Effect of elevated temperatures on growth and defence of *Vachellia sieberiana* seedlings grown with or without grass

by

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PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Grassland Science, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg Campus, South Africa. The research was financially supported by the Agricultural Research Council (ARC) and the National Research Foundation (NRF).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate. The data chapters of the dissertation were prepared as papers prepared according to the format of the *African Journal of Range and Forage Science* where they will be submitted for publication.

We confirm that the above information is correct,

Signed: Prof. Peter Scogings

Date:

___20/01/21____________________

Signed: Dr Ntuthuko Mkhize

Date:

DECLARATION 1: PLAGIARISM

I, Lusanda Ncisana (Student number: 217047385), declare that:

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

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

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

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

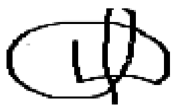
(a) their words have been re-written, but the general information attributed to them has been referenced;

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



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DECLARATION 2: CONFERENCE PROCEEDINGS

My role in each paper and presentation is indicated. The * indicates corresponding author.

1. Ncisana L*, Scogings PF, Mkhize NR. 2018. The effect of elevated temperatures on growth and defense of *Vachellia sieberiana* grown with or without grass. Paper presented to the School of Life Sciences Annual Post Graduate Research Day, 17 May 2017, Pietermaritzburg, South Africa. *(Platform)*. Presented by L Ncisana. My role: I designed the experiment, collected and analysed the data, and wrote the paper.

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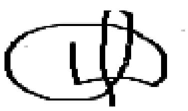

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ABSTRACT

Warming is suggested to increase globally in the next few decades. Warming, soil nutrients, water, CO_2 and sunlight are the most important environmental factors for plant life. Elevated temperatures can highly impact plant metabolism, photosynthesis and consequently woody plant performance and fecundity. An increase in minimum temperatures will possibly result in the transformation of grasslands to savannas. The effects of rising temperatures on growth and defence of woody plant seedlings and trade-offs between growth and physical defence particularly thorn length of woody plants that potentially invade grasslands have been studied utilising open-top warming chambers (OTCs). Furthermore, it is important to study the effect of warming on woody plant growth and defence when competing with grass. Field experiments were conducted in three different seasons to determine the effect of warming on growth and defence of *Vachellia sieberiana* seedlings growing with or without grass, and the effect of warming on trade-offs between growth and defence of *V. sieberiana* seedlings growing with or without grass. It was predicted that elevated temperatures would increase growth and thorn length of *V. sieberiana* seedlings growing (1) with or without grass in the dormant season and early growing season, but (2) in the later part of the growing season only when grass cover is absent. It was also predicted that warming, with or without grass cover increases seedling growth, but elevated temperatures would decrease investment in defences relative to growth of *V. sieberiana* seedlings when grass cover is absent. To test these predictions, 120 seedlings that were three weeks old were transplanted into 20 field plots. Ten plots were warmed, and the other ten plots were not warmed. In both warmed and unwarmed plots the grass was either cleared or not. OTCs raised air temperature by 1.0 to 2.5 °C. Stem length, plant height, stem diameter, thorn length, and dry mass of shoot, leaf, and root were measured after 6 weeks for the dormant season, and after 6 weeks and 12 weeks in the growing season for the first experiments. For the second experiment, plant height, stem length, stem diameter and thorn length were measured after 6 weeks. To determine effects of warming and grass cover on the relationship between defence and growth, ratios of thorn length (a measure of defence) to plant height, stem length and stem diameter (measures of growth) were calculated. The first experiment revealed that warming increased growth of *V. sieberiana* seedlings in all seasons. Defence was low in the presence of grass cover in the growing season, but not in the dormant season. The second experiment revealed that warming and grass cover significantly and independently reduced the thorn length: plant height ratio and thorn length: stem length ratio.

There was a significant interaction effect between warming and grass cover on the thorn length: stem diameter ratio. Lastly these results suggest that, with an increase of 1 – 2.5 °C regardless of grass cover at the time of seedlings establishment, the rate of woody encroachment will increase as temperature rises. The findings also suggest that there are trade-offs between the growth of *V. sieberiana* seedlings and physical defence in terms of thorn length.

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Firstly, I would like to thank my creator, God, who gave me strength and courage to conquer all the forces that were on my way. This study was made possible by many institutions and generous human beings that deserve to be acknowledged. The Agricultural Research Council and the National Research Foundation of South Africa are thanked for financial assistance.

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CHAPTER 1: INTRODUCTION

The increase of atmospheric gases has been suggested to result in warmer temperatures in the next few decades globally (IPCC 2014). The increase in temperatures has been documented to increase woody plants abundance (Way and Oren 2010). The increase in woody legumes in southern African rangeland has caused hot debates between scientists. The claim is that it is caused by absence of grass cover due to overgrazing (Smit 2004; Ward 2005), but others say it is caused by CO_2 (Kgope et al. 2010; Bond and Midgley 2012).

Much has been said about the role of CO_2 in woody thickening or encroachment in rangelands, but the role of increased temperature, which is caused by increased CO_2, has not been explored in as much detail. Global warming is one established problem, and woody encroachment in rangelands is another established and further threatening problem, but the role of warming in driving woody encroachment in rangelands has been understudied compared to the roles of overgrazing and increased CO_2 level.

One mechanism by which warming may play an important role in woody encroachment is through effects on seedling growth rate. The faster a seedling grows, the sooner it reaches reproductive age or size (Gleason et al. 2018), thus promoting encroachment. Among the many other factors that affect woody growth rate is grass cover. Elevated temperatures have been suggested to increase the growth of woody seedlings (Way and Oren 2010; Carlson et al. 2018). However, grasses compete with seedlings for resources such as water, space, nutrients and sunlight, thus limiting seedling growth rate (Tedder et al. 2014), and herbivores consume seedlings, which requires seedlings to divert resources from growth to defence, thus also potentially limiting growth rate (Herms and Mattson 1992). Hence, the aim of the study was to determine the effects of warming, with or without grass cover, on the growth and defences of seedlings of a typical woody encroacher species such as *Vachellia sieberiana*.

Some of the communal grasslands of KwaZulu-Natal are encroached by *V. sieberiana* and encroaching *V. sieberiana* can cover the whole surface layer of grassland (Grellier et al. 2012). The encroaching of grassland by these typical species has a direct effect on grazing livestock by reducing their grazing material or forage, and indirectly affect human beings through food insecurity due to low animal production.

Hypotheses and Objectives

The hypotheses tested in this study are premised from the fact that an increase of ambient temperature by a few °C benefits the growth of woody seedlings when plant growth is limited by low temperatures (Way and Oren 2010). Grasses start growing later than woody plants, so competition becomes more intense later when grasses have accumulated maximum biomass, implying that grasses suppress growth of woody seedlings (Whitecross et al. 2017). Grasses strongly compete with woody seedlings for resources and suppress woody seedlings' growth and resources are diverted to defence due to low resource availability (Wigley et al. 2015). Therefore, the broad hypothesis is that in the absence of grasses competition under elevated warming, woody seedlings attain high growth. On the other hand, the presence of grass cover is hypothesized to result in low growth of woody seedlings and high defence under warming. The objective of the study was to test the study predictions, and thus determine the effect of warming on growth and defence of woody seedlings that have the potential to invade grasslands.

Dissertation structure

This dissertation has been prepared as a series of two experimental chapters formatted as papers. Chapter 1 gives a brief general introduction with motivation, hypothesis and objectives for the study. In Chapter 2, the effect of warming on plant growth, the role of grass in woody encroachment, plant defence hypotheses, and the trade-offs between growth and defence of woody plants are discussed in detail. Chapter 3 addresses the effects of warming on growth and defence of *V. sieberiana* woody seedlings growing with or without grass in different seasons. It was predicted that elevated temperatures would increase growth and thorn length of *V. sieberiana* seedlings growing (1) with or without grass in the dormant season and early growing season, but (2) in the later part of the growing season only when grass cover is absent. Chapter 4 reports data from a field experiment to determine the effect of warming on trade-offs between growth and defence of *V. sieberiana* woody seedlings growing with or without grass. It was hypothesized that warming, with or without grass cover, increases *V. sieberiana* seedling growth, but decreases thorn length in relation to growth when grass cover is absent. These chapters 3 and 4 are independent chapters formatted as papers, and all figures and tables are placed at the end of each chapter. The experimental set-up is explained in detail in each chapter. Chapter 5 gives a general conclusion highlighting the main findings of the work and recommendations for further studies.

All data were collected between June 2017 and May 2018 at Ukulinga Research Farm and greenhouse of the University of KwaZulu-Natal, Pietermaritzburg, South Africa.

CHAPTER 2: LITERATURE REVIEW

Introduction

Global warming is the increase in temperature which results from rise of concentration of atmospheric greenhouse gases. Nitrous oxide (N_2O), methane (CH_4), and carbon dioxide (CO_2) are the main gases that contribute in the course of trapping thermal radiation. As per the predictions of Intergovernmental Panel on Climate Change (2014), mean global temperature will increase by 1.8 - 4.0 °C by 2099, and 0.4 °C rise has been experienced from 1906 to 2005. The basic problem is that global climate is known to be changing such that increased temperature is expected in the near future. Bush encroachment is an established problem that has been studied for decades and about which quite a lot is known (including the impact of CO_2), but very little is known about how temperature will affect this phenomenon, especially in savannas.

Warming is an important environmental factor for plant life and elevated temperatures can highly impact plant metabolism, photosynthesis and consequently woody performance and fecundity (Ensslin et al. 2018; Shen et al. 2018). Rises in minimum temperatures possibly will cause a transformation of grasslands to savannas (Wakeling et al. 2012; Carlson et al. 2018). As temperature rises, water requirement for plants increases, with CO_2 concentration (de Boer et. al 2011), as such C_3 trees outcompete C_4 grasses due to their rooting system which can penetrate deeper in search of water. Globally, longer growing period, higher biomass allocation towards roots, higher woody plant fecundity and possible shifts towards woody plant dominated biomes are predicted due to rising temperature (Scheiter and Higgins 2009; Rouget et al. 2016).

