Effects of increased temperature on growth and nutritional value of mesic grasslands, with or without woody legume seedling competition

By

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Submitted in fulfilment of the academic requirements of:

Master of Science

in

Ecology

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg,

South Africa

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PREFACE

The research contained in this thesis was performed in the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The study commenced in January 2018 and ran up until November 2020 under the supervision of Dr. M. J. Tedder and co-supervised by Prof. P. F. Scogings and Dr. N. R. Mkhize.

This research has not been submitted for examination to any university and except where other researchers' work has been acknowledged, the results reported here are solely due to investigations by the candidate.

Nikilitha Gili

We confirm that the above information is correct,

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DECLARATION: PLAGIARISM

I, Gili Nikilita, declare that:

(i) the research is an outcome of my own work, except where it is indicated otherwise;

(ii) this dissertation has not been previously submitted for examination at any university;

(iii) where reference of other researchers' work has been made, it is acknowledged in the text and the words are re-written;

(iv) this dissertation is prepared by myself from materials collected in published journal articles and posters;

(v) this dissertation contains no copied and pasted texts, graphics and tables from the Internet, unless stated otherwise and acknowledged in the dissertation and the References section.

Signed: Gili Nikilita

Date: 03/12/2020

ABSTRACT

Mesic grasslands are complex ecosystems covered in grasses and other graminoid vegetation. The species composition varies due to variation in rainfall and temperature; these grasslands are climatically supported. They also vary in nutritive value and grasslands with high species richness have low nutritive value because grasses differ genetically. Grasses' response to high temperature and competition is species dependent. Grasslands are ideal for ecological experiments because grasses grow fast and their response to environmental changes is noticeable. Therefore, an experiment of induced warming with legume seedlings interaction was conducted at the University of KwaZulu-Natal, using open top chambers and *Vachellia sieberiana* var. *woodii*. This was done to determine the effect of increased temperature on the biomass, growth, morphology and nutritive value of *Themeda triandra* and *Aristida junciformis*. These species were chosen because they occur naturally and dominate in the Ukulinga farm, where the experiment was conducted. They also have contrasting palatability, *T. triandra* is highly palatable and *A. junciformis* is less palatable. *Vachellia sieberiana* seedlings were grown from seed and transplanted after two months to the field to interact with grasses for four months. The results suggest that the interaction of warming and woody seedlings reduces the biomass of the investigated species. This implies that warming reduces grass biomass. Plant traits such as grass height, leaf area, tiller width and tuft diameter responded differently to the treatments. The fibre (neutral detergent fibre) of *T. triandra* was increased by warming. The interaction of warming and woody seedlings had no effect on the regrowth fibre content. The interaction of warming and woody seedlings increased the protein content of *A. junciformis*. Warming and woody seedlings independently increased the protein content of *T. triandra*. The response of plants to increased warming will help ecologists understand the effects of global warming. To provide more insight into these findings, further research on specific species with longer experimental duration and high woody seedling neighbour density is of importance.

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ACKNOWLEDGEMENTS

First and most importantly, I thank God the almighty for granting me the strength and capacity to complete this thesis.

I am grateful for the guidance and support from my supervisors Michelle Tedder, Peter Scogings, and Ntuthuko Mkhize throughout this study. The patience, planning, and comments made this project a success.

For field assistance

- Mr Welcome Ngcobo
- Miss Zinhle Lembede
- Miss Khululwa Ndabankulu

For support
- Grassland Science lab members
- Mr Athi Zangwa
- Miss Ntomboxolo Msengana

DEDICATED TO MY FAMILY

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CHAPTER ONE: INTRODUCTION

Rangelands are terrestrial ecosystems that are dominated by grasses, forbs, and/or shrubs (Hoffman and Vogel, 2008; Roselle *et al*., 2012; Boone *et al*., 2018). They are characterized by diverse vegetation physiology (Dumont *et al*., 2015), and plant-animal interactions due to variation in precipitation and temperature (Hobbs *et al*., 2008). Furthermore, rangelands are known to occupy 50% of the Earth's surface (Scholes, 2003) and produce 30% of the aboveground production (Xu *et al*., 2013). In semi-arid regions, an increase in rainfall promotes grass growth, because grasses have a more rapid response than trees; whereas in mesic regions it negatively affects grass cover by promoting tree growth (Bond, 2008). In water-limited conditions, rainfall variation directly influences plant-plant interactions by intensifying resource competition (Synodinos *et al*., 2018). In mesic grasslands, low rainfall for a short period during the growing season does not result in resource limitation (Xu *et al*., 2013; Synodinos *et al*., 2018). The South African grassy biomes (Grassland and Savanna) are threatened because of loss of habitat and the threats include soil erosion, soil salinization and soil compaction; only 26% is used for animal grazing and game foraging (Reyers *et al*., 2001). Plant production is increased when tree cover increases but rangeland nutritive value is reduced because grazeable species are limited (Xu *et al*., 2013). In rangelands, herbivory, fire and soil interact with rainfall and manipulate plant growth. In semi-arid rangelands, grazing clears the grass cover, therefore, reduces grass competition towards trees (Synodinos *et al*., 2018). The reliance on rangelands for livestock production is expected to grow (Hoffman and Vogel, 2008); and grasslands are sensitive to future increased temperature hence, it is crucial to understand its response (Klein *et al*., 2007). In this study the response of mesic grasses to warming has been investigated in a Southern African rangeland.

Global warming is any rise that occurs in mean air temperature over time; it may occur because of nature's unpredictability or be triggered by human activity such as burning fuel (IPCC, 2014; Shahzad, 2015). Global warming takes place when atmospheric greenhouse gases and aerosol concentration increases (Biggs *et al*., 2004). When sunlight reaches the Earth's surface, only 30% of the heat is sent back to the atmosphere (Shahzad, 2015). The residual heat captured by the land, air and ocean results in the heating up of the Earth (Shahzad, 2015). Global warming effects, including elevated temperatures and reduced

rainfall, shift the ecological zone and reduce overall terrestrial net primary productivity (Boko *et al*., 2007).

Rangeland quality and composition are influenced by many factors including atmospheric CO_2 concentration, precipitation and temperature, which interact with grazing (Hoffman and Vogel, 2008). Elevated warming increases water-limitation stress in plants as well as lignification of the cell wall content (Buhrmann *et al*., 2017) which, according to Thornton *et al*. (2007), has a negative influence on both plant digestibility and the degree of nutrient decomposition. Precipitation frequency and intensity have an impact on both short- and long-term plant species composition, mainly because of alterations in the development and reproductive physiology of grasses (Ketter and Holdo, 2018). Perennial plants are deep rooted and the roots bind the soil particles and protect it from soil erosion. Annual grass species can rapidly replace perennial plants during prolonged drought (Hein, 2006). Furthermore, the replacement of perennial plants results in a decrease of rangeland productivity because perennials use less soil nutrients compared to annual plants (McCollum *et al*., 2011).

Increased precipitation promotes the growth of woody plants and could result in bush encroachment; a common problem in Africa (Hoffman and Vogel, 2008). Bush encroachment outcomes are an ecological shift from grass dominance to woody dominance, therefore, decreasing rangeland productivity but increasing vegetative biomass (Hoffman and Vogel, 2008). Moreover, the length of the growing season for shorter growth forms (perennial herbs) depends primarily on water availability and plant competitive ability that is determined by the stage of growth (Hoffman and Vogel, 2008). The height of trees increases with an increase in water availability thereby increasing their ability to compete for light, thus suppressing any shorter growth forms i.e. perennial herbs (Bond and Midgley, 2000). Grasses can outcompete tree seedlings when the woody cover is low, by limiting belowground resources (nutrients, space, and water) and by keeping them within the fire trap (Dohn *et al*., 2013). When water is the limiting factor, grasses are assumed to outcompete tree seedlings because of their adventitious deep root systems and greater transpiration rates (Ludwig *et al*., 2008). Adventitious roots allow grasses to access surface water and water from light rain (Ludwig *et al*., 2008). The interaction between tree seedlings and grasses depends on the functional traits of seedlings and not the root depth (Ketter and Holdo, 2018). Grasses do not solely depend on the few centimeters (cm) of the top-soil, (Cramer *et al*., 2007) but are deeper-rooted than tree seedlings but this does not reflect their functional rooting profile (Ketter and Holdo, 2018).

Functional root traits; length, diameter and tissue density determines the belowground competitive ability of plants (Fort *et al*., 2012). Deep roots are crucial for ecosystem functions such as moisture content regulation and soil carbon sequestration (Pierret *et al*., 2016). Therefore, root niche separation is more noticeable in the arid than the mesic rangelands (Ketter and Holdo, 2018). The details about how seedlings and grasses interact with each other are still unknown (Cramer *et al*., 2007).

Rangelands that have the potential to be grazed should produce enough feed for the production of animals to be sustainable. The feed must achieve an appropriate balance of total ration of nutrient composition and meet the animals' nutritional requirements (Ball *et al*., 2001). This can only be achieved by knowing the nutrient content of the grasses available in the field (Klein *et al*., 2007). Tremendous variation exists in nutrient composition between plants in rangelands (Zhang *et al*., 2018) because rangelands encompass an exceptional diversity in species composition, habitat and climatic regions (Klein *et al*., 2007). Hence, it is difficult to make broad generalizations on how rangelands are impacted by rising temperatures (Klein *et al*., 2007). Forages harvested off the same rangeland within the same year can have very different nutrient compositions influenced by environmental conditions and harvesting season (Zhang *et al*., 2018). Low-quality feeds have fewer nutrients available for animal absorption; therefore, large amounts of animal feed supplements need to be added which becomes costly to the farmers (Ball *et al*., 2001).

The nutritive value of any feed is defined by the quality of a well-balanced ration and potential digestibility (Moore, 1994). Nutritional value is controlled by the physical and chemical functioning of the plants, which is dependent on climatic conditions as an external factor (Moore, 1994). The percentage of acid detergent fibre (ADF) and neutral detergent fibre (NDF) in a feed is an indicator of the quality of forage (Stergiadis *et al*., 2015). Acid detergent fibre and neutral detergent fibre levels are importance because they affect digestibility (Raffrenato *et al*., 2017). The structural components of the plant are the source of fibres and are least digestible (Raffrenato *et al*., 2017). When discussing animal feeds, digestibility is the most crucial concept. Digestibility of feed is determined by the nutrients that are available for animal growth and reproduction, excluding the indigestible parts of the feed (Ball *et al*., 2001). Where livestock production relies on native forage, it is severely affected by low-quality forage, especially during the dry season (Adebisi and Bosch, 2004; Grant *et al*., 2015).

AIM, OBJECTIVES, RESEARCH QUESTIONS AND HYPOTHESES

This research aimed to determine the effects of the interaction between the induced increased temperature and woody legume competition on the growth and nutritional value of mesic rangeland grasses.

Objectives:
1. To determine the effect of increased temperature on the biomass and morphology of mesic rangeland grasses with and without woody legume seedling competition.
2. To determine the effect of increased temperature on the nutritional value of mesic rangeland grasses with and without woody legume seedling competition.

Research Questions and Hypotheses:
1. The first objective addresses the question, how does increased temperature affect the biomass and morphology of mesic rangeland grasses when growing with woody legume seedlings? It was hypothesized that warming will decrease the grass biomass and because grasses are strong competitors compared to woody seedlings, seedlings will not have any effect on the grass biomass production. The presence of woody seedlings will not affect the morphology of grasses; there will be no interaction between the two factors, but rather a warming effect.
2. The second objective gave rise to the question, how does increased temperature affect the nutritive value of mesic rangeland grasses when growing with woody legume seedlings? It was hypothesized that warming will increase fibre content and reduce the nitrogen content of grasses; the presence of woody seedlings will not affect the nitrogen content of grasses because the seedlings are young.

CHAPTER TWO: LITERATURE REVIEW

The Earth has an atmosphere, which provides a protective layer against heat and radiation coming from the Sun (UCAR, 2015). The energy exerted by the Sun to the Earth is affecting the living organisms (Mann *et al*., 2008). The process of the exchange of energy among the Sun, the atmosphere and the Earth is a biogeochemical system (Sharp, 2017). The system is so complex that the amount of energy change is scientifically uncertain but there are qualitative projections that lead to an understanding of human impacts (UCAR, 2015).

The atmospheric system is made up of different layers, each with specific traits (UCAR, 2015). The troposphere is closest to the Earth's surface (UCAR, 2015; Sharp, 2017) and is in constant motion (Sharp, 2017). The environments in this layer control the Earth's weather pattern. The constant motion diffuses pollutants and changes the quality of air by reducing harmful impacts on a local level (Mann *et al*., 2008). The next layer is the stratosphere. The ozone layer is found here and absorbs harmful ultraviolet (UV) radiation from the Sun (Sharp, 2017). In contrast to the troposphere, the air in the stratosphere is not turbulent and is stable and dry; hence, it is warmer. Unlike the troposphere, pollutants here are not diffused and persist in the atmosphere for a long period (Mann *et al*., 2008).

Above the stratosphere is the mesosphere (UCAR, 2015; Sharp, 2017). The top part of the mesosphere, the mesopause is cold with an average temperature of -90ºC. The air in this layer is far too thin to breathe; air pressure is less than 1% and continues to drop when approaching the top (Mann *et al*., 2008; Sharp, 2017). It is difficult to study this layer. It is known that meteors, small bodies of matter from outer space (fireballs), burn up in this layer (Mann *et al*., 2008; UCAR, 2015; Sharp, 2017). After the mesosphere is the ionosphere which is not a distinct layer; instead, it is a series of isolated gas molecules broken into ions by solar radiation from the Sun (Weart, 2008; UCAR, 2015; Sharp, 2017). The layer above the mesosphere is the thermosphere. The height of this layer and the temperature within it are influenced by variation in the amount of energy coming from the Sun (Sharp, 2017). The thermosphere blocks high-energy harmful cosmic radiation from the Sun, including X-rays, gamma rays and ultraviolet radiation (UCAR, 2015).

GLOBAL WARMING

The atmosphere is a thin layer of gas that works like a layer of glass in a greenhouse to cover and protect the planet. The greenhouse effect results from variation in the ratio of radiation that heats the Earth (Shahzad, 2015). Air, land and oceans capture the ultraviolet radiation that passes through the atmosphere; the infrared radiation does not pass through the ozone layer and is trapped, therefore warming the planet (Grant *et al*., 2015; Shahzad, 2015). The trapped hot air cannot rise and no energy is lost through convection (Shahzad, 2015). Global warming is initiated when carbon dioxide and methane, that comes from animal and plant respiration, and nitrous oxide from the combustion of fuel and nitrogen fertilizers, increase in concentration and alter the electromagnetic energy transfer (radiative) equilibrium in the atmosphere, causing the Earth to heat up (Collins *et al*., 2013; Grant *et al*., 2015; Shahzad, 2015). These gases (carbon dioxide, methane and nitrous oxide) have heat-trapping abilities and are called greenhouse gases (Grant *et al*., 2015). These alterations to the chemical composition of the atmosphere lead to global warming (Grant et al., 2015).

There are aerosols, the fine solid units or liquid condensations, present in the atmosphere that are responsible for global warming. Aerosols have different effects; some aerosols (black carbon and soot) warm the Earth, while others (mist) act as coolants. These aerosols can be natural (fog, dust and forest exudates) or from anthropogenic activities (internal combustion engines, electric geysers) (Shahzad, 2015). Aerosols scatter and absorb radiation from the sun, and boost cloud forming, while greenhouse gases absorb and emit infrared radiation (Collins *et al*., 2013). The aerosols do not interfere with the greenhouse effect and remain in the atmosphere for shorter time than greenhouse gas.

Global warming is currently occurring; it begins when the sun rays hit the surface of the Earth and only 30% of the heat waves are reflected back to the atmosphere (Shahzad, 2015). Some of the outgoing radiation from the troposphere is returned to Earth and is re-absorbed by carbon dioxide, water vapour and ozone (Grant *et al*., 2015; Shahzad, 2015). The radiation re-absorption keeps the Earth cool; the problem is the alteration of the concentration of these gasses by human activity (Shahzad, 2015). The mean surface air temperature of the Earth increased by 0.6 to 0.9ºC between 1906 and 2006 (Grant *et al*., 2015; Shahzad, 2015). The Representative Concentration Pathway satellite (RCP 4.5) showed an increase between 1.1 to 2.6ºC in the average annual air temperature of the Earth from 1986 to 2005 (Collins *et al*., 2013). In the high altitudes, where maximum warming is expected to occur, temperatures may reach +7ºC hotter during winter by the end of the 21st century (Dumont *et al*., 2015).

