treatments, with higher increases observed in 50%, 75% and 100% removal treatments. Grass production in site 2 may have suppressed the growth of seedlings in all treatments. The results from site 2 are consistent with those of Morrison *et al.* (2018) who showed that, in the Serengeti ecosystem in Tanzania, increased grass production hinders the growth of *V. tortilis* and *V. robusta* seedlings. This pattern was confirmed by Pierce *et al.* (2019) who reported that in New Mexico (USA), grasses negatively affected the performance of *Prosopis glandulosa* seedlings. Vadigi and Ward (2014) also demonstrated the negative effects of grass competition on humid (> 1000 mm mean annual rainfall) and mesic (about 750 mm mean annual rainfall) tree saplings in north-eastern coastal region of KwaZulu-Natal, South Africa.

The results from site 1 could be related to undetermined factors such as the predation of *V. tortilis* seeds by insects and a possible reduction in the soil seed bank (possibly caused by rainfall-induced soil erosion) in the study site (Jiao *et al.* 2009; Ward *et al.* 2010). Nonetheless, the results from study site 1 were consistent with the results of Brudvig and Asbjornsen (2008), who reported that in Iowa (USA), tree removal did not have any significant effects on the density of white oak *Quercus alba* seedlings. We attributed the results from site 2 to the higher grass biomass production after tree removal in 50%, 75%, and 100% removal treatments, which may have possibly suppressed the establishment of tree seedlings (see also Grellier *et al.* 2012). Additional research has shown that grasses suppress seedling establishment and survival (Ward and Esler 2011; Grellier *et al.* 2012; Vadigi and Ward 2013; Morrison *et al.* 2018; Pillay and Ward 2020). For instance, in the Northern Cape Province in South Africa (mean annual rainfall

= 350 mm), Ward and Esler (2011) found a significant negative effect of grass cover on *Senegalia* (formerly *Acacia*) *mellifera* seedling establishment, a finding that was consistent with Cramer *et al.* (2007) from the east coast of KwaZulu-Natal province (South Africa) with a much higher rainfall (ca. 1,000 mm per annum). These effects were also reported by Grellier *et al.* (2012), who showed that grass cover negatively affected *Vachellia* (formerly *Acacia*) *sieberiana* seedling establishment. Our results suggest that changes in grass biomass after tree removal play a vital role in tree seedling establishment, seedling survival and growth, and consequently woody plant encroachment in savannas.

4.4.3. *The impact of tree removal on large tree growth*

Our data from both study sites were consistent with the prediction that large trees from moderate (50%) to high (75%) removal-intensities will significantly increase in growth (stem diameter, height and canopy area). This is also consistent with the results from similar studies that investigated the effects of tree removal on the growth of the remaining individuals (Smit 2001; Brudvig *et al.* 2011; Kambatuku *et al.* 2011a). For example, in a *Colophospermum mopane* savanna in South Africa, Smit (2001) reported that tree removal reduced inter-tree competition, which resulted in a significant increase in the vegetative growth of the remaining trees, a finding that was consistent with Brudvig *et al.* (2011). This pattern was also confirmed by Kambatuku *et al.* (2011a), who showed that the removal of neighbouring woody plants results in greater growth of the remaining trees. Our results suggest that reduced tree competition through moderate to high intensities of tree removal may facilitate the growth of the remaining trees. However, we caution against high intensities (75 –100%) of tree removal as this may result in large gaps between the remaining trees and/or lack of woody vegetation, which may favour an increase in soil erosion, particularly when the grass biomass is compromised (Smit 2014).

4.5. Conclusion

While tree removal may increase standing grass biomass in multi-tree-species systems on healthy soils, it may not be effective in monospecific stands especially on eroded clay soils. We suggest that future research including grazing animals will be helpful in identifying long-term management options for controlling woody plant encroachment while promoting the herbaceous layer, as will studies that tests the effects of tree removal on species composition. The implications of our results for woody plant encroachment and management are that in rangelands that are severely affected by woody plant encroachment, the removal of some of the

woody material may release the remaining individuals from competition-induced size limits. A further implication of these findings is that the recovery of key ecosystem services such as an increased forage production may not be realised, regardless of investment in woody species control. However, we results may be system-specific. In other systems encroached rangelands the absence of management interventions such as tree removal may compromise grass production.

4.6. Conflicts of Interest

The authors declare no conflicts of interest.

4.7. Declaration of Funding

The current study was funded by the National Research Foundation (grant number: 99405) and the Agricultural Research Council.

4.8. Data availability statement

The data that support this study will be shared upon reasonable request to the corresponding author.

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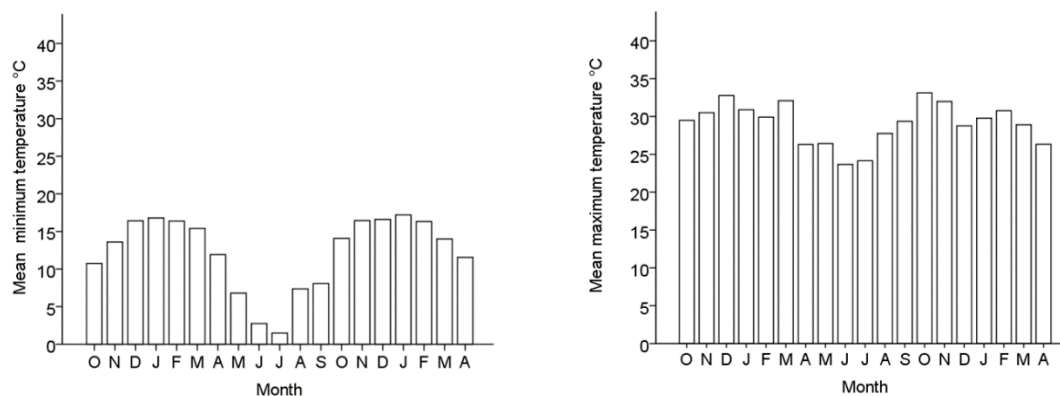
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2682 Fig. 4.1. Mean monthly temperatures (°C) recorded at the Roodeplaat farm during the
 2683 experimental period (2018/2019, 2019/2020).

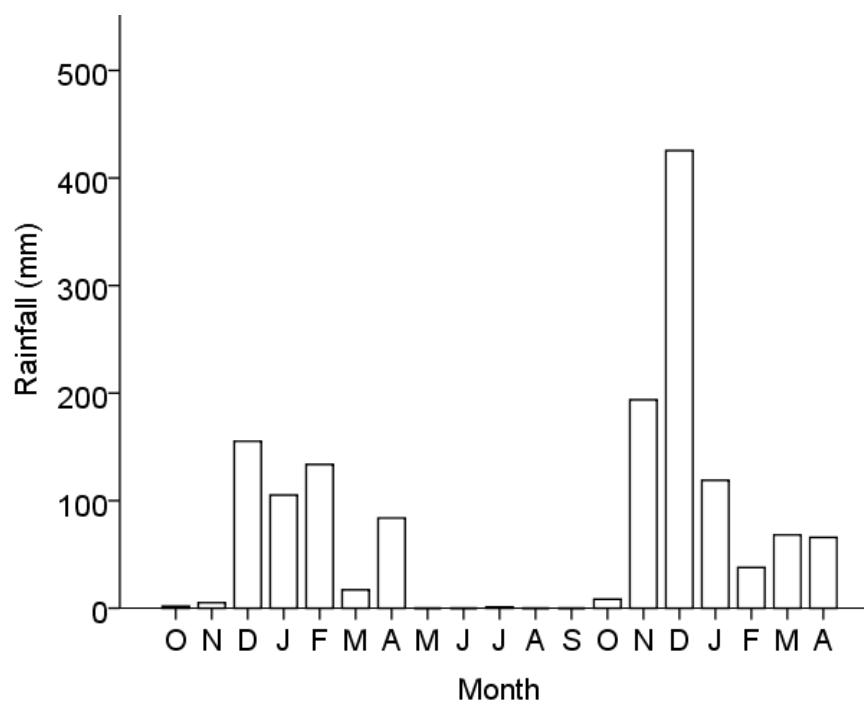


Fig. 4.2. Monthly total-rainfall recorded at Roodeplaat experimental farm during the two growing seasons (October-April) of the experimental period (2018/2019, 2019/2020).

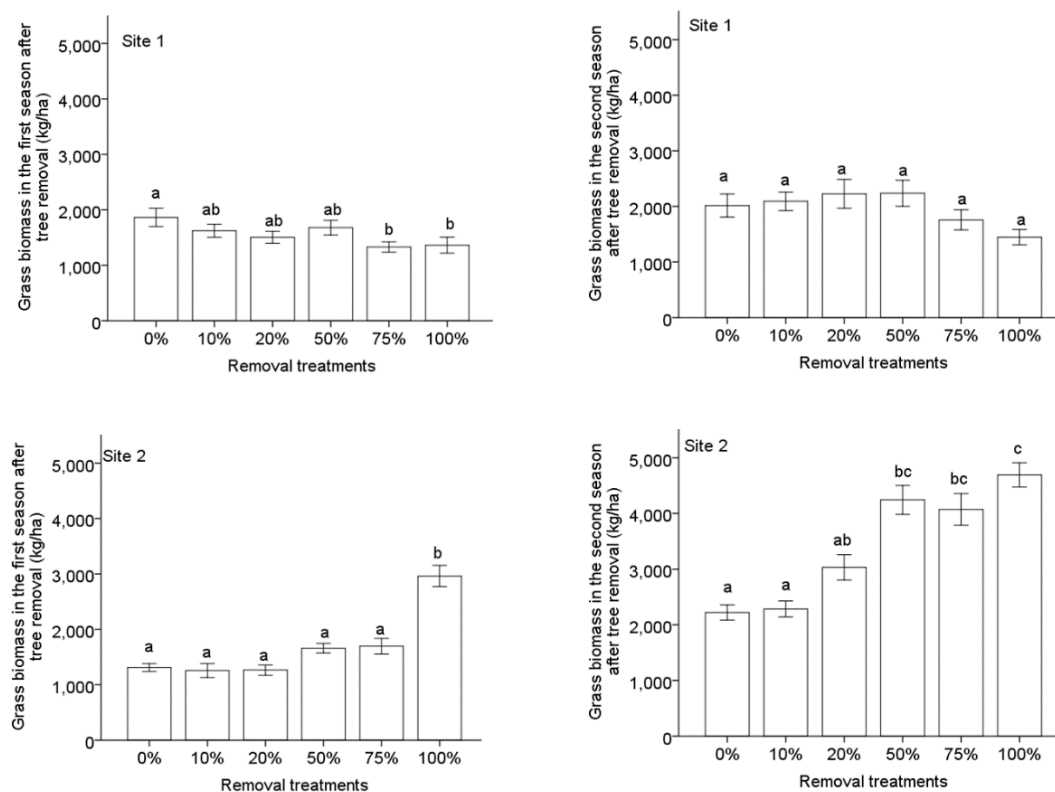


Fig. 4.3. Mean (\pm 1 S.E.) grass biomass production after tree removal in study sites 1 (ST1) and 2 (ST2). The different superscripts represent significant differences from a Bonferroni *post hoc* test. Treatments range from 0% = no removal (control) to 100 % removal = complete tree removal.