Over the past five decades, the invasion of woody plants in savannas and grassland biomes have been noticed throughout the world (Stevens et al. 2016). This phenomenon of increase in woody density is called bush encroachment (Van Auken 2009). Southern African savannas and grasslands are changing their land cover because of woody encroachment (Mureva et al. 2018). Woody encroachment has been suggested to increase total carbon stock on rangelands (Birhane et al. 2017; Gobelle and Gure 2018).

Increased woody plants which are notorious invaders of rangelands, impacting their ecosystem services such as grass production, is a threat to food security. In southern Africa, the grazing capacity of most rangelands has been declining due to abundance of woody plants that invade these rangelands (Scholes and Archer 1997). This increase has negative impacts on livestock farmers because of low forage production which results in low animal production. The aim of this review is to examine the factors that contribute to promotion of bush encroachment, and the effects of warming and grass cover on woody seedlings.

The role of grass cover in woody encroachment

Savanna ecosystems are characterized by a mixed community of woody plants and grasses. They occur in many regions of the world, including Africa, Australia, South America and North America (Scholes and Archer 1997). Savannas are divided into two broad groups. Dry savannas include arid and semi-arid savannas receiving a rainfall of approximately 400 – 1000 mm per annum (Sankaran et al. 2005; Donzelli et al. 2013). Wet savannas, also known as moist savannas, receive 800–2000 mm per annum (Sankaran et al. 2005; Donzelli et al. 2013). It is reported that water and nutrient availability are the main limiting factors as annual precipitation decreases (Kraaij and Ward 2006).

Distribution and abundance of plant species and their related populations are influenced by environmental factors such as nutrient availability, temperature, rainfall, altitude and latitude in savannas (Callaway et al. 2002; Barron-Gafford et al. 2017). Several studies have attempted to explain the mechanisms of tree-grass co-existence in savannas (Walter 1971; Scholes and Archer, 1997; Sankaran et al. 2004; Rossatto et al. 2014; d'Onofrio et al. 2015; Smit and Prins 2015; Synodinos et al. 2015; Accatino et al. 2016; Barron-Gafford et al. 2017). Walter's (1971) 'two-layer hypothesis' suggested that grasses have better access to the shallow soil resources, while trees have better access to deeper soil layers. In arid regions where woody plant growth is water limited, grasses can be displaced by woody plants (Yu et al. 2017; Holdo et al. 2018). Woody plants in savannas are viewed as having higher nutrient capture ability because of their more extensive spread of roots than grasses, which reduce grass biomass (Scholes and Archer, 1997; Priyadarshini et al. 2016). This theory suggests the relationship between grasses and woody plants reaches equilibrium due to long term dynamics of vegetation in dry savannas (Sankaran et al. 2004; Ward et al. 2013).

Contrary studies have been shown in temperate savannas. One reason could be that the separation depend on the type of ecosystem and ecological conditions that enhance it (Holdo et al. 2018). The two-layer hypothesis can be used to explain soil-water separation and tree-grass co-existence in dry savannas if it is used from its original context (Ward et al. 2013). Yu et al. (2017) also agrees that it can be applied in dry savannas. During the seedling stage of woody plants where they use the same top-soil layer as grasses, the two-layer hypothesis alone cannot be used to explain woody plant encroachment (Ward et al. 2013).

It has been suggested that there is strong competition between woody plants and grasses at many demographic stages. However grasses compete better at the seedling stage of woody plants where they suppress the growth and establishment of seedlings (Higgins et al. 2000; Tedder et al. 2014; Campbell and Holdo, 2017). Grass suppresses some humid and mesic savannas woody saplings growth (Vagidi and Ward 2014). African savanna woody seedlings are suppressed by C_4 grasses, which result in high decrease in woody growth rates (Campbell and Holdo 2017). Decrease in woody growth is due to interspecific differences in woody plant response to grass competition which is negatively related to carbon assimilation in woody species (Campbell and Holdo 2017). Additionally, absence of grass cover promotes woody plant seedlings and presence of grass cover suppress woody plant seedling establishment of the tropical riparian pastures in south Mexico (Meli et al. 2015).

Similarly, low grass cover promotes woody seedling establishment and high biomass of *Vachellia karroo* saplings due to reduction of grass biomass and high availability of moisture and light (Tedder et al. 2014). Additionally, dry savanna woody seedlings were established in the absence of grass cover (Morrison et al. 2018). Grasses suppressed the growth of woody plant seedlings (Manea and Lishnmen 2015). de Dios et al. (2014) reported that their findings were in line with other studies that suggest woody plant seedling recruitment and growth is strongly suppressed by grass cover.

Another factor that contributes to the role of grass cover in woody encroachment is resource availability. The amount of rain received has the ability to change an ecosystem through affecting the availability of soil water to plants, soil fauna and microorganisms (Honda and Durigan 2016). In savannas it is suggested that tree-grass interaction is due to competition for resources like soil water availability and nutrient supply (Kambatuku et al. 2011; Donzelli et al. 2013). Wet savannas have been suggested to be less fertile than dry savannas due to limited phosphorus which is a result of high rainfall that leaches the soil nutrients (Donzelli et al. 2013). However, Morrison et al. (2019) found that Serengeti grasses and savanna woody plants were competing for resources other than soil water.

The absence of woody plants in wet savanna regions has been reported to be due to low availability of nutrients since infertile soils limit woody plant growth (Bond 2010). In savannas where water is the limiting factor, woody plants have the advantage of allocating additional carbon to below ground (Devine et al. 2017). Grass competition is significant in decreasing growth rates of saplings on infertile soils (Tedder et al. 2014). However, grasses compete with seedlings for resources, thus limiting seedling growth rate, and herbivores consume seedlings, which requires seedlings to divert resources from growth to defence, thus also potentially limiting growth rate.

The removal of grass cover, resource availability and global warming are all playing part in the growth of woody seedlings which have potential to invade grassland. The competition of grasses and woody plants also depend on the type of savanna. In wet savannas there is high leaching of nutrients due to high rainfall, implying that woody seedlings and grasses compete for limited resources. In dry savannas woody seedlings and grasses compete for resources other than water. Woody plant performance in the absence of grass cover also suggests the promotion of woody plant encroachment. Elevated temperatures are a major factor that may contribute to woody plant encroachment. The contribution of this important factor to woody encroachment has rarely been explored.

Herbivory, fire and cultivation as processes causing grass removal in rangelands

Rangelands are home to millions of people and animals. Rangelands are covered by grasses shrubs, forbs and trees (Lund 2007), and they are used by grazing animals. In southern Africa, communal rangelands are used for grazing animals such as cattle, sheep and goats (Squires et al. 1992). There are no supplementary feeds for these animals due to lack of resources such as financial capacity (Ngongoni et al. 2007). This has led to change of land use management and poor rangeland management that results in removal of the grass layer. The deterioration of rangelands is due to overstocking and poor veld management skills (Squires et al. 1992; Hoffman and Ashwell 2001).

Animals modify vegetation in different ways because of their different feeding behaviour and preference (eg sheep graze with more of a biting action than cattle and are well adapted to graze short herbage and are classified as selective grazers). The heavy grazing by these animals results in loss of more palatable grass species and promotes less palatable grass species (Radácsi and Czeglédi 2005). This is because grass species with erect growth form and exposed buds and stems are more vulnerable to heavy grazing. Overgrazing creates an environment that results in reduction of soil infiltration, soil moisture and fertility, and accelerates run-off and soil erosion (Radácsi and Czeglédi 2005). The prolonged grazing by sheep and cattle results in removal of grass cover (Kilgore 1981). Heavy grazing and selective grazing results in the removal of grass cover under poor rangeland management. The reduction of natural fires frequency, fire intensity due to low biomass or fuel load in arid savannas is because of overgrazing (Saintilan and Rogers 2014; Stevens et al. 2016; Devine et al. 2017).

The physical and chemical process known as combustion is called fire. The combustion reaction takes place when chemical energy (biomass fuel), thermal energy (heat from an ignition source) and oxygen (O_2) are present (Neary et al. 1999). In the process of combustion, soil is heated to different temperatures. The soil temperatures of 40 – 70 °C disrupt the biological processes and results in protein degradation and death of plant tissue, while seed mortality takes place at 70 - 90 °C (Neary et al. 1999). This makes grass cover vulnerable when there is heavy rain or heavy grazing.

The loss of perennial grass species has been shown where there is lower biomass since fire tends to burn more patchily (Trollope and Trollope 2004). The post-burning management is critical because fire stimulates the growth of grasses or biomass production. Therefore, the introduction of animals immediately after the rangeland is burnt results in the loss or removal of grass species due to overgrazing by different herbivores with different diet preferences (Savadogo et al. 2007).

The high increase of human population and livestock in rangelands has caused drastic changes in land use management (Squires et al. 1992). The 50% increase in human population in some semi-arid rangelands of the Eastern Cape, South Africa, between 1954 and 1988 has been reported (Kakembo and Rowntree 2003). This increase has resulted in low crop production. The decline in crop production has been experienced in semi-arid and arid rangelands of the Eastern Cape South Africa (Mbuti 2000).

Effects of warming on plant growth

Expected warming will not affect the world equally, with higher latitudes experiencing larger increases (Way and Montgomery 2015). Effect of elevated temperatures on vegetation will be different for different seasons (Tan et al. 2015). Warming affects woody plant growth according to their age (Way and Oren 2010). The dormant season is the period where the minimum temperatures are low and there is accumulation of snow on the ground in some areas, and the growing season experiences the opposite (Williams et al. 2015). Elevated temperatures change the plant’s micro climate due to snow melting during dormant season (Khorsand et al. 2015; Williams et al. 2015). Warming increases biological or biochemical processes such as photosynthesis and respiration due to quicker enzyme function (Way and Oren 2010).

Therefore, increase in biological processes can benefit woody plant growth during the dormant season (Williams et al. 2015).