Warming differs with season and region, with winter and spring showing a faster increase in air temperature (Xia *et al*., 2014).

MESIC AND ARID GRASSLANDS

Grasslands and savannas are complex systems and it is difficult to understand their structural functioning (Wills, 2015). Blair *et al*. (2014) defined grasslands as open canopy ecosystems with extensive grass cover. The species composition in these ecosystems is primarily influenced by climate, fire and herbivory (Blair *et al*., 2014; Wills, 2015). These factors affect the aboveground primary productivity of grasslands, for instance, herbivores select palatable grasses and mature dry grasses fuel fire (Blair *et al*., 2014). C_4 grasses currently dominate the open savannas because a decrease in CO_2 aided in developing a photosynthetic pathway that helps them efficiently use water in warm conditions when compared with C_3 plants (Wills, 2015).

Mesic grassland soils, world-wide, are geologically older than arid grasslands because of rapid weathering (Blair *et al*., 2014). In Africa, grasslands are climatically distinct from each other. Grasslands in regions receiving rainfall ranging from 250 mm/year to 500 mm/year are said to be arid, mesic regions receive rainfall more than 500 mm/year but less than 1 000 mm/year and tropical grasslands are in regions receiving an average rainfall of 1 000 mm/year or more (Wills, 2015). Mesic grasslands occur in regions where woodlands can be climatically supported. Therefore, they are said to be disturbance-dependent communities where periodic fire and drought keep the grassland from transitioning (Wills, 2015). In mesic grasslands, plant dormancy occurs as a mechanism to survive winter low temperatures (Wills, 2015). In arid grasslands, plant dormancy is driven by summer drought (Wills, 2015). Grasslands provide forage and habitat and are a source of drinking water to livestock and wildlife. Grasses grow rapidly and respond quickly to manipulations which makes grasslands ideal for ecological experiments.

Mesic Grasslands

Grant *et al*. (2015) defined mesic grasslands as systems where the herbaceous vegetation is rarely stressed during the growing season because of high soil moisture. Mesic grasslands are in regions receiving rainfall of 1 000 mm or more per annum on average. Mesic grasslands face stress when the precipitation events are intense and infrequent as this increases the

variability of the soil water content (Grant *et al*., 2015). Generally, if the air temperature is the only factor that is increased, plant productivity shows a positive response (Grant *et al*., 2015). Experimental warming increases aboveground net primary productivity only when the ambient temperature is normally cool throughout the growing season (Grant *et al*., 2015). During water-limited periods, warming increases water stress and negatively affects net primary productivity. Mesic grasslands have a rapid decomposition rate and plants are less lignified. As a result, there is greater soil biodiversity compared to arid grasslands (Grant *et al*., 2015). In mesic grasslands, the response of plant species composition to climate variability has rarely been studied (Sala *et al*., 1996).

TEMPERATURE VARIABILITY AND PRODUCTIVITY

IPCC (2007) stated that when other climatic factors are not considered, high temperatures increase plant primary productivity. Higher temperatures may benefit pasture productivity in temperate regions when the frequency of extreme events is not considered (IPCC, 2007). In tropical and sub-tropical regions moderate warming may reduce plant productivity (IPCC, 2007). A local mean temperature increase of 1-3ºC, which is normally associated with atmospheric CO_2 increase, improves plant productivity of temperate rangelands (Dumont *et al*., 2015). Further increases in average temperature reduces the yield (Zhao *et* al., 2017).

EFFECTS OF WARMING ON GRASSLANDS

Elevated temperature affects vegetation structure and composition differently according to the region and local changes in greenhouse gas concentration. The effect of increased temperatures on grasslands is significant to consider because they have high biodiversity (Buhrmann *et al*., 2017). In South Africa, many grassland types are threatened by woody encroachment and land use transformation (Hoffman and Vogel, 2008). The temperature effect is likely to reduce biodiversity in grasslands, worldwide (Sala, 2001). Grasslands play a crucial role in recycling soil nutrients (Sala, 2001). Poor management, land-use changes, and increasing temperatures damage grassland structure and function (Sala, 2001; Buhrmann *et al*., 2017).

When plants are subjected to increased temperatures, they experience physiological modifications such as altered carbon assimilation rates, higher photosynthetic rates or

increased evapotranspiration rates (Sala, 2001). Water deficit, which occurs because of elevated temperature, restricts photosynthesis and vegetation growth, leading to reduced quantity and quality of forage (De Boeck *et al*., 2007). The most noticeable effect of elevated temperature is the alteration of plant yield (Guoju *et al*., 2005; Buhrmann *et al*., 2017). The net primary productivity of plants is the C gain integrated with plant foliage over some time (Buhrmann *et al*., 2017). Net primary productivity could be increased by elevated temperatures where plant carbon assimilation is restricted by cold weather (De Boeck *et al*., 2007). Conversely, grass productivity is reduced by warming due to increased heat stress and a decrease in soil moisture (Sebastia, 2007). High temperatures modify the rate at which photosynthetic enzymes function and changes the leaf-to-air vapour pressure; indirectly influencing stomatal conductance (Amedie, 2013). The photosynthetic enzymes lose their shape and functionality causing photosynthetic rates to decline rapidly High temperatures indirectly affect net primary productivity by reducing available soil nitrogen (Amedie, 2013). An increase in mean annual temperature of 0.5 ℃ to 1.00 ℃ increases soil N mineralization and organic matter decomposition; leading to increased net primary production (Amedie, 2013).

SEASONAL GROWTH AND PRIMARY PRODUCTIVITY

Global climate change, specifically increasing temperature, is going to have an undesirable outcome on plant community composition (Grant *et al*., 2014) as climate change affects species turnover, persistence, and recruitment (Adler *et al*., 2006). The existing research only predicts the effect of continuous warming and it is currently not possible to forecast the impacts of non-uniform warming (Xia *et al*., 2014). Non-uniform warming alters precipitation and disturbance occurrence, such as wildfire, and is associated with increased temperature extremes (Xia *et al*., 2014). Plant biomass and photosynthetic rate decrease when warming experiments induce moisture stress (De Boeck *et al*., 2007). Responses of plants to available resource fluctuations and temperature result in species dominance and composition shift (Grant *et al*., 2015). Findings on species composition and function during summer high temperatures are controversial (Grant *et al*., 2015). In some regions, summer high temperatures are coupled with rainfall resulting in the continuous cover of the soil and balanced species composition (De Boeck *et al*., 2007). In other areas, summer high

temperatures result in drought and dormancy of grass seeds (Grant *et al*., 2014). Thus, there is a negative balance between soil moisture availability and evaporation (Knapp *et al*., 2002).

FACTORS AFFECTING NUTRITIVE VALUE OF GRASSLANDS

Buxton (1996) stated that grassland forage quality is influenced by nutrient availability, temperature and moisture variability, plant growth stage, and species composition. As the plant ages, it becomes more fibrous because the protein and soluble carbohydrates are reduced (Buxton, 1996). Plant digestibility also declines as the plant matures with the stem (fibrous part) becoming increasingly more difficult to digest than the leaves (less-fibrous part) (Buxton and Fales, 1994; Buxton, 1996; Grant *et al*., 2015). Plants at the same stage of growth can also have different nutritive values (Grant *et al*., 2015) because of different functional traits. The nutritional content of grasslands is determined by botanic diversity, species' nutritive value and the ages of leaves and tillers when harvested or grazed (Grant *et al*., 2015). Forages harvested off the same rangeland within the same year can have very different nutrient compositions because of variation in environmental conditions and harvesting season (Zhang *et al*., 2018).

Increasing temperature and decreasing rainfall diminish rangeland quality by reducing crude protein content and digestibility of organic matter (Grant *et al*., 2015). A slight increase of 1ºC would need 200 mm/annum precipitation increase to preserve the same quality of forage (Craine *et al*., 2010 cited in Grant *et al*., 2015). Hence, it is difficult to make broad generalizations on how rangelands are or may become impacted by rising temperatures (Klein *et al*., 2007).

WARMING EFFECT ON FORAGE QUALITY

Feed quality is determined by the digestibility of the feed (Dumont *et al*., 2015) and strongly affects animal performance (Ball *et al*., 2001; Adebisi and Bosch, 2004; Dumont *et al*., 2015). High temperatures indirectly affect animal performance by altering forage physical and chemical characteristics (Dumont *et al*., 2015). Cell-wall content has lignin that hinders the microbial enzymes by interfering with digestion (Wilson *et al*., 1991; Dumont *et al*., 2015). Warm environmental conditions directly affect animal performance through feed intake and digestive processes (Adebisi and Bosch, 2004). In ruminants, most heat is

produced during rumen fermentation, therefore; feed intake by animals is reduced when temperatures are high due to thermoregulation (Adebisi and Bosch, 2004).

Temperature determines the forage nutritive value (Buxton and Fales, 1994). A 10% decrease in the proportion of grass biomass production was observed when the average temperature was 3.5ºC warmer (Dumont *et al*., 2015). Warmer temperatures reduce soil moisture leading to heat stress that consequently affects the availability of soil N for plant uptake. This results in contrasting outcomes of warming on forage N content (Dumont *et al*., 2015). Dumont *et al*. (2015) emphasized that experimental investigations into the warming effect on forage quality is rare.

VEGETATION ADAPTATION

Elevated warming mitigation and adaptation issues have been discussed intensely (Elum *et al*., 2017) where mitigation was defined as an important long-term solution that involves anthropogenic activities that aim to reduce greenhouse emissions and address on-going threats. Adaptation of plants refers to the adjustments in the natural response to the increasing temperature and taking advantage of the situation (Elum *et al*., 2017). Adaptation is the process that enables vegetation to be successful in its environment for future climatic conditions by taking proper measures (UNFCCC, 2007). Plants growing in dry regions have structural adaptations such as large root systems, small leaf surface area to reduce water loss, waxy leaf surfaces, and water storage tissues. The degree of adaptation to warming primarily depends on the vulnerability of plants to warm temperatures that is determined by the sensitivity of plants and time of exposure to increased temperature (Elum *et al*., 2017). African countries are known to be susceptible to the impacts of elevated warming, with no exclusion of South Africa (IPCC, 2014). All countries are susceptible to negative impacts of global warming because of a lack of awareness, dependence on natural resources, and poverty (Fereja, 2017). Understanding how plants are affected by warming will help farmers identify adaptation strategies for future vegetation responses (Elum *et al*., 2017).

OPEN TOP CHAMBERS

Open top chambers are constructed with slanted sidewalls that are transparent (polyvinyl chloride, Plexiglas) with a frustum at the top. The frustum allows the exchange of air to

balance temperature and humidity inside the chamber (Jach and Ceulemans, 1999; Uprety *et al*., 2006). The closed walls and an open frustum generate a synthetic microclimate and that makes open top chambers the most widely used and cost effective method to study the response of plants to elevated temperature, altered humidity, and photosynthetically active radiation (PAR) (Uprety *et al*., 2006; Macháčová, 2010). The effect of the chambers varies with plant species (Macháčová, 2010). Open top chambers are often used to study the physiological changes that occur in plants due to increased CO_2 concentration under environmental conditions adjacent to the native conditions in the field (Macháčová, 2010). The open top chambers do not alter the flow of air around the plant but rather increase the temperature by 2°C to 3°C.

The responses of grasses to the effects of open top chambers vary (Klein *et al*., 2004) with plant species (Macháčová, 2010). Open top chambers decrease the reproductive success of plants, thereafter reducing species diversity in rangelands (Klein *et al*., 2004). Arft *et al*. (1999) noted that flowering and seed production increase after three to four years of manipulation when subjected to OTC warming. This shows that reproduction mechanisms are limited for plants that are inside the OTCs. However, OTCs can also increase plant reproduction in colder regions where soil moisture and relative humidity will not decline drastically (Klein *et al*., 2004).

RESPONSE OF VEGETATION TO ELEVATED WARMING

Predicting the response of the ecosystem to global warming is becoming significantly important (Laurance *et al*., 2011) because rangelands occupy almost 50% of land cover, globally (Buhrmann *et al*., 2017). Plant response to rising temperature is a species-specific trait and life-form dependant (Buhrmann *et al*., 2017). The response depends on a species' ability to be physiologically adapted to the environmental changes or to migrate to other terrains (Grant *et al*., 2015). The level of warming determines the physical and chemical changes when vegetation responds to high-temperature stress (Dumont *et al*., 2015). The speed of global warming negatively affects species survival; for plants to adapt or migrate, they require spatiotemporal abilities; the developmental sequences which modifies the performance (Grant *et al*., 2015). The impact of global climate variation includes biodiversity loss (Sala, 2001), shifts in community compositions and species ranges (Sebastia, 2007), and a drop in ANPP (Dumont *et al*., 2015).

Grant *et al*. (2015) stated that mitigation and adaptation are the most crucial response strategies for global warming. The mitigation and adaptation approaches minimize the negative effects caused by elevated warming (IPCC, 2012; Grant *et al*., 2015). One cannot replace the other but rather they supplement one another (Elum *et al*., 2017). Warmer temperatures accelerate the organic material decomposition rate and increase the temperate grassland's productivity (Elum *et al*., 2017). In contrast, high temperatures cause loss of soil C reducing grassland's ability to be carbon sinks and making them carbon sources (Grant *et al*., 2015). Mitigation strategies are the first techniques in trying to maintain grassland productivity. Adaptation takes time to implement and adaptation strategies for increased climate variability differ from adaptation strategies to changes in mean conditions (Bryan *et al*., 2009). Improvement of soil water availability reduces drought stress and increases plant resilience, this is an adaptation strategy for increased temperature variability (Elum *et al*., 2017). Grazing mitigation measures for increased temperatures are still unknown.

An experiment done on wild grasses showed that the net primary productivity of C_3 and C_4 plant species increase under conditions of elevated temperatures (Grant *et al*., 2015). A 33% increase in C_3 grass biomass was shown by greater tiller formation whereas, C_4 plants increase leaf area by 44% (Wand *et al*., 1999). Plants' interaction with the ecosystem and climate variability is complex because responses to climate change vary with physical, biological, and chemical processes (Wand *et al*., 1999). How biodiversity and biological system functioning are influenced by climate change and altered ecosystem processes is critical to understand.

PLANT-PLANT INTERACTIONS

Biotic interactions are crucial determinants of ecosystem function and structure. These biotic interactions affect species abundance and distribution (Grant *et al*., 2015). During extreme environmental conditions, abiotic stress severely affects the competitive species and the stress-tolerant species persevere (Grant *et al*., 2015). As a result of this climatic conditions are able to alter species composition. Plant interactions are greatly influenced by plant density, physiology, and life stage (Callaway and Walker, 1997).

 Plant-plant interactions can be either competitive or facilitative depending on the establishment of plants, abundance and plant-species distribution (Dohn *et al*., 2013). In a

community, plants compete for available resources (light, nutrients, and water) (Grant *et al*., 2015) and the coexisting species differ in their environmental requirements (Grant *et al*., 2015). The neighbour effect can shift as climatic conditions change because what is facilitative to one plant can be harmful to the other plant (Zhang *et al*., 2018). Thus, shifts in the neighbour effect among species determine the plant community productivity when subjected to harsh climatic events (Grant *et al*., 2015). When plants improve the environment, the interaction is facilitative (Grant *et al*., 2015). For example, legumes have nodules that help them fix atmospheric nitrogen and promote growth and establishment of the neighbouring plants through increased soil nitrogen. Some plants provide shade to neighbouring plants; therefore, reducing transpiration and increasing soil water availability (Grant *et al*., 2015). Facilitative interaction patterns between plant communities are disrupted by temperature and precipitation variability (Scholes and Archer, 1997; Grant *et al*., 2015). Competitive species are more prone to environmental stress than stress-tolerant species (Grant *et al*. 2015).

