

**Interactive effects of fire history and elevated
temperature on aboveground productivity in a high-
altitude mesic grassland in South Africa**

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**Submitted in fulfilment of the academic requirements for the
degree of
Master of Science**

in the Discipline of Ecological Sciences

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

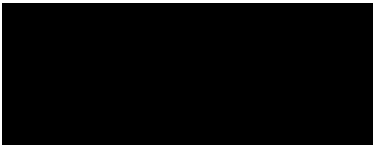
Pietermaritzburg Campus

2021

PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Ecological Sciences, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg Campus, South Africa. The candidate was supervised by Dr. Michelle Tedder and co-supervised by Dr. Mariska te Beest and the research was financially supported by the National Research Foundation.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.



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DECLARATION 1: PLAGIARISM

I, Thembeke Ayanda Mvelase declare that:

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

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

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

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

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

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

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

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

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



Signed: Thembeke Ayanda Mvelase

Date: 09/04/2021

DECLARATION 2: CONFERENCE/WORKSHOP PROCEEDINGS

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

1. Mvelase TA*, Tedder TJ, Te Beest M. Effects of elevated ambient and soil temperature on above-ground productivity of high-altitude grassland of South Africa. In: 53rd Annual Congress of the Grassland Society of Southern Africa, July 2018, Pretoria, South Africa. Presented by Mvelase TA.
2. Mvelase TA*, Tedder TJ, Te Beest M. Effects of elevated ambient and soil temperature on above-ground productivity of high-altitude grassland of South Africa. In: School of Life Sciences Annual Post-Grad Research Day, May 2018, Pietermaritzburg, South Africa. Presented by Mvelase TA.
3. Te Beest M * Mvelase TA, Tedder MJ, Van Rensburg S. Interactive effects of fire and experimental warming on C4 grasslands in South Africa. In: The 16th Annual Savanna Science Networking Meeting, March 2018, Kruger National Park, South Africa. Presented by Te Beest M.
4. Mvelase TA*, Tedder TJ, Te Beest M. Legacy-effects of long-term fire manipulation on aboveground productivity of a high-altitude mesic grassland in South Africa. In: SAEON Indibano Graduate Student Network, September 2017, Cape Town, South Africa. Presented by Mvelase TA.

ABSTRACT

Climatic variables, coupled with the fire regime (and herbivory), are the main factors that affect the distribution and the ecology of grassland systems. Variables such as temperature, precipitation, but also the frequency and season of burn have significant impacts on the overall productivity of grassy biomes. Climate change studies have predicted a temperature increase of up to 3°C in the African continent in the next 30 years. In South Africa, annual average temperatures have risen by over 1.5 times the detected global mean of 0.65°C in the last 50 years, making climate change a pressing concern. This significant increase in temperature will severely impact the grassland biome, and will ultimately also affect the fire regime, one of the most vital drives of grassland systems.

This research aimed to investigate the legacy effects of long-term burning and elevated temperature on aboveground productivity in a high-altitude mesic grassland in South Africa. It was conducted in the Brotherton burning trials in Cathedral Peak, KZN Drakensberg. These trials were established in 1980 to assess long-term fire effects on the grassland. In May 2016, an arson fire swept through the Brotherton fire experimental trials. This fire provided the ideal opportunity for our first experiment to examine the legacy effects of long-term burning on aboveground biomass, basal cover, and species composition of a montane grassland. We used the comparative yield method, the dry weight rank method, the disc pasture meter, and the quadrat method to measure aboveground plant growth. Generalized linear models (GLZM) were used to determine the legacy effects of fire on biomass and basal cover, while the effects on species composition were examined using the Principal Correspondence Analysis (PCA). The first experiment showed that the no burn treatment had the greatest aboveground biomass ($474.2 \text{ g/m}^2 \pm 16.14$), while the annually burnt treatments had the least biomass ($331.67 \text{ g/m}^2 \pm 12.55$). Season of burn had no significant effect on aboveground biomass. Basal cover was not significantly affected by the frequency of burning but rather by the season of burning, where basal cover was highest in spring burns and lowest in autumn burns. The Principal Components Analysis showed that frequently burned plots were dominated by *Themeda triandra*, quinquennial burns were dominated by *Tristachya leucothrix* and the no-burn treatment by *Harpochloa falx*. Overall, our results show that the legacy effects of long-term fire, rather than the time since fire, determine aboveground grassland productivity in the

Brotherton trials. The second experiment investigated the effects of elevated air and soil temperature on aboveground productivity in the same study site. Experimental open-top chambers (OTCs) were used to simulate *in situ* temperature increases. OTCs in this study increased midday air temperature by about 4 °C and soil temperatures by up to 1.5 °C. Average daily air temperatures were increased by 1 °C and soil temperature by 0.7 °C. Our results show that warming significantly increased aboveground biomass in the mid-winter season while it had no impact in the late spring and the late summer seasons. Temperature increases were also found to significantly reduce soil moisture content, particularly in spring and summer seasons. There were no interactive effects of warming and fire in neither biomass nor soil moisture content. There were also no apparent effects of warming on species composition, due to the short timeframe of the study. Outcomes of this study are a significant benchmark for the continuous monitoring of climate change impacts on high-altitude fire-climax grasslands, and they accentuate the demand for further studies on responses of these grasslands to a variety of climate change scenarios.

ACKNOWLEDGMENTS

I would first like to grant my most sincere gratitude to my supervisors: Dr Tedder and Dr Te Beest for their input in this whole thesis, their corrections, words of encouragement, and mostly for not giving up on me, none of this would have been possible without your consistent guidance and support. I would then like to thank Sue van Rensburg: for igniting the spark that made this whole research possible. For believing that I was worthy of this degree, and for your never-ending support and reassurance. I appreciated it so much.

To the SAEON WGF node team: Paul, Thami, Aobakwe, Sue, Byron, Manish, Kent and Siphile for assistance with fieldwork and data collection. Paul for your support and overall input in this project, it is all highly appreciated.

To the UKZN Grassland lab team: Lindo, Naledi, Stuart, Nolwazi, for your support and words of encouragement, especially Stuart for assisting with analysis and Lindo for always being available to read my work, it was always highly appreciated.

To my loving family: My dear Mother, Maggie, for your support and patience and love throughout this lengthy academic journey. My little sister, for always having my back and believing in me and this degree. To all my family members, for their consistent support, this degree is for all of you.