Many studies have documented an increased length of the growing season due to elevated temperatures in different regions globally (Way and Oren 2010; Marchin et al. 2015; Khorsand et al. 2015; Williams et al. 2015; Way and Montgomery 2015; Fridley et al. 2016; Kueppers et al. 2017). The growing season may be divided into early, mid, and late growing season and the timing of plant growth differs (Ernakovich et al. 2014). Global warming has been shown to change the start of the growing season and extend it in the Arctic (Khorsand et al. 2015). It has been suggested that the growing season could extend by 10-20 day under elevated temperatures (Khorsand et al. 2015). The elevated temperatures melt the frost which implies that winter days temperatures will be increased compared to the past thereby extending the growing season which favours woody plant growth as they will outcompete the grasses due to their deep root system. Elevated temperatures will not only increase the length of the growing season (Reyes-Fox et al. 2014), but also increase growth of woody plants during the growing season (Way and Montgomery 2015). In some semi-arid regions of Africa, the growing season extension has been observed due to retention of leaves for a longer time (Stevens et al. 2016). However, an increase of 5 °C higher than normal temperatures can also reduce plant growth during the growing season (Hatfield and Prueger 2015). It is because extreme temperatures slow down the photosynthesis and increase rate of respiration, consequently plant growth is reduced.

Elevated temperatures have negative impact on growth of woody seedlings at high elevation forests in the absence of soil moisture (Lazarus et al. 2018), while mature plants have been shown to increase growth under warming in forests and in alpine areas (Lazarus et al. 2018). However, woody seedlings of *Platanus occidentalis* at elevated temperature have increased stem height growth, shoots, plant height, leaf mass and leaf surface area (Ultra and Han 2015). In contrast, elevated temperatures did not reduce the growth of tropical saplings.

Defence hypotheses

Herbivory plays a major role in ecosystem functioning in the semi-arid regions of African savannas, while the interaction between the plants and animals in savannas are not well comprehended (Scholes 1997; Scogings 2003). Woody plants in African savannas and herbivores coevolved, with woody plants developing physical and chemical defence against herbivores (Du Toit 2003; Mkhize et al. 2015). The study of why some plants have good defence while others do not, has led to the development of several hypotheses that have been fundamental in guiding ecological and evolutionary investigation on plant defences (Stamp 2003; Ferrenberg et al. 2015).

Carbon nutrient balance hypothesis postulates that secondary metabolites in plant tissues are controlled by the availability of carbon and nitrogen in the soil (Bryant et al. 1983). This hypothesis has been successfully used to predict and explain differences in plant resistance to herbivores, then again some research disagreed with this hypothesis (Herms and Mattson 1992; Koricheva et al. 1998). There are some assumptions pertaining to this hypothesis, the first one, is that secondary plant metabolites production will always come second after growth (Tuomi et al. 1991). This means that the carbon and nitrogen can be invested to growth first and once the requirements of growth are met, then they will be allocated to secondary metabolites production.

Light is one of the most important abiotic factors for plant growth (Giertych et al. 2015). It is assumed that light-demanding species invest more carbon in growth and less in the production of secondary metabolites that act as defence to deter herbivores (Coley et al. 1985), while the species that require less light, invest their carbon in chemical defence (Coley 1987), such as tannins, flavonoids and phenolic acids (Bennett and Wallsgrove 1994).

Optimal defence theory states that chemical and morphological defences of plants are costly and resources are invested in defences that optimise plants in terms of fitness (Rhoades, 1979). Plants deploy different types of chemical defence to deter herbivores, and these chemical compounds are within plants tissues (McCall and Fordyce 2010). Therefore, optimal defence theory was developed to predict and explain the distribution of chemical compounds within the plant (McKey 1974). This theory has been useful in predicting some intra-plant distributions of secondary compounds (Zangerl and Rutledge 1996). The prediction of root density using optimal defence model has also been developed after three decades (Craine 2006). McCall and Fordyce (2010) showed that optimal defences theory is useful in predicting the allocation of defensive compounds among tissues of different plant age. In the meta-analysis study of McCall and Fordyce (2010), they found that younger leaves are better chemically defended than older leaves.

Growth differentiation balance hypothesis states that there are physiological trade-offs between growth and defences, but the trade-offs depend on resource availability (Herms and Mattson 1992). Any process that involves cell division and elongation is called growth. Whereas, cell differentiation, is whereby the structure and functioning of cells changes, leads to different tissues and different organs such as leaves or roots. The thickening of leaf cuticle, trichome production and secondary metabolites are some of the differentiation related processes that deter herbivores (Herms and Mattson 1992). Investment to differentiation is at the cost of enzymes, transport and storage of constitutive defences (Stamp 2004). Growth and secondary metabolites can compete for available sugars and other substances that are produced by photosynthesis (Mooney and Chu 1974), and therefore there is a trade-off for carbon allocation (Stamp 2004). The limitation of nutrients and water slows down growth, while photosynthesis is less affected by limited water and nutrients (Herms and Mattson 1992).

The growth rate hypothesis is also known as the resource availability hypothesis which postulates that plants from high-resource areas grow fast and allocate less in herbivore resistant traits, while plants in low resource locations grow slowly and are more resistant to herbivores (Coley et al. 1985; Endara and Coley 2011; Hattas et al. 2017; Coley et al. 2018).

Physical defence

African savannas are commonly invaded by deciduous plants that show thorns, spines, and prickles (Hattas et al. 2017). During anatomical plant development there is formation of plant defence, whereby leaves are physically modified and there is a need of investing carbon in the form of complex organic polymers such as lignin (Barton 2016). There are three types of spinescence in woody plants and these mechanical defences hinder herbivory (Barton 2016). Spines are modified leaves, prickles are projections from cortex and thorns are modified stems (Tomlinson et al. 2016; Barton 2016). Physical plant defences have been suggested to deter herbivory and affect foraging behaviour by decreasing browsing rate (Papachristou et al. 2003; Wigley et al. 2015; Barton 2016). Goats browsing on the woody plants that were physically defended showed lower foraging rate than those that were not physically defended (Gowda 1996). Examples of woody encroacher species with spines include *V. sieberiana*, with prickles include *S. Senegal*, and with thorns include *Gymnosporia senegalensis*. The function of thorns in *Vachellia* species has been reported as a protection of stems rather than leaves (Midgely et al. 2001).

Trade-offs between defence and growth

The survival and reproduction of plants depend on growth and defence of the plant. Plants have evolved and developed strategies to balance growth and defence (Huot et al. 2014; Barton 2016). Therefore, trade-offs between growth and defence have significant ecological impact (Huot et al. 2014). Plants depend on defence to protect them from herbivores and these defences are the results of resources that they invested at the cost of growth and reproduction (Rodner and Ward, 1997: Koricheva 2002; Ferrenberg et al. 2015; Sebeta 2016). Fast growing plants invest less in defence than slow growing plants and these effects are more noticeable for seedlings and saplings than for adult plants (Endara and Coley 2011). In contrast, plants growing in fertile soils can invest resources more in constitutive defences (Stamp et al. 2003). Constitutive defences are defences that are always present on the plant as compared to induced defences which are produced by plants when the plant is injured or attacked. However, plants can invest in both growth and defence at the same time (Mundim et al. 2017).

The other factor that contributes to trade-offs between growth and defence is competition for nutrients from other plants (Züst et al. 2015). Nutrient availability is the major determinant in trade-offs between growth and defence of woody plants (Mundim et al. 2017). Grasses strongly compete with woody seedlings for resources and suppress woody seedling growth, and resources are diverted to defence due to low resource availability (Wigley et al. 2015). Clearing of grass cover results in high woody seedling growth due to competitive release (Meli et al. 2015). Yet plants growing without neighbours can invest more resources in defence than the ones with neighbours (Cipollini 2010; Fernandez et al. 2016), because the manufacture of physical defences that deter herbivory is not cheap in the presence of neighbouring plants (Cipollini 2010).

Conclusion

The knowledge of the causes of bush encroachment in a changing climate are very important in agriculture and wild life conservation (O'Connor et al. 2014). Herbivory, global warming, carbon dioxide and nutrient availability are suggested to be some of the major contributors in promoting bush encroachment. Warming increases the growth of woody seedlings, while grass cover reduces the growth of woody seedlings. The defence of these encroaching species may play an important role in deterring herbivores such as goats that are used to control bush encroachment.

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CHAPTER 3: EFFECT OF ELEVATED TEMPERATURES IN DIFFERENT SEASONS ON GROWTH AND DEFENCE OF *VACHELLIA SIEBERIANA* SEEDLINGS GROWN WITH OR WITHOUT GRASS

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Abstract

The effects of rising temperature on grasslands have been studied utilizing open-top warming chambers (OTCs), but little is known of warming effects on growth and defence of woody seedlings that potentially invade grasslands. Predictions that elevated temperatures would increase growth and thorn length of *Vachellia sieberiana* seedlings growing (1) with or without grass in the dormant season and early growing season, but (2) in the later part of the growing season only when grass cover is absent were tested. To test these predictions, 120 three-week old seedlings were transplanted into 20 field plots in July 2017 (dormant season) and October 2017 (start of the growing season). Ten plots were warmed and ten plots were not warmed. Each plot was either cleared of grass or not. Open-top warming chambers raised air temperature by 1.0 to 2.5 °C. Stem length, plant height, stem diameter, thorn length, biomass of shoot, leaf, root and total plant were measured after six weeks for the dormant season, and after six weeks and twelve weeks in the growing seasons. Study predictions were not consistently supported. Warming increased plant height, stem length, and stem diameter in early and late growing seasons, and only stem diameter in the dormant season. The increase of shoot, leaf, root and total biomass was only found during the dormant season and late growing season. In the dormant season thorn length was longer in warmed plots irrespective of grass cover, while in the growing season longer thorn length were only found in the absence of grass cover.

Warming to a level expected in the next few decades clearly was more beneficial than grass cover removal for *V. sieberiana* seedling growth irrespective of seasons. The results imply that whatever the future scenario is, in terms of warmer climate, *V. sieberiana* will thrive irrespective of grass cover.