COMPETITIVE EFFECT OF GRASSES

Tree-grass competitive interactions are well documented but the interaction between grasses and newly established tree seedlings remains unclear (Ketter and Holdo, 2018). Plant-plant relations are a multifaceted combination of effects and the results depend on the combination of biotic and edaphic factors (Dohn *et al*., 2013). The persistence and abundance of plants is attributed to the ability of plants to compete with other plant species (Peltzer and Köchy, 2001).

Interaction between tree seedlings and grasses are either competitive or facilitative (Scholes and Archer, 1997). Grasses provide fire fuel load and influence the abundance of trees by hindering the recruitment of seedlings to adult trees (Cramer *et al*., 2007). For the aboveground competition, there is a relatively large competitive effect exerted by large plants (Scholes and Archer, 1997), but for belowground resources, it varies with plant species (Cramer *et al*., 2007). Many studies state that grasses compete with seedlings but the degree of competition is not constant for all grasses and differs with grass size, structure, ecological status, and factors affecting grass vigour (Cramer *et al*., 2007). Overgrazing is a major source of bush encroachment because it reduces grass competitive effect and results in a species shift from more competitive climax grasses to less competitive grasses (Ash *et al*., 2011). Wand *et*

al., (1999) stated that the potential competitive advantage and distribution of C_4 plant species are dictated by climate and CO_2 concentration.

Effect of Grasses on Woody Seedlings

The response of trees to perennial grass competition does not depend on root depth but rather on tree seedling traits (Holdo and Brocato, 2015). Grasses strongly compete with tree seedlings (Cramer *et al*., 2012). There is no difference in the root depth of grasses and seedlings (Ketter and Holdo, 2018). In some cases, grasses may appear to have deeper roots than tree seedlings but the rooting depth does not reflect a functional rooting profile (Nippert and Knapp, 2007). Deep roots are important for biological functions such as soil C sequestration and moisture content regulation (Pierret *et al*., 2016). The functional rooting profile indicates that roots are physically different and play different roles, depending on the soil profile (Pierret *et al*., 2016; Ketter and Holdo, 2018). This shows that grasses do not solely depend on the few centimeters (cm) of the top-soil (Cramer *et al*., 2007). Root niche separation occurs less or may be completely absent in mesic regions and is more apparent in arid regions (Mordelet *et al*., 1997). Perennial, tussock-forming grasses exhibit an intense competitive effect on seedlings during the establishment phase (Ketter and Holdo, 2018). When grown with grass *Acacia nigrescens* seedlings experienced a strong reduction in photosynthesis (56%) and stomatal conductance (60%) but in *Colophospermum mopane* 40% and 44% reduction in photosynthesis and stomatal conductance occur, respectively (Ketter and Holdo, 2018). Grass shade on tree seedling has no significant effect on dry mass and leaf physiology (Ketter and Holdo, 2018)

Grasses strongly compete with tree seedlings (Riginos, 2009; Cramer *et al*., 2012). In savannas, tree recruitment is promoted by grass disturbances and by removal of browsers and mixed-feeders that temporarily remove grass cover (Wakeling *et al*., 2011). During seedling establishment, grass competition is great because the entire tree root is occupying the same soil horizon as the grass (Cramer *et al*., 2012). N_2-fixing leguminous seedlings ameliorate the environment by increasing soil N availability to plants (Cramer *et al*., 2012). Grasses are superior competitors because of their root morphology, although intensity of competition depends on the biomass of the competing species (Wakeling *et al*., 2011). When tree seedlings are transplanted into dense grass sward, they are easily outcompeted by grasses due

to limited soil resources resulting from the reduced soil volume available (Cramer *et al*., 2012). Thus, seedlings are susceptible to belowground resource competition because of root constraints (Cramer *et al*., 2012). This shows that different root profiles result in contrasting interaction outcomes depending on the availability of soil moisture (Kulmatiski and Beard, 2013).

LIVESTOCK FARMING

Pastoralists and smallholder farmers in communal areas (Mpanza, 2015) commonly practice livestock farming. Animal production is severely constrained by a shortage of quality feed (Adebisi and Bosch, 2004). In smallholder farms, livestock relies on communal natural grazing pastures (Dziba *et al*., 2007; Mpanza, 2015) that are insufficient and become poor in quality, predominantly throughout the dry season (Adebisi and Bosch, 2004). Many natural pastures in communal areas have very low crude protein content and high fibre content, particularly during the dry season. Animal feed that has crude protein below the threshold (7%) restricts microbial activity in the rumen and results in poor digestibility (Hariadi and Santoso, 2010). In South Africa, communal farmers have a high number of animals but production is low (Thomas *et al*., 2007). Variations in forage quantity and quality severely affect livestock production (Mpanza, 2015) and lead to overutilization of communal natural vegetation (Masafu, 2006; Sultan *et al*., 2008). Livestock mortality due to parasite infestation and poor nutrition is a common problem for communal farmers (Adebisi and Bosch, 2004; Mpanza, 2007). Feed shortage results in slow growth and low reproduction (Ajayi *et al*., 2007). South Africa is becoming increasingly arid and this is caused by the increasing temperature that results in low soil moisture and reduced biomass production (O'Connor and Kikker, 2004).

Challenges Faced by Livestock Producers

Livestock production by smallholder farmers is exposed to several challenges (Kosgey, 2004). These challenges include fluctuation of feed availability and quality (Scogings *et al*., 2004), poor grazing management (Abusuwar and Ahmed, 2010), and disease prevalence (Mpanza, 2007). In communal areas, grazing on native pasture is the mostly used system of feeding for livestock production (Abusuwar and Ahmed, 2010). Natural pastures have high

energy and protein content during early growth stages (vegetative stage). However, forage quality in rangelands varies as the growing season progresses and declines when the plants mature (Dziba *et al*. 2007). Forage digestibility, intake, and palatability are negatively affected by low protein and soluble sugar content in the feed because fibre contents are high (Moyo *et al*., 2012). Consequently, weight loss and high mortality rates occur during the dry season because low-quality feed hinders animal production (Adebisi and Bosch, 2004). Soil nitrogen (N) deficiency results in low soil fertility which reduces forage yield and quality (Mpanza, 2007). Continuous cultivation and overgrazing affect soil fertility; these are common problems in Africa (Mpanza, 2007).

BRIEF DESCRIPTION OF GRASS SPECIES USED IN THIS STUDY

Themeda triandra, which is normally called the red grass, is dominant in the Africa, Australia, south-east Asia, and India (Leistner, 2000). It grows well under a variety of climatic conditions and ecosystem substrates (Leistner, 2000). *Themeda triandra* is vulnerable to change and disappears rapidly when ecological conditions are changing, such as under selective grazing pressure or reduced precipitation (Van Oudtshoorn, 1999). Reduced abundance of *T. triandra* in grasslands shows a decline in ecosystem function, grazing value, and species richness. This tufted grass varies in appearance from green to blue-green with flushes of pink that turns red with age and varies in height from 0.3 to 0.5 m (Zacharias, 1990; Leistner, 2000). It flowers from October to July. The grass grows in various soil types but it grows well in fertile soils (Van Oudtshoorn, 1999; Leistner, 2000).

Aristida junciformis (Ngongoni grass) occurs in coastal areas of KwaZulu-Natal and Eastern Cape. *Aristida juniforms* is a tufted, ornamental grass with thin leaves and it appears green with shades of light brown. It tolerates almost all soil types. *Aristida junciformis* offers excellent cover and is traditionally used to make brooms. It flowers from November to May and the size varies between 60- 80 cm, but can also reach 1 m depending on the habitat (Särkijärvi *et al*., 2012). *Aristida junciformis* provides habitat for grassland or wetland wildlife, it is not desired by farmers because it is unpalatable to animals and is an indicator of overgrazing. *A. junciformis* is a pioneer grass and is useful for preventing soil erosion (Särkijärvi *et al*., 2012).

CHAPTER THREE: THE EFFECT OF INDUCED INCREASED TEMPERATURE ON GRASS BIOMASS AND MORPHOLOGY

ABSTRACT

Rangelands are characterized by diverse vegetation physiology and plant-animal interactions due to variation in precipitation and temperature. South African grassland and savanna biomes produce the majority of the forage for livestock and wildlife. The composition and productivity of grassland and savanna are determined mainly by rainfall and temperature. A field experiment was conducted to determine how induced increased temperature (using open top warming chambers, OTCs) and the presence of *Vachellia sieberiana* var. *woodii* seedlings affect grass biomass production and morphology. Two widespread grass species of contrasting palatability and ecophysiology were the focus of this study. *Themeda triandra* is palatable and valuable in the animal production enterprise while *Aristida junciformis* is a sign of degraded rangeland as it is unpalatable.

The aboveground biomass of *T. triandra* was significantly (P= 0.008) reduced by woody seedlings in warmed plots. Warming significantly (P= 0.001) reduced the biomass of *T. triandra. Aristida junciformis* aboveground biomass was significantly (P= 0.018) reduced in warmed plots compared to unwarmed plots. Woody seedlings significantly (P=0.035) reduced *A. junciformis* biomass. There was no significant (p= 0.887) interaction between warming and *V. sieberiana* seedlings on biomass of *A. junciformis*. The mean leaf area of *T. triandra* was significantly (P= 0.005) reduced by warming in the presence of woody seedlings. The interaction of warming and woody seedlings significantly (P= 0.002) reduced mean leaf area of *A. junciformis*. Neither warming (P=0.315) nor woody seedlings (P=0.597) had a significant effect on the height of *T. triandra*. The height of *A. junciformis* tufts was significantly (P< 0.001) increased by woody seedlings present in the warmed plots. Neither warming (P= 0.395) nor woody seedlings (P= 0.142) had a significant effect on the tiller width of *T. triandra*. For *A. junciformis* tufts in plots that are warmed and had woody seedlings had significantly (P= 0.041) wider mean tiller width. Warming (P= 0.950) and woody seedlings (P= 560) had no significant effect on the tuft diameter of *T. triandra*. However, woody seedlings (P= 0.006) promoted the expansion of the tuft diameter of *A. junciformis*.

In this study, open top chambers and therefore increased temperature reduced biomass of both *A. junciformis* and *T. triandra*. *Themeda triandra* biomass was facilitated by the interaction of woody seedlings and was negatively affected by warming. This shows that global warming will reduce the available forage in rangelands.

Keywords: biomass, leaf area, height, tiller width, tuft diameter, warming, woody seedlings, open top chambers, *Themeda triandra* and *Aristida junciformis*

INTRODUCTION

Global warming is a rise in mean temperature that occurs over time, due to either climatic variability or human activity (IPCC, 2014). An increase in the mean air temperature is caused by alterations in the concentration of greenhouse gases, aerosols, and solar radiation (Biggs *et al*., 2004). The effects of increased temperature and reduced rainfall together with other stresses that include more frequent floods and increased intensity of storms result in a reduction in primary production in Africa (Biggs *et al*., 2004). There are predictions of increased wet days in high latitudes because of higher intensity of precipitation, and increased drought across mid-latitudes. However, the degree of increase in temperature is uncertain (Christensen *et al*., 2007). Precipitation tends to be the limiting factor affecting rangeland productivity (McCollum *et al*., 2011). Thus, how much the rangelands and society will be affected by increased temperature is probably going to differ according to the present vegetation and its condition (McCollum *et al*., 2011).

Rangeland is a land cover that is dominated by grasses, forbs, and/or shrubs (Boone *et al*., 2018) and provides ecosystem functions such as maintaining biodiversity (Hobbs *et al*., 2008) and producing forage for animal production (Thornton, 2010; Boone *et al*., 2018). It is characterized by variable precipitation, diverse vegetation physiology, and plant life-forms (Weber *et al*., 2000). Grasses produce approximately 20-25% of terrestrial net primary production, globally (Shoko *et al*., 2019). Biomes are characterized by different vegetation structures that are controlled by atmospheric CO_2, climate, and soil (Rutherford *et al*., 2006; Botha *et al*., 2016). The grassland biome in Africa contains many endemic/native plant species; therefore, it is recognized as a unique biome (Botha *et al*., 2016). South African grassland and savanna biomes produce most forage for animal grazing (Botha *et al*., 2016).

The composition and productivity of rangelands are determined mainly by fire, grazing, rainfall and soil; although temperature and CO_2 concentration changes need to be considered (Hoffman and Vogel, 2008; McCollum *et al*., 2011; Fereja, 2017). Temperature is crucial during all the stages of grass growth and species differ significantly based on the temperature requirement (Rutherford *et al*., 1999). Grass species' soil water requirements and nutrient absorption ability are determined by temperature. Heat differentiates species based on the plants' ability to endure extra external temperature stress (Rutherford *et al*., 1999). During the 20th century, temperature in Africa has risen by 0.5ºC (Hoffman and Vogel, 2008) whereas the global mean air temperature has risen by 0.8ºC, and an increase of 1.4-5.8ºC is estimated to occur in the 21st century (IPCC, 2012).

Increasing temperature is expected to have numerous effects on plant populations, globally (Buhrmann *et al*., 2017). In arid regions, the increasing temperature has a negative effect on grasses, as it is believed to promote bush encroachment as a result of a prolonged growing season allowing more biomass to be allocated to woody plant roots (Hoffman and Vogel, 2008). The main effect of increased temperature is the alteration of grass productivity, and changes in species composition (Buhrmann *et al*., 2017). An increase is expected to occur in mesic rangelands because semi-arid rangelands are likely to have shorter growing seasons than mesic rangelands; hence, the productivity of semi-arid rangeland decreases (Hoffman and Vogel, 2008). Klein *et al*. (2004) stated that the plants' response to experimental warming is species-specific and may be influenced by belowground resources and vegetative heat stress tolerance. The maximum temperature of 45ºC to 47ºC is the leaf area threshold for grasses; above this temperature, leaves start to wilt. This is defined as the maximum heat plants can tolerate (Klein *et al*., 2004). The plant leaves experience an excessive evaporative cooling due to high temperature; this induces water stress and reduces species richness (Chirara, 2001; Buhrmann *et al*., 2017). Grass vigour is reduced and this decreases the sward competitiveness towards the neighbour plant (Chirara, 2001). Grasses outcompete trees for resources close to the surface because tree roots have greater access to the deeper layers of the soil (Cramer *et al*., 2007; Ketter and Holdo, 2018). Trees and grasses can only compete for the topsoil resources when their roots overlap (Fetene, 2003). However, during the development stage, woody seedlings and established grass swards share resources and therefore woody seedlings are exposed to competitive stress (Chirara, 2001). Woody seedlings established within a grass community are outcompeted by grasses for the available resources and may result in mortality among seedlings (Pillay and Ward, 2014).

So far, no studies have been done on the interaction of increased induced warming and legume woody seedlings on grass growth and morphology. This experiment aimed to determine the effects of induced increased temperature on the growth and morphology of mesic rangeland grasses with and without woody legume seedlings competition. The first objective was to determine the effects of increased temperature on the leaf area, tiller width, tuft diameter, height, and biomass of mesic rangeland grasses. The second objective was to determine how woody legume seedlings affect mesic rangeland grasses' growth. These objectives gave rise to the question, what is the effect of increased temperature on the leaf area, tiller width, tuft diameter, height and biomass of mesic rangeland grasses with and without woody legume seedlings? It was hypothesised that induced increased temperatures will enhance the growth of grasses grown without woody legume seedling competition. The interaction of temperature and woody seedling would have an adverse effect on grass growth.

MATERIALS AND METHODS

Study Site

The research study was conducted at Ukulinga Research Farm in Pietermaritzburg, KwaZulu-Natal, South Africa. The farm is situated at latitude 29º 66' S and 30º 41' E where the summer mean temperature is 21ºC and winter mean temperature is 15.4ºC. The mean annual rainfall is 659 mm; the rainy period starts in October and ends in April. The highest rainfall occurs between December and January. Due to variations in temperature and landscapes, there is a combination of vegetation types that are related to the grassland biome. It is classified as the transition between KwaZulu-Natal Hinderland Thornveld and Ngongoni Veld (Mucina and Rutherford, 2006).