To my dear friends: Silindile, Pumla, Nqobile, Keamogetse, Sinenhlanhla, and all of you who I could not mention, thank you for loving me and crying with me. It sure made things a little bearable.

I would like to thank the National Research Foundation (NRF) for financial support and SAEON (WGF node) for research equipment, project operational costs and assistance, which this project would not be possible without.

I dedicate this to my Princess, Fanelabongwe Mvelase

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CHAPTER 1: LITERATURE REVIEW

1.1 Introduction

1.1.1. Grasslands

There is no one straight forward, all-inclusive definition of the term grassland as they have been defined and distinguished from other biomes in many ways. Some studies categorize and distinguish grasslands by the type of vegetation they are made of (Ellery and Mentis 1992), while others use temperature, soil type, and human use of the ecosystem to categorize them. White et al. (2000) defines grasslands as ‘terrestrial ecosystems dominated by herbaceous and shrub vegetation and maintained by fire, grazing, drought and/or freezing temperatures’ while Carbutt et al. (2011) refers to a grassland as ‘a single-layered herbaceous plant community, with a few woody plants, which are usually restricted to specific habitats, including drainage lines and rocky hilltops. Grasslands are generally found in areas dominated by grasses with a rare occurrence of other grassy vegetation such as sedges, where there is irregular or absent woody vegetation (Huntley 1984). The grassland biome encompasses more than 40% of the world’s total land surface (Egoh et al. 2011; Boval and Dixon 2012; Blair et al. 2014) and is found on every continent in the world except Antarctica (White et al. 2000; Leys et al. 2018), covering more terrestrial surface than any other single biome type (Egoh et al. 2011; Blair et al. 2014). These systems are found in varying environmental conditions, ranging from the Arctic to the tropics, from sea-level to high-altitude and from areas that have deep nutrient rich soils, to thin nutrient poor soils (Huntley 1984; Blair et al. 2014; Leys et al. 2018). Grasslands play an important role in the Earths systems and processes, particularly in nutrient cycling, water provision, carbon sequestration and for sustaining biodiversity, wild animals and livestock (Parr et al. 2014; Leys et al. 2018).

1.1.2. Grasslands in South Africa

Grasslands in South Africa cover over 360 589 km², stretching from the high plateau (Highveld) to the montane areas of Lesotho, all the way to the uplands of KwaZulu-Natal, Eastern Cape and Mpumalanga (Carbutt et al. 2011). This biome, one of the nine terrestrial biomes in this country, is the second largest biome after the savanna and accounts for approximately 28% of the total terrestrial surface (Mucina and Rutherford 2006). It has different types of landscapes that range from gently rolling flat surfaces, hills, and valleys,

to mountain slopes (Palmer and Ainslie 2005; Blair et al. 2014). South African grasslands typically have cold and dry winters, with frost and snow falling frequently at higher altitudes (Huntley 1984; Mucina and Rutherford 2006). They have highly variable and seasonal rainfall, from 400 mm to 2500 mm per annum, and a growing season that lasts for nearly half the year (Huntley 1984; Carbutt et al. 2011). There are three centers of plant endemism (Drakensberg Alpine Center, Wolkberg Center, and the Midlands Putative Center) and three world heritage sites (uKhahlamba Drakensberg, Cradle of Humankind, and Vrederford Dome) in the grassland biome in South Africa (Carbutt et al. 2011).

For many centuries, this biome has been the foundation for human survival around the world both directly (through food production) and indirectly (through carbon sequestration and nutrient recycling) (Egoh et al. 2011; Blair et al. 2014; Parr et al. 2014). Globally, more than one billion people depend on grasslands either directly for livestock feed, growing their crops, and collecting thatch grass and medicinal plants, (Dzerefos and Witkowski 2001) or indirectly for nutrient cycling (Gill et al. 2002; Boval and Dixon 2012; Blair et al. 2014), carbon sequestration (Sala and Paruelo 1997; Egoh et al. 2011) and water production (Campbell et al. 1997; Everson et al. 2011). Grassland soils store large volumes of carbon and other important nutrients (such as Nitrogen) and therefore play a tremendous role in biochemical cycles worldwide (Blair et al. 2014). The grassland biome in South Africa has a unique biodiversity that is of global significance (O'Connor and Kuyler 2009; Haddad and Butler 2018). The plant diversity in this biome is the second highest, after the fynbos biome, with over 3000 plant species (Reyers and Tosh 2003; O'Connor and Kuyler 2009; Cadman et al. 2013). This biome also boasts high levels of endemic, rare, and endangered mammals, reptiles, butterflies, and other fauna, with 52 of the country's 122 important bird species and more than 10% of threate[ned butterflies found in this biome (Boval and Dixon 2012; Cadman et al. 2013). In South Africa, this biome supports most of this country's economic activities, and is home to millions of people, especially in rural areas (Reyers and Tosh 2003; Palmer and Ainslie 2005; Egoh et al. 2011). One of the most important services rendered by grasslands is that of water supply (Egoh et al. 2011). These systems contribute immensely to the hydrological cycle through reducing runoff and erosion, and by storing runoff and groundwater (Murray et al. 2000; Palmer and Ainslie 2005; Egoh et al. 2011). The majority of the catchment zones for South Africa's water resources are covered by grasslands (Egoh et al. 2011), grasslands are therefore one of the country's Strategic Water Source Areas (Cadman et al. 2013). Some of

South Africa's main river systems, namely: Gariep, Vaal, Thukela, Mzimvubu, and Kei Rivers, have their headwaters in grasslands, making this biome a significant landscape for water production, comprising of 42 river ecosystems and a number of threatened wetlands (Cadman et al. 2013).

1.2. Fire in grasslands

1.2.1. Fire history in southern African grasslands

Earth systems have been driven in one way or the other, by naturally occurring fire for millions of years (Hall 1984; Everson 1985; Archibald et al. 2013). There is limited information about the historical fire regimes before humans started manipulating fire, mostly because it is difficult to differentiate between natural and anthropogenic fires in paleontological evidence (Hall 1984; Everson 1999; Short 2001). However, it has been well documented that fire has been an important ecological phenomenon in shaping the South African grassland biome long before the emergence of hominids (Hall 1984; Everson 1985).