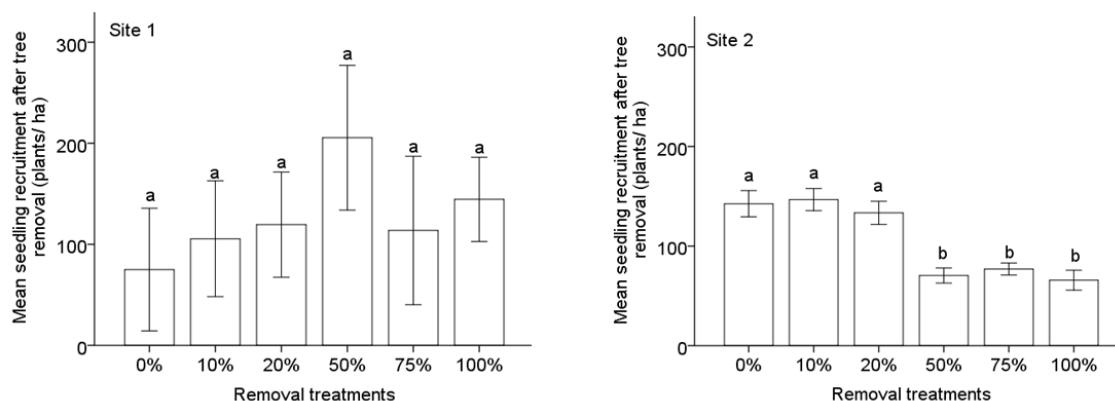


Fig. 4.4. Mean (± 1 S.E.) seedling recruitment after tree removal in sites 1 and 2 (ST1, ST2, respectively). Different superscript letters represent significant differences among treatments, based on a Bonferroni *post hoc* test. Treatments range from 0% = no removal (control) to 100% = complete removal of trees. Mean seedling recruitment after tree removal was significantly different between the 50-100% removed and the 0-20% removed in study site 2.

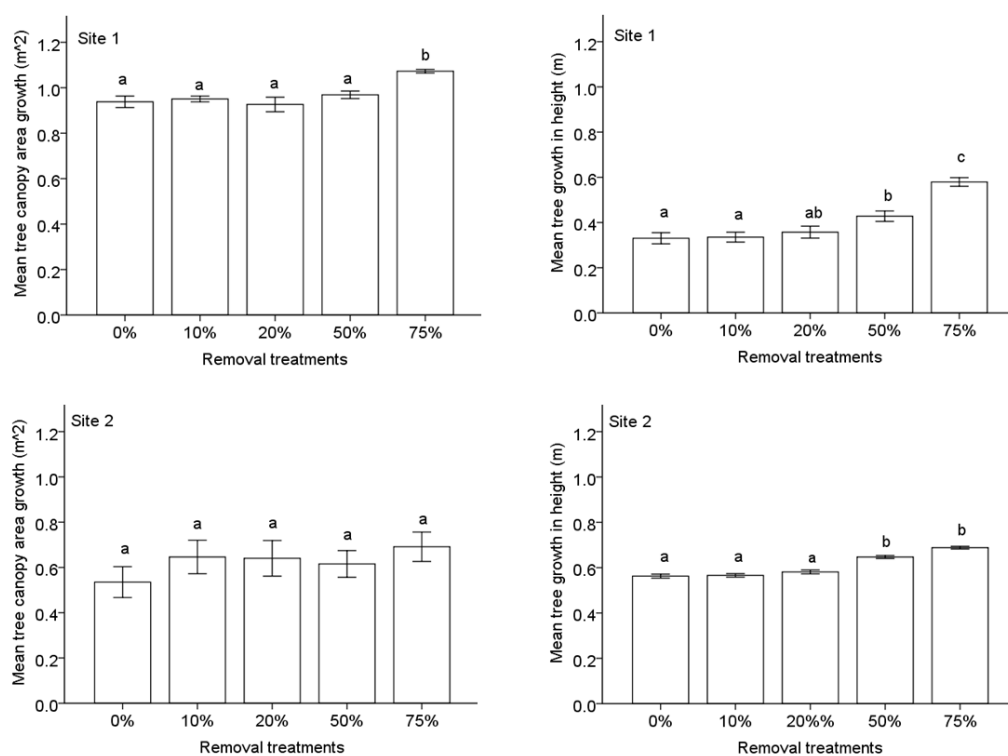


Fig. 4.5. Mean (± 1 S.E.) height- and canopy area growth of large trees. Different superscript letters represent significant differences based on a Bonferroni *post hoc* test. Treatments range from 0% = no removal (control) to 75% removal of trees.

Chapter 5: Short-term effects of fire on vegetation dynamics in a *Vachellia karroo* woodland

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Abstract

Fire is a common ecological process that affects the structure and composition of savanna ecosystems globally. In this study, we investigated the effects of 5 years of annual burning on the growth (i.e. height, stem diameter and canopy size) and density of young and adult *Vachellia karroo* plants. In addition, we determined the impact of annual burning on grass species composition and diversity, using 25 m x 25 m plots dominated by *V. karroo* seedlings and saplings. Measurements of *V. karroo* tree densities and growth were carried out in each plot before treatment application and after five years of annual burning. Grass surveys were conducted before treatment application in 2013 during the wet season and again in the years 2016 and 2018. Our results supported the “fire-trap” paradigm by demonstrating substantially higher densities of young plants in the burned plots than in the unburned plots. In addition, the recruitment of young plants and saplings into adult trees was significantly greater in the unburned plots than in the burned plots. *V. karroo* trees substantially increased in growth (height and basal diameter) in the unburned plots. The grasses changed in abundance in response to annual burning in burned plots. However, there were no significant changes in grass species diversity between the treatments. We found that the removal of the grass layer by fire and repeated topkill of trees increased the number of young *V. karroo* individuals. Annual burning limited *V. karroo* juveniles and saplings from reaching an adult size class that may have detrimental effects on the herbaceous layer. We demonstrated that grass species composition is more prone to fire-induced changes than species diversity and richness in our study area. In conclusion, we show that annual burning can be used to achieve specific objectives such as a reduction in woody cover in our study area.

Keywords: Fire ecology, firetrap, rangeland management, tree recruitment bottleneck, woody plant encroachment

5.1. Introduction

The increasing density of woody plants in savannas threatens these ecosystems worldwide (Van Auken 2009; Naito and Cairns 2011; D’Odorico et al. 2012; Mitchard and Flintrop 2013; Stevens et al. 2016). The proliferation of trees and shrubs threatens the herbaceous layer, which provides forage for livestock and wildlife (Wigley et al 2010). In primary grasslands, the herbaceous layer is also highly diverse, with many endemics (Bond 2016). Thus, woody plant encroachment is regarded as a form of rangeland degradation (Ward 2005; Okin et al. 2006; Scholes 2009). This is because grazing which is the dominant land use over many rangelands where woody plant encroachment occurs, is mostly based on grasses, which are frequently outcompeted by woody plants (Ward 2005; Archer and Predick 2014; Maestre et al. 2017). The negative effects of woody plant encroachment on animal production makes this problem an important concern for both human livelihoods and nature conservation (Wigley et al. 2009; O’Connor et al. 2014). Although woody plant encroachment is of global concern (Scholes and Archer 1997; Brown and Archer 1999; Kraaij and Ward 2006; Wiegand et al. 2006; Britz and Ward 2007), its management is local in scale (Archer and Predick 2014).

Changes in woody plant density and structure, which may depend on local management may contribute to woody encroachment in savannas (Case and Staver 2017; Hoffmann et al. 2020). Disturbances such as fire play an important role in regulating plant cover (Bond 2008; Staver et al. 2009; Gordijn et al. 2014; Hoffmann et al. 2020). Globally, the fire-mediated bottleneck has been used to explain how fire regulates savanna woody structure (Prior et al. 2010, Bond et al. 2012, Freeman et al. 2017, Nguyen et al. 2019). Frequent fires reduce mature-tree cover and maintain vegetation in a juvenile state by top-killing saplings and seedlings thereby retarding their transition to adulthood (Higgins et al. 2000; Bond et al. 2003, 2005), which result in a high density of fire-trapped stems. Lower densities of mature trees are crucial for the development of a grass layer (Smit 2004, 2005; Ward 2005). Tree-density reduction may enhance fuel loads for fires that could aid in maintaining low densities of woody plants (Bowles et al. 2017).

Fire can also facilitate encroachment by creating open spaces for woody plant seedling recruitment (Grellier et al. 2012, 2013; Tjelele et al. 2015). The removal of the grass biomass by fire may allow tree seeds to germinate *en masse* (Tjelele et al. 2015). Numerous studies have demonstrated that competition from grasses negatively affect seedling germination, survival and growth (Kambatuku et al. 2011, Ward and Esler 2011; Grellier et al. 2012; Vadigi and Ward 2013; Wakeling et al. 2015; Bhadouria et al. 2016; Morrison et al. 2018), which may

limit the recruitment of tree seedlings into adult trees. In addition, fire may increase the abundance of young plants, which are able to persist even under frequent fires through resprouting (Keeley 2006; Prior et al. 2010; Pausas and Keeley 2014, 2017). Resprouting allows individual plants to regenerate after the elimination of the aboveground biomass and persist in ecosystems with recurrent disturbances such as frequent fires (Vesk 2006; Nzunda et al. 2014; Pausas and Keeley 2014).

Studies have shown that fire does not only affect the woody layer but can also have profound effects on the grass layer (O'Connor et al. 2004; Uys et al. 2004). Savanna fires are ground fires and because of this, the understory layer is burned prior to the onset of burning of woody material. Thus, frequent fires are expected to have a substantial effect on understory plant communities (Ripley et al. 2015). One of the key steps for understanding the effects of fire on the grass layer is to determine how plant communities react to burning. Fire can influence the diversity and composition of the herbaceous layer by removing the aboveground biomass of herbaceous species indiscriminately (Bond and Keeley 2005; Bassest et al. 2020), which may shift species composition of grasses (O'Connor et al. 2004). This is because in fire-managed systems only grasses that can regrow their aboveground parts quickly are expected to increase in abundance relative to those that grow slowly (Ripley et al. 2015).