Keywords: Climate change, dormant season, growing seasons, open-top warming chamber, spinescence, woody encroachment

Introduction

Change in global climate is causing an increase in the daily, seasonal and annual mean air temperatures to which plants are subjected (Yamori et al. 2014). The increasing greenhouse gases in the atmosphere are predicted to raise mean temperatures up to 4.5 °C in the near future (IPCC 2014). This rise in mean air temperature is suggested to result in a longer growing season, higher fecundity, and higher biomass allocation towards roots by plants and possible transformation of grasslands to savannas (Scheiter and Higgins 2009). Elevated temperatures increase the growth of woody plants. However the effect of elevated temperatures on woody plants have been mainly studied on adult plants. Therefore, there is little information on how southern African savanna woody seedlings will respond to the warming climate. Responses in woody seedling growth and defence to global warming will possibly depend on many factors, which include competition for resources with grasses, as well as season. For example, grasses compete better with woody seedlings for resources (Wagner et al. 2018) and during the growing season, competition can be intense while in the dormant season where grasses are not actively growing, woody seedlings may outcompete grasses (Bargués et al. 2017).

Woody legumes are notorious invaders of rangelands, reducing their ecosystem services such as grass production (Stafford et al. 2017) and they are a threat to food security due to reduction of agro-ecosystems. They are the threat to food security because they decrease grazing capacity which results in low production of red meat and milk. Therefore, the knowledge of how these woody seedlings will respond to elevated temperatures may help in the future conservation and management of rangeland (Thuiller et al. 2008).

Elevated temperatures are expected to be greater in winter and spring than summer and autumn, and warming effects have been shown to be seasonal (Andersen et al. 2017; Asse et al. 2018). Elevated temperatures can enhance growth in height of woody seedlings (Lett et al. 2017; Gamm et al. 2018). Warming has more effects on shoot length, leaf biomass and stem biomass of different woody seedlings during the mid-growing season than early growing season (An et al. 2017). Even a low increase in minimum air temperature enhances the growth of woody plants during the growing season (Camac et al. 2017). Consequently, enhancement of woody seedlings growth under elevated temperatures is due to biochemical processes, like photosynthesis and respiration, due to their high rate of enzyme function when exposed to warming (Way and Oren 2010).

Growth is important for a woody seedling to reach reproductive age or size as fast as possible (Gleason et al. 2018), while the presence of herbivores requires plants to invest resources in defences (Coley et al. 1985; Wigley et al. 2018). However, the diversion of resources to defence is costly for plants because plants need resources to grow and reproduce (Coley et al. 1985; Herms and Mattson 1992; Koricheva 2002; Moreira et al. 2015; Wigley et al. 2018). In addition to investment in defence, another factor that reduces plant growth is competition. Under elevated temperatures, competition effects supress plant growth, whereby an individual plant is disadvantaged by its neighbour's presence (Adler et al. 2009; Dohn et al. 2017). Additionally, savanna woody plant growth rate decreases in the presence of neighbours compared to the absence of neighbours (Dohn et al. 2017). Furthermore, the absence of grass cover promotes *Vachellia sieberiana* seedling establishment and high biomass due to both absence of grass cover and high availability of light and moisture (Grellier et al. 2012). Therefore, grass can suppress the woody seedling growth (Kambutuku et al. 2011).

A small increase in temperature benefits the growth of woody seedlings during the dormant season when plant growth is limited by low temperatures (Way and Oren 2010). During the dormant season and early part of the growing season warming benefits woody seedlings because grasses are less competitive for water at the time (Bargués et al. 2017; Wagner et al. 2018). Yet in the later stage of the growing season grasses pose strong competition to woody seedlings due to high accumulation of biomass (Wagner et al. 2018). Woody plants generally start to grow before the grasses because they have more water stored in their roots and stems and have tap roots that may be able to access water at deeper soil depths (Whitecross et al. 2017; Holdo et al. 2018). *Vachellia* seedlings have high root/shoot ratios when they are subjected to dry condition in the presence of grass cover, implying that woody seedlings have an advantage over grasses when accessing water and other resources (Chirara 2001).

The effects of rising temperature on grasslands have been studied utilizing open-top warming chambers (OTCs), however little research has been done on the effect of warming in different seasons on the growth of woody plants that potentially invade grasslands. Thus, since woody plant growth is potentially affected by investment in defence and competition from grasses, the objective of the study was to determine the effect of warming on woody seedling growth and defence when growing with or without grass competition in the dormant season and at different stages of the growing season. It was predicted that elevated temperatures would increase growth and thorn length of *Vachellia sieberiana* seedlings growing (1) with or without grass in the dormant season and early growing season, but (2) in the later part of the growing season only when grass cover is absent.

Materials and methods

Study site

Field experiments were carried out at a fenced site at Ukulinga Research Farm of the University of KwaZulu-Natal, Pietermaritzburg, South Africa (29°24'E, 30°24'S). The site receives a mean annual rainfall of 694 mm, with most of it occurring between September and April. The place experience the mean maximum temperature of 26.4 °C during growing season in February, while winters are not too cold with 8.8 °C mean minimum temperature and some frost in July. The growing season is from October to April. The vegetation is classified as grassland biome (Rutherford and Westfall 2003), and the site is classified as Natal Mist Belt 'Ngongoni Veld, dominated by *Themeda triandra*, *Aristida junciformis*, and *Tristachya leucothrix* (Acocks 1988), that falls into the transition zone between Ngongoni Veld and KwaZulu-Natal Hinterland thornveld (Mucina and Rutherford 2006). Westleigh soil forms are dominant at Ukulinga (Soil Classification Working Group 1991), with permanent field capacity of 228–233 $mm \cdot m^{-1}$ and wilting point of 172–194 $mm \cdot m^{-1}$. The soil is clay loam, with clay content increasing from 29% to 35% with depth (Moodley et al. 2004).

Seed collection and germination

Seeds of *Vachellia sieberiana* were collected from different parent trees around Pietermaritzburg. Two hundred seeds of *V. sieberiana* were soaked for 30 minutes in sodium hypochlorite (4% concentration) and put in a beaker with a magnetic stirrer for sterilization of the seed coat for 30 min. Then, promotion of seed germination was done by scarifying the seeds using nail clippers. Agar gel was prepared by adding 8 grams of nutrient agar powder into 1000 millilitre (mL) of water in a 2000 mL beaker then put in a microwave oven for 5 min with occasional stirring. The agar gel was then transferred to Petri-dishes and the gel was allowed 15 min to properly set. Scarified seeds were placed in the gel and the Petri-dishes were sealed with Parafilm® immediately. After a week the germinated seeds were transplanted into plastic pots that were 1.0 litre (L) in volume and filled with sandy soil in a greenhouse at the University of KwaZulu-Natal, Pietermaritzburg, South Africa, and grown for three weeks. Water was provided to the seedlings every two days. Eighty seedlings were oven dried for 48 hours (hrs) at 60 °C to provide data for developing a regression model so that initial plant dry biomass in milligrams (mg) at the start of the experiment could be determined from stem diameter measurements.

Experimental design

One hundred and twenty seedlings at a mean height, stem diameter and total biomass of 133 mm (SEM; ± 1.7), 2.12 mm (SEM; ± 0.03) and 798.40 mg (SEM; ± 76.64), respectively, were transplanted into field plots that were either cleared of grass or not in July 2017 (dormant season). In October 2017 (start of the growing season), the same procedure was used, but seedlings had a mean height, stem diameter and total biomass of 135 mm (SEM; ± 2.60), 2.16 mm (SEM; ± 0.03) and 862.60 mg (SEM; ± 76.56), respectively. The plots to which seedlings were transplanted were 2 m x 2 m, and were separated from each other by 1 m. A fully crossed randomised design was used to assign treatments, which were grass present, grass absent, warming and no warming. In plots with no grass, the grass was removed to ground level with a spade from the base of the grass plant and its roots were left intact so it could regrow. Dominant grass species on plots with grass were *Themeda triandra*, *Eragrostis capensis* and *Sporobolus africanus*. To simulate temperatures expected in the future (IPCC 2014), open-top warming chambers were randomly assigned to ten plots, while the other ten plots were not warmed. The OTC design that was utilised in this study was based on the design of the International Tundra Experiment (Molau and Magaard 1996). The chambers were constructed of clear polycarbonate sheets (Maizey Plastics, Pietermaritzburg, South Africa) that had a light transmittance of 90% and was 2 mm thick (https://www.maizey.co.za/; Buhrman et al. 2016).

Ambient temperature was increased by 1.0 °C during the growing season and by 2.5 °C during the dormant season, according to data collected by use of temperature loggers placed inside and outside the OTCs. Six *V. sieberiana* seedlings were transplanted into each plot. In plots with OTCs, seedlings were planted 30 cm apart and 40 cm in from the base of the OTC.

In the remaining plots, the same configuration of seedlings was followed. In cleared plots, grass was removed from the hexagonal area under the OTC or, if no warming was applied to the plot, then from an area that would have been covered by an OTC. Plots with no grass were weeded every fortnight and 500 ml water supplied to each seedling periodically to facilitate establishment for ten days.

Plant height, stem length, stem diameter and length of the longest thorn were measured in early September 2017, early December 2017 and mid-January 2018. The plant height and stem length were measured, rather than just one of them because plant height alone can be misleading if the plant leans to one side. The seedlings planted in July were all harvested in early September 2017, but of those planted in October, half were randomly selected and harvested in early December 2017 and the remainder were harvested in January 2018. A 30 cm ruler was used to mark an area of 400 cm^2 above ground in order to collect all the roots that were within the area since it is not practical to collect all the roots in the field. A spade was used to dig the seedlings out to harvest the roots. Harvested plants were oven-dried at 60 °C for 48 hours. Leaves, roots and thorns were separated from shoots and weighed.

Statistical Analysis

The IBM SPSS statistical software version 25 (www.spss.com) was used to conduct statistical analysis. Two-way ANOVA was used to test the effects of warming as the first independent variable (factor) with two levels (i.e. warming vs no warming) and grass competition as another factor with two levels (i.e. with vs. without grass cover). All measured variables were used in the ANOVA as dependent variables. Data from each experimental period were analysed separately. Variables that were not normally distributed were successfully $\log_{10}$ transformed for analysis. Bonferroni *post hoc* test was used to compare means. Significance was declared when $p < 0.05$.