Numerous studies agree that hominids have inhabited the southern African hemisphere for some 3 million years (Beaumont et al. 1978; Tobias 1981; Volman 1984; Berger 1998; Coppens 2013) and have affected the structure of vegetation communities for several thousands of years (Hall 1984; Sheuyange et al. 2005; Coppens 2013). However, there is uncertainty surrounding the exact period that hominids started directly manipulating the structure of grassland systems. In South Africa, the earliest evidence of the use of fire dates to roughly 1 - 1.5 million years BP, and according to Brian and Sillent (1988), these fires occurred in the Swartkrans cave (now the Cradle of Humankind Heritage site in Johannesburg, South Africa). However, understanding of the precise influence of human activities and that of fire on grassland vegetation communities is limited before the Upper Pleistocene (128 000 years BP) (Hall 1984; Uys 2000). With the introduction of livestock farming and production 1800 years BP, there was an increase in the use of anthropogenic fires (Uys 2000). It was only in the Holocene (4000 – 1000 years BP), where climatic conditions were more favorable for terrestrial plants, that anthropogenic fires were common (Hall 1984; Everson 1985; Uys 2000). It is believed that it was only by the early eighteen century that the grassland biome was subjected to regular fires by the Bantu-

speaking people who mostly burnt grazing lawns for their livestock feed and also to facilitate hunting (Everson 1985; Uys 2000). These fires played a huge role in shaping vegetation communities (Hall 1984; Sheuyange et al. 2005; Sheuyange et al. 2014).

1.2.2. Fire in the Drakensberg

There is evidence suggesting that modern man has occupied southern Africa for at least 115 000 years and the Drakensberg for at least 7000 years (Beaumont et al. 1978). However, the population of the modern man was regarded too small to have significant impacts on the vegetation and the biome at large (Uys 2000). Lightning was the main natural source of fire in these mountains before San hunter-gathers started to apply fire for hunting purposes in the Drakensberg, about 8000 to 5000 BP (Hall 1984). The Drakensberg Mountains have high lightning strike densities in South Africa, with more than 15 strikes per square kilometer that would have sustained these regular fires (Manry 1983; Edwards, 1984; Manry and Knight 1986). Modern-day fires in the foothills of Natal Drakensberg are deliberate fires, set and controlled by management to sustain the integrity of the montane grasslands (Morris et al. 2020), or by accident due to runaway firebreaks (Nänni 1969; Gordijn et al. 2018). The role of fire in the evolution of the current structure and composition in the Drakensberg grassland has been quite significant (Morris et al. 2020). The majority of the KwaZulu-Natal Drakensberg is currently managed by Ezemvelo KZN Wildlife, which has executed a flexible burning regime over the past ~ 38 years to promote species diversity and habitat heterogeneity (Morris et al. 1999; Gordijn et al. 2018). Ezemvelo KZN Wildlife has two main management objectives for the Drakensberg, one, the production of high-quality water (Everson 1985; Everson 2000; Taylor et al. 2016); and two, to sustain grassland structure and composition for soil preservation (Mentis et al. 1974; Gordijn et al. 2018; Morris et al 2020). The historical fire regimes in terms of frequency and season of burn in the Drakensberg is unknown and possibly variable (Gordijn et al. 2018). Biennial burning in these mountains is commonly recommended for increasing basal cover and to promote aboveground productivity and structural heterogeneity (Nänni 1969; Everson 1985). Frequent burning also reduces the fuel load, thereby minimizing the probability of hazardous wildfires (Morris et al. 1999; Morris et al. 2020).

1.2.3. Effects of fire on grassland vegetation

Numerous studies (e.g., Kozlowksi and Ahlgren 1974; Oosterheld et al. 1999; Uys et al. 2004; Anderson 2012; Blair et al. 2014; Bachinger et al. 2016) agree that fire (and herbivory) are the most important factors responsible for the development and maintenance of grassland ecosystems. Fire in these systems maintain vegetation in various ways (Anguyi 2010). These include reducing the encroachment of trees and shrubby plants (Oosterheld et al. 1999; Leys et al. 2018) influencing changes in species composition (Guevara et al. 1999; Smith et al. 2013) minimizing diseases and pests (van Wilgen and Scholes 1997; Anguyi 2010), and most importantly, improving the production and quality of livestock feed (de Villiers and O'Connor 2011; Li et al. 2013; Little et al. 2015). The primary intention of grassland fires is to remove aboveground biomass (van Wilgen and Schole 1997; Scheintaub et al. 2009; Little et al. 2015), which is often the accumulated moribund litter in the dormant season (Ojima et al. 1994; Scheintaub et al. 2009). In more productive grasslands, the removal of litter provides more solar radiation to the soil surface (Uys et al. 2006), thereby leading to a quicker, prolonged growing season (Scheintaub et al. 2009). Litter removal through burning also results in reduced competition for light, and possibly changes in the availability of nutrients in warmer soils (Evans et al. 1989; Oluwole et al. 2008; Scheintaub et al. 2009; Anguyi 2010). Access to light is a vital factor in mesic (high precipitation) grasslands, thus shading out caused by moribund material is unfavourable to the survival of some grasses (e.g., *Themeda triandra*) (Short 2010). The burning of moribund biomass will encourage tillering (Mentis et al. 1974; Short 2010), consequently resulting in a more uniform utilization of the grassland throughout the growing season (Househam 2017). All these factors generally increase vegetation productivity and influence community structure in burnt systems (Higgins et al. 2000; Uys et al. 2006). However, litter removal through burning does not always have positive effects on plant biomass productivity (Oosterheld et al. 1999). According to Blair (1997), productivity might be limited by soil moisture content, which generally decreases with the removal of aboveground biomass.

Moreover, studies have shown that excluding fire in grassland systems drastically reduces grassland net productivity (Sheuyange et al. 2005; Snyman 2006; Li et al. 2013). According to Van Staden et al. (2000), this is because most grassy species have evolved reproductive strategies that are adapted to fire (or factors associated with fire), and

therefore prohibiting fire could be detrimental to such species. Titshall et al. (2000) also mentioned that grassland responses to fire and fire exclusion are not uniform across species or grasslands. Climatic variables such as temperature, precipitation, and topography also have an effect on species' responses to fire (Polley et al. 2013). For example, Holocene paleofire studies revealed a positive relationship between precipitation and fire, where fire frequency was found to be higher in areas that were wet (Grimm et al. 2011; Leys et al. 2018). Temperature has also been reported to increase biomass burning in grasslands (Daniau et al. 2012; Daniau et al. 2013).