In this study, we evaluated the effects of annual burning on tree density and growth in a *Vachellia karroo* woodland at Roodeplaat farm in Gauteng Province of South Africa. In addition, we assessed the effects of annual burning on grass composition and richness. We focused on *V. karroo* because it is one of the most common woody plant encroachers in southern Africa (O'Connor et al. 2014). To achieve the study objectives, we established the following hypotheses:

- 1) Annual burning will increase the density of young *V. karroo* plants.
- 2) *V. karroo* seedlings and saplings in unburned plots will substantially increase in height, basal diameter and canopy size, which will result in a higher density of adults.
- 3) Annual burning will change grass species composition, diversity and richness.

5.2. Materials and methods

5.2.1. Study area

Field experiments were carried out at Roodeplaat farm of the Agricultural Research Council, Pretoria, South Africa (25°36'29"S, 28°2'08"E). The area is about 2100 ha and is primarily used for beef and game farming. Study site receives a mean annual rainfall of 687 mm, with most of

it occurring between November and March. The place experience a mean maximum temperature of 20-29 °C during the growing season (summer), while during dry season (winter) mean minimum temperature drops to 2-16°C. The soils of the area are classified as Vertisols, Ferralsols and Luvisols. Mucina and Rutherford (2006) classified the vegetation as Marikana Thornveld, which is dominated by *Vacchellia karroo* (formerly *Acacia*) and *Senegalia caffra* (formerly *Acacia*) (Kyalangalilwa et al. 2013). However, *Vachellia tortilis* (formerly *Acacia*), *Ziziphus mucronata* and some *Euclea* tree species are also dominant. Coates-Palgrave's (2002) nomenclature was used for tree species. The herbaceous layer is covered by *Digitaria eriantha*, *Eragrostis curvula*, *Melinis repens*, *Panicum maximum*, *Setaria sphacelata* and *Sporobolus africanus*. Other important grasses include *Themeda triandra*, and *Heteropogon contortus* (Van Rooyen 1983). van Oudtshoorn's (2006) nomenclature is followed for grass species. The study area is situated on the Roodeplaat Igneous Complex, which belongs to the Post-Waterberg Formation (Panagos et al. 1998). The Roodeplaat Igneous Complex is a unique ring-shaped structure with a diameter of approximately 16 km and is also referred to as the "Roodeplaat volcano" (Panagos et al. 1998).

At the beginning when the experiment was set-up, the study site was dominated by *V. karroo* seedlings (76% of the total density) followed by saplings (14%) and adult trees (8%), respectively. The study site was under crop cultivation more than 20 years ago and there was no record of fire management prior to the study. The study site was selected because research studies have reported that fire can be most effective in the control of young trees (< 2m in height) as compared with old trees that have escaped the "fire trap" (Bond 2008; Lohmann et al. 2014).

5.2.2. Study design

Sixteen plots of 25 m x 25 m were used in this study. Eight plots were randomly selected and burned annually during the dry season for five years (2013-2017). The other eight plots were not burned. We note that the timing of fire needs to be strictly controlled (Govender et al. 2006). In general, if fires occur towards the beginning of the wet season (i.e. before trees produce), then fire creates space in the grass sward (which is the primary fuel load) for the tree seeds to germinate *en masse*, resulting in bush encroachment. However, if fires occur at the beginning of the dry season, the fire will kill those young tree seedlings that have managed to recruit during the wet season, and the savanna will remain open (Frost and Robertson 1985; Ward 2005). Thus, plots were burned at the early stages of the dry season of each year.

Measurements of *V. karroo* densities and growth were undertaken along a 25 m x 5 m rectangular transect placed at the center of each plot before treatment application and five years after the last annual burning. In this study, we define young plants as trees < 1 m in height, saplings as trees between 1 and 2 m, and adults as trees greater than > 2 m (*sensu* escape height; Bond 2008). Young plants consisted of newly established seedlings and resprouting plants that were killed by fire. Tree growth measurements consisted of (i) tree height, (ii) canopy size in two perpendicular directions, and (iii) stem basal diameter. To ensure consistency, stem basal diameter was measured at the base of every plant.

Grass species composition and diversity were determined using the nearest plant species technique described by Hardy and Tainton (1993). Because our plots were relatively small (25 m x 25 m), we assessed the closest species and basal strikes along a 25 m line transect in each plot. At 1-m intervals, a metal rod was dropped and any herbaceous species on which the rod struck (basal strikes) were identified. When the distance to the nearest plant was 30 cm from the marked step point, “bare ground” was recorded. Tefera et al. (2010) showed that this technique is sufficient to obtain reliable results. The herbaceous surveys were conducted before treatment application in the year 2013 (February) during the wet season. The measurements were collected again during the wet seasons of the years 2016 and 2018. Grass species richness was calculated by summing the total number of plant species in each plot. Shannon-Wiener index of species diversity was calculated for each plot. Pielou's Evenness Index was used to calculate grass species evenness. In addition, β diversity was calculated using Sørensen's index between each pair of treatments (no-burn vs burn treatments), using the formula $C_s = 2j/(a + b)$, where “j” is the number of species shared between two treatments and “a” and b are the numbers of species unique to each treatment (Sørensen 1948). Rainfall data for the study area was received from the accredited Institute for Soil, Climate and Water of the ARC (Fig. 5.1).

5.2.3. Statistical analysis

Multivariate analysis of covariance (MANCOVA) was used to investigate the effects of fire on the density of young plants, saplings and adult trees of *V. karroo*. Initial density of *V. karroo* young plants, saplings and adult tree densities recorded before treatment application were used as covariates. The density of *V. karroo* (young plants, saplings and adult trees) plants recorded after five years of burning were considered the dependent variables. We also used MANCOVA to determine the effects of fire on tree growth (height, basal stem diameter and canopy size), where the initial height, basal stem diameter and canopy size were used as covariates.

MANCOVA was also applied to test whether there were fire effects on grass species richness and diversity. The initial species richness and diversity recorded before treatment application were used as covariates. MANCOVA was used to reduce Type 1 error caused by testing multiple dependent variables. Data for *V. karroo* densities and growth were analysed separately. IBM SPSS v. 26 (IBM 2019) was used for data analysis. Canonical correspondence analysis was used to determine the effects of annual burning on grass species composition (Masunga et al. 2013). Species composition analyses were performed using XLSTAT software (version 2020.5, Addinsoft, New York, USA).

5.3. Results

We found significant differences in *V. karroo* densities between burned and unburned plots (Wilks' $\lambda = 0.338$; $F = 5.867$; $P < 0.017$). ANOVA results showed that the density of young *V. karroo* plants was significantly higher in burned plots than in unburned plots and adult tree densities higher in the no-burn treatment (Fig 5.2). However, sapling densities were similar between treatments. There were significant differences in plant growth between the treatments (Wilks' $\lambda = 0.865$; $F = 8.462$; $P < 0.001$). ANOVA results showed that the differences were in tree height ($F = 17.919$; $P < 0.001$) and basal stem diameter ($F = 11.486$; $P < 0.001$) (Fig. 5.3), which were greater in the no-burn treatment than in burned plots. However, there were no significant differences in canopy size between the treatments ($F = 2.429$; $P > 0.121$).

There was a significant association between the grass species and the treatments ($\chi^2 = 751.75$, $P < 0.001$) (Fig. 5.5). *Bothriochloa insculpta* was the most dominant grass species that increased in abundance in both treatments after 3 years. Grass species *Aristida congesta* subsp. *congesta*, *Cenchrus ciliaris* and *Digitaria filiformis* increased in abundance in the burn treatment at the end of the study period. Also, at the end of the study period *Panicum maximum* started to show an increase in abundance in the no-burn treatment. Values for grass species richness and evenness are presented in Table 5.2. We found no significant effect of burning on grass species richness and grass diversity between the treatments (Wilks' $\lambda = 0.711$; $F = 0.731$; $P > 0.618$ and Wilks' $\lambda = 0.784$; $F = 1.655$; $P > 0.232$, respectively (Table 5.3).

5.4. Discussion

This study indicates that fire played a prominent role on *V. karroo* tree densities, which also affects vegetation structure. These results show that the “fire-trap” paradigm holds in the *V. karroo*-dominated area by supporting the following constituents of the model: 1) burned plots

had a substantially higher abundance of *V. karroo* seedlings and saplings that are prone to repeated fires than unburned plots; 2) the recruitment of young plants and saplings into mature trees was significantly higher in the unburned plots than in the burned plots (Table 5.1). Furthermore, the abundance of different grass species changed in response to annual burning after three years of annual burning. We found annual burning to change the grass species composition again after five years. However, grass species diversity, richness and evenness did not change as a result of annual burning.

5.4.1. Effects of annual burning on tree dynamics

Our results supported the notion that burning would increase young *V. karroo* plants because of resprouting stems and new tree seedling recruits. A similar study undertaken in the same ecosystem also showed that tree seedling densities of *V. nilotica* and *Dichrostachys cinerea* increased with burning (Tjelele et al. 2015). Increased densities of young plants in burned plots suggest that the removal of the grass layer by fire relieves *V. karroo* seedlings from competitive effect of grasses (Ward and Esler 2011; Pillay and Ward 2020). Additionally, the resprouting ability of *V. karroo* after the loss of aboveground biomass may also explain the substantial abundance of young plants in the burned plots. These results are similar to the findings of Wigley et al. (2009), who demonstrated resprouting of *V. karroo* plants from the base after losing all the above-ground parts due to burning, which may have resulted in a high density of young plants. In this regard, the use of heavy browsing to restrict the growth and survival of juvenile *V. karroo* plants could be vital in reducing the encroachment of this species. Our results show that the removal of the grass layer by fire and repeated “top kill” of woody plants enhances the abundance of young *V. karroo* individuals (see also Prior et al. 2010; Tjelele et al. 2015).

These results are consistent with the prediction that adult *V. karroo* plants would substantially increase in density in the unburned plots whereas fire reduces adult tree densities (D’Odorico et al. 2006; Hanan et al. 2008; Smit et al. 2010). Prior et al. (2010) demonstrated that repeated annual fires reduced the density of adult trees in an Australian mesic savanna. Similarly, Sankaran et al. (2008) reported that frequent fires reduced woody plant cover and maintained most of the woody plants in a juvenile state. In addition, the results reported by Higgins et al. (2007) who demonstrated that fire suppresses tree density and cover of adult trees supported our findings. The results of this study showed that the absence of fire in rangelands dominated by young *V. karroo* plants increases the density of adult trees, which may have negative outcomes for rangeland productivity (Gordijn et al. 2012).