Results

In the dormant season, none of the measured variables was significantly affected by the interaction between warming and grass cover (Table 3.1). Plant height was not affected by either warming or grass cover. Warming significantly increased stem diameter (2.63 mm ± 0.07 vs 2.13 mm ± 0.09), shoot biomass (442.00 mg ± 14.45 vs 334.00 mg ± 8.88), root biomass (564.06 mg ± 13. 19 vs 421.75 mg ± 14.67), total biomass (1040.75 mg ± 27.78 vs 805.95 mg ± 23. 58) and thorn length (4.89 mm ± 0.37 vs 3.3 mm ± 0.25) (Tables 3.1), but reduced leaf biomass (40.11 mg ± 5.33 vs 50.20 mg ± 8.38). Grass cover significantly reduced shoot biomass (367.50 mg ± 17.91 vs 395.23 mg ± 20.74), root biomass (478.75 mg ± 27.67 vs 495.00 mg ± 24.97) and total biomass (888.50 mg ± 43.01 vs 937.96 mg ± 44.93) (Table 3.1).

In the early growing season warming and grass cover had significant interacting effects on thorn length resulting in longer thorns when grass cover was absent under warming (Figure 3.1). Warming significantly increased plant height (248.63 mm ± 14.50 vs 216.95 mm ± 10.58), stem length (228.44 mm ± 12.80 vs 191.97 mm ± 11.14) and stem diameter (3.48 mm ± 0.13 vs 2.87 mm ± 0.27) (Table 3.2). Shoot biomass, leaf biomass, root biomass and total biomass were not significantly affected by either warming or grass cover (Table 3.2). During the later stage of growing season warming and grass cover had significant interacting effects on thorn length resulting in longer thorns when grass cover was absent under warming (Figure 3.2). Warming significantly increased plant height (377.98 mm ± 23.29 vs 286.82 mm ± 21.12), stem length (345.72 mm ± 19.91 vs 256.09 mm ± 19.45), stem diameter (3.87 mm ± 0.18 vs 2.77 mm ± 0.80), leaf biomass (833.89 mg ± 176.83 vs 469.26 mg ± 69.89), shoot biomass (1596.97 mg ± 376.23 vs 662.52 mg ± 90.87), root biomass (1942.30 mg ± 226.43 vs 960.71 mg ± 134.19) and total biomass (4373.16 mg ± 670.39 vs 2092.49 mg ± 263.39) (Table 3.3). The grass cover significantly reduced shoot biomass (367.50 mg ± 17.91 vs 395.23 mg ± 20.74), leaf biomass (406.26 mg ± 70.65 vs 847.82 mg ± 151.12) and total biomass (2299.92 mg ± 336.85 vs 3979.15 mg ± 682.09) (Table 3.3).

Discussion

Effect of warming on woody plant growth and defence

The first prediction that warming would increase the growth and defence during the dormant season and early-growing season was not consistently supported by the study results. During the early-growing season, only plant height, stem length, stem diameter and thorn length of seedlings were affected positively by warming. The current study result showed stem diameter, shoot biomass, leaf biomass, roots biomass and total biomass increase during the dormant season under warming. Thorn length was longer in treatments that were warmed with or without grass. One possible reason could be that plants can experience heat stress when temperatures are high, affecting many biochemical and physiological processes which control growth of plants, as a result of that stem height, leaf biomass, and stomatal conductance decrease (Mu et al. 2018; Meineke and Frank 2018). Another reason could be that grass cover poses strong competition to seedlings during the early-growing season, while during the dormant season grasses are not active enough to compete with *V. sieberiana* seedlings. Additionally, resources were abundant to be invested to both growth and defence. Similarly, Mundim et al. (2017) argue that plants can invest in both growth and defence at the same time. The possible reason for the low thorn length of seedlings on plots warmed and growing with grass in the early-growing season could be the competition with grass, with resources allocated to growth in order to escape competition (Herms and Mattson 1992).

Way and Oren (2010) suggested that elevated temperatures could increase woody plant growth irrespective of water stress and resource availability due to acclimation of woody plants to warming. This could be one of the reasons that the study found high stem diameter, shoot, root and total biomass during the dormant season. However, the low leaf biomass under warming and absence of grass cover during the dormant season could be due to decrease in water content which resulted in high transpiration rate (Sardans et al. 2008). In contrast, much of the biomass is allocated to leaf biomass when woody plants are exposed to warming (Way and Oren 2010; Sivadasan et al. 2018). The increase in growth of woody seedling in dormant and growing seasons under warming treatments in this study have been found in other studies (Way and Oren 2010; An et al. 2017; Li et al. 2017; Carlson et al. 2018).

The second prediction that warming would increase woody seedlings growth and defence only when grass cover is absent was not consistently supported by results because growth was high irrespective of grass cover but defence was high in the absence of grass cover. Competition of grass cover to woody seedlings could be the major contributor for not finding support for the second prediction, that high growth and defence will be achieved in the absence of grass cover in mid-growing season. However, the high growth during the mid-growing season is similar to the findings of An et al. (2017). They found that elevated temperatures increased shoot length, leaf biomass, and stem biomass of *Quercus variabilis* seedlings, while shoot length and leaf biomass increase was found during the mid-growing season compared to the early-growing season (An et al. 2017). The reason for high growth during the mid-growing season at 1.0 °C could be that seedlings were experiencing strong competition from grass and were seeking to escape shade from grass (Payne 2008).

Another reason that could contribute to high growth increase could be soil moisture. Meineke and Frank (2018) suggested that warming can increase the growth rate and photosynthesis of woody plants when there is sufficient water availability and temperatures are not higher than that required for physiological activities of plants. This could be another reason for biomass increase in the mid-growing season than the early-growing season, since high rainfall was received in later stages of the growing season than the early-growing season. Dev (2012) suggested that C_4 plants performed better under rain availability during the mid-growing season. Sonko et al. (2016) found that soil nutrients were more abundant during the growing season than dormant season, and indicated that soil moisture is more available during the growing season than dormant season, implying that plants can have high growth when there is high soil moisture.

Furthermore, elevated temperatures enhance the nitrogen fixation by woody plants (Wang et al. 2018). These could be the reasons for high root biomass on warmed plots in both the dormant season and later stage of the growing season, and *Vachellia sieberiana* is a legume species that can fix nitrogen. However, Way and Oren (2010) are in disagreement with the study results, because they found that elevated temperatures reduce root biomass.

The seedling stage of woody plants is important for plant population dynamics as they lack the structural strength of mature plants, and therefore they need to grow fast and establish roots so that they can compete for resources and develop physical and chemical defences to deter herbivory (Perez-Sanchez et al. 2015). Warming increased thorn length in the mid-growing season when grass cover was absent, which supported part of the second prediction. Plants in the control plots without grass competition were the second most defended in the growing season, which may be due to abundant resources which were allocated to both growth and defence. However, Wigley et al. (2018) suggested that most defence theory is based on chemical defence and there is less knowledge on physical defence like thorn length. We are unaware of any study that investigated the effect of elevated temperatures and grass competition on structural defence particularly thorn length. In contrast to our findings, plants prioritise growth when there is high resource availability and defence when there is resource limitation, however these suggestions do not specify the difference between above and below ground plant production (Mundim et al. 2017).

Conclusion

Warming to a level expected in the next few decades clearly was more beneficial than grass cover removal for *V. sieberiana* seedlings growth irrespective of seasons. Our study suggest that, regardless of grass cover at the time of seedling establishment during the dormant season and growing season, the rate of woody plant encroachment will increase as temperature rises.

In the absence of grass cover and a temperature increase of 1.0 – 2.5 °C, high growth and thorn length of *V. sieberiana* seedlings was shown. Mundim et al. (2017) argue that plants can invest in both growth and defence simultaneously. However, when conditions are the same in the presence of grass cover, woody seedlings have high growth and possess less defence or low thorn length during the growing season. The findings showed that there is a possibility of increased forage availability for browsers during the growing season since thorn length is the primary line of defence against browsers foraging on leguminous woody plants in semi-arid savannas of southern Africa.

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Table 3.1: Analysis of variance of plant height (mm), stem diameter (mm), thorn length (mm), shoot biomass (mg), leaf biomass (mg), root biomass (mg) and total biomass (mg) of *V. sieberiana* seedlings during the dormant season

Dependent variable	Source of variation	df	Mean Square	F-ratio	P-value
Plant height	Warming	1	190.615	0.687	0.420
	Grass	1	620.136	2.236	0.156
	Warming*Grass	1	98.023	0.353	0.561
	Error	15	277.332		
Stem diameter	Warming	1	0.209	52.250	**<0.001**
	Grass	1	0.010	2.500	0.143
	Warming*Grass	1	0.006	1.500	0.953
	Error	15	0.004		
Shoot biomass	Warming	1	58716.739	121.532	**<0.001**
	Grass	1	14452.316	29.913	**<0.001**
	Warming*Grass	1	641.739	1.328	0.267
	Error	15	483.139		
Leaf biomass	Warming	1	7403.088	86.303	**<0.001**
	Grass	1	0.935	0.011	0.918
	Warming*Grass	1	2.954	0.034	0.855
	Error	15	85.780		
Root biomass	Warming	1	105061.226	139.748	**<0.001**
	Grass	1	18245.841	24.270	**<0.001**
	Warming*Grass	1	1892.596	2.517	0.133
	Error	15	751.792		
Total biomass	Warming	1	297043.670	119.636	**<0.001**
	Grass	1	68198.900	27.467	**<0.001**
	Warming*Grass	1	10.155	0.004	0.950
	Error	15	2482.901		
Thorn length	Warming	1	5.219	6.014	**0.040**
	Grass	1	1.169	1.347	0.279
	Warming*Grass	1	0.853	0.983	0.350
	Error	8	0.868		

Bold numbers mean significance

Table 3.2: Analysis of variance of plant height (mm), stem length (mm), stem diameter (mm), thorn length (mm), shoot biomass (mg), leaf biomass (mg), root biomass (mg) and total biomass (mg) of *V. sieberiana* seedlings during the early-growing season