1.2.4. Brotherton fire trials

Located in the northern part of the Maloti-Drakensberg Park near the Cathedral Peak are the Brotherton trials, classified by Mucina and Rutherford (2006) as Basalt grasslands. These trials were established in 1980 to assess long and short-term effects of fire frequency and seasonality on plant community dynamics in fire-climax grasslands (Morris et al. 1999; Short 2001; Short 2004). Understanding ecosystem dynamics and processes (e.g., grassland composition and structure) is vital for assessing the health and condition of southern African grasslands (Tainton 1999). These grasslands are also recognized as a biodiversity hotspot and are therefore of conservation importance (Cowling and Hilton-Taylor 1994; Mucina and Rutherford 2006; Gordijn et al. 2018). Fire is an important ecological process driving these grasslands and has significant effects on biodiversity and ecosystem functioning (Everson 1985; Morris et al. 1999; Short 2004; Gordijn et al. 2018). The Brotherton fire trials are among the longest running fire trials in South Africa, together with the Ukulinga Burning & Mowing experiment (since 1950) and the Skukuza long-term burn plots (since 1954). Long-term experiments such as these are unique and highly valuable and have been an important foundation for long-term invaluable knowledge in southern African grasslands (Morris et al. 1999; Uys 2000; Short 2004; Short 2007). The main objective of the Brotherton fire trials was to determine the effects of burning at different frequencies (annual, biennial, triennial, quinquennial, and fire protection) and in different seasons (spring, autumn and winter) on grassland composition and structure (basal cover) in the natural grassland catchments of the Drakensberg (Short 2004; Manson et al. 2007; Short 2007). Botanical surveys of species composition in the plots were conducted biennially from 1981 – 1992 (Morris et al. 1999; Short 2004), but consistent sampling was discontinued after 1992 due to limitations in funding and other human

resources in the Ezemvelo KZN Wildlife formerly known as the Department of Forestry, then Natal Parks Board (Morris et al. 1999; Short 2004). A collaboration between Ezemvelo KZN Wildlife and South African Environmental Observation Network (SAEON) in 2012 enabled consistent sampling in order to realize the original objectives. Treatments were continued throughout. Recognizing the value and importance of long-term trials, other ecological surveys were carried out in addition to the botanical surveys, including entomological (Uys and Hamer 2006) and soil surveys (Manson et al. 2007). Short (2007) also emphasized the value of these trials, especially for climate change studies and the ecological importance of long-term studies.

The layout of the Brotherton trials was a replicated randomized block design that was made up of three blocks, each consisting of at least one of the main fire treatments. There are 12 treatments and 45 plots in total ([See Figure 2.1](#)). The plots are 25×25 m, and they all have a 5 m wide pathway between them. The pathway was regularly burnt to prevent the buildup of dead material which could act as an unintended fire ignition hazard, and also to limit the establishment of invasive plants.

There have been several short and long-term studies that have been conducted in the Brotherton Fire trials. For example, Morris et al. (1999) conducted a study in these trials which investigated compositional and diversity data in order to understand the effects of burning on the temporal dynamics of montane grasslands. The general conclusion from this study was that burning biennially in spring maintained sward heterogeneity and species richness. Manson et al. (2007) examined the long-term effects of fire on basal cover, soil properties and landscape functioning in these trials. They found that fire protection yielded the lowest basal cover, and that there were no significant burning effects on the amount of organic matter. They, similar to Morris et al. (1999) and Short et al. (2003) respectively, also found reduced basal cover in infrequently burnt treatments. Everson and Everson (2016) investigated long-term burning effects on grassland productivity in the Brotherton trials and they found that unburnt plots had 20% lower productivity and also lower crude protein when compared to plots that were burnt either annually or biennially. They came to the conclusion that burning annually or biennially in the dormant season promoted high long-term production in this montane grassland (Everson and Everson 2016). Other studies that have emerged from these trials also

include effects of long-term fire treatment on invertebrate abundance (Uys and Hamer, 2007); forb diversity and species composition (Uys et al. 2004) to name but a few.

1.3. Climate change

Before defining climate change, why it is of importance, its consequences and impacts, it is important to first understand what climate is. The basic definition of climate is ‘weather patterns over long periods of time’ or ‘average weather patterns over several years to tens of years’ (Quante 2010). Climate change therefore is, according to Unganai (1996) a shift in climatic conditions in a gradual way, with significant changes in climatic elements (such as temperature, rainfall, wind, atmospheric pressure), while the Intergovernmental Panel on Climate Change (IPCC 2001) defined climate change as “statistically significant variations in climate that persist for an extended period, usually decades or longer”. These variations include but are not limited to changes in the occurrence and magnitude of periodic weather patterns and also the steady continuous rise in global average surface temperatures (IPCC 2001). The climate of the earth has always naturally reformed and evolved, therefore, climate change is a natural phenomenon (Solomon 2007). However, historically this change was mostly due to variations on solar radiation emitted by the sun, volcanic eruptions, and the discrepancies in solar radiation caused by the Milankovitch cycles (Roe 2006; Quante 2010). These changes used to occur every 10 000 years, were entirely natural and were never regarded as problematic. However, the clearing, development, and transformation of land for food production over the last thousand years has resulted in immense instabilities in the Earth’s climate (IPCC 2001; Quante 2010). With the development of agriculture some 1000 years ago, humans began to significantly alter global climate, mainly via the additional release of greenhouse gases (GHG) (Anderson et al. 2016), changes in the Earth’s albedo and changes in biogeographical cycles from land use change (Quante 2010; Dhillon and Wuenhlish 2013). The Earth’s albedo is the reflected solar energy scattered back by the earth, which plays an important role in the Earth’s energy balance and the processes that govern the Earth’s climate and climate change (Stephens et al. 2015). The burning of fossil fuels has also significantly affected the rate of the changing climate. Over the last 200 years, concentrations of greenhouse gases (such as carbon dioxide, methane, water vapor, ozone, and nitrous oxide) have increased considerably due to human activities, consequently increasing global temperatures (Venkataramanan 2011; Jian-Bin et al. 2012; Al-Ghussain 2019). It is

important to note that without these greenhouse gasses in the atmosphere, surface temperatures would be about -21°C and the Earth would not be habitable for most living organisms (Polley et al. 2017). However, as crucial as these gases are, their atmospheric concentrations are rising at a rate that is far from natural, enhancing the natural greenhouse effect, thereby causing the Earth to warm up quicker (IPCC 2001; Polley et al. 2017). The development of coal-burning factories, power plants, and motorized vehicles also significantly contributed to the high volumes of carbon dioxide released into the atmosphere (IPCC 2007). The most significant anthropogenic source of global warming, carbon dioxide, has increased by at least 30% since 1950 (Al-Ghussian 2019) and causes nearly 25% of the greenhouse effect. The burning of crude oil, coal, and natural gases, which are the primary fossil fuels, is the most significant anthropogenic cause of global warming (Venkataramanan 2011; Jian-Bin et al. 2012).