Weak competitive interactions among *V. karroo* trees may explain our canopy size results (Pillay and Ward 2012, 2014; Mureva and Ward 2016). In a humid savanna in KwaZulu-Natal, South Africa, Pillay and Ward (2012) showed that the competitive interactions among *V. karroo* trees are relatively weak and thus results in smaller canopy sizes. Additionally, Archibald and Bond (2003) showed that *V. karroo* trees in savannas grow taller instead of wide to avoid disturbances such as fire. Nonetheless, annual burning in our study suppressed the growth in height of *V. karroo* trees through repeated top kill, thereby providing little opportunity for the plants to grow into the taller fire-resistant size classes (Bond et al. 2012; Hoffmann et al. 2020). Moreover, even without fire-induced mortality, repeated top kill could prevent the recruitment of reproductive individuals, reducing the possibility of woody plant encroachment (Higgins et al. 2000). Repeated top-kill may also reduce time to replenish belowground resources that are necessary for resprouting (Nzunda et al. 2014). The results from the current study suggest that recurring annual fire may significantly prevent *V. karroo* juveniles and saplings from growing outside the flame zone, which may have detrimental effects by suppressing the herbaceous layer.

5.4.2. Effects of annual burning on grass dynamics

Despite the distinct grass species assemblages for fire and no-fire treatments (Fig. 4), it was difficult to single out specific grass species that were consistently associated with either burned or unburned plots. For example, the abundance of *Bothriochloa insculpta* was associated with both treatments after 3 years of annual burning. Although *B. insculpta* is a fire tolerant grass (Plumptre et al. 2010), the results from this study show that this species is able to increase in abundance in plots where fire is not a treatment. Nonetheless, after five years of annual burning, grass species such as *Aristida congesta subsp. congesta*, *Cenchrus ciliaris* (another fire tolerant grass) and *Digitaria filiformis* that may have been favoured by frequent fires were responsible for changes in grass composition in the fire treatment. Moreover, *Panicum maximum* that is known to be sensitive to disturbances started to show an increase in abundance in the control plots after 5 years in the unburned plots, a result similar with the findings of Smith et al. (2013) who showed an increase of *P. maximum* in unburned plots. Fynn et al. (2005) also demonstrated that tall-stature grasses such *P. maximum* increase in abundance in unburned plots. Our results concur with Smith et al. (2013) who showed that annual burning changed grass species composition in a South African savanna. These results demonstrate that annual burning in our study area caused a shift of grass species composition.

The lack of a fire effects on grass species richness and diversity can be attributed to the short duration of this study. Long-term fire application studies often report an increase in grass species diversity and richness, although this may be site-specific (Smith et al. 2013). Nonetheless, our β diversity values shown that the treatments were similar in grass species composition over the study period (Table 5.2), which was not surprising considering that many grass species that were common before treatment application remained common after 5 years of burning. Our findings concur with the findings from other studies that demonstrated that grass species composition is more prone to changes than species richness after frequent fire application (O'Connor et al. 2004; Uys et al. 2004). These findings suggest that grass communities in our study area are resilient to annual fire disturbances. Alternatively, 5 years of fire application was insufficient to shift patterns of species diversity and richness.

5.5. Conclusion

We showed that annual burning can be used to reduce woody cover in the study area, which may lead to an increase in grass production. We found that the removal of the grass layer by fire and repeated topkill of woody plants increased the abundance of young *V. karroo* trees. Annual burning also prevented *V. karroo* tree seedlings and saplings from reaching an adult tree stage where they can possibly reproduce and produce seeds that would further increase encroachment of the rangeland (Bond 2008). We also showed that fire suppression allows *V. karroo* trees to increase in stem growth and height, whose shading effects on herbaceous plants including grasses may result in reduced fuel loads. Thus, successful rehabilitation of woody-plant encroached rangelands may require structural interventions such as tree thinning in addition to the use of fire (Smit 2004, 2005; 2014; Bassett et al. 2020). This is because fire can be insufficient for killing large trees (Lohmann et al. 2014). An implication of these results is that fire should be applied to control *V. karroo* plants when they are still in their juvenile stage to avoid having to resort to costly approaches such as chemical or mechanical treatments. Nonetheless, annual burning did not have significant effects on grass species richness and diversity. However, grass species composition changed in the burn treatment, as annually burned plots showed a clear separation of grass species between the treatments over the study period.

5.6. References

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Wigley, B.J., Bond, W.J., Hoffman, M.T., 2009. Bush encroachment under three contrasting land-use practices in a mesic South African savanna. *African Journal of Ecology* 47: 62-70. <https://doi.org/10.1111/j.1365-2028.2008.01051.x>.

3330 Table 5.1. Mean (\pm S.E.) *Vachellia karroo* plant densities before (2013) and after (2018)
 3331 treatment application in burned (n = 8) and unburned (n = 8) plots at Roodeplaat farm.

Treatment	<i>V. karroo</i> density (number of plants /ha)					
	Juveniles		Saplings		Adults	
	Before	After	Before	After	Before	After
Fire	270 \pm 13	1010 \pm 21	310 \pm 12	520 \pm 11	30 \pm 6	450 \pm 17
No fire	220 \pm 14	350 \pm 29	320 \pm 11	410 \pm 21	70 \pm 8	1180 \pm 24

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3355 Table 5.2. Grass species richness and evenness in the fire and no-fire treatments over the study
 3356 period.

Treatments	Period	Richness	Evenness
Fire	2013	9 ± 8.7	0.8
No-fire	2013	7 ± 12.8	0.8
Fire	2016	7 ± 10.9	0.8
No-fire	2016	9 ± 7.2	0.8
Fire	2018	13 ± 4.8	0.9
No-fire	2018	13 ± 4.6	0.8

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3378 Table 5.3. β diversity (calculated as Sørensen's index) of grasses between and within treatments
 3379 over the study period.

Treatments	Period	β diversity
Fire vs no fire	2013	0.9
Fire vs no fire	2016	1
Fire vs no fire	2018	0.8
Fire vs no fire	2013 vs 2016	0.9
Fire vs no fire	2013 vs 2018	0.6
Fire vs fire	2016 vs 2018	0.7
No fire vs no fire	2013 vs 2016	0.7
No fire vs no fire	2013 vs 2018	0.6
No fire vs no fire	2016 vs 2018	0.7