Dependent variable	Source of variation	df	Mean Square	F-ratio	P-value
Plant height	Warming	1	4722.258	4.901	**0.043**
	Grass	1	508.230	0.528	0.479
	Warming*Grass	1	2935.473	3.047	0.101
	Error	15	963.455		
Stem length	Warming	1	6412.874	7.320	**0. 016**
	Grass	1	772.790	0. 882	0. 363
	Warming*Grass	1	2019.786	2.305	0. 150
	Error	15	876.105		
Stem diameter	Warming	1	2.083	23.090	**<0.001**
	Grass	1	0.004	0.049	0.827
	Warming*Grass	1	0.074	0.818	0.380
	Error	15	0.090		
Log shoot biomass	Warming	1	0.031	1.579	0.228
	Grass	1	0.067	3.432	0.084
	Warming*Grass	1	0.043	2.169	0.161
	Error	15	0.020		
Log leaf biomass	Warming	1	0.055	1.712	0.210
	Grass	1	0.006	0.200	0.661
	Warming*Grass	1	0.010	0.298	0.593
	Error	15	0.032		
Log root biomass	Warming	1	0.029	0.443	0.516
	Grass	1	0.0002	0.003	0.949
	Warming*Grass	1	0.001	0.015	0.894
	Error	15	0.066		
Total biomass	Warming	1	1057686.982	2.467	0.137
	Grass	1	10059.648	0.023	0.880
	Warming*Grass	1	919863.429	2.146	0.164
	Error	15	428656.173		
Thorn length	Warming	1	4.349	1.300	0.272
	Grass	1	4.271	1.277	0.276
	Warming*Grass	1	15.531	4.644	**0.048**

Error	15	3.344

Bold numbers mean significance

Table 3.3: Analysis of variance of plant height (mm), stem length (mm), stem diameter (mm), thorn length (mm), shoot biomass (mg), leaf biomass (mg), root biomass (mg), and total biomass (mg) of *V. sieberiana* seedlings during the mid-growing season

Dependent variable	Source of variation	df	Mean Square	F-ratio	P-value
Plant height	Warming	1	33572.367	7.953	**0.014**
	Grass	1	5570.911	1.320	0.270
	Warming*Grass	1	6515.256	1.543	0.235
	Error	14	4221.575		
Stem length	Warming	1	32864.741	9.913	**0.007**
	Grass	1	4574.846	1.380	0.260
	Warming*Grass	1	4764.519	1.437	0.251
	Error	14	3315.466		
Stem diameter	Warming	1	5.197	32.465	**<0.001**
	Grass	1	0.405	2.532	0.134
	Warming*Grass	1	0.149	0.930	0.351
	Error	14	0.160		
Log shoot biomass	Warming	1	0.391	10.480	**0.006**
	Grass	1	0.581	15.544	**0.001**
	Warming*Grass	1	0.090	2.408	0.143
	Error	14	0.037		
Leaf biomass	Warming	1	524292.962	4.660	**0.049**
	Grass	1	866553.323	7.702	**0.015**
	Warming*Grass	1	161337.981	1.434	0.251
	Error	14	112514.125		
Root biomass	Warming	1	4135851.129	12.839	**0.003**
	Grass	1	375122.652	1.165	0.299
	Warming*Grass	1	103254.389	0.321	0.580
	Error	14	322127.727		
Total biomass	Warming	1	20935268.445	14.340	**0.002**
	Grass	1	12532584.820	8.584	**0.011**
	Warming*Grass	1	4381553.700	3.001	0.105
	Error	14	1459938.426		
Thorn length	Warming	1	9.889	0.984	0.338
	Grass	1	149.082	14.830	**0.002**
	Warming*Grass	1	56.803	5.650	**0.032**

Error	14	10.053

Bold numbers mean significance

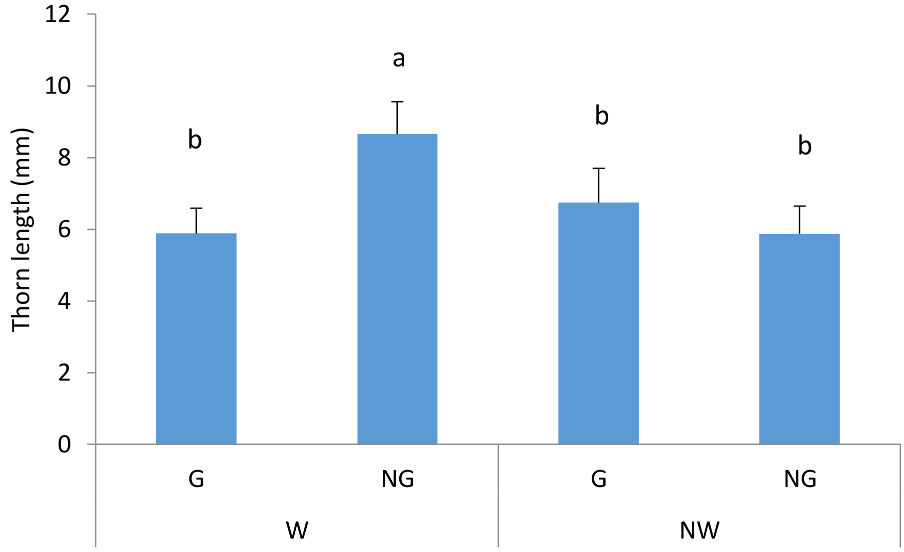

Figure 3.1: Mean thorn length of *Vachellia sieberiana* seedlings grown with or without warming (W vs NW), and with or without grass cover (G vs NG) during the early-growing season (n = 5). Error bars represent standard errors of the means. Letters above error bars indicate significant differences ($p < 0.05$).

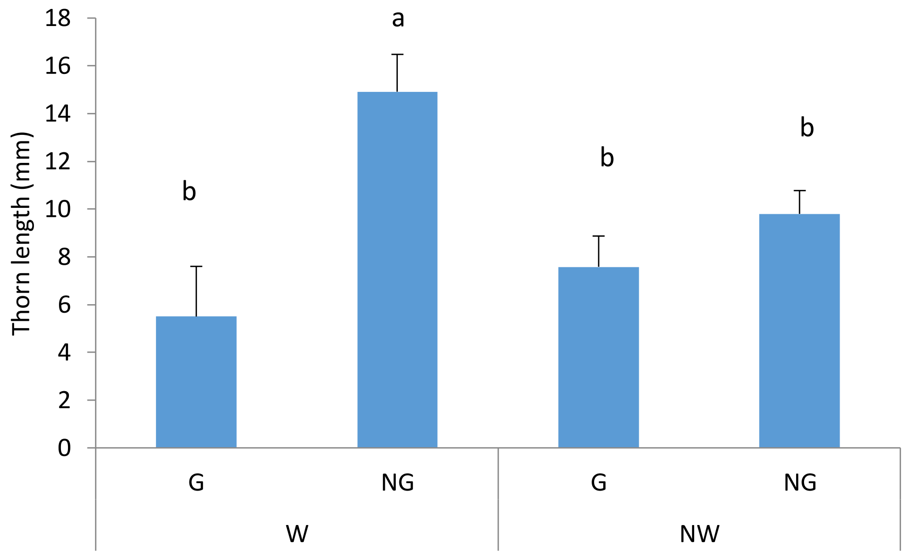

Figure 3.2: Mean thorn length of *Vachellia sieberiana* seedlings grown with or without warming (W vs NW), and with or without grass cover (G vs NG) during the mid-growing season (n = 5). Error bars represent standard errors of the means. Letters above error bars indicate significant differences ($p < 0.05$).

CHAPTER 4: WARMING EFFECT ON TRADE-OFFS BETWEEN GROWTH AND DEFENCE OF *VACHELLIA SIEBERIANA* SEEDLINGS GROWING WITH OR WITHOUT GRASS

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Abstract

Little is known about the effect of warming on the trade-offs between growth and physical defence particularly thorn length of woody plants that potentially invade grasslands of southern Africa. This study tested the hypothesis that elevated temperatures would decrease thorn length in relation to growth of *Vachellia sieberiana* seedlings only when grass cover is absent. To test the hypothesis, 120 seedlings that were three weeks old were transplanted into 20 field plots in March 2018. Ten plots were warmed with open-top chambers (OTC) and ten plots were not warmed. Each plot was either cleared of grass or not. Open-top warming chambers raised air temperature by 1.5 °C. Plant height, stem length, stem diameter and thorn length were measured after six weeks. To determine effects of warming and grass cover on the relationship between defence and growth, ratios of thorn length (a measure of defence) to plant height, stem length and stem diameter (measures of growth) were calculated. Warming and grass cover significantly and independently reduced the thorn length: plant height ratio. Likewise, the thorn length: stem length ratio was significantly and independently reduced by both warming and grass cover. There was a significant interaction effect between warming and grass on the thorn length: stem diameter ratio. Warming significantly reduced the thorn length: stem diameter ratio when grass cover was present, but not when grass cover was absent. Warming to a level expected in the next few decades clearly was more effective than grass cover removal for *V. sieberiana* seedlings growth and defence relationship. Our results

suggest that in veld that has good grass cover the forage for browsers will increase, but not when the veld has poor grass cover as temperature rises to 1.5 °C.

Key words: climate change, open-top warming chamber, physical defence, spinescence

Introduction

Temperature is one of the vital abiotic factors that will determine the responses of woody plants to climate change (Randriamanana et al. 2015). Global mean minimum air temperatures are increasing and are expected to rise by up to 4.5 °C by 2050 due to the increase in greenhouse gases in the atmosphere (IPCC 2014). While the semi-arid regions of southern Africa will experience a minimum increase of 1.6 °C by 2050 (IPCC 2014), it is not clear how woody plant resource partitioning will be affected by this predicted increase.

Investment of resources in defence is assumed to trade-off with plant growth (Koricheva 2002; Moles et al. 2013). While most documented literature has been focused on trade-offs between growth and chemical defence, most of the encroaching southern African leguminous woody plants rely on physical defence to deter large herbivores (Wigley et al. 2015). With limited knowledge of trade-offs between growth and physical defence, it is not easy to understand the effect of warming on growth and physical defence, particularly thorn length. Thus, it is vital to improve the understanding of the trade-offs between plant growth and defence.