1.3.1. Global warming

Venkataramanan (2011) defines global warming as the increase of the Earth's average surface temperatures which is caused primarily by a surge in the greenhouse gas concentrations. Changes in global temperatures have occurred throughout human history (Solomon 2007) however, these changes began occurring at a significantly increased rate in the 20th century (Dhillon and Wuehlisch 2013). There has been a lot of research showing that the recent increases in surface temperature are due to the enhancement of the greenhouse layer, which is mostly due to anthropogenic activities, such as the burning of fossil fuels, deforestation and other industrial and agricultural processes (e.g., IPCC 2007; Houghton 2009; Venkataramanam 2011; Dhillon and Wuenhlish 2013; Xia et al. 2014). The increase in global temperatures has a wide range of impacts, affecting all that inhabits the earth (Venkataramanan 2011). Consequences of global warming include the melting of glacial ice, the rise in sea level, increased variation in rainfall patterns, frequent floods, severe storms and droughts, species extinction, and overall disruption of ecosystem processes (Melillo et al. 1993; IPCC 2007; Dhillon and Wuehlisch 2013). All of these have unsettling effects on the economy (Adams 1989), ecology (Scheiter and Higgins 2009) and human society at large (IPPC 2007; Seddon et al. 2016).

1.3.2. Climate change impacts

As explained above, there is strong scientific evidence that climate change is mostly a consequence of anthropogenic activities (Suliman 1990; Rind 1999; IPCC 2007; Trenberth et al. 2007; Kruger and Sekele 2013). One of the most significant ramifications of climate change is the consequent increase in temperature and changes in temperature extremes across the world (Gunn and Farral 1999; IPCC 2007; Solomon 2007; Kruger and Sekele 2013; IPCC 2014). Numerous studies (Hulme et al. 2001; Kruger and Shongwe 2004; IPCC 2007; Kruger and Sekele 2013; Al-Ghussian 2019) reported that the rate at which global temperatures have elevated over the past century is almost twice as that of the previous century ($0.13 \pm 0.03^{\circ}\text{C}$ vs $0.07 \pm 0.02^{\circ}\text{C}$ per decade). Additionally, studies reported a decline in the number of cold nights occurring, while a significant increase in the occurrence of warm nights was reported (Kruger and Sekele 2004; Yang et al. 2017).

The African continent is regarded as especially susceptible to significant climate change impacts due to its low adaptive ability, poverty, limited access to capital and resources, high dependence on agriculture, and advanced ecosystem degradation (Callaway 2004; Boko et al. 2007; Manase 2010; Kusangaya et al. 2014; IPCC 2014). The continent's high exposure to climate change risks such as floods, storms and extreme droughts make this continent highly vulnerable to climate change impacts (IPCC 2014; Vogel and Scholes 2015). According to Olsson et al (2014), Africa and other undeveloped marginalized regions generally have the least safety measures to help against climate-related hazards, hence suffer the most impacts and have little recovery time.

Climate change studies (Hulme et al. 2001; Kruger and Shongwe 2004; Nicholson et al. 2013) found that during the last 5 decades to a century, surface temperatures in Africa have increased by at least 0.5°C , where minimum temperatures were observed to increase more rapidly than maximum temperatures (New et al. 2006). The IPCC (2007) predicted that in the next 30 years, average temperatures on the African continent would have increased by $1.5 - 3^{\circ}\text{C}$ and by $2 - 6^{\circ}\text{C}$ in the next century (Hulme et al. 2001; Christensen et al. 2007), making temperature increases in Africa second greatest in the world (IPCC 2007; Sanderson et al. 2011; Gemedi and Sima 2015; Hummel 2016), after the Arctic region, which is predicted to increase by $7 - 8^{\circ}\text{C}$ within the next century (Bjorkman et al. 2018). In South Africa, numerous studies (Hughes and Balling 1996; Unganai 1996; Kruger and Shongwe 2004; New et al. 2006; Ziervogel et al. 2014) have observed a trend

of warming over the past decade. According to Ziervogel et al. (2014), mean annual temperatures have increased by at least 0.975 °C, which is significantly higher than the global mean of 0.65°C in the half-century, making climate change an imperative concern in this country (IPCC 2007). Predictions report that temperatures will continue to increase as human populations continue to grow and release more greenhouse gases into the atmosphere (Schulze 2000; Ziervogel et al. 2014; Al-Ghussian 2019), though the extent and implications of this increase will differ from region to region (Suliman 1990; Shaver et al. 2000). Even though Africa has the lowest GHG emissions compared to other continents, (due to low levels of industrial development), it still remains the most vulnerable continent to drastic climate change impacts and this is attributed to its high human population growth (Huq et al. 2004).

Changes in climate will also result in major changes in rainfall patterns, thereby significantly affecting water resources worldwide (IPCC 2007; Urama and Ozor 2010; Gemedu and Sima 2015; Li et al. 2018). Considering that climatic factors in the southern African region are spatially and temporally variable, impacts of climate change on water resources in this region are likely to be more evident in the future than formerly anticipated (IPCC 2007; Galley-Ayala and Juizo 2011; Li et al. 2018). The African continent is generally thought of as a water-scarce continent, therefore climate change is expected to have severe impacts on the water resources in this region (Suliman 1990). Potential and noticeable climate change impacts on African water resources include flooding, drought, changes in distribution and occurrence of rainfall, drying up of rivers, and a rise in sea-level (Saxe et al. 2001; Levy et al. 2004; Gemedu and Sima 2015; Li et al. 2018). Increasing temperature is also projected to increase air vapor pressure deficit (Saxe et al. 2001), resulting in enhanced transpiration rates, which could have severe effects on arid and semi-arid regions (James 2010). Generally, increases in temperature result in increased evaporation and therefore increased precipitation, however, projections do not show a significant increase in global precipitation (James 2010). Significant increases in precipitation are expected in humid and high-altitude regions, while declines in precipitation are expected for arid and semi-arid, low-altitude regions (Urama and Ozor 2010; Li et al. 2018). Until the end of the 21st century, the spatial extent of severe shortages in soil moisture and short-term droughts are projected to double, while long-term droughts are expected to triple in frequency, particularly in arid regions (IPCC 2007; Füssel 2009).