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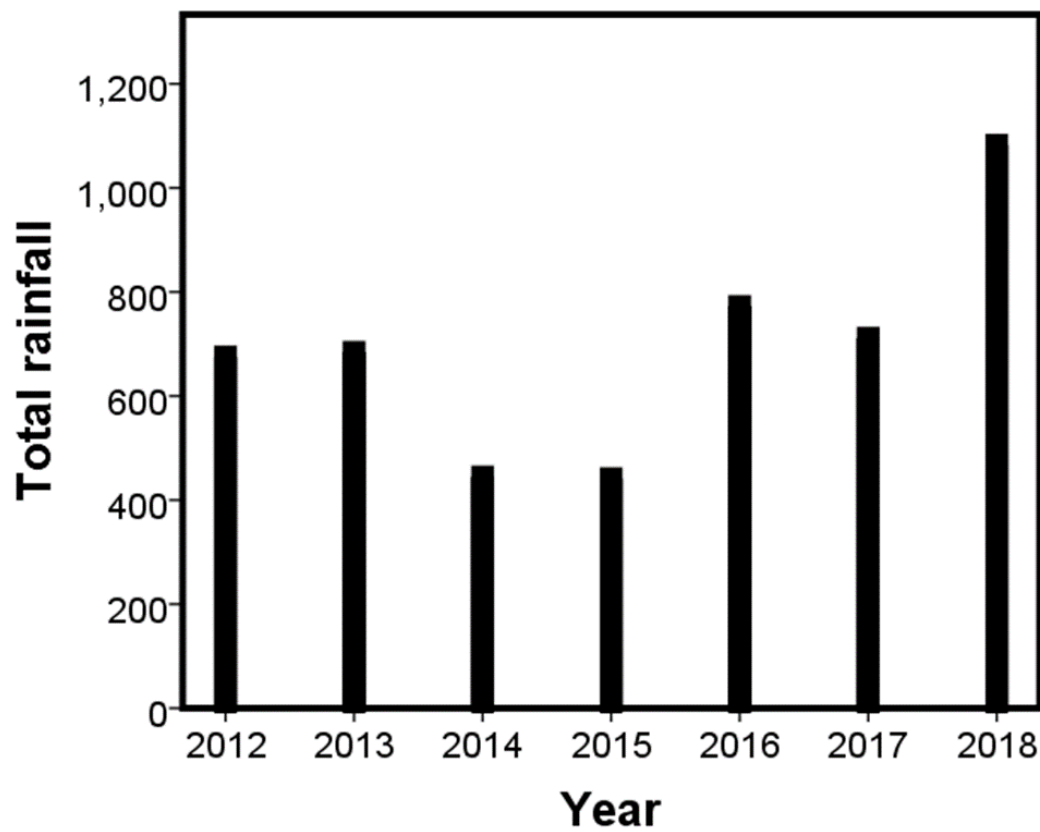
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3388 Figure 5.1. Yearly total-rainfall recorded at Roodeplaat farm during the experimental period
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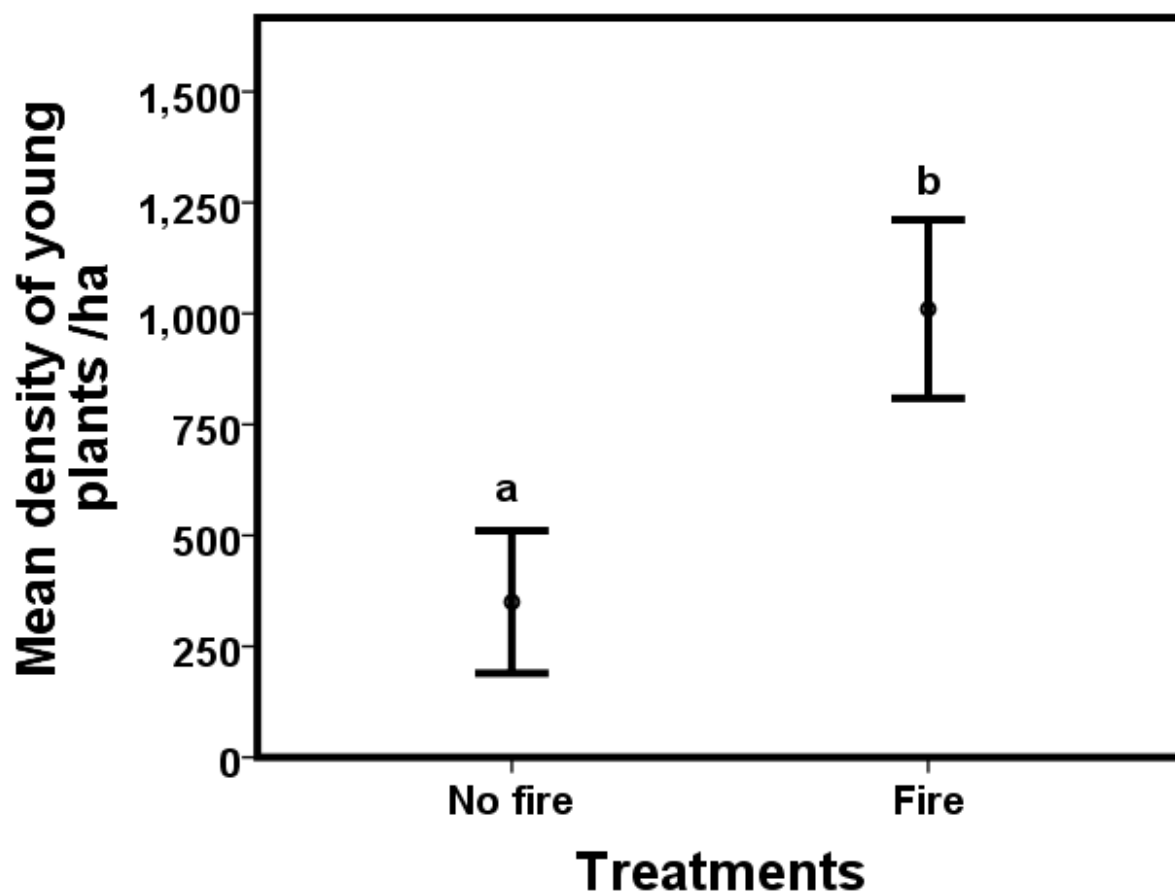
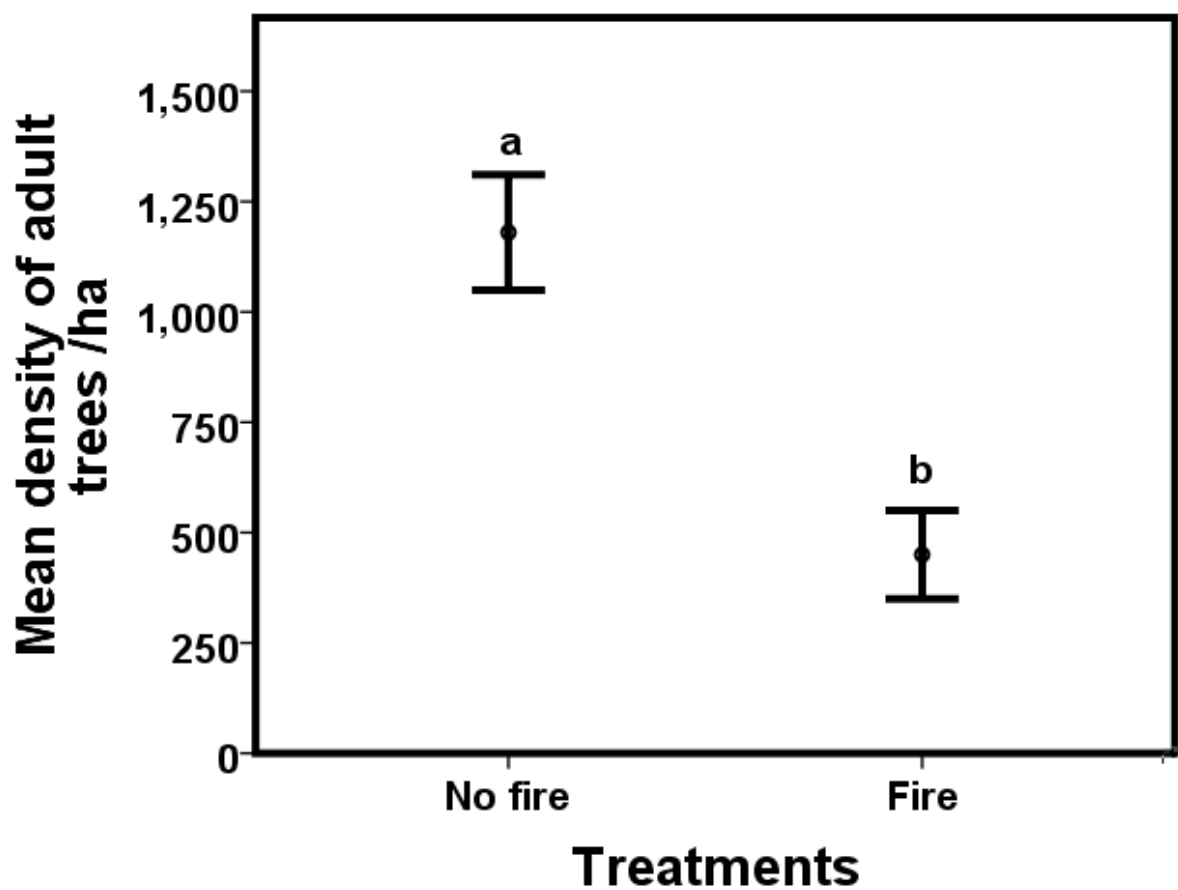


Figure 5.2. Mean (± 1 S.E.) density of young *V. karroo* plants in fire and no-fire treatments over the study period at Roodeplaat farm.



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3411 Figure 5.3. Mean (± 1 S.E.) density of adult *V. karroo* plants in fire and no-fire treatments over
3412 the study period at Roodeplaat farm.

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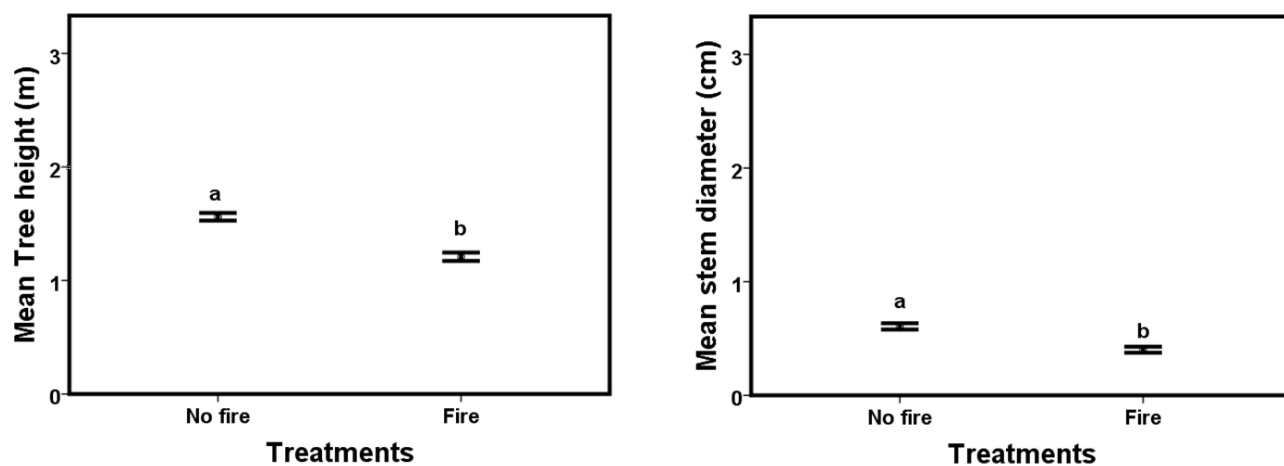


Figure 5.4. Mean (± 1 S.E.) height- and stem basal diameter growth of *V. karroo* plants in the fire and no-fire treatments.