Experimental Design

Two hundred seeds of *Vachellia sieberiana* var. *woodii* were scarified by soaking in boiling water that was allowed to cool overnight. After soaking to soften the seed coat, each seed was sown into a 12 cm pot filled with sandy soil and grown in a greenhouse at the NM Tainton Arboretum, University of KwaZulu-Natal. Seeds were germinated and grown in the pots for two months from November 2018. Water was provided every day to the seedlings, then the seedlings were transplanted to the plots in the field, where they were watered every day for the first two weeks to help them adapt and establish. After two weeks, seedlings were

watered every second day for three weeks. After five weeks, seedlings were not watered regularly, only on hot days (when day temperatures were >28ºC).

The trial was arranged using a completely randomized experimental design, replicated six times. Forty-eight plots each measuring 2 x 2 m with a one-meter corridor between plots were marked using rope and pegs. Plots were on fairly flat terrain thus there was not much of a difference in nutrient flow in and out of the plots. The trial had two treatments: *Vachellia sieberiana* seedlings or no seedlings and open top chamber or no chamber, which were applied to pots containing largely monospecific stands of two grass species, *T. triandra* and *A. junciformis*. 24 plots were dominated by *T. triandra* and the other 24 plots by *A. junciformis*. These grasses were chosen because they occur naturally as dominant species at Ukulinga Research Farm and they differ dramatically in terms of their palatability. *Themeda triandra* is a palatable species that dominates throughout southern and eastern African savannas and grasslands and has significant ecological and economic importance (Snyman *et al*., 2013). *Themeda triandra* provides forage for animals. *Aristida junciformis* is an unpalatable tufted, evergreen species associated with the degeneration of rangelands. It is native to South Africa. In each of the treatments with woody seedlings present six *V. sieberiana* seedlings were planted. The grasses were cut to the ground level before beginning the trial, this was done to reduce aboveground competition. The seedlings were arranged in a hexagon shape following the shape of the chamber. The trial ran for four months (from January to April 2019).

Chamber Construction

The design of the open top chambers (OTCs) that were utilized for this experiment was founded by the International Tundra Experiment (ITE) (Molau and Mølgaard, 1996). Open top chambers were constructed using polycarbonate clear sheets from Maizey Plastics (Pty) Ltd, South Africa. The sheets have a light transmittance of 90% and are 2 mm thick. The sheets were cut into 100 (bottom) x 67 (top) cm trapezium shapes. Cable ties were used to assemble the chamber using six sections per chamber resulting in a hexagon shape. The OTCs used are inert because they trapped solar energy inside the chamber and do not allow any direct manipulation of temperature (Buhrmann *et al*., 2017).

Figure 3.1: Open top chambers on an area dominated by *Themeda triandra*. Plot corners are denoted by white markers.

Temperature and Humidity

Air temperature and the relative humidity were measured at 15 minute intervals for the duration of the trial at 50 cm height within the OTCs and in control plots through data loggers (U23-004 HOBO ProV2, Onset, Bourne, MA). The open top chambers were not adjusted as the grass was growing; the adjustments were going to interfere with the results of the experiment. The OTCs increased the average maximum day temperature by 3ºC and reduced the relative humidity by 32% during the day. The average maximum chamber and ambient temperature were 40ºC and 37ºC, respectively. Minimum night temperature and relative humidity were not different between the chamber and the ambient readings.

Data Collection

Biomass Production and Morphology

In the field, the grasses were allowed four months to interact with the *V. sieberiana* seedlings. Four grass tufts were marked in each plot. One leaf per tuft was randomly picked and leaf area was measured every second week using Licor LI- 3000C Portable Area Meter. Leaf area was measured every second week so that biomass will not be reduced by picking the leaves. The height of each tuft was measured from the ground to the top, this was done every week for seven weeks. Tuft diameter and tiller width were measured every week for seven weeks. Tiller width was measured using a Master-craft^TM GS5071522 digital Vernier caliper. Tiller with was measured using a measuring tape. At the end of the trial, the grass tufts were harvested, using sheep shears, placed in paper-bags inside plastic bags to retain moisture, and

immediately weighed to determine the fresh weight. After weighing the grass samples were each placed in a paper bag and dried in an oven at 60°C for 48 hours. After oven drying, each sample was then weighed to attain the dry weight.

The relative interaction intensity (RII) was determined using the following formula:

$$RII = \frac{Bw - Bo}{Bw + Bo}$$

where Bw is the dry weight of the grass plants that is observed when it is grown with woody seedlings.

Bo is the potential dry weight of the grass plants achieved in the absence of woody seedlings interaction (Armas *et al*., 2004).

The RII values are limited between -1 and +1. The negative values mean that there was a competitive interaction between the grasses and woody seedlings. Positive values show that the interaction among grasses and woody seedlings was facilitative.

Statistical Analysis

Biomass

The data were analysed using SPSS. For both grass species, a two-way analysis of variance (ANOVA) was performed after the assumption of normality of data and homogeneity of variance were met. *Themeda triandra* normality was tested using a Kolmogorov-Smirnov test, while *A. junciformis* normality was tested with Shapiro-Wilk's test because when Kolmogorov-Smirnov test was used, the data for *A. junciformis* was not normal. When interactions were not significant ($P>0.05$); the main effects were analysed separately using the independent samples t-test with the option of equal variances. When the ANOVA revealed significant difference, Tukey's test (HSD) was used to separate the means.

For leaf area, height, tiller width and tuft diameter a two-way repeated measures ANOVA was performed to test for a significant interaction between woody seedlings and warming. For leaf area *T. triandra* normality was met when tested using a Kolmogorov-Smirnov test, while *A. junciformis* normality was met after log transformation. For both *T. triandra* and *A. junciformis*, normality was met when tested with Shapiro-Wilk, when measuring the height. When measuring the tiller width and tuft diameter, data for *T. triandra* was normally

distributed whereas *A. junciformis* normality was met when tested using Shapiro-Wilk's Test. Mauchley's Test of Sphericity showed that the assumption of sphericity was met. When the ANOVA revealed significant difference, Tukey's test (HSD) was used to separate the means. This was also done when measuring height, tiller width and tuft diameter.

RESULTS

Biomass

There was a significant (P= 0.008; Table 3.1) interaction between warming and woody seedlings for *T. triandra*, showing that warming in the presence of woody seedlings reduced grass biomass (Figure 3.1 A). Warming also significantly (P= 0.001; Table 3.1) reduced the biomass of *T. triandra*. There was a no significant (P>0.05) interaction between warming and woody seedlings for *A. junciformis*. Warming and woody seedlings independently and significantly reduced biomass of *A. junciformis* (Figures 3.1 B and C). There was a significant interaction between warming and woody seedlings in *T. triandra* Figure 3.1 A showed the interaction.

TABLE 3. 1: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the biomass of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

Source of variation	*Themeda triandra*				*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	1078.499	10.799	**0.001**	84.356	5.802	**0.018**
Seedlings	1	348.044	3.485	0.065	66.683	4.587	**0.035**
Warming * Seedlings	1	730.241	7.312	**0.008**	0.296	0.020	0.887
Error	92	99.871			14.539		
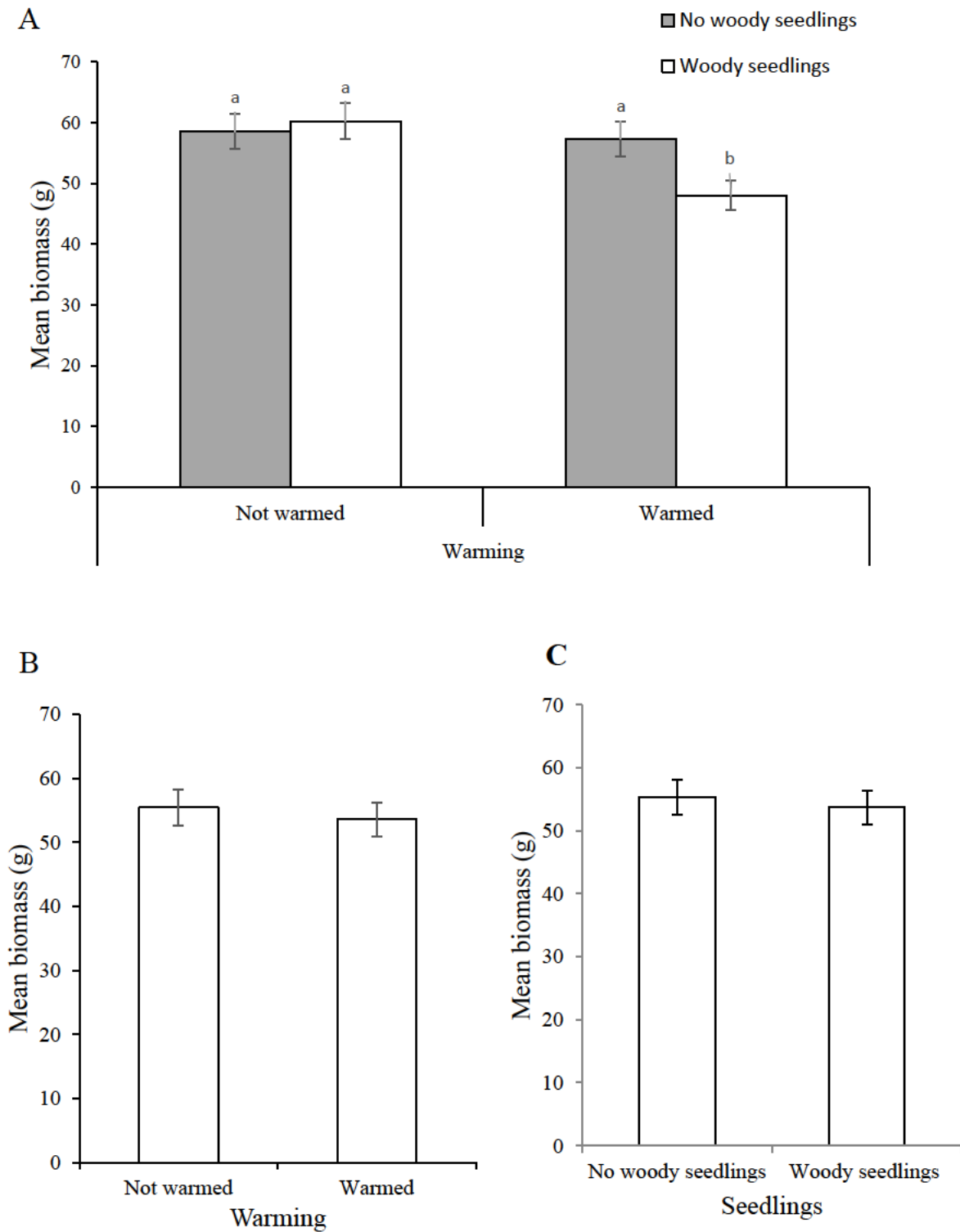
Figure 3. 1: The mean ± SE biomass g/plot of *Themeda triandra* (A) and *Aristida junciformis* (B and C). The interaction for *A. junciformis* was not significant and so only the main effects were graphed. SE= standard error. Letters in common indicate non-significance (P>0.05). B and C have no letters to indicate significance.

Leaf Area

The two-way repeated measures ANOVA revealed that there was a significant interaction between warming and woody seedlings for both *A. junciformis* and *T. triandra* (Table 3.2) showing that warming in the presence of woody seedlings reduced the mean leaf area when compared to unwarmed plots with woody seedlings.

Themeda triandra final leaf area was greater in unwarmed plots that had woody seedlings, followed by warmed plots with no woody seedlings (Figure 3.2 A). The same trend was observed in *A. junciformis* (Figure 3.2 B). The least mean leaf area for *A. junciformis* was found in warmed with woody seedlings (Figure 3.2 B). When leaf area was measured the second time, it is assumed that grasses were recovering from cutting and not producing new leaves instead of growing the already formed leaves.

TABLE 3. 2: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the leaf area of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

Source of variation		*Themeda triandra*			*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	2	0.202	0.675	0.515	0.081	0.710	0.498
Seedlings	2	0.374	1.251	0.297	0.019	0.169	0.845
Warming * Seedlings	4	1.847	6.174	**0.005**	0.840	7.326	**0.002**
Error	40	0.299			0.115		
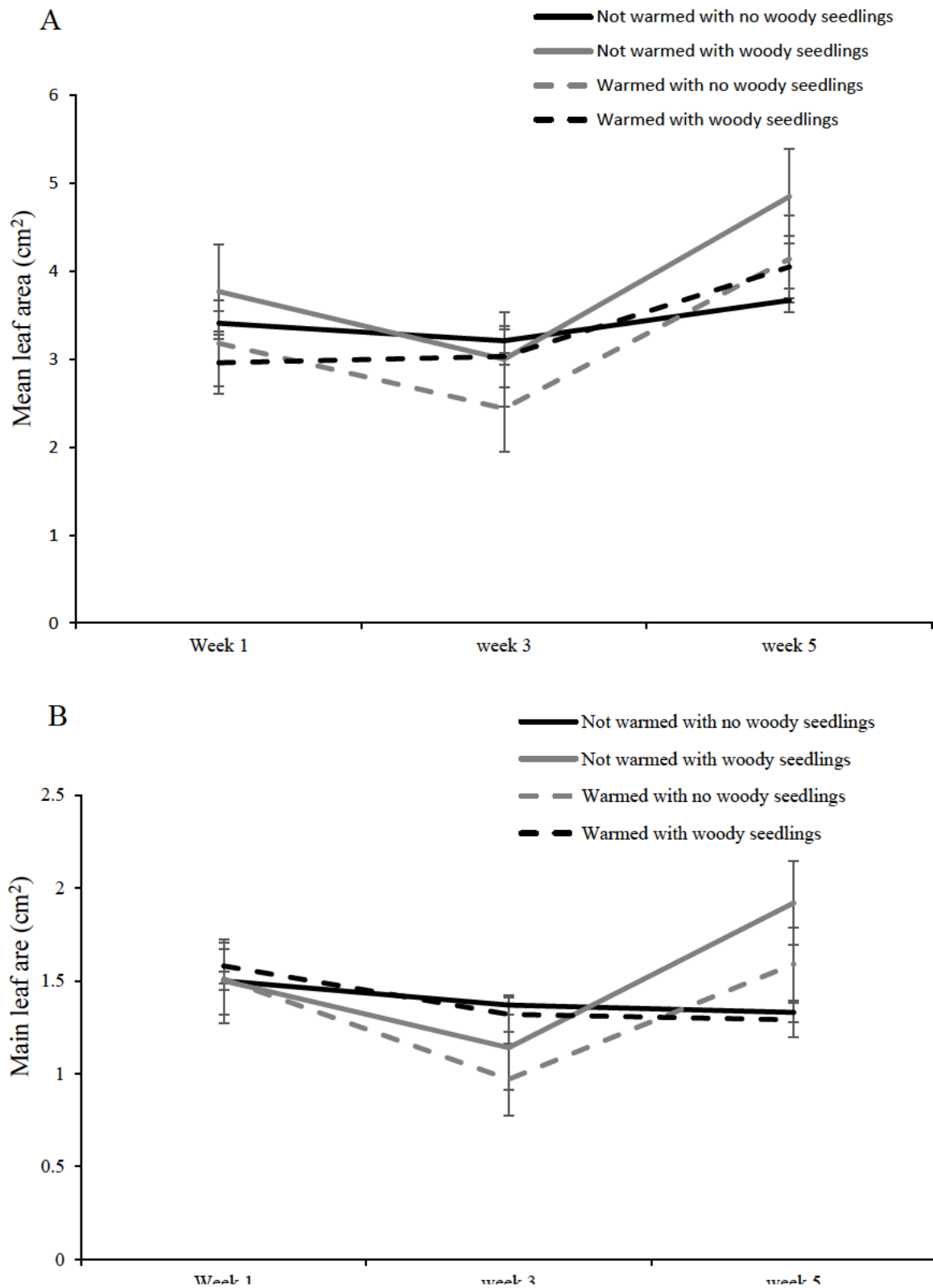
Figure 3. 2: A) *Themeda triandra* and B) *Aristida junciformis* mean ± SE leaf area (cm^2) over time. Abbreviation: SE-Standard Error.

Height

Warming significantly increased (P< 0.001; Table 3.3) the height of *A. junciformis* (warmed plots: 52.98 ± 1.403 cm; unwarmed plots: 46.58 ± 1.621 cm). There was no significant difference in the height of *T. triandra* with neither warming nor woody seedlings (Table 3.3).