Theoretically, woody plants need to grow as fast as possible to avoid suppression by their neighbours while simultaneously defending themselves from herbivores (Ballaré 2014). The allocation of resources to growth can cost defence, and allocation to defence can suppress growth and reduce competitive ability against neighbours (Herms and Mattson 1992; Cipollini 2004; Ballaré 2014). Plants in infertile soils invest in defences because they grow slowly and cannot regrow rapidly after herbivory (Endara and Coley 2011; Moreira et al. 2014). They grow slowly because of low resource availability (Endara and Coley 2011).

Plants and herbivores coevolved, with woody plants developing physical and chemical defences against herbivores (Du Toit 2003; Mkhize et al. 2015). When resources are invested in physical defence, savanna woody plants benefit because thorns have been shown to decrease browsing rate (e.g Wigley et al. 2015; Gowda 1996; Milewski et al. 1991; Cooper and Owen-Smith 1986). The possible consequence may be that resources used to develop physical defences could have been allocated to plant growth in the absence of herbivory.

The other factor that contributes to trade-offs between woody plant growth and defence is competition for resources from other plants (Züst et al. 2015). Grasses strongly compete with woody seedlings for resources and suppress woody seedling growth and resources are diverted to defence due to low resource availability (Wigley et al. 2015). There is evidence that clearing of grass cover results in high woody seedling growth due to competitive release (Meli et al. 2015). Yet plants growing without neighbours can invest more resources in defence than the ones with neighbours (Cipollini 2010; Fernandez et al. 2016). That is because the manufacture of physical defences that deter herbivory is not cheap in the presence of neighbouring plants (Cipollini 2010).

Although trade-offs between woody plant growth and chemical defence have been studied in southern Africa (Wigley et al. 2015), little is known about the effect of warming on trade-offs between growth and physical defence. Additionally, it is not known how woody plant growth and physical defences will respond to the predicted elevated temperatures (Kgope et al. 2010). The aim of the study was to determine the effect of warming on trade-offs between woody seedling growth and defence when growing with or without grass. To achieve this aim, Open Top Chambers (OTCs) were used to test the hypothesis that, warming, with or without grass cover increases seedling growth (Chapter 3), and then elevated temperatures would decrease thorn length in relation to growth of *Vachellia sieberiana* seedlings only when grass cover is absent.

Materials and methods

Study site

The field trial was conducted at Ukulinga Research Farm of the University of KwaZulu-Natal, Pietermaritzburg, South Africa (29°24'E, 30°24'S). The mean annual rainfall is 694 mm, mostly occurring from September to April. There is high temperature during the growing season with mean maximum temperature of 26.4 °C in February; winters are cool with 8.8 °C mean minimum temperature in July. The growing season normally runs from October to April. Vegetation type is described as Grassland biome by Rutherford and Westfall (2003) and classified as Natal Mist Belt 'Ngongoni Veld with the dominance of *Themeda triandra, Aristida junciformis*, and *Tristachya leucothrix* (Acocks 1988). According to Mucina and Rutherford (2006), it falls into the transition zone between Ngononi Veld and KwaZulu-Natal Hinterland thornveld. The soil form that dominates the farm is Westleigh as classified by Soil

Classification Working Group (1991) with field capacity ranging between 228–233 mm·m^{-1} and permanent wilting point between 172–194 mm·m^{-1}. According to Moodley et al. (2004), the soil texture is a clay loam, with clay content increasing from 29% to 35% with depth.

Seed collection and germination

Seed collection was done around Pietermaritzburg to get a total of 200 seeds of *V. sieberiana* from different parent trees. Seeds were soaked in sodium hypochlorite (4% concentration) for 30 minutes and put in a beaker with magnetic stirrer for 30 minutes in order to sterilize them. The seeds were scarified using nail clippers in order to break the seed coat and promote seed germination. The preparation of agar gel was done by mixing 8 g of nutrient agar powder with 1000 mL of water in a 2000 mL beaker then boiled in a microwave oven for 5 minutes with occasional stirring, followed by transferring it to Petri-dishes to set for 15 minutes. The scarified seeds were put in Petri dishes with the gel and properly sealed with Parafilm®. Germination occurred after seven days and seeds were transplanted to 1 L plastic pots filled with sandy soil in a greenhouse of the University of KwaZulu-Natal, Pietermaritzburg, South Africa, and were allowed to grow for 21 days. Watering was done every two days. A sample of eighty seedlings was harvested and oven dried for 48 hrs at 60 °C in order to provide data for development of a regression model to determine initial plant dry biomass in milligrams (mg) from stem diameter measurements prior to the field experiment.

Experimental design

In March 2018, 120 seedlings of *V. sieberiana* were transplanted to 20 field plots. In each plot, six seedlings were transplanted. Each plot was 4 m^2 and 1 m apart from each other. Each plot contained six seedlings of *V. sieberiana* with inter-plant spacing of 30 cm. The experimental site was dominated by *Themeda triandra*, *Eragrostis capensis* and *Sporobolus africanus* grasses. The seedlings had a mean height of 157 mm (SEM: 2.6), stem diameter of 1.85 mm (SEM: 0.029) and total biomass of 343.5 mg (SEM: 3.02) at planting. Treatments were assigned based on grass and warming in a fully crossed randomised design, namely grass present, grass absent, warming and no warming. Ten plots had grass removed from the surface using a spade. The study used open top chambers (OTCs) based on the design of the International Tundra Experiment (Molau and Magaard 1996). The OTCs were randomly assigned to ten plots to simulate temperatures expected in the next few decades (IPCC 2014). The OTCs were made up of polycarbonate clear sheet (Maizey Plastics, Pietermaritzburg, South Africa) with a light transmittance of 90% and 2 mm thickness (maizey.co.za; Buhrman et al. 2016). In plots with OTCs, seedlings were planted 30 cm apart and 40 cm in from the base of the OTC and in all the plots without OTC same procedure was followed. Temperature loggers were placed inside and outside the OTCs to capture temperature data. The ambient temperature was increased by 1.5 °C by the OTCs. Weeding was done fortnightly using a spade on plots without grass cover. All seedlings received 500 ml of water for ten days to facilitate establishment. In early May 2018, data on plant height, stem length, stem diameter and the longest thorn length was collected. Plant height and stem length were measured because measuring of one of them can be misleading when the plant is leaning to one side.

Statistical analysis

Two-way analysis of variance (ANOVA) was conducted to test warming and grass effects as independent factors with two levels (warming against no warming, grass cover against no grass cover, respectively). The statistical analysis was done using IBM SPSS statical software version 25 (www. spss.com). To determine effects of warming and grass cover on the relationship between defence and growth, ratios of thorn length (a measure of defence) to plant height, stem length and stem diameter (measures of growth) were calculated and subjected to 2-factor ANOVA. This was done instead of regression analysis of thorn length on each growth variable because of the low number of replicates. The reduction in these ratios by either factor in terms of the trade-off between growth and defence suggest amplification of the trade-off, while an increase would suggest the opposite. Variables were normally distributed and therefore did not require transformation for analysis. Bonferroni post hoc test was used to compare means. Significance was declared when $p < 0.05$.

Results

There was a significant interaction effect between warming and grass on the thorn length: stem diameter ratio, resulting in longer thorn length when grass cover was absent under warming (Table 4.1 and Figure 4.1). Independently, warming and grass cover significantly reduced the thorn length: plant height ratio (0.031 ± 0.004 vs 0.039 ± 0.003 and 0.026 ± 0.002 vs 0.043 ± 0.003, respectively). Likewise, the thorn length: stem length ratio was significantly reduced by either warming and grass cover (0.033 ± 0.004 vs 0.051 ± 0.005 and 0.032 ± 0.004 vs 0.052 ± 0.005, respectively). Warming significantly reduced the thorn length: stem diameter ratio when grass cover was present, but not when grass cover was absent (Figure 4.1).

Discussion

Warming effect on trade-offs between growth and defence

Our study is the first to determine the effect of elevated temperatures on woody seedling trade-offs between growth and physical defence when grown with or without grass in southern Africa. Temperature is one of the vital abiotic factors that will determine the response of woody plants to climate change (Randriamanana et al. 2015). Vetteli et al. (2006) suggested that temperature is the critical limiting factor for woody plant growth in different regions of the world. On the basis of an assumed trade-off between growth and defences (Herms and Mattson, 1992), it was hypothesised that elevated temperatures would decrease thorn length in relation to growth of *Vachellia sieberiana* seedlings growing with or without grass. This hypothesis was partially supported by the results.

The effect of warming resulted in enhanced trade-offs between thorn length and plant height, thorn length and stem length and thorn length and stem diameter. Many studies have suggested an increase in woody plant height, stem length and stem diameter under warming (Vetteli et al. 2006; Way and Oren 2010; Lett et al. 2017; Andersen et al. 2017; Camac et al. 2017; Asse et al. 2018; Gamm et al. 2018; Carlson et al. 2018). However, an increase in growth of *Vachellia sieberiana* seedlings at the cost of thorn length was noticed in the current study. Similarly, Sivadasan et al. (2018) also showed that warming increased plant height, stem diameter and stem length of woody plants but reduced the phenolic concentration. The growth and chemical defence trade-offs supports the results of this study, assuming that there is no trade-off in chemical and mechanical defence of southern African woody plants (Rohner and Ward 2007).

Effect of grass cover on trade-offs between growth and defence

Plants depend on defence to protect them from herbivores and these defences result from resources that they invested at the cost of growth and reproduction (Rodner and Ward 1997; Koricheva 2002; Ferrenberg et al. 2015; Sebata 2016). When many nutrients are limited in the soil, this can influence the relationship between defence and growth (Karasov et al. 2017). In the review of 50 studies which focused on woody plant growth and defence, it was found that fast-growing plants invest less in chemical and mechanical defence than slow-growing plants (Endara and Coley 2011). This was the same scenario in this current study, where resources were allocated to growth rather than defence in the presence of grass cover in all warmed plots. This may be due to limited resources in the presence of grass cover and growth of woody seedlings was prioritised to escape competition.