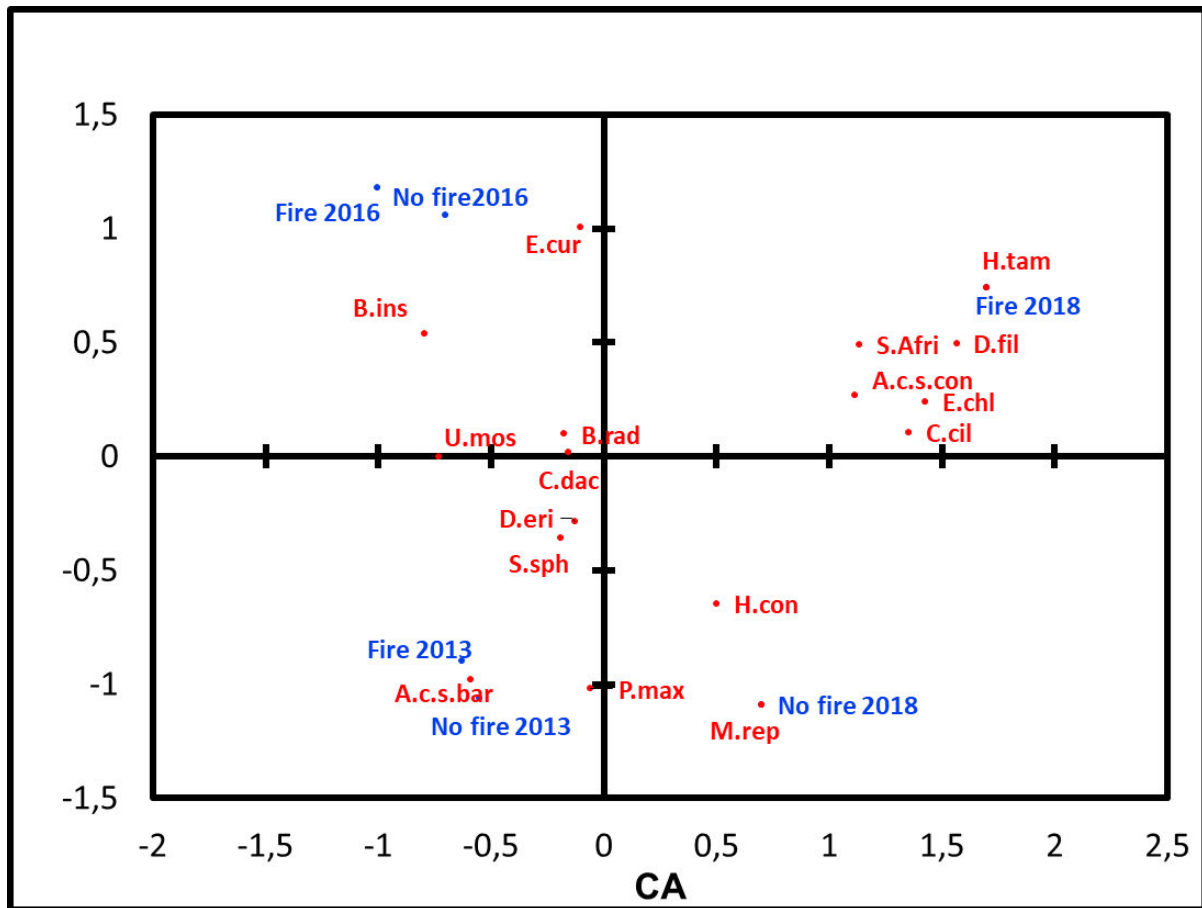


Figure 5.5. Correspondence analysis (CA) scatterplot showing grass species assemblages in fire and no-fire treatments during the study period at Roodeplaat farm. Species names are: A.con = *Aristida congesta subsp. congesta*; A.cs = *Aristida congesta subsp. barbicollis*; B.ins = *Bothriochloa insculpta*; B.rad = *Bothriochloa radicans*; C.cil = *Cenchrus ciliaris*; C.dac = *Cynodon dactylon*; D.eri = *Digitaria eriantha*; D.fil = *Digitaria filiformis*; E.chl = *Eragrostis chloromelas*; E. cur = *Eragrostis curvula*; H.con = *Heteropogon contortus*; H.tam = *Hyparrhenia tamba*; M.rep = *Melinis repens*; P.max = *Panicum maximum*; S.sph = *Seteria sphacelata*; S.afri = *Sporobolus africanus*; U. mos = *Urochloa mossambicensis*. After 5 years of annual fire, burned plots were more associated with *A. congesta subsp. congesta*, *C. ciliaris* and *D. filiformis*, *E. chloromelas* and *S. africanus*. In addition, *M. repens* and *P. maximum* were associated with no-fire treatment.

Chapter 6: The impact of woody plant control on rangeland productivity in a southern African savanna: Synthesis and future directions

6.1. Introduction

The negative effects of woody plant encroachment on ecosystem functioning are well known, particularly where pastoralism is the primary land use (Hoffman and Ashwell 2001; Ward 2005; Bond 2008; Archer et al. 2011; Eldridge et al. 2011; O'Connor et al. 2014). Woody plant encroachment is generally associated with reductions in forage production and biodiversity, and has the potential to threaten the social and economic viability of rangelands (Smit 2005). Therefore, when considering the detrimental effects of woody plant encroachment, it is not surprising that management of woody plants and rehabilitation of ecosystems affected by this problem have become of priority to ecologists and land managers globally (Ding and Eldridge 2019).

Many African woody plants harbour nitrogen-fixing bacteria in their root nodules (Cramer et al. 2010; Kambatuku et al. 2013b), which may result in greater soil nutrient concentrations (Ward et al. 2018). Also, this may promote ecohydrological functions (Kambatuku et al. 2013a; Eldridge and Soliveres 2015) and improve vegetation cover and consequently reduce soil erosion (Ndhlovu et al. 2016). Developing appropriate strategies that could help promote forage production and biodiversity, while encouraging the benefits of woody plants in savannas is central to rangeland productivity (Smit 2005; Ding and Eldridge 2019). Tree clearing and the application of fire are some of the main control methods often applied to combat woody plant encroachment in savanna rangelands (Smit 2004; 2005; Ding and Eldridge 2019). However, knowledge gaps still exist on rangeland recovery following the application of tree control measures. These gaps make it difficult to determine if further management is needed to achieve sustainable rangeland recovery for improved livestock production. In addition, monitoring the recovery of the rangeland after treatment application may help land managers choose management options suitable for their rangelands. In this chapter, I summarize and integrate the results obtained in the preceding chapters, and discuss new perspectives contributed through this thesis to the current understanding of tree thinning and range burning on rangelands productivity. This study investigated the following:

1. Effects of chemical and mechanical control of woody plants on resprouting potential and tree seedling populations in a savanna,

2. Short-term responses of grass species richness, composition, β diversity and soil dynamics after tree thinning in a South African savanna,
3. The impact of tree thinning on seedling recruitment and growth of woody plant species, and
4. Short-term effects of fire on vegetation dynamics in a *Vachellia karroo* dominated woodland

6.2. Stem size is a more important predictor of resprouting than herbicide application and tree thinning on savanna tree species

In chapter two (*Chemical and mechanical control of woody plants on resprouting and seedling production in communal rangelands*), our prediction that all the tree species in this study will resprout following cutting was supported by the study findings. The study plants demonstrated their ability to regenerate from the damaged tissues. Different intensities of tree thinning were not important predictors of resprouting potential. Herbicide application was important in suppressing resprouting ability of four of the 12 species studied. However, I found that stump diameter was the most important determinant of resprouting ability of the study species post-tree thinning. However, the effect of stump diameter on resprouting abilities in trees varies across ecosystems (Lévesque et al. 2011; Syampungani et al. 2017). I also showed that woody plants are more likely to resprout and survive disturbances as juveniles than as adults in southern African savannas. These findings contradict the results reported by Shackleton (2000, 2001), conducted in a southern African savanna. I explained that these resprouting patterns by woody plants may be influenced by plant age, which is related to bud senescence (Waters et al. 2010). Thick bark in older trees may inhibit resprouting abilities because it may hinder bud emergence (Clarke et al. 2013; Charles-Dominique et al. 2015). Although I did not measure tree bark thickness, the postulation about tree age, which is measured by stem diameter at the time of disturbance, is supported by empirical evidence (Clarke et al. 2013; Charles-Dominique et al. 2015).

In chapter two, I also established that the effectiveness of herbicide application on preventing stump regeneration is species specific. I explained that the inconsistency of herbicide application across species may be attributed to the amount of picloram applied to the cut stumps and time of application for each plant species. Enloe et al. (2015) showed that tree species react differently to the amount of herbicide applied. In addition, trees in this study were

cut and treated with herbicide during the wet season. The seasonal timing of herbicide application on cut stumps has been shown to have a significant impact on subsequent resprouting of woody plants (Badalamenti et al. 2015; Enloe et al. 2016, 2018). The control of woody plants with herbicides is more effective during the dry season (Enloe et al. 2018).

Chapter two also investigated the effectiveness of Tree Poppers[®] (hand-held tools) to mechanically uproot tree seedlings and saplings of eight dominant species in the study area. This was important because, in southern Africa, the problem of woody plant encroachment is often more severe in communal rangelands (Mograbi et al. 2015). Communal rangelands in South Africa cover nearly 6 million ha (Shackleton et al. 2001), and are used by resource-constrained rural communities mostly for livestock production (Vetter 2013). Therefore, alternative low-cost strategies that are effective, less complex and that can control the growth and survival of young trees in small-scale rangeland systems are essential. I expected that the effectiveness of Tree Poppers[®] depended on seedling height and root morphology of the study plants. I found that Tree Poppers[®] were effective in controlling shallow-rooted tree seedlings such as *Dichrostachys cinerea*, *Ehretia rigida*, *Euclea crispa*, *Gymnosporia buxifolia* and *Ziziphus mucronata*. Tree Poppers[®] were not effective in controlling the *Vachellia* (*V. karroo*, *V. nilotica* and *V. tortilis*) tree seedlings used in the study that have been reported to be among the major woody plant encroachers in southern African savannas (Hoffman and Ashwell 2001; Kraaij and Ward 2006; O'Connor et al. 2014). I explained that the ineffectiveness of the tool was because many *Vachellia* species have a long taproot to access underground water (Ward and Esler 2011; Kambatuku et al. 2013a). This kind of root system makes it difficult to uproot seedlings of these species. The Tree Popper[®] harvesting tool was, however, effective in controlling the *D. cinerea* seedlings, which is also among the major woody plant encroachers in southern African savannas (Kraaij and Ward 2006; O'Connor et al. 2014). The results provided a scientific basis for deciding whether Tree Poppers[®] are viable rehabilitation tools for managing tree seedlings in communal rangelands.

6.3. The effects of tree thinning on grass species richness, composition, β diversity and soil dynamics

Chapter three (*Short-term responses of grass species richness, composition, β diversity and soil dynamics after tree thinning in a South African savanna*) examined the effects of tree thinning on grass species richness, composition and β diversity. Additionally, I tested the effects of tree

thinning on soil fertility and cover. β diversity findings from this study demonstrated that tree thinning may change grass species composition, although this may be site-specific. The emergence and disappearance of certain grass species during the study period was responsible for the change in species composition (see also Dodson and Peterson 2010). I also showed in this chapter that tree thinning does not cause significant changes in grass species richness. These findings suggest that grass species richness in these savannas is resistant to thinning-imposed changes. However, the duration of the study may have been insufficient to cause significant changes. Importantly, I also found that tree thinning stimulated the abundance of the dominant grasses *Digitaria eriantha* and *Panicum maximum*, which are highly palatable grass species. These results are important for provision of ecosystem services such as forage production that may support livestock and wild herbivores in savannas. However, the nitrophilous *P. maximum* will likely decline in abundance with time in high-removal treatments (75% and 100%) because this species prefers fertile islands created by N-fixing tree species (Smit 2005).

Contrary to expectations, tree clearing did not have a significant impact on soil fertility in either of the two study sites used for chapter 3. Studies on tree clearing have shown that soil properties relating to soil fertility may take longer periods (between five and seven years) to change (Sangha et al. 2005; Kaur et al. 2007). I explained that the lack of a significant reduction in soil fertility in high-tree thinning treatments (particularly complete removal of trees) in this study may be due to the temporary legacy of nitrogen fixation and nutrient accumulation by woody plants (Ward et al. 1998; Ward and Ngairorue 2000; Sangha et al. 2005). Similar to the findings of Ding and Eldridge (2019), there was no evidence that tree thinning changes the amount of soil cover.