The trend observed in grass height was the same for all treatments. The height of both *T. triandra* and *A. junciformis* fluctuated with treatments (Figure 3.4). The grass continued to grow taller over time and *T. triandra* had the tallest height in plots that had OTCs and woody seedlings (33.17 ± 1.370 cm) (Figure 3.4 A). Warming together with woody seedlings interaction had a positive outcome as tufts in these plots had the tallest *A. junciformis* tufts (53.58 ± 2.292 cm) (Figure 3.4 B).

TABLE 3. 3: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the height of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

Source of variation		*Themeda triandra*			*Aristida* junciformis		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	6	4.633	1.193	0.315	56.303	9.371	**<0.001**
Seedlings	6	2.986	0.767	0.597	3.074	0.512	0.799
Warming * Seedlings	6	1.407	0.362	0.901	6.008	1.000	0.429
Error	120	3.884			6.008		

A

Legend:
- Not warmed with no woody seedlings
- Not warmed with woody seedlings
- Warmed with no woody seedlings
- Warmed with woody seedlings

B

Legend:
- Not warmed with no woody seedlings
- Not warmed with woody seedlings
- Warmed with no woody seedlings
- Warmed with woody seedlings
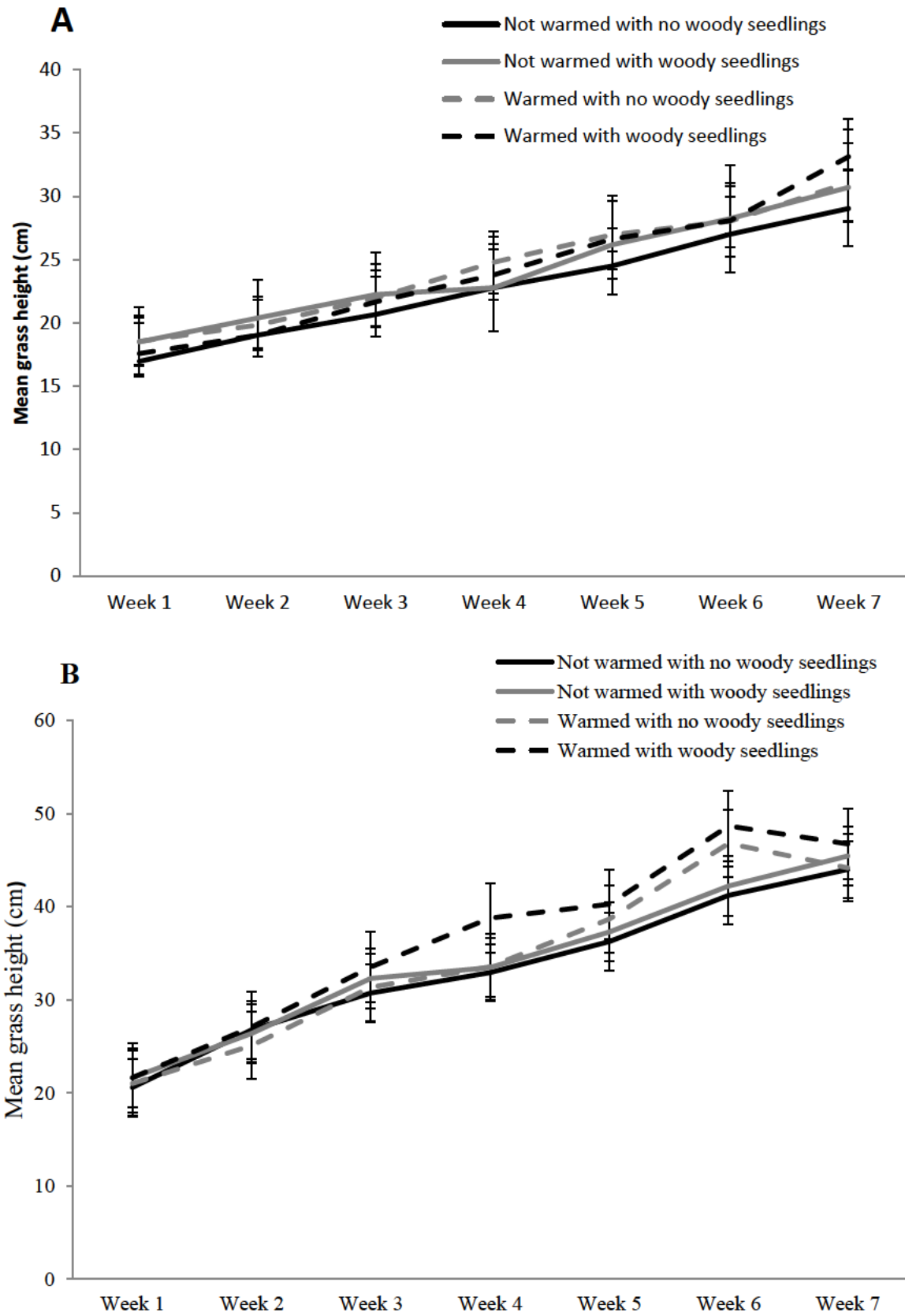
Figure 3. 3: *Themeda triandra* (A) and *Aristida junciformis* (B) mean± SE height over time. Abbreviation: SE-Standard Error.

Tiller Width

Woody seedlings in the presence of OTCs significantly (P= 0.041) increased the tiller width of *A. junciformis* (1.03 ± 0.046 cm) compared to tufts in the warmed plots with no woody seedlings which did not increase tiller width (0.94 ± 0.032 cm). For *T. triandra* neither warming nor woody seedlings had a significant effect on tiller width (P>0.05 in both cases, Table 3.4).

The mean tiller width of *T. triandra* decreased rapidly from week 1 to week 2 and was thereafter constant. The tiller width growth changed over time irrespective of the treatments (Figure 3.4 A). The mean tiller width of *A. junciformis* shrank over time. The plots that had OTCs and no woody seedlings appeared to have the lowest mean for the first 5 weeks (Figure 3.4 B). There was a general decrease in the tiller width of both *A. junciformis* and *T. triandra* over time and it does not appear to be a clear treatment effect.

TABLE 3. 4: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the tiller width of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

| Source of variation		*Themeda triandra*			*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	6	0.253	1.052	0.395	0.087	3.307	**0.005**
Seedlings	6	0.395	1.641	0.142	0.037	1.289	0.225
Warming * Seedlings	6	0.242	1.005	0.425	0.060	2.268	**0.041**
Error	120	0.240			0.026		
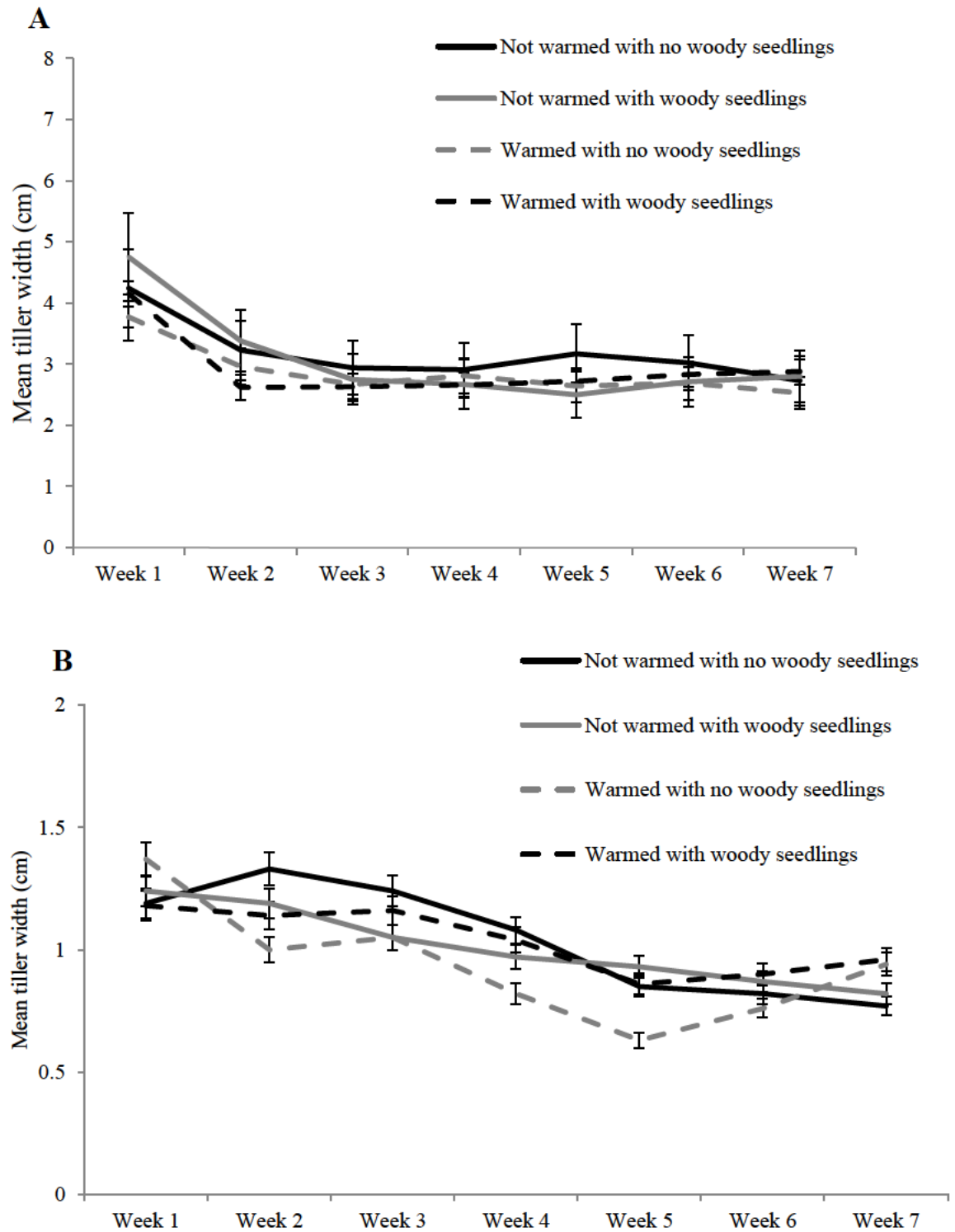
Figure 3. 4: A) *Themeda triandra* and B) *Aristida junciformis* mean± SE tiller width (cm) over time. Abbreviation: SE- Standard Error.

Tuft Diameter

Woody seedlings independently and significantly (P= 0.006; Table 3.5) increased the tuft diameter of *A. junciformis* (warmed plots: 10.14 ± 0.263 cm; unwarmed plots: 9.02 ± 0.273 cm). The ANOVA revealed that neither warming nor seedlings had a significant on the tuft diameter of *T. triandra* (P>0.05 in both cases; Table 3.5).

The mean tuft diameter of *T. triandra* of all treatments decreased from week 1 to week 3 (Figure 3.5 A). Plots that had no OTCs and had woody seedlings had the greatest tuft diameter (Figure 3.5 A). The mean tuft diameter of *A. junciformis* from week 1 to week 2 decreased in all treatments and control plots had the greatest mean tuft diameter for the first 5 weeks (Figure 3.5 B). However, plots that had OTCs and woody seedlings had the least tuft diameter throughout the trial (Figure 3.5 B). After initial declines, there was a general increase in tuft diameter for both species in all treatments over the 7 weeks of the trial. There was more variation in *A. junciformis* tuft diameter than in *T. triandra* tuft diameter between the treatments.

TABLE 3. 5: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the tuft diameter of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold

| Source of variation	d.f	*Themeda triandra*			*Aristida junciformis*		
		m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	6	1.769	0.950	0.463	1.284	0.919	0.484
Seedlings	6	1.044	0.560	0.761	4.417	3.164	**0.006**
Warming * Seedlings	6	0.660	0.354	0.906	0.384	0.275	0.948
Error	120	1.863			1.396		
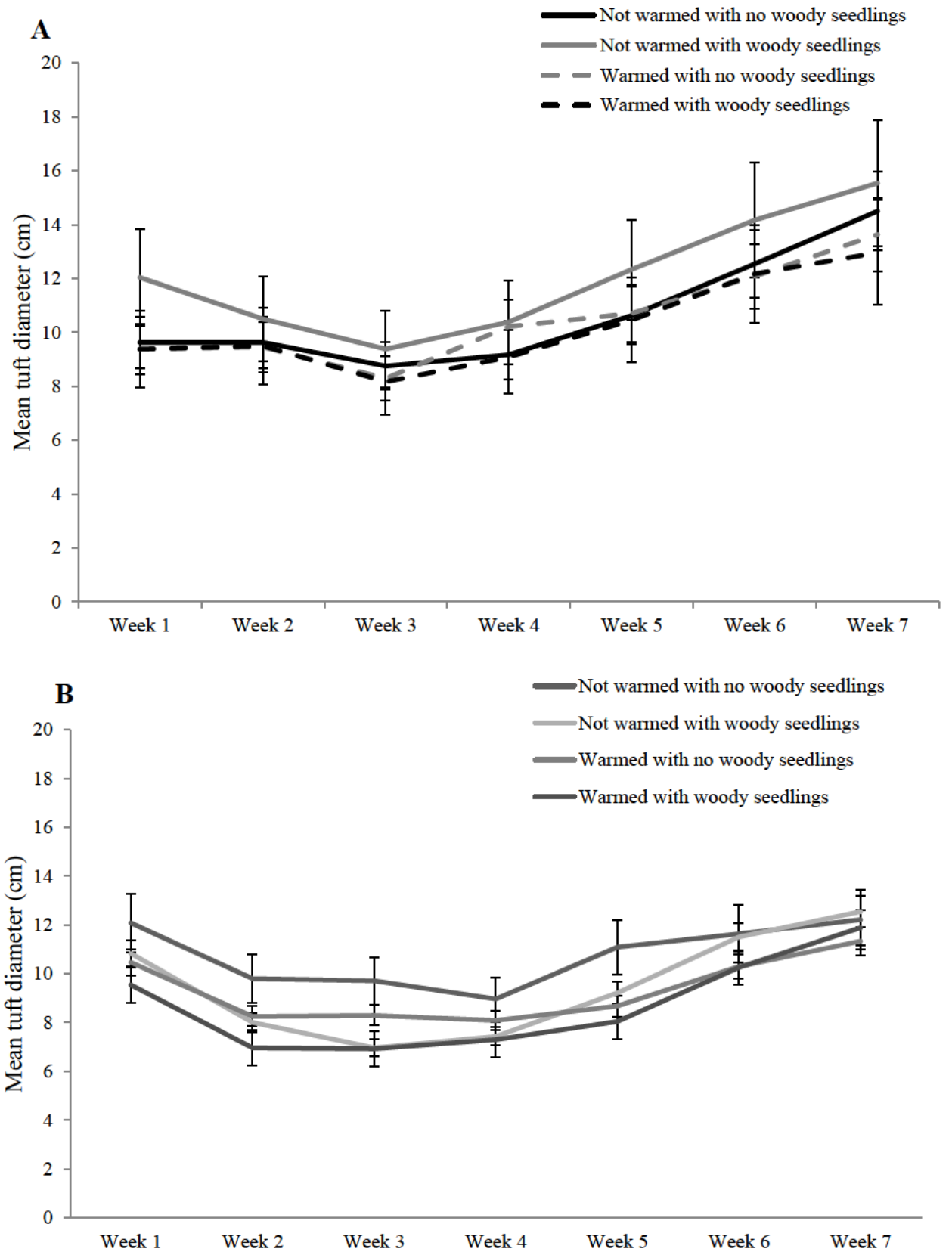
Figure 3. 5: A) *Themeda triandra* and B) *Aristida junciformis* mean± SE tuft diameter over time. Abbreviation: SE- Standard Error.

Relative Interaction Intensity

The overall interaction of *T. triandra* and the woody seedlings (-0.034) was competitive. There was a competitive interaction between *T. triandra* and woody seedlings (-0.088) in warmed plots. The interaction between *T. triandra* and the woody seedlings (0.014) was facilitative when warming was not included. There was a competitive interaction between *A. junciformis* and the woody seedlings (-0.015) regardless of warming. Competition occurred between *A. junciformis* and woody seedlings (warmed plots: -0.017; unwarmed plots: -0.014).