However, Karasov et al. (2017) suggest that an increase in defence may result in reduction of growth due to limited resources. Plants that grow without neighbours allocate resources to defence than plants growing in the presence of neighbours (Cipollini 2010; Fernandez et al. 2016). However, in the absence of grass cover, resources may have been invested in both growth and defence at the same time.

Conclusion

Warming to a level expected in the next few decades clearly was more effective than grass cover removal for *V. sieberiana* seedling growth and defence relationship. Warming resulted in trade-offs between growth and defence. Warming increased the growth and reduced thorn length of *V. sieberiana* seedlings when grass cover was present but not in the absence of grass cover. Our results suggest that in veld that has good grass cover the forage for browsers will increase, but not when the veld has poor grass cover as temperature rise by 1.5 °C.

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Table 4.1: Analysis of variance of thorn length: plant height ratio, thorn length: stem length ratio, thorn length: stem diameter ratio of *V. sieberiana* seedlings grown with or without grass with warming or without warming

Dependant variable	Source of variation	df	Mean Square	F-ratio	P-value
Thorn length: Plant height	Warming	1	31.454	5.744	**0.029**
	Grass	1	136.856	24.992	<**0.001**
	Warm * Grass	1	7.513	1.372	0.259
	Error	16	5.476		
Thorn length: Stem length	Warming	1	21.613	14.574	**0.002**
	Grass	1	28.792	19.415	<**0.001**
	Warm * Grass	1	0.178	0.120	0.734
	Error	16	1.483		
Thorn length: Stem diameter	Warming	1	1.739	9.349	**0.008**
	Grass	1	3.528	18.968	<**0.001**
	Warm * Grass	1	1.368	7.355	**0.015**
	Error	16	0.186		

Bold numbers mean significance

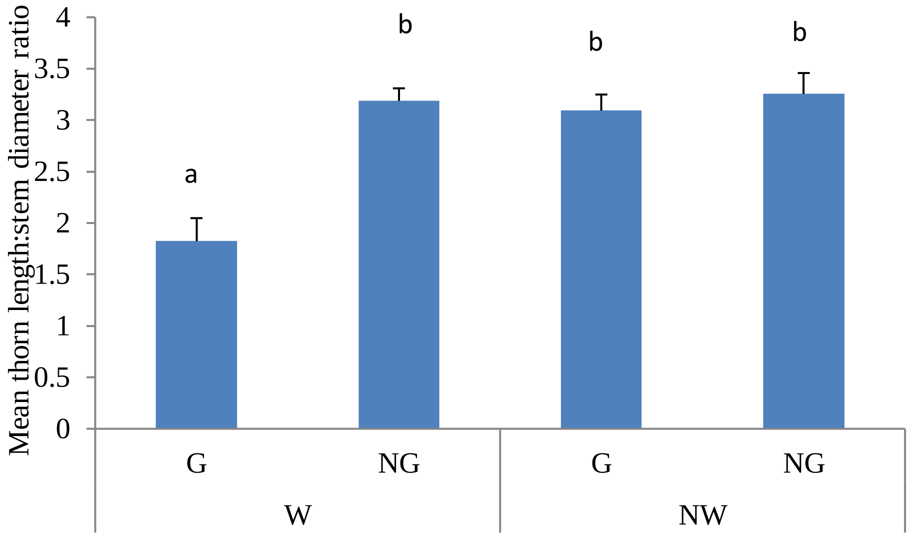

Figure 4.1: Effect of warming (W) vs no warming (NW), with grass cover (G) or without grass cover (NG), on mean thorn length: stem diameter ratio of *Vachellia sieberiana* seedlings. Error bars represent standard errors of the means and letters above error bars indicate significant differences ($p < 0.05$).

CHAPTER 5: CONCLUSION AND RECOMMENDATIONS FOR FUTURE RESEARCH

Introduction

Over the past years, rapidly increasing evidence has shown that savannas throughout the globe are altered by the phenomenon called bush encroachment (Acher et al. 1995; O'Connor and Crow 1999; Moleele et al. 2002; Ward 2005; Devine et al. 2017). These encroacher species reduce the grazing capacity of rangeland and consequently results in low optimum animal production. However, much interest has been concentrating on the effect of CO_2 on the growth of woody plants and chemical defence. Less attention has been paid to knowing the effect of warming on woody seedlings growth and defence competing with or without grass cover at different seasons. In addition, the effect of warming on trade-offs between growth and defence growing with or without grass using open top warming chambers in southern Africa has been not studied. Global warming is suggested to increase woody seedling growth. Grass cover has been documented to suppress woody seedlings, but reduction in grass cover can enhance the growth of woody plants that have potential to encroach grasslands and savannas in southern Africa.

Aims

The aim of the study was to determine the effects of warming, with or without grass cover, on the growth and defences of seedlings of a typical woody encroacher species.

Summary

The first and second chapters of this dissertation examined the factors that contribute to bush encroachment. Effects of herbivores on woody seedlings require seedlings to divert resources from growth to defence, which potentially limit growth of the seedlings. This study has investigated the effect of warming on growth and defence of *Vachellia sieberiana* seedlings growing with or without grass cover at different seasons (Chapter 3). Change in global climate is causing an increase in daily, seasonal and annual mean air temperatures to which plants are subjected (Yamori et al. 2014). The increase of mean minimum temperatures by 4.5 °C globally is predicted in the near future due to increasing amount of greenhouse gases in the atmosphere (IPCC 2014). In Africa, this rise in minimum air temperature is suggested to result in longer growing seasons, high fecundity and higher biomass allocation towards roots by plants and possible transformation of grassland to savannas (Scheiter and Higgins 2009).

Increase in temperature by a few degrees benefits the growth of woody seedlings during the dormant season when plant growth is limited by low temperatures (Way and Oren 2010). During the dormant season, and early-growing season, warming benefits woody seedlings because grasses pose less competition for water (Bargués et al. 2017; Wagner et al. 2018). Yet in the mid-growing season, grasses pose strong competition to woody seedlings due to high accumulation of biomass (Wagner et al. 2018).

In the current study, it was found that warming was more beneficial than grass cover on the woody seedlings growth in all seasons. Longer thorns were noticed under warming treatments without grass cover during the growing season. However, in the dormant season longer thorns were found in warming treatments irrespective of grass cover. Way and Oren (2010) suggested that elevated temperatures can increase woody plant growth irrespective of water stress and resource availability due to acclimation of woody plants to warming.

These results imply that as temperature increases, woody plant encroachment will be extended irrespective of grass cover. Poor grass cover in grasslands and savannas during the growing season will result in longer thorns, which are suggested to reduce the browsing rate of herbivores, while in the dormant season, longer thorns will be found as temperature rises irrespective of grass cover.

In chapter 4, the effect of warming on trade-offs between growth and defence of *Vachellia sieberiana* seedlings growing with or without grass cover was determined. The major determinants in allocation of resources to growth and defence are resource availability, competition and herbivores (Stamp 2003; Li et al. 2015).

Investment of resources to defence is assumed to trade-off with plant growth (Koricheva 2002; Moles et al. 2013). However, many studies have focused on trade-offs between growth and chemical defence rather than growth and physical defence. Yet, most of the leguminous woody plants that are encroaching in southern Africa rely on physical defence to deter large herbivores (Wigley et al. 2015). This study revealed that warming resulted in enhanced trade-offs between growth and defence. Warming increased the growth and, relative to growth, reduced thorn length of *V. sieberiana* seedlings when grass cover was present but not when grass was absent. Our results suggest that in veld that has good grass cover the browsing rate will increase, but not when the veld has poor grass cover as temperature rise to 1.5 °C. Plants growing without neighbours allocate more resources to defence than plants growing in the presence of neighbours, which allocate resources to growth (Fernandez et al. 2016).

Further research

There is plenty of potential research that may help rangeland managers and conservationists for future management as temperatures continue to rise. The clipping of woody seedlings under warming may help in understanding of how woody plants will respond to rising temperatures. Browsers have been used as biological control of bush encroachment in most savannas and grasslands of Africa. Therefore, clipping of woody seedlings under warming treatments may help rangeland managers to plan for effective biological control measures for bush encroachment.

Another interesting area for future study would be determining the effect of warming and carbon dioxide on growth and defence of *Vachellia* woody seedlings growing with or without grass, and the study should be allowed to run about a year or longer. The potential differential impacts of elevated atmospheric CO_2 concentration and temperature on plant growth and defence may affect both plant and animal populations by means of effect on competition and herbivory (Idso et al. 1987).

Recommendations

Proper rangeland management which results in good grass cover is important, because this study revealed that when grass cover is absent, woody seedlings have longer thorns which reduce browsing rate. This implies that under poor rangeland management, which results in poor or no grass cover, there is possibility of biological control for bush encroachment being not effective. Little is known about the effect of warming on growth and defence of woody seedlings growing with or without grass cover at different seasons and warming effect on trade-offs between growth and physical defence of woody seedlings. This will help improve knowledge and understanding of warming effect on woody plant growth and defence that have potential to invade grasslands and savannas of southern Africa.

The knowledge gained from this research is important for improving literature on causes of bush encroachment in savannas and grasslands of southern Africa. Rangeland managers and conservationist benefit from the findings of this study to gaining rangeland management strategies as temperature rises by 1.0 - 2.5 °C.

It is suggested that less defended plants have potential to be heavily browsed by browsers. Woody plants form major sources of feed for many herbivores. During the dormant season when there is shortage of feed, cattle and sheep who are grazers feed on woody plants (Scogings 2003). Therefore, the results suggest that during the dormant season browsers and grazers' browsing rate will decrease due to longer thorns.

Conclusions

This dissertation reveals that the global warming that is predicted to increase in the next few decades will be more effective in promoting bush encroachment than the absence of grass cover in both growing and dormant seasons. The study shows that warming resulted in trade-offs between growth and defence of *V. sieberiana* seedlings. Furthermore, in some of the grasslands and savannas of southern Africa, browsers are used in control of bush encroachment when the plant is 1.5 m or less. Then the longer thorns of *V. sieberiana* seedlings under warming in the absence of grass cover might result in ineffective biological control of bush encroachment, since longer thorns are suggested to reduce browsing rate for browsers.

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