1.3.3. Warming impacts on grasslands

All ecosystem processes and organic matter pools will be affected by warming, even though the rate of impact will differ from one ecosystem and environment to the next (Morison and Lawrol 1999). These will vary over time amongst ecosystems and will depend mostly on the initial physical and chemical environment, the dominant species in that ecosystem, and the interaction between those species (Shaver et al. 2000; Mueller et al. 2016). Temperature, unlike carbon dioxide, essentially affects all chemical and biological processes, whereas CO₂ only impacts on respiration and photosynthesis (Shaver et al. 2000). Warming can affect plant communities in many terrestrial systems by changing the availability of the two most important resources, water, and nutrients (Whittaker 1970; Walther 2003; De Boeck et al. 2007). Significant warming-induced changes in these resources have been reported to have severe implications on the growing season (Levy et al. 2004); plant productivity (Lou et al. 2008; Mueller et al. 2016); species composition and community structure (Harte and Shaw 1995; Slingsby et al. 2019; Wang et al. 2019); physiological processes (Shaver et al. 2000; Charles and Dukes 2009); and might even lead to local species extinction (Klein et al. 2004; Levy et al. 2004; Thomas et al. 2004; Houghton 2009).

Numerous studies agree that there has been a consistent trend of increases in surface temperature over the last decade in southern Africa (Hughes and Balling 1996; Unganai 1996; Kruger and Shongwe 2004; Warburton et al. 2005; New et al. 2006; Kusangaya et al. 2014). The Millennium Ecosystem Assessment (MEA 2005) recognizes climate change as the greatest imminent threat to natural systems and their biodiversity (Klein et al. 2004; Malcolm et al. 2006; Thuiller et al. 2008; Scheiter and Higgins 2009). Several experimental studies on climate change and simulated temperature increases have shown that warming generally increases plant growth in many ecosystems (Wu et al. 2011; Morgan et al. 2011; De Boeck et al. 2007). Some studies predict that temperature increases and the consequent rise in CO₂ would favor C3 trees over C4 grasses, thereby promoting woody species encroachment in grassland systems (Ceballos et al. 2010; Moncrieff et al. 2015). This is due to potentially higher benefits that C3 plants would gain over C4 plants as temperature and CO₂ increase (Briggs et al. 2005). Another climate model added to this perspective whereby they predicted that as surface temperature continues to rise, 34.6% of global grasslands would be transformed into savannas by the year 2100 (Scheiter and Higgins 2009). These findings were contrasted by Peterson et al. (2014), who predicted

that an increase in temperature would instead increase the rate of C3 photosynthesis and evaporative demand, thereby promoting fire, which would then favor grasses over woody plants and trees. Precipitation also plays an important role when determining warming effects on plant communities. While some studies have suggested that aboveground productivity is mostly controlled by precipitation and not temperature in grasslands (Mowll et al. 2015; Mueller et al. 2016), other studies suggest that temperature plays an equally vital role in the productivity of grasslands in arid and semi-arid regions (Wertin et al. 2017). In grasslands where water is not a limiting factor (such as the Brotherton trials), it has been shown that grass production is positively impacted by soil warming, therefore making temperature the limiting factor in overall grassland productivity in these areas (Buhrmann et al. 2016). Grasslands at higher altitudes have also been predicted to be more sensitive to warming impacts (Rustad et al. 2001), and this is because high-altitude ecosystems are generally limited in both temperature and nutrients (Rustad et al. 2001). However, regions that generally have limited precipitation are predicted to experience massive declines in productivity when temperature is increased (Reeves et al. 2014). A recent experimental study in an arid grassland in the US found that 2 - 4 °C temperature increases reduced the rate of photosynthesis and aboveground biomass accumulation in some C3 and C4 plant species, and that combined effects of reduced moisture and warming could result in severe negative impacts on plant productivity (Wertin et al. 2015). However, Rustad et al. (2001) found that elevation in air and soil temperature increased the rate at which soil organic matter decomposes, which therefore increases nutrient availability, plant growth, and the overall net primary production (Xu et al. 2013).

1.4. Experimental warming

Impacts of warming on ecosystems can differ either as a result of the period or length the experiment takes, or the temporal variability of additional environmental aspects such as the weather, that affect these warming impacts (Mueller et al. 2016). For example, the initial physiological vegetation response to warming could be the most important factor determining the amount and direction of plant production in the first months or years of an experiment, while over the years, soil resource availability and the cumulative effects of physiological responses on community composition might indirectly determine plant production (Smith et al. 2009; Polley et al. 2013; Mueller et al. 2016). Over time, other environmental factors such as precipitation, which also control ecological interactions and

physiological processes (Shaver et al. 2000), should also influence the variable impacts of warming on ecosystem functioning (Hoeppner and Dukes 2012).

1.4.1. Open-top chambers (OTCs)

Studies that focus on assessing current and future climate change impacts on natural systems are of ecological value and they are currently getting a lot of attention (Hollister et al. 2006; Godfree et al. 2011). Through the years, there have been numerous approaches and systems that have been used to manipulate temperature for evaluating climate warming impacts on plant communities (e.g., Henry and Molau 1997; Marion et al. 1997; Arft et al. 1999; Kimball 2005; Buhrmann et al. 2016). This is mostly due to the global concerns regarding climate warming on terrestrial and other ecosystems. These concerns regarding warming impacts have led to an increase in field studies conducted in various ecosystems to manipulate temperature (Marion et al. 1997; Godfree et al. 2010; Hollister et al. 2006). One of the most common techniques for such studies is the use of passive systems (Marion et al. 1997), which passively heat small plots of vegetation by trapping solar energy and protecting against the wind (De Frenne et al. 2010). One of the most extensively used passive systems is open-top chambers (OTCs) (Marion et al. 1997; Godfree et al. 2011; De Frenne et al. 2010). OTCs are small, in situ, hexagonal greenhouses made of transparent thick Perspex sheeting with inclined walls and open-tops (De Frenne et al. 2010). The type of OTCs used in this study are based on a design that was developed for the International Tundra Experiment (ITEX) (Marion 1996; Henry and Molau 1997; Marion et al. 1997).