DISCUSSION

Biomass

The plant community structure is determined by temperature (Saleska *et al*., 2002), herbivory and fire. Increased temperatures associated with reduced rainfall decrease grassland productivity, which modifies ecosystem function (Burnamm *et al*., 2017). Higher temperatures indirectly prolong the growing season then affect soil nitrogen mineralization and accessibility to plants, which then affect N uptake by plants' roots (Wan *et al*., 2005).

In this study, grasses that were grown in open top chambers had lower biomass compared to grasses that were not subjected to increased temperature. A decrease in aboveground net primary productivity (40 g/m^2) has been observed in other studies when grasses were subjected to warming (Klein *et al*., 2007). However, in a study in Durban, South Africa, the aboveground production of graminoids increased by ± 19.9% when subjected to higher temperatures during autumn and spring seasons (Buhrmann *et al*., 2017). In Colorado where there is mosaic vegetation type, soil warming reduced plant productivity (Saleska *et al*., 2002). In a meta-analysis it was observed that experimental warming either increases ANPP or have no effect at all (Walker *et al*., 2006). However, in this study it has been observed that warming decreased the biomass of investigated grasses; this may be due to edaphic and climatic changes

Experimental warming increases aboveground net primary productivity only when the ambient temperature is cool during the growing season (Grant *et al*., 2015). When the

ambient temperature is hot and water is limited period, warming increases water stress and negatively affects ANPP (Schwartz *et al*., 2006). In a warming experiment through transplanting that was conducted in a mesic grassland in the Pyrenees, warming increased biomass of plants that were transplanted to the cold and dry lowland (Sebastia, 2007). Therefore, the effect of high temperatures on grassland productivity remains complex (Burnamm *et al*., 2016).

Woody seedlings negatively affected the biomass of *A. junciformis*. In plots that had woody seedlings, the biomass was reduced compared to plots that had no woody seedlings. This indicates that woody seedlings were competing with grasses for the available resources. Tussock grasses are known to out-compete tree seedlings (Holdo and Brocato, 2015) during the establishment phase (Ketter and Holdo, 2018). The interaction between grasses and woody seedlings does not depend on the depth of roots but it depends on the traits of woody seedlings (Ketter and Holdo, 2018). The interaction of warming and woody seedlings negatively affected the biomass of *T. triandra*. Warming decreased grass biomass in monoculture and a drastic drop in yield was observed when warming was combined with woody seedlings. Klein *et al*. (2007) stated that experimental warming decreases total ANPP and these results are in line with the findings in this study.

When plants are growing close to each other they compete for available resources; the nurse effect which results in a facilitative interaction when environmental amelioration outweighs the negative impacts of warming (Callaway and Walker, 1997). The synergistic interactions between warming and woody seedlings show that the combined effect cannot be predicted from a single factor study. *T. triandra* is considered as a highly palatable grass; the decrease in the biomass caused by the interaction of warming and woody seedlings may result in the shortage of palatable biomass for herbivores in extensive rangelands.

Leaf Area

Leaf area, which was collected every second week so as not to affect the biomass, showed the same trend for both *A. junciformis* and *T. triandra*. The wide leaves in unwarmed plots that had woody seedlings occur because leguminous woody seedlings produce N which is available for plant uptake. In plots that had OTCs and no woody seedlings, the leaf area was not affected. However, *A. junciformis* had the widest leaves in the unwarmed plots with woody seedling interaction; narrow leaves were found in warmed plots that had woody

seedlings as well. This may be because woody seedlings improved the soil to favour the growth of the leaf area under cool conditions. Open top chambers increase the ambient temperature by 3°C, this builds up heat around the leaf surface and they do not allow heat dissipation through air movement (Klein *et al*., 2004). The interaction of warming and woody seedlings reduced the leaf area, these results are associated with the relative rates of leaf extension given that the grass was cut before starting the experiment (Saleska *et al*., 2002).

During the early recruitment stages of woody seedlings, these legumes ameliorated the soil and facilitated the grass growth (leaf expansion); later legumes out-competed the neighbour plant (Wagner *et al*., 2018). Findings in this study are consistent with Wagner *et al*. (2018) who found that either legume seedlings gain strength over time or active tussock grasses reduced competitive ability. The main impact of competition was retardation of growth rates, which is a typical way in which competition expresses itself in all kinds of herbaceous vegetation (Wilson and Tilman 1991). In regions with wet growing seasons, soil moisture is not a restrictive factor; hence, warming makes more N to be available to the soil. Leaf area is important because it controls photosynthesis, respiration and water use processes which results in the primary productivity of leaves (Quetin and Swann, 2018). Warming increases vapour pressure deficit which increases water demand in plants, this leads to hydraulic damage in leaves which later results in reduced leaf area (Quetin and Swann, 2018).

Height

Open top chambers significantly increased the grass height of *A. junciformis*. OTCs exert heat that damages plant tissues (Klein *et al*., 2007). Plant tissues develop a heat tolerance threshold that reduces heat stress (Klein *et al*., 2007); the same trend was observed in *A. junciformis* plots because the height was increased by warming. Klein *et al*. (2007) stated that regions with limited N for plant uptake and cooler air temperature experience greater species loss with warming.

Themeda triandra did not show visible differences in height in all treatments. However, when comparing the biomass, *T. triandra* was shorter than *A. junciformis*, but produced greater yields indicating that the tufts were denser. This shows that increased grass height does not necessarily mean that the grass will produce more biomass. The *A. junciformis* sward provides soil cover but not the much-needed forage because it is unpalatable. When soil moisture was considered, warming effect on plant height increase was more evident in mesic

regions compared to semi-arid regions (Klein *et al*., 2007). Grass height is important because it is associated with life span and time to maturity. It is noted that low production grass species that are less palatable are taller that the more palatable grasses (Moles *et al*., 2009). This was also noted in this study as *A. junciformis* was taller than *T. triandra*. The variation in tallness may be due to environmental adaptation. Taller grasses have great ability to compete for light compared to shorter grasses because of correlation between height and leaf area (Moles *et al*., 2009).

Tiller Width

The overall tiller width of *A. junciformis* was greater in control plots and warmed plots with woody seedlings interaction. The tiller width of both *T. triandra* and *A. junciformis* when the data was first collected was large and slowly decreased. This is because the grasses were cut before starting the experiment and the tillers that were measured were the ones that were growing. The grass was cut to reduce resource competition when interacting with newly transplanted woody seedlings. Tiller width of both *A. junciformis* and *T. triandra* followed the same trend irrespective of treatments. These trends were not uniform; there were variations from one week to the following week. *A. junciformis* tiller width in plots that had OTCs was greater compared to plots that had no OTCs, whether or not there were woody seedlings. For *T. triandra* the tiller width was almost the same in all the treatments. This shows that *A. junciformis* was adapting to the increased warming as OTCs induce heat stress.

Tuft Diameter

Warming generally decreases tuft diameter. Ketter and Holdo (2018) stated that plants compete for resources other than water. Both *A. junciformis* and *T. triandra* had wider tuft diameter in the unwarmed plots compared to warmed plots. These outcomes are in line with Saleska *et al*. (2002), who stated that warming shifts the competitive balance of plants. Warming posed a facilitative impact towards *A. junciformis* and *T. triandra* and resulted in the expansion of tuft diameter. It is believed that the positive outcomes that occur due to experimental warming occurs because the dominant plant species takes advantage of the favourable micro-environment (Walker *et al*., 2006). Woody seedlings also increased the turf diameter of *A. junciformis*. This shows that the interaction between woody seedlings and grasses was facilitative. Plots that had OTCs had the least tuft diameter because *T. triandra* is susceptible to heat stress (Van Oudtshoorn, 1999). Positive and negative interactions tend to

be species- and/or habitat-specific (Callaway, 1997). However, the relative interaction intensity showed that the interaction of *T. triandra* and woody seedlings in unwarmed plots was facilitative and this was the only facilitative interaction in this trial. The interaction of *A. junciformis* and woody seedlings was competitive, regardless of warming.

CONCLUSION

Warming was shown to negatively affect the biomass of grasses. Woody seedlings reduced the biomass of *A. junciformis*, regardless of warming, which means even though tussock grasses are known to be strong competitors, woody seedlings outcompeted *A. junciformis*. The combined treatment of warming and woody seedlings had no effect on the biomass of *A. junciformis*. Even though warming reduced biomass, *A. junciformis* tufts were tallest in warmed plots. The interaction of warming and woody seedlings reduced *T. triandra* biomass. Surprisingly, *T. triandra* had greater biomass than *A. junciformis* but *A. junciformis* was taller than *T. triandra* indicating that height is a poor proxy for biomass in tufted grasses.

Leaf area of both *A. junciformis* and *T. triandra* was significantly reduced by woody seedlings in warmed plots. This explains the reduction of biomass in warmed plots that had woody seedlings. The tiller width of *T. triandra* was not affected by the treatments. *Aristida junciformis* warmed plots with no woody seedlings had the thinnest tillers. Warming and woody seedlings had no effect on the tiller width of *T. triandra*. That is, the combined treatments resulted in no effect on the tiller width of *T. triandra*. Woody seedlings independently reduced the tuft diameter of *A. junciformis*. Warming promoted height and tuft diameter of *A. junciformis*.

The different responses of plants to experimental warming occurs as a result of different geographic regions that have different soil moisture content. The different morphological responses of these grasses to warming shows that as global warming is occurring, the palatable biomass will be reduced compared to unpalatable biomass. Understanding the plant traits and processes is ecologically important to help in developing strategies to overcome the current effects of global warming.

CHAPTER FOUR: INTERACTIVE EFFECTS OF WARMING AND LEGUME SEEDINGS ON NUTRITITIVE VALUE OF TWO RANGELAND GRASSES

ABSTRACT

Increases in the average surface air temperature has negative effects on the flora, globally. Global warming negatively affects the herbage production and nutritive value by reducing soil moisture. Bush encroachment is also a major problem in Africa. Therefore, to understand the effect of the interaction of induced increased temperatures (using open top warming chambers, OTCs) and the presence of *Vachellia sieberiana* var. *woodii* seedlings on the regrowth biomass and nutritive value of palatable and unpalatable grasses, a field experiment was conducted at Ukulinga Research Farm over 4 months. Two grass species that dominate and occur naturally in mesic grasslands were the main focus in this study. *Themeda triandra* is palatable and is a sign of good veld condition while *Aristida junciformis* is unpalatable and a sign of degraded rangeland.

The regrowth aboveground biomass of *T. triandra* was significantly ($P<0.001$) reduced by the interaction of warming and woody seedlings. Warming independently reduced ($P<0.001$) biomass of an unpalatable *A. junciformis*. Neither warming ($P= 0.490$) nor woody seedlings ($P= 0.312$) had a significant effect on the acid detergent fibre of *T. triandra*. Warming ($P= 0.486$) and woody seedlings ($P= 0.313$) had no significant effect on the acid detergent fibre of *A. junciformis*. The neutral detergent fibre of *T. triandra* was significantly ($P=0.002$) increased by warming. Warming and woody seedlings interaction had no significant ($P= 0.344$) effect on the neutral detergent fibre of *A. junciformis*. Warming and woody seedlings had no significant effect on the fibre of regrowth of both grass species ($P>0.05$). Woody seedlings significantly ($P<0.05$) increased the N content of both primary growth and regrowth of *T. triandra*. Warming together with woody seedlings interaction increased nitrogen content of both primary growth ($P=0.043$) and regrowth ($P=0.003$) of *A. junciformis*.

Aristida junciformis improved quality only when warming interacted with leguminous woody seedlings. Leguminous woody seedlings improve the N content of these grasses and the seed pods of legumes can be used as the supplement when low-quality forage is abundant. Warming is known to decrease the nutritive value of grasses by increasing maturity and fibre content. This was shown by the response of *T. triandra* to warming.

INTRODUCTION

Global warming, defined as the rise in average temperature conditions over time, is evident through extreme weather events which include storms, floods and drought (Shahzad, 2015). The Earth's air temperature has increased by 0.6 to 0.9 ℃ between 1906 and 2006, (Shahzad, 2015). Between 1986 and 2005, an increase of 1.1 to 2.6 ℃ in air temperature occurred (Collins *et al*., 2013). Due to increased warming, carbon cycling also fluctuates; altering plant productivity (Shahzad, 2015). In some areas, global warming will result in reduced palatable biomass mostly in areas where the temperatures are already high (Shahzad, 2015). Grassland yield and high-quality results in profitable production. Primary growth has low yield and constitutes low crude protein compared to regrowth (Naadland *et al*., 2017). Grass regrowth has low neutral detergent fibre and its digestibility is higher than that of primary growth (Naadland *et al*., 2017). Few studies have investigated the nutritional quality of plants in the vegetative stage.

Grasslands are terrestrial ecosystems that are covered by graminoid plants and scattered woody vegetation (Boone *et al*., 2018). Heat and precipitation are the main factors controlling the vegetation distribution and aboveground productivity, even though grazing and fire play an important role (Hobbs *et al*., 2008). Climate changes do not only affect productivity but also alters plants' physiological processes and nutrient availability and may decrease forage quality (Xu *et al*., 2013). The nutritive value of rangelands is mainly affected by heat, rainfall availability and soil nutrients; plant age at harvest and also by species composition (Xu *et al*., 2013). Forage quality decreases as the plant grows because protein and absolute carbohydrates decline with age (Buxton, 1996). Effects such as increased maturity rate result in low nutrient content and high water stress increases cellulose content (Hoffman and Vogel, 2008). Even so, plants have different forage quality at the same stage of maturity. That is why grasslands with diverse vegetation have lower forage quality than grasslands with fewer species (Ball *et al*., 2001; Klein *et al*., 2007). Consequently, grass-fed livestock production is severely constrained by low-quality forage (Adebisi and Bosch, 2004; Dumont *et al*., 2015). High quality forage is needed to meet the animal requirements (Lovejoy, 2005).

Mature plants have a low leaf-to-stem ratio and high cell-wall content (Ball *et al*., 2001; Dumont *et al*., 2015). Grasses in tropical regions are known to have high fibre and low protein contents when compared with grasses in cooler regions (Habermann *et al*., 2019). Increased temperatures usually stimulate plant growth and lignify cell wall which increases the acid detergent fibre and neutral detergent fibre contents (Lee *et al*., 2017; Habermann *et al*., 2019). Neutral detergent fibre in the feed limits ingestion by animals and promotes peristalsis (Zang *et al*., 2018). Acid detergent fibre binds the feed and making it hard for animals to absorb (Zang *et al*., 2018). Therefore, the high fibre content in feed results in lower quality and consequently interferes with the digestion of plants by herbivores (Ball *et al*., 2001). There are other factors, other than temperature that decrease forage quality; such as the time during harvest, maturity at harvest, and water deficit (Habermann *et al*., 2019).

High temperatures indirectly affect plants' chemical composition by warming the soil and increasing soil N availability and plant N uptake (Buxton and Fales, 1994). In contrast, warming reduces soil moisture and leads to water stress which reduces the effect of plant N uptake. This results in contrasting outcomes of warming on forage N content (Dumont *et al*., 2015). Experimental investigation on the warming effect on forage quality is rare (Dumont *et al*., 2015).

Plant-plant interaction (competitive and facilitative) occurs and it varies with plant traits, region, and climatic conditions (Dohn *et al*., 2013). Plants in the same community compete for the same available resources (light, nutrients, and water) (Grant *et al*., 2015). Trees compete with each other and their underground competition is said to occur in the deeper layers of the soil, depending on the soil profile. Grasses are strong competitors compared to trees when the interaction is taking place on the top layers of the soil (Cramer *et al*., 2007; Ketter and Holdo, 2018). However, grasses can outcompete trees, especially during the juvenile stage (Cramer *et al*., 2012). This is because the roots of the establishing seedlings and roots of grasses occur in the top layer of the soil (Cramer *et al*., 2012). Thus belowground competition is more evident than aboveground competition. Through environmental amelioration, nitrogen-fixing legumes promote neighbouring plants by increasing soil nitrogen; this is called the nursing effect (Amedie, 2013). Plants differ genetically, hence the rate of maturity is species dependent (Zang *et al*., 2018), that is why the two grass species used in this study were not compared to each other but rather to their regrowth nutritive component.