6.4. The impact of tree removal on grass biomass production, seedling emergence and growth of woody species

In chapter four (*The impact of tree removal on grass biomass production, seedling recruitment and growth of woody species*), I tested the effects of tree thinning on grass biomass production, tree-seedling emergence and growth, and the growth of the remaining mature trees in two study sites (hereafter site 1 and site 2) that differ in soil texture and woody species. Site 1 was located on clay-dominated soils on land that was previously cultivated. The soils are severely eroded, and were encroached by *Vachellia tortilis*. Site 2 was located on sandy soils with no history of cultivation, and with mixed species of woody plants. In site 1, I found that tree thinning

significantly reduced grass biomass production after the first growing season, whereas there was no change in the second growing season. I explained that the diminished grass biomass production during the first growing season in site 1 can be attributed to the ability of *Vachellia tortilis* (the only tree species in site 1) to facilitate herbaceous biomass under their canopies, as has been reported by other studies for this tree (e.g. Yadeta et al. 2018; Abdallah et al. 2008). *V. tortilis* is known to enhance water infiltration and amounts of soil nutrients underneath their canopies (Ludwig et al. 2003; Abdallah et al. 2008). For example, Yadeta et al. (2018) demonstrated that herbaceous biomass increases under *V. tortilis* canopies rather than in open spaces. In addition, the overall diminished grass biomass production in site 1 after the two growing seasons may possibly be related to the occurrence of soil erosion. Studies have shown that soil erosion leads to a decline of the herbaceous layer thereby increasing runoff of the topsoil and reduced water infiltration (Chartier et al. 2013). In addition, I found that tree thinning did not affect seedling emergence in site 1.

In site 2, tree thinning increased grass biomass production with substantial increases in 50%, 75% and 100% (complete removal) thinning treatments, which was also associated with substantial reduction in tree-seedling emergence. Additionally, for two study sites I found that the removal had no effect on tree-seedling growth. However, tree thinning substantially increased the growth (canopy area and tree height) of the remaining trees where 50% and 75% of the woody layer was removed in both sites. I argued that the lack of significant differences in tree-seedling establishment in site 1 could be related to undetermined factors such as the removal of *V. tortilis* seeds by insects and a possible reduction in the soil seed bank (possibly caused by rainfall-induced soil erosion) in the study site (Jiao et al. 2009; Ward et al. 2010). Furthermore, I explained that the lack of substantial differences in growth response of the tree seedlings could be attributed to the negative and positive responses of the herbaceous layer after tree thinning in both study sites. In site 1, diminished grass production across all treatments may have provided seedlings with an equal opportunity for growth, resulting in the lack of substantial differences in seedling growth among the treatments (Grellier et al. 2012). In site 2, the increased grass production may have suppressed seedling growth across all treatments, with the highest increases observed in 50%, 75%, and 100% thinning treatments. Research has shown that grasses suppress seedling recruitment and growth (Ward and Esler 2011; Grellier et al. 2012; Vadigi and Ward 2013; Morrison et al. 2018). The results found in chapter four suggest that increased and/or diminished grass-biomass production after tree thinning played a vital role on seedling recruitment and growth.

In chapter four, I also predicted that the remaining mature trees from moderate (50%) to high (75%) tree removal-intensities will significantly increase in growth (stem diameter, height and canopy area) because of the reduced tree competition. I found that reduced tree density in the moderate and high intensities of tree removal treatments facilitated the growth of the remaining mature trees. These results are consistent with those from similar studies that investigated the effects of tree removal on the growth of the remaining individuals in contrasting habitats (Smit 2001; Brudvig et al. 2011; Kambatuku et al. 2011a).

6.5. The effects of annual burning on vegetation dynamics in a *Vachellia karroo* woodland

Chapter five (*Short-term effects of fire on vegetation dynamics in a *Vachellia karroo* dominated woodland*) investigated the effects of five years of annual burning on the density of young and adult *Vachellia karroo* trees. I also determined the effects of annual burning on tree growth (i.e. total plant height, stem diameter and canopy size). In addition, I examined the impact of annual burning on grass species composition and richness. The results supported the “fire-trap” paradigm by demonstrating substantially higher densities of young plants in the burned plots than in the unburned plots. Moreover, the recruitment of young *V. karroo* trees into adult trees was significantly higher in the unburned plots than in the burned plots. Also, *V. karroo* trees substantially increased in height and basal diameter growth in the unburned plots. I argued that the removal of the grass layer by fire and the ability of *V. karroo* to resprout from the base after topkill led to a significant increase of young plants in burned plots (Wigley et al. 2009; Pillay and Ward 2020). These findings are consistent with the results from similar studies, which reported that frequent fires reduce woody cover and maintain most of the woody vegetation in a juvenile state (Higgins et al. 2007; Sankaran et al. 2008; Prior et al. 2010).

Annual burning was found to be ineffective in influencing grass species composition and diversity in our savanna site. I explained that long-term studies on fire application (see Smith et al. 2010) usually report a change in grass species richness and diversity. Thus, these findings suggest that grass communities in savannas are resistant to change by annual fires, and/or the duration of fire application was insufficient to change grass diversity and richness. However, there was evidence that grass species composition was changing in the burn treatment, as annually burned plots showed a clear separation of grass species between the burning treatments.

6.7. Management implications

6.7.1. Pastoralism

Tree thinning has been widely employed to improve the quality and quantity of forage production and maintain the economic viability of rangeland that are affected by woody plant encroachment (Smit 2005; Ndhlovu et al. 2016), particularly where pastoralism is the main land use. Although, the study was not conducted in an area used purely for pastoralism, tree species examined in this study negatively affect many pastoral areas in South Africa (O'Connor et al. 2014). I showed in this study that cut trees have the ability to resprout from the cut stems. In this case, stump treatment with chemicals may be helpful. However, in the scenario of resource-constrained communal farmers, stump burning might be a viable option (see also Dreber et al. 2019). Regardless of the general notion that tree-thinning increases grass production, I showed that thinning may have both positive and negative effects on grass production. Thus, the effects of tree thinning on grass production are site specific. Factors such as tree species (see Ding and Eldridge 2019), soil type and possibly erosion (in the current study) may determine the success of tree thinning on grass biomass production. I recommend the implementation of preventative soil-erosion measures before applying tree-removal practices in eroded rangelands. Additionally, in systems where the recovery of the herbaceous layer does not occur naturally, I recommend restorative interventions such as the re-introduction of perennial grasses from seeds and/or planting grasses (e.g. Falcão et al. 2020). However, in chapter 3, I also showed that tree thinning does not have negative effects on the density of palatable grass species. The implications of the effects of tree thinning on palatable grass species for pastoralism is that adequate production of good quality forage that may support livestock and wild herbivores in savannas may be enhanced. Nonetheless, in rangelands where the objective is to relieve the herbaceous layer from the suppressive effects of woody plants, I recommend maintaining the equivalent stand density of 50% (depending on the original density). Removing higher intensities (75-100%) of trees may result in large gaps between the remaining trees, which may favour subsequent woody plant encroachment or invasion by alien plants and possibly an increase in soil erosion (see also Smit 2014; Ndhlovu et al. 2016).

Where tree thinning improves understory production (particularly grasses), the increased grass biomass may suppress tree seedling performance. By constraining seedling establishment and growth, grasses may limit woody plant encroachment (Kambatuku et al. 2011b). However, grazing animals may remove grasses, and allow tree seedlings to grow into

mature trees that could re-encroach rangelands (Sankaran et al. 2008). Thus, an adjusted management system and reduced stocking rate might prevent woody plant encroachment by maintaining the suppressive effects of grasses on tree seedlings. Additionally, the recruitment of shallow-rooted tree seedlings of certain species should be reduced by making use of hand-held mechanical instruments such as the weed wrench (Tree Poppers®) (see chapter two).

Reduced tree competition had a significant effect on the growth of the remaining mature trees regardless of tree species or site. The implications of these results for management of woody plant encroachment in impacted rangelands is that the removal of some of the woody plants may release the remaining individuals from competition-induced size limits. Scattered large trees are important in rangelands for improving hydrological functions because they possess deeper roots, and produce a greater cover and mass of litter, which can increase infiltration by promoting aggregation and accumulation of soil organic matter (Bronick and Lal 2005; Marquart et al. 2019). Thus, scattered large trees have the potential to achieve greater N fixation rates than smaller trees, which can improve grass production, which may benefit pastoralism in savanna rangelands.

The implications of annual burning for bush encroachment control are that burning reduces woody plant cover (Bond 2008; Prior et al. 2010), which leads to an open savanna. An open savanna benefits pastoralism by increasing light intensities that may improve production of herbaceous vegetation for grazers (Smith et al. 2013). Also, reduced woody cover may reduce the competitive effects of woody plants on grasses, which may increase the abundance of various grass species (chapters 3 and 5). An increase in the abundance of different grass species may not only benefit animal production, but may also shield the soil layer from erosion (Berendse et al. 2015). An increase in forage production and a reduction of soil erosion may benefit range managers economically.

6.7.2. Biodiversity

Savanna rangelands provide habitat for game and non-game wildlife and thus have a considerable multidimensional value (Archer and Predick 2014; Stevens et al. 2016; Archer et al. 2017). It is important to keep some of the woody plants while promoting the herbaceous layer (Smit 2005; Archer and Predick 2014). Consequently, high intensities of tree thinning and/or total clearing of woody plants may not only worsen the rangeland in the long run (Smit 2014), but may also affect the biodiversity of rangelands (Martin and McIntyre 2007; Kutt and Martin 2010; Isaacs et al. 2013). Management practices that avoid total removal of woody

plants are expected to not only benefit pastoralism in terms of forage production but may also have positive effects on biodiversity (Kutiel et al. 2000; Fulbright et al. 2013; Hale et al. 2020). For example, Kutiel et al. (2000) showed that total clearing of woody plants reduces the abundance of small mammals such as rodents in cleared areas. Rodents play a vital role in savannas by performing the role of seed predators (Kappler et al. 2012; Hale et al. 2020), which may help reduce woody plant encroachment. In addition, total removal of the woody layer may negatively affect food availability of rodents. Furthermore, studies have shown that bird species that spend most of their time foraging on the ground but nest in the mid-canopy are reduced in numbers where woody vegetation has been cleared (Woinarski and Catterall 2004; Kutt and Martin 2010). Thus, tree clearing may alter birds' habitat. Woody plant clearing may also have a negative effect on browsing mammals (Isaac et al. 2013; Inman et al. 2020). Thus, high intensities of tree removal may alter ecosystem functions and reduce biodiversity. It is therefore, important to maintain a certain density of the woody layer that will not negatively affect pastoralism, rangeland biodiversity and nature conservation.