OTCs have been used in ecosystem warming studies in many different short stature plant communities (Bokhorst et al. 2013), are the cheapest and simplest method for ecological research (De Frenne et al. 2010) and have been shown to elevate air temperatures by 1.0 – 1.8°C and soil temperature by at least 0.6 - 3 °C (Gedan and Bertness 2009; Bokhost et al. 2013). The amount of air and soil temperature increase in the OTCs is directly regulated by the relative surface area of the inside diameter of the chamber (Aronson and McNulty 2009). Therefore, the smaller the open-top relative to the height of the chamber, the higher the temperature increase (Aronson and McNulty 2009). The ratio of the open-top to chamber height also has effects on other environmental variables such as the amount of light, precipitation, and also the humidity inside the chamber (Marion et al. 1997; Aronson and McNulty 2009; Buhrmann et al. 2016).

1.4.2. Limitations of OTCs

One of the most common limitations of OTCs is that they are usually small in size (~ 30 – 50 cm high), therefore only limiting their use to short stature plant communities (Gedal and Bertness 2009). Even though OTCs undoubtedly elevate average temperatures by approximately the same predicted amounts projected by general circulation models (Marion et al. 1997; Bokhorst et al. 2013), they affect other microclimatic variables as well (Aronson and McNulty 2009; De Boeck et al. 2012; Bokhorst et al. 2013). These include lower incident radiation and light intensity (Godfree et al. 2011), reduced relative humidity (Marion et al. 1997), reduced wind speed (Gedal and Bertness 2009) and decreased soil moisture (Arft et al. 1999; Aronson and McNulty 2009; De Boeck et al. 2012). Additionally, Henry and Molau (1997) further reported that the use of OTCs affects pollinator activity and herbivory, thereby affecting the accuracy of chambers in simulating natural climate scenarios. These chambers have also been reported to produce minimal heating/cooling at nighttime (Godfree et al. 2011). Studies by Marion et al. (1997) and Musil et al. (2004) found that OTCs can elevate maximum temperatures by an unrealistic 5°C or more. Such extreme temperature estimates are inconsistent with climate change predictions and are likely incoherent with future climates in many regions around the world (Kennedy 1995; Hollister et al. 2006). While some researchers are confident that these chambers provide reasonable warming based on plant responses (Arft et al. 1999; Hollister and Webber 2000; Buhrmann et al. 2016), others (Kennedy 1995; Musil et al. 2004; Marchand et al. 2006) argue that the biological plant responses observed may not be direct passive warming responses, but rather responses due to extreme temperatures and other non-temperature microclimate impacts (Bokhorst et al. 2013). Moreover, Aronson and McNulty (2009) reported that climatic perturbations that occur outside the growing season may significantly affect biotic responses during the growing season if the chambers are deployed year-round (Aronson and McNulty 2009; Bokhorst et al. 2013). Problems of experimental artifacts are not exclusive to OTC warming, other methods such as mechanical heating devices also have similar problems (Hollister et al. 2006). Not having total experimental control together with the experimental artifacts are common tradeoffs to in situ studies, therefore it is vital that such impediments are properly documented and addressed in all field studies (Hollister et al. 2006).

The majority of experimental warming using OTC studies have been on tundra systems (Arft et al. 1999; Rustad et al. 2001; Aronson and McNulty 2009) with little research done on the effects of temperature warming on the mesic high-altitude grasslands. To date, no studies have been conducted on the combined effects of fire and warming in these systems. This is worrying, considering how high-altitude systems are likely to experience the greatest loss in biodiversity and species shift (Thuiller et al. 2008; Gedan and Bertness 2009), and also potentially losing some of their important services due to warming. This motivated the present study, to assess the interactive effects of fire history and elevated temperature on grassland productivity in a mesic high-altitude grassland in the Cathedral Peak, KZN Drakensberg.

1.5. This study

In May 2016, an unplanned arson fire swept through most of the Cathedral peak catchments, including all the Brotherton fire experimental trials, removing all aboveground biomass and effectively setting the time since last burn to zero in all fire treatments. This prompted this research, to investigate the legacy effects of over 38 years of fire on grassland productivity, and also the combined effects of long-term fire and elevated temperature on grassland vegetation.

1.5.1. Dissertation outline, aim, and research questions.

Chapter 1: Literature review

An overview of the literature on grasslands, the history of grasslands and their relationship with fire. This chapter also included climate change, global warming, and their impacts on grasslands.

Chapter 2: Legacy effects of long-term fire manipulation on aboveground grassland productivity of a high-altitude mesic grassland in South Africa.

This experiment aimed to examine the legacy effects of long-term burning on aboveground biomass, basal cover and species composition of a montane grassland, post arson fire.

There were two main research questions for this experiment:

1. Are there significant differences in the aboveground biomass between the different fire regimes, after the arson fire has invalidated the effects of time-since-burn?

2. How does 38-years of consistent burning management affect basal cover and species composition within the different fire regimes?

Chapter 3: Effects of elevated air and soil temperature on aboveground productivity of high-altitude grassland in South Africa.

The aim of this experiment was to determine the effects of warming and long-term burning and their interactive effects, on grassland productivity.

These were the main questions for this experiment:

1. Can OTCs imitate temperature increases that are consistent with the predictions that are accurate and realistic for this century in a high-altitude grassland in southern Africa?
2. How does temperature increase affect aboveground biomass in interaction with different fire regimes?
3. How does temperature increase in interaction with different fire regimes affect soil moisture content?
4. Does an increase in temperature affect species compositional structure within the different fire regimes?

Chapter 4: Synthesis and Recommendations

The last chapter of this dissertation provides a summary of the main findings from the data chapters and also the recommendations for future research opportunities.

CHAPTER 2: LEGACY-EFFECTS OF LONG-TERM FIRE MANIPULATION ON ABOVEGROUND PRODUCTIVITY OF A HIGH- ALTITUDE MESIC GRASSLAND IN SOUTH AFRICA

(Prepared according to the format guidelines of the African Journal of Range and Forage Science)