Thus far, few studies have comprehensively quantified the interaction effect of warming and woody seedlings on the chemical composition of grasses and the regrowth nutritional value. To address this gap, a field experiment was conducted to determine the effects of induced increased temperature on the nutritive value of mesic rangeland grasses with and without competition from seedlings of a woody legume. The objective was to determine the effects of increased temperature on the nutritive value of mesic rangeland grasses with and without woody legume seedlings. The objective gave rise to the question, what is the effect of induced increased temperature on the nutritive value of mesic rangeland grasses with and without woody legume seedlings? It was hypothesised that induced increased temperature would increase the fibre content of grasses grown without woody legume seedlings competition but it will have no effect on the regrowth fibre content. The interaction of temperature and woody seedlings would increase the crude protein of both primary growth and the regrowth of grasses.

MATERIALS AND METHODS

This section has been explained in the previous chapter

Data Collection

Biomass Production

The samples were then milled with a small grinder and sieved through 1mm for chemical analysis. The samples were analysed for acid detergent fibre (ADF) and neutral detergent fibre (NDF) using the method described by Van Soest *et al.* (1991) at Cedara, KwaZulu-Natal. Neutral detergent fibre is hemicellulose, cellulose and lignin. Acid detergent fibre is cellulose and lignin. Hemicellulose and cellulose are structural carbohydrates that can be digested by ruminants. Lignin is an indigestible compound.

To determine crude protein, the portions of grass samples were milled to fine powder in a Precellys® Evolution homogeniser. Then nitrogen was analysed in an elementar rapid N cube using the Dumas method, after which crude protein was calculated from nitrogen multiplied by 6.25.

STATISTICAL ANALYSIS

Regrowth Biomass

The *T. triandra* regrowth biomass was normally distributed after Log transformation when using the Kolmogorov-Smirnov test. Shapiro-Wilk's test showed that the *A. junciformis* biomass was also normally distributed. An ANOVA for *T. triandra* was used to test significance among warming and woody seedlings as well as the interaction effect. In cases where there was no significant interaction effect, an independent sample T-test with an option of equal variance was run to test the main effects separately at P<0.05.

Nutritive Value

Data for all fibres (ADF and NDF) were normally distributed except for ADF of *T. triandra* that was normal after arcsine transformation. A Kolmogorov-Smirnov test showed that the crude protein content of both *T. triandra* and *A. junciformis* was normally distributed. An ANOVA was used to test for significance among warming and woody seedlings. Where there was no significant interaction effect, an independent samples T-test with an option of equal variance was used to test the main effects separately. When there was a significant interaction, a post-hoc test using Turkey's HSD test was used to separate the means at P< 0.05.

RESULTS

Regrowth Biomass

The biomass of *T. triandra* was significantly (P<0.001; Table 4.1) reduced by woody seedlings in warmed plots while, unwarmed plots with woody seedlings produced the greatest yield (Figure 4.1 A). *Aristida junciformis* regrowth biomass was significantly (P< 0.001; Table 4.1) reduced in warmed plots (Figure 3.1 B) compared to unwarmed plots. Woody seedlings had no significant (P= 0.313; Table 4.1) effect on the regrowth biomass of *A. junciformis*.

TABLE 4. 1: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the regrowth biomass of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

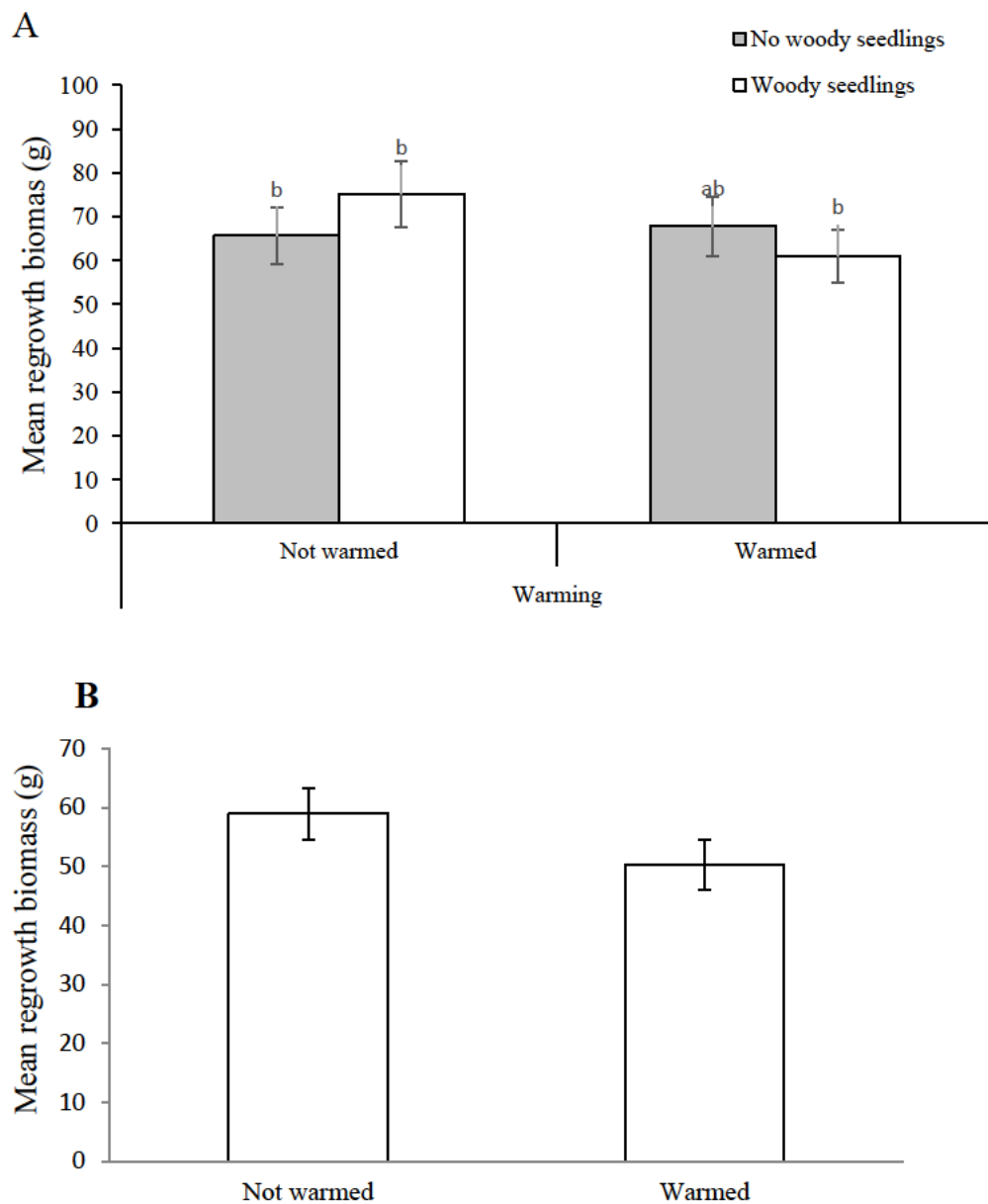| Source of variation		*Themeda triandra*			*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	863.220	6.997	**0.010**	1819.258	12.966	**<0.001**
Seedlings	1	44.187	0.358	0.551	144.134	1.027	0.313
Warming * Seedlings	1	1617.124	13.108	**<0.001**	3.631	0.026	0.873
Error	92	123.863			140.310		

Figure 4 1: The mean ± SE regrowth biomass (g/plot) of *Themeda triandra* (A) and *Aristida junciformis* (B). SE= standard error. Letters in common indicate non-significance (P>0.05).

Fibres

Warming independently and significantly (P= 0.002; Table 4.3) increased neutral detergent fibre of *T. triandra* (warmed plots: 74.68 ± 0.295 g/plot, unwarmed plots: 73.22 ± 0.418 g/plot). Warming had no significant (P= 0.490; Table 4.2) effect on the acid detergent fibre of *T. triandra*. Warming and woody seedlings had no significant (P= 0.145; Table 4.2) effect on ADF of *A. junciformis*. There was no interaction between warming and seedlings in the NDF of *A. junciformis* (P>0.05; Table 4.3). There were no significant differences in the fibres of grass regrowth among the warming and woody seedling treatments as shown in Table 4.4 and 4.5.

TABLE 4. 2: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the ADF of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown.

Source of variation		*Themeda triandra*			*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	0.007	0.495	0.490	1.535	0.504	0.486
Seedlings	1	0.014	1.077	0.312	4.167	1.027	0.313
Warming * Seedlings	1	0.029	2.213	0.152	7.009	2.302	0.145
Error	20	0.013			3.044		

TABLE 4. 3: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the NDF of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

Source of variation		*Themeda triandra*			*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	12.790	12.206	**0.002**	5.097	2.854	0.107
Seedlings	1	0.022	0.021	0.889	0.177	0.099	0.756
Warming * Seedlings	1	0.807	0.770	0.391	1.675	0.938	0.344
Error	20	1.048			1.786		

TABLE 4. 4: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the ADF regrowth of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown.

Source of variation	*Themeda triandra*				*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	0.353	0.197	0.680	2.020	0.662	0.462
Seedlings	1	0.115	0.064	0.812	1.638	0.237	0.504
Warming * Seedlings	1	4.090	2.284	0.205	1.110	0.364	0.579
Error	4	1.791			3.052		

TABLE 4. 5: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the NDF regrowth of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown.

Source of variation	*Themeda triandra*				*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	0.414	0.130	0.736	1.584	0.342	0.590
Seedlings	1	0.068	0.022	0.890	0.925	0.200	0.678
Warming * Seedlings	1	5.281	1.664	0.265	2.554	0.552	0.499
Error	4	3.175			4.629		
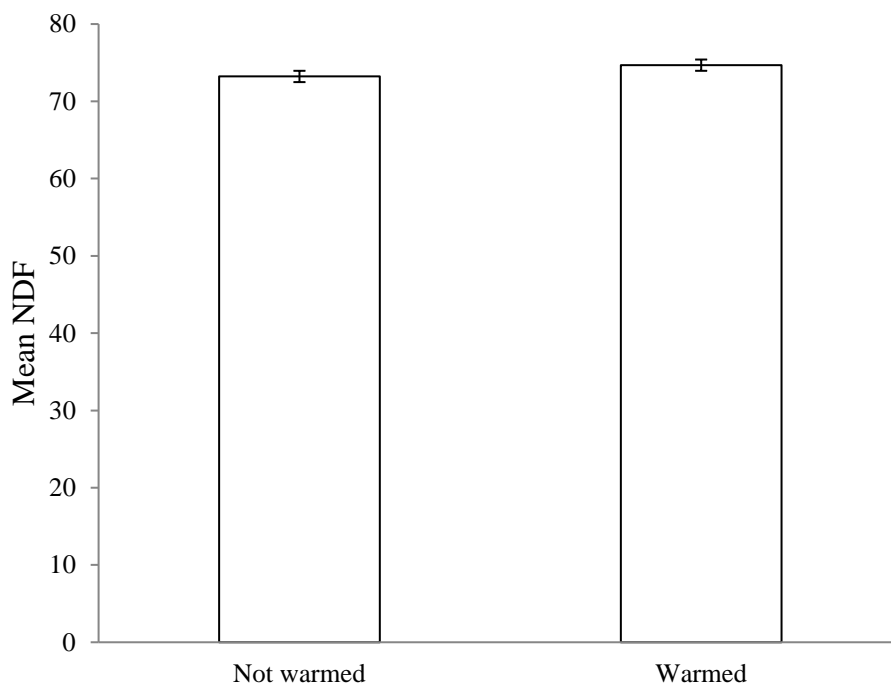
Figure 4 2: The mean ± SE neutral detergent fibre of *Themeda triandra*. SE= standard error.

Protein Content

Warming and woody seedlings independently and significantly (Table 4.6) increased the protein content of *T. triandra*. Warming together with woody seedlings interaction significantly (P= 0.043; Table 4.6) increased the protein content of *A. junciformis* (Figure 4.2 B). Woody seedlings significantly (P=0.043; Table 4.6) increased the protein content of *A. junciformis* (with woody seedlings: 6.48 ± 0.105, without woody seedlings: 6.18 ± 0.125; P< 0.05).

TABLE 4. 6: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the protein of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

Source of variation		*Themeda triandra*			*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	0.888	5.134	**0.035**	0.105	0.841	0.370
Seedlings	1	1.258	7.273	**0.014**	0.559	4.470	**0.047**
Warming * Seedlings	1	0.288	1.665	0.212	0.583	4.663	**0.043**
Error	4	0.173			0.125		

A
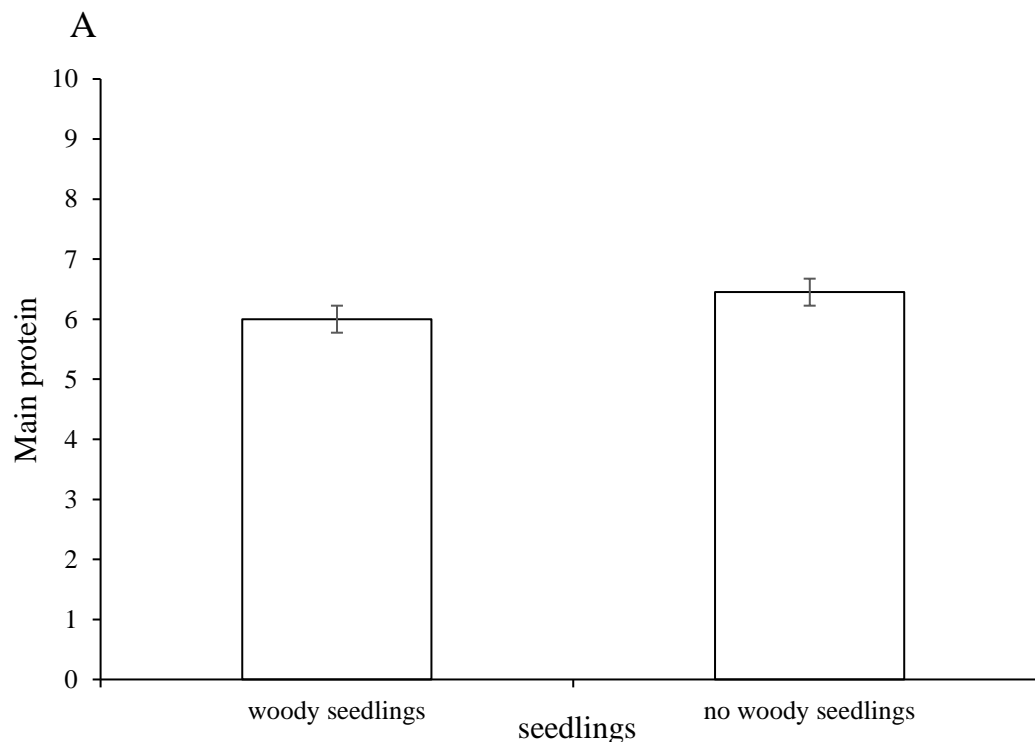
B
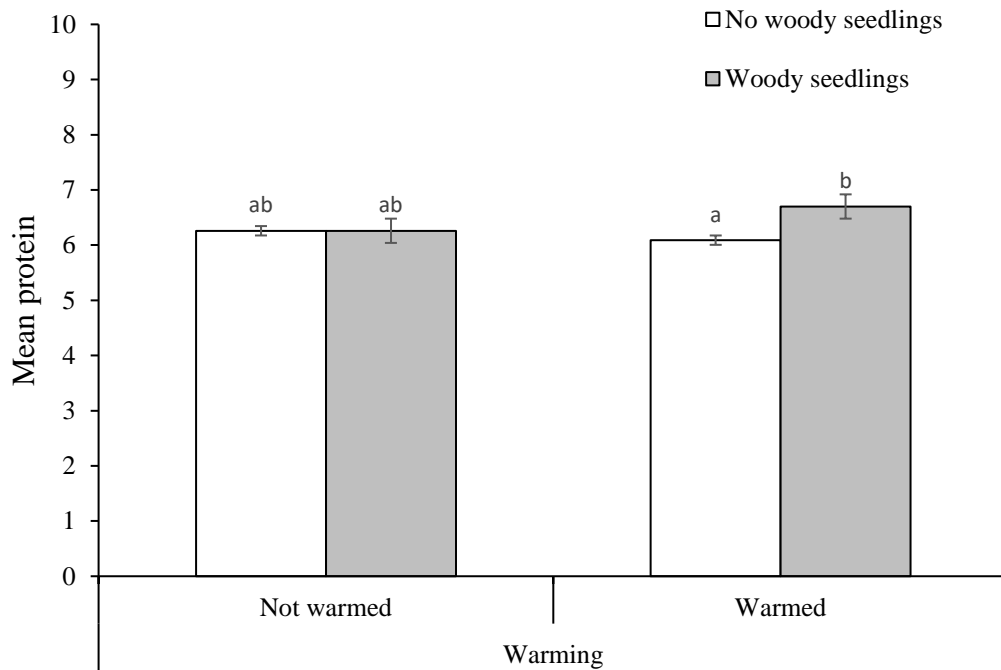
Figure 4 3: The mean ± SE protein content of *Themeda triandra* (A) and *Aristida junciformis* (B). SE= standard error. The interaction for *T. triandra* was not significant, only the main effect for woody seedlings was graphed. Letters in common indicate non-significance (P>0.05).