Although the primary impact of fire is on the vegetation, burning may have profound effects on fauna, particularly in protected areas where the main objective is the conservation of biodiversity (Murphy et al. 2010). Fire has both direct and indirect effects on biodiversity (Andersen et al. 2012). However, fire-induced mortality of animals is often low (Andersen et al. 2012). This is because the majority of animals in fire-prone areas are well adapted to it, and have consequently developed a range of responses to fire (Frost 1984). Range burning may indirectly affect biodiversity by altering vegetation structure and composition (Bond 2008). This can result in changes in quantity and quality of forage, vegetation cover, and micro-site characteristics (Murphy et al. 2010), which may negatively affect animal populations. Moreover, range burning may lead to open fields that may reduce predation because visibility is improved (Isaac et al. 2013). Consequently, other animal species may become vulnerable to predation. Thus, in rangelands where pastoralism is the main objective, land managers may trade off conserving biodiversity for increased forage production for livestock. The negative effects of fire on biodiversity may be reduced by the retention of nearby unburnt habitat. However, this does not suggest complete fire exclusion. Long-term fire exclusion may cause detrimental changes to habitats via woody plant encroachment (Gordijn et al. 2012).

6.8. Future research

The encroachment of woody plants into open savannas, woodlands and grasslands has long been of concern to managers in areas where pastoralism is the primary land use (e.g. Fisher 1950). Future research studies must develop appropriate management strategies aimed at controlling woody plant encroachment while promoting ecosystem functions of rangelands. In chapter two, herbicide application failed to control the stumps of all the tree species and thus it is important to determine all dynamics related to stumps treatment following cutting. Furthermore, it will also be crucial to contribute to closing the research and knowledge gaps identified in this thesis.

6.8.1. The influence of herbicide concentration, application timing and stump burning on resprouting patterns of woody species

The ability of trees to resprout following cutting is one of the challenges rangelands managers are faced with when thinning the density of woody vegetation (Archer and Predick 2014). This challenge renders further treatment of the stumps necessary in order to completely control the plant (Badalamenti et al. 2015). Stump treatment is therefore vital in maintaining long-term herbaceous production and low woody plant cover. Herbicide application and stump burning are some of the viable options that land managers could employ (Enloe et al. 2018; Dreber et al. 2019). The effectiveness of herbicide application has been demonstrated to depend on a number of factors such as tree species, type of herbicide, herbicide concentrations and the timing of herbicide application (Badalamenti et al. 2016; Enloe et al. 2015, 2016, 2018). For instance, in chapter two I showed that herbicide application controlled four of the 12 woody species examined. Testing the amount of herbicide concentration needed to kill certain woody species may be of importance for land users in southern African savannas. Moreover, the seasonal timing of herbicide application on cut stumps has been reported to influence subsequent resprouting of woody plants (Badalamenti et al. 2016; Enloe et al. 2016, 2018). Future research should focus on testing the adequate concentrations and time (wet or dry season) of application of different herbicides needed to kill the stumps of certain tree species.

Applying fire to tree stumps has also been shown to be a viable option to limit resprouting by woody plants (Dreber et al. 2019; Hare et al. 2020). This technique involves treating stem basal area of individual trees with fire (Hare et al. 2020), which may be time consuming and laborious. Thus, a better approach is needed, particularly in systems where

tree thinning may increase the density and biomass of herbaceous layer including fuel loads. Plot-level fire application in these systems may prevent the regeneration of tree stumps. This may be a viable option for resource-constrained communal ranchers who cannot normally afford treatments such as herbicides. Therefore, future studies should examine the effects of whole-plot (block burning) fire application on the resprouting dynamics of woody species after the recovery of the herbaceous layer. This information may inform land managers on economic approaches to suppress tree stump regeneration after tree thinning.

6.8.2. Can a combination of tree thinning, application of soil erosion control measures and re-introduction of perennial grasses rehabilitate eroded rangelands of different soil textures?

In arid and semi-arid ecosystems, soil erosion has been recognized as a major feature of soil degradation, and is considered one of the main factors responsible for reduced soil fertility and desertification (Michaelides et al. 2009). At low densities, woody plants have been reported to protect the soil from erosion by improving herbaceous vegetation cover (Marquart et al. 2019), which promotes infiltration and reduces runoff (Herrick et al. 2005; Ndhlovu et al. 2016). However, in the current study I observed that tree thinning in the clay soil-dominated study site further degraded the rangelands, possibly because of soil erosion. This was not the case in the sandy-dominated site. These results suggest that the success of tree-removal may largely depend on factors such as soil erosion and soil texture. Soil texture is known to directly affect soil aeration, water infiltration, nutrient retention capacity and erodibility (Hare et al. 2020). Water infiltration and permeability is slow in clay soils and rapid in sandy soils (Coppock 1994). The observations from the current study suggest that the removal of woody plants in clay-dominated soils may severely affect hydrological functions, which may result in diminished herbaceous plant production.

In most cases, a single method is not always effective to achieve sustainable control of woody plant encroachment. Therefore, a combination of different techniques may successfully rehabilitate rangelands affected by woody plant encroachment (Bassett et al. 2020; Hare et al. 2020). Future research may reveal whether a combination of tree thinning, soil-erosion control measures and the re-introduction of perennial grasses will rehabilitate eroded rangelands, particularly in clay-dominated areas.

6.8.3. Effects of fire application and tree thinning on the herbaceous layer and ecosystem structure

Woody plant encroachment caused by fire suppression and overgrazing (among other causes) may limit the effectiveness of fire for achieving target structure and composition (Ward 2005; Bond 2008; Lohmann et al. 2014). Therefore, successful rehabilitation of rangelands encroached by woody plants may require a combination of mechanical thinning and fire application (Bassett et al. 2020). Additionally, savanna trees may escape the “fire trap” by growing tall (*sensu* Higgins et al. 2000; Grady and Hoffmann 2012; Keeley et al. 2011; Dantas and Pausas 2013). Consequently, the application of fire alone may not be sufficient to cause any substantial changes in woody cover (Lohmann et al. 2014). Future studies that focus on the interaction between tree thinning and fire may inform land managers on effective woody plant control methods.

6.9. Conclusions

This thesis demonstrated that mechanical- and chemical -control, as well as fire application influences the structure and functioning of savannas. These management strategies may help increase the economic viability of savanna ecosystems by creating gaps that increase forage production. However, despite the notion that reduced tree densities improves ecosystem functions, this thesis shows that the effects of these control measures (particularly tree thinning) on forage production are not consistent across savanna sites (see also Ding and Eldridge 2019). Apart from promoting the growth of the remaining large trees, in other sites tree thinning may also diminish grass biomass, which may potentially intensify land degradation. Thus, the success of tree thinning may depend on local drivers of encroachment (Figure 6.1). In addition, this thesis demonstrated that the positive effects of tree thinning on grass production may relatively be short-lived (c.a. 5 years) because of the ability of cut trees to resprout (*sensu* Archer et al. 2011).

This thesis also shows that management with prescribed annual fire reduced woody plant encroachment across the 5-year study, demonstrating that fire management may be effective and should be explored as a management strategy. In addition, this study supported the existence of a fire-mediated recruitment bottleneck in *V. karroo* dominated stands. Thus, land owners and/or managers should consider the most appropriate control methods (i.e. mechanical, chemical or fire) for specific goals based on the target species in order to manage savannas. In conclusion, this thesis demonstrated that regardless of the substantial costs of

woody plant control, the recovery of key ecosystem services such as an increased forage production may not be realised. However, I recognize that this may be system-specific. In other systems, the absence of management interventions such as tree thinning may compromise provision of ecosystem services and ecosystem functioning (see Archer and Predick 2014). In addition, this thesis shows that land managers of savannas may use annual burning to achieve specific vegetation structural objectives, particularly in rangelands that are dominated by woody plants whose sizes are within the flame zone of grass fires (Lohmann et al. 2014).

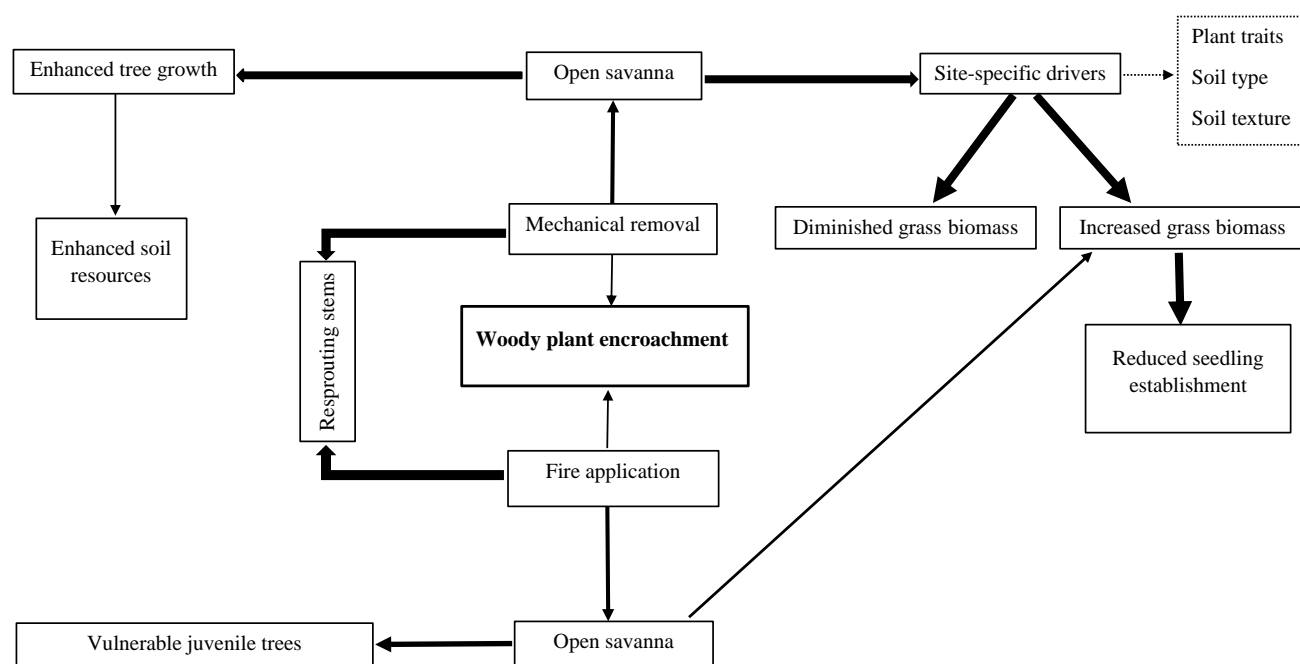


Figure 6.1. The conceptual framework of the components summarised in this chapter. The thickness of the arrows indicates the factor's significance.

6.10. References

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