Regrowth Protein Content

Warming significantly P< 0.010) increased the protein content of *T. triandra* regardless of woody seedlings (warmed: 7.73 ± 0.130; unwarmed: 6.70 ± 0.184). Woody seedlings independently and significantly increased the protein content of *T. triandra* (with woody seedlings: 7.66 ± 0.130; without woody seedlings: 6.77 ± 0.101, P= 0.001). The interaction of warming and woody seedlings significantly increased the protein content of *A. junciformis* (Table 4.7).

TABLE 4. 7: Results of analysis of variance of the main effects and interaction of warming and woody seedlings on the protein regrowth of *T. triandra* and *A. junciformis*. The degrees of freedom (d.f), mean of squares (m.s), F-ratio and P-values are shown with significant values in bold.

Source of variation	*Themeda triandra*				*Aristida junciformis*		
	d.f	m.s	F-ratio	P-value	m.s	F-ratio	P-value
Warming	1	3.211	31.766	**<0.001**	0.013	0.134	0.724

Seedlings	1	2.358	23.327	**0.001**	0.031	0.314	0.591
Warming * Seedlings	1	0.008	0.078	0.787	1.718	17.275	**0.003**
Error	4	0.101			0.099		
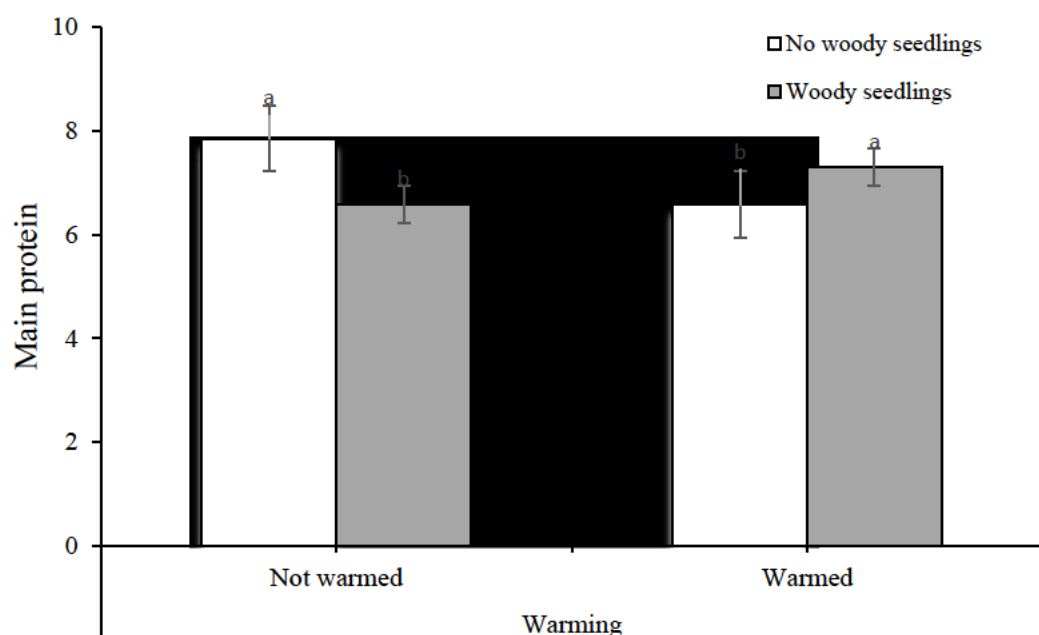
Figure 4 4: The mean ± SE protein content of *Aristida junciformis*. SE= standard error. The interaction for *T. triandra* was not significant. Letters in common indicate non-significance (P>0.05).

DISCUSSION

Global warming is changing the vegetation distribution in South Africa (Moncrieff *et al*., 2014); these vegetation modifications will result in shifts in rangeland productivity. Developing strategies to overcome these changes is of critical importance. Natural pastures have high energy and protein content during early growth stages (vegetative stage). However, forage quality in rangelands varies as the growing season progresses, it decreases as the plants mature (Dziba *et al*. 2007). During the dry season, when the available forage is inadequate and has low quality, animal production that solely depends on native vegetation is negatively affected. To improve the poor-quality forage, supplementation with high protein feed is needed and becomes costly to farmers. Klein *et al*. (2007) stated that warming reduces rangeland quality by decreasing species variability and forage quality. A one-month regrowth of grasses was monitored and in this study, the observed biomass differed with treatment. Biomass for both grass species in plots that had OTCs was significantly reduced. This means warming reduces grass biomass.

Themeda triandra unwarmed plots that had woody seedlings produced the greatest biomass. This is evidence of the nursing effect because *T. triandra* was complemented by the woody seedlings. However, the biomass of *T. triandra* in plots that had OTCs and woody seedlings was significantly reduced. This shows that the interaction between woody seedlings and *T. triandra* was facilitative when warming was not included. Generally, legume woody seedlings improve soil conditions by fixing atmospheric N making N available to the soil (Ketter and Holdo, 2018). Woody seedlings ameliorated the soil, and soil moisture and temperature have shown to favour grass growth. Therefore, the increase in biomass of *T. triandra* may be due to facilitative interaction and nitrogen availability to the soil.

The stage of plant regrowth highly affects forage quality because of decreased leaf-to-stem ratio (Boval and Dixon, 2012). Physiological changes that occur as the plant matures negatively affect forage quality by increasing fibres (Klein *et al*., 2007; Zang *et al*., 2018). The interaction of warming and woody seedlings had no significant effect on the ADF of the primary growth of both *A. junciformis* and *T. triandra*. In contrast, a meta-analysis revealed that NDF increases by 0.4% for every 1°C rise in temperature (Blaser *et al*., 2007). However, Lee *et al*. (2017) stated that fibre contents increase by 13% for every 1°C rise in air temperature. The NDF content is also a photosynthetic dependant pathway (Lee *et al*., 2017). However, the hypothesis that induced increased temperature will increase the fibre content of primary growth was met in this study as warming alone significantly increased the NDF of *T. triandra*. The regrowth of both *A. junciformis* and *T. triandra* had no significant differences in the fibre content. These results are in line with the findings of Dumont *et al*. (2015) who reported that warming has no significant effect on ADF and NDF. Different results are obtained in different studies because different species were studied and species are affected differently by warming.

The competition which is known to occur when a plant uses resources (nutrients, space, and water) that are needed by the neighbouring plant has an impact on the quality of forage (Dohn *et al*., 2013). Warming has contrasting results on forage quality. Grass tussocks can maintain soil humidity and that facilitates the woody seedlings-grass interaction (Wagner *et al*., 2018) even though the interaction varies with the treatment. There was a neutral interaction of woody seedlings and grasses on the ADF of grasses. All treatments did not affect the fibre contents of *A. junciformis*. However, warming significantly increased NDF of the primary growth of *T. triandra* but it did not affect the regrowth. The woody seedlings had no effect on

the NDF of grasses. This shows that grasses were aggressive towards the woody seedlings or there was some degree of resource complementarity. Warming other than any factor is the determinant of the fibre content of *T. triandra*. Protein is essential in animals because it promotes development, growth, reproduction, and organ repair. Protein improves the nutritional value of animal feed; hence, feeds with low protein content restrict animal performance and must be supplemented with high energy feeds (Adebisi and Bosch, 2004; Dumont *et al*., 2015).

In this study, warming had no significant effect on the N content of the primary growth of *T. triandra* but it increased the N content of the regrowth. Dumont *et al*. (2015) stated that warming has no significant effect on N contents. The interaction of warming and woody seedlings significantly increased the N content of both primary growth and regrowth of *A. junciformis*. Early harvested primary growth has low crude protein content and it is increased in the regrowth (Naadland *et al*., 2017). Regrowth usually has more crude protein than primary growth because primary growth contains a higher amount of indigestible neutral detergent fibre (Naadland *et al*., 2017). However, experimental warming has no effect on foliar N of grasses (Klein *et al*., 2007). This explains the contrasting results obtained in the warming effect on the N content of the forage.

N-fixing woody plants are the main plants that increase soil N more than any other plant (Blaser *et al*., 2007). Through soil amelioration, plant species facilitate coexistence (Fetene, 2003). Leguminous woody plants do not compete for soil N because they can fix atmospheric N and promote N uptake by the neighbour plant (Fetene, 2003). This study shows that leguminous woody seedlings significantly increased N content of *T. triandra*. Blaser *et al*. (2007) stated that leguminous plants that are able to fix atmospheric N increase soil N because they are producing more biomass instead of competing with the grasses. Positive interaction occurs when the resources are sufficient and the soil amelioration outweighs the warming effect and allows plants to obtain resources (Callaway and Walker, 1997).

CONCLUSION

There are uncertainties about the effect of global warming and they are expected to reduce rangeland production. Climate change influences the ability of plants to uptake nutrients and thereby influencing the productivity of rangelands. Woody seedlings improved the regrowth biomass of *T. triandra* in unwarmed plots. This shows that leguminous woody seedlings can

be used to increase biomass of *T. triandra* as it also increased the protein content. Under global warming and woody encroachment *A. junciformis* may become palatable. However, warming had a negative effect on the regrowth biomass of *A. junciformis*. Warming increased neutral detergent fibre of *T. triandra*. Warming and woody seedlings independently increased the protein content of *T. triandra*.

Warming promoted nutritive quality of *T. triandra* regrowth whereas woody seedlings promoted the nutritive value of *T. triandra* primary growth. The interaction of warming and woody seedlings improved the nutritive quality of *A. junciformis* by increasing the protein content. The protein content of the *A. junciformis* regrowth was greater in control plots and warmed plots with woody seedlings. This shows that *A. junciformis* will strive through global warming and the encroaching leguminous species may improve the protein content of *A. junciformis* at any stage of growth.

CHAPTER FIVE: CONCLUSION AND RECOMMENDATIONS FOR FURTHER RESEARCH

Rangeland ecosystems are complex and dynamic systems that consist of various vegetation growth forms (Roselle *et al*., 2012) and animal interaction that is controlled by rainfall, temperature and fires (Hoobs *et al*., 2008; Dumont *et al*., 2015). Climate change is altering the resources available to plants; increased temperatures reduce soil moisture and consequently alter the nutrient uptake by plants (Synodinos *et al*., 2018). This results in resource limitation and changes the plants' ability to compete with neighbour plants. In rangelands, precipitation increases plant productivity but reduces rangeland nutritive value by increasing aboveground biomass of hardy plants. Grazing clears the grass cover; therefore, reduces grass competition towards trees (Botha *et al.,* 2016). Tremendous variation exists in nutrient composition between plants in rangelands because rangelands encompass an exceptional diversity in species composition, habitat and climatic regions. Hence, it is difficult to make broad generalizations on how rangelands are impacted by rising temperatures. The response of grasses to experimental warming varies with plant traits, season and the region as explained in chapters three and four of this thesis.

The results and recommendations of these experiments are limited to two grass species and can be used in grasslands that are dominated by them.

AIM

This research aimed to determine the effect of the interaction of induced increased temperature on the growth and nutritional value of mesic rangeland grasses with and without woody legume seedling competition.

STUDY CONCLUSIONS

There are uncertainties about the effects of global warming and these effects are expected to reduce rangeland production. The morphological characteristics of plants have different responses to the interaction of warming and woody seedlings. Knowing how woody seedlings and grasses interact in order to coexist will help in coming up with adaptation strategies to

mitigate global warming effects. Grasslands are important ecosystems because they provide forage and habitat for a large number of animals. Grass family is the most important plant family in the world. A more severe problem is an invasion of fertile land by unpalatable plants. In the 21st century, climate change and rising temperature are projected to change the distribution of South African biomes dramatically. *Aristida junciformis* is an aggressive invader and is able to grow in most grasslands. In KwaZulu-Natal, *A. junciformis* is expanding and it is deteriorating the grasslands. This expansion has taken place in the Ngongoni veld and it is severely affecting the grazing land. Van Zyl (1998) has referred to Ngongoni veld as the most useless veld grass in South Africa because it could not produce biomass of 20 kg/ha in a year. *Aristida junciformis* is unpalatable because it has high tensile strength in the cell wall due to high distribution of lignin. The fibrous leaves are difficult to digest by grazing animals once the height of *A. junciformis* reaches 30cm. Animals can however, obtain the nutrients from *A. junciformis* during the regrowth stage or when the grass is producing leaves. *Themeda triandra* is an important grass species that proved conservation of biodiversity and it is crucial for animal production because it is the most palatable grass. It is an indicator of grasslands in good conditions. *Themeda triandra* is a leafy grass and its palatability is influenced by availability of water, presence of lignin and crude protein. During high temperatures, the leaves of *T. triandra* become thin and narrow and this leads to reduction of leaf area. Competition has a significant influence on plant composition. Competition results in an avoidable increase in the density of plant communities when an inadequate amount of restrictive resource can be received by some plants in a group. Soil moisture competition occurs both within and between plant species. Competition between mature plants and seedlings determines the survival of seedlings. Increased competition intensity from mature plants restricts the survival of seedlings attempting to establish. Unless the canopy of adult plants is reduced, seedlings growing in close corporation with adult plants may fail. Findings in this dissertation suggest that warming negatively affected the biomass of grasses. Woody seedlings increased regrowth biomass of *T. triandra* in unwamred plots and also increased its protein content. Although this is a good outcome regarding animal production, woody encroachment is a big problem in Africa. The interaction of warming and woody seedlings improved the protein content of *A. junciformis*. This shows that *A. junciformis* can be grown with leguminous woody seedlings to improve its nutritive value. There will be special management skills required as the seedlings may encroach the grassland. Clipping and fire may be used to control growth and development of woody

seedlings, grasses provide fire fuel to eliminate recruitment of undesirable plant species. It is recommended that *A. junciformis* should be grazed during the vegetative stage.

CHALLENGES

The first challenge that was faced in this research is that in November 2018, the *Vachellia sieberiana* seedlings dried out after transplanting to the field due to high temperatures. The *V. sieberiana* seeds had to be germinated and regrow the seedlings in a controlled environment then transplant the seedlings in January 2019. This shortened the interaction period between the woody seedlings and the grasses in the field. One of the disadvantages of OTCs is the short height, so woody seedlings can rapidly grow out through the opening and therefore not get the full warming effect. Another disadvantage is the use of polycarbonate because it blocks UV light and so alters light quality for the plants.

Thus, the findings are limited because the experiment ran for one season.

FURTHER RESEARCH

Many future studies can be done for this research. The limited time span of this study prevented more essential conclusion to be made. Letting the plants interact in the field for four seasons or more would give a more practical indication of how global warming will affect grasslands. Understanding the effect of belowground competition by analysing functional rooting profile, use other grass species and use another leguminous plant can be used. Also increasing the neighbour density of woody legume seedlings is of importance for future research. Due to the challenge where seedlings died in the field, seedlings can grow for more than two months before being transplanted to the field.

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