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2.1. Abstract

Climate and fire are important drivers of the distribution and ecological attributes of grassy biomes. Although prescribed fires have been used to attain important management goals, we still have a poor understanding of the long-term effects of burning on species composition and overall grassland productivity, especially in high-altitude grasslands. This study was conducted in the Brotherton burning trials, which were established in 1980 to assess long-term fire impacts on the grassland. An arson fire swept through these trials in May 2016, removing all aboveground biomass and setting time since last burn to zero. The objective of this study was to determine the legacy effects of frequency and season of burn on aboveground biomass, basal cover and species composition on the Brotherton fire trials in the KwaZulu-Natal Drakensberg. Sampling for biomass were in April 2017, species composition sampling was conducted April 2017 and February 2018 respectively, while basal cover sampling was conducted at the peak of the summer in January 2018. In terms of burn frequency, the no burn treatment had the greatest biomass ($474.2 \text{ g/m}^2 \pm 16.14$), while annual had the least biomass ($331.67 \text{ g/m}^2 \pm 12.55$). Season of burn had no significant effect on aboveground biomass ($p = 0.871$). Basal cover was also not significantly affected by the frequency of burning ($p = 0.119$) but rather by the season of burning ($p < 0.001$), where basal cover was highest in spring burns ($24.63 \% \pm 1.37$) and lowest in autumn burns ($16.95 \% \pm 1.945$). The Principal Components Analysis revealed that in the 2017 data set, frequently burned plots were dominated by *Themeda triandra*, quinquennial burns were dominated by *Tristachya leucothrix* and the no burn treatment by

Harpochloa falx. The 2018 dataset however, showed no clear trend of fire frequency or season to species composition; this is with exception to the no burn treatment. Overall results show that the legacy effects of long-term fire treatment are responsible for grassland productivity and species compositional changes.

Keywords: *fire, aboveground biomass, grassland, species composition, Brotherton trials*

2.2. Introduction

Fire, herbivory and climate are important factors that determine the distribution and ecology of grassy biomes (Bond et al. 2003). The notion that climate was the main determinant of ecosystem characteristics has prevailed for a long time in ecology (Bond et al. 2003). Such ecosystems are referred to as climax vegetation (Selleck 1960; Bond et al. 2005). However, ecologists then became cognizant that many grassy biomes were in fact driven by the presence and/or absence of fire rather than climate (Phillips 1930; Bond et al. 2003). Acocks (1953) labelled these grassy ecosystems whose distribution and vegetation were controlled by fire as ‘false’ or fire-climax grasslands. In the African continent, fire is a core component for determining the distribution and ecology of grassy biomes (Bond et al. 2005; Archibald et al. 2009; Blair et al. 2014), and for the proper functioning and conservation of these biomes worldwide (Trollope and Trollope 2010; Allen and Palmer 2011). Grassland fires evolved naturally from lightning (Edwards 1984). Lightning influenced the frequency, season and spread of fires through landscape for centuries before humans started controlling fire as a dominant driver of the grassland landscape (Guevara et al. 1999). Currently, fire is generally ignited by humans, mostly as a veld management tool (Manson et al. 2007) and for shaping vegetation distribution (Archibald et al. 2013; Li et al. 2013). To achieve different management objectives, humans can directly change fire dynamics by changing the timing and frequency of fires (Archibald 2016; Alvarado et al. 2018).

Numerous studies (e.g., Kzlowksi and Ahlgren 1974; Oosterheld et al. 1999; Uys et al. 2004; Bond and Keeley 2005; Blair et al. 2014; Bachinger et al. 2016) agree that fire, herbivory, and frost are the most important controlling factors responsible for the development and maintenance of grassland ecosystems. Fire in these grasslands maintains vegetation in several ways (Archibald et al. 2009; Anguyi 2010). These include regulating plant community structure and species composition (Tainton and Mentis 1984; Uys et al. 2006; Manson et al. 2007; Alvarado et al. 2018), inhibiting the intrusion of woody plants

and maintaining open vegetation (Oosterheld et al. 1999; Alvarado et al. 2018), minimizing diseases and pests (Anguyi 2010), and improving primary production and the quality of livestock feed (Bond et al. 2005; Uys et al. 2006; Li et al. 2013; Blair et al. 2014; Morris et al. 2020).

The primary purpose of grassland fires is to remove moribund aboveground biomass and to encourage new growth (Bond 1997; van Wilgen and Scholes 1997; Scheintaub et al. 2009). In grasslands that have high productivity, this removal of moribund biomass leads to increased solar radiation reaching the soil surface (Uys et al. 2006), which promotes seed germination and the development of new tufts, thereby prolonging the growing season (Fynn et al. 2005; Scheintaub et al. 2009; Blair et al. 2014). Litter removal through burning also minimizes competition for light and nutrients, especially in warmer soils (Bond et al. 2005). All these factors generally increase the vegetation's productivity after a fire has occurred (Scheintaub et al. 2009).

Over the years, studies related to fire in grassland ecosystems have mostly focused on the agricultural perspective rather than the ecological perspective (Bond and Keeley 2005; Trollope and Trollope 2010). Although prescribed fires have been used to attain important management goals, such as those mentioned previously, there is still a gap in the scientific literature about the long-term effects of burning on species composition and overall grassland productivity (Gordijn et al. 2018). This has resulted in controversy over different burning regimes that have been used in the past (Everson 1985). For example, it was suggested by Nänni (1969) that an unbalanced, irregular fire regime would be the best for maintaining the optimal grassland condition in terms of grass productivity and species diversity in the Drakensberg, while Tainton and Mentis (1984) suggested grasslands should be burned every second year in order to maintain maximum productivity, and that these burns should occur in winter to encourage *Themeda triandra*. By contrast, Uys et al. (2004) found that the exclusion of fire for ten years or more resulted in significant changes in species composition, with grasslands becoming invaded by woody vegetation. In another long-term study in the KwaZulu-Natal Drakensberg, Everson and Tainton (1984), found that 30-years of annual and biennial spring burns did not significantly change the condition of the grassland with regards to species composition and productivity, while excluding fire for five years resulted in significant species compositional change, which affected the overall production and quality of the grassland (Everson and Tainton 1984; Everson and Everson 2016).

There has been a lot of research on fire effects on grassland vegetation, particularly in the KwaZulu-Natal Drakensberg mountains (e.g. Everson 1985; Uys 2000; Short et al. 2003; Short 2004; Manson et al. 2007; Everson and Everson 2016; Gordijn et al. 2018; Morris et al. 2020). This study adds on the body of literature on the legacy effects of fire on grassland vegetation. Situated in the northern part of the Maloti-Drakensberg Park near Cathedral Peak are the long-term Brotherton fire trials. These trials were established in 1980 to assess long and short-term effects of fire frequency and seasonality on plant community dynamics in fire-climax grasslands (Short 2004). Even though management of the Drakensberg grasslands aims at implementing a range of burning regimes to maintain a mosaic of differing vegetation composition and cover while also reducing fire danger, the Drakensberg grasslands continue to have wildfires and or arson fires almost every year. These unplanned fires often occur in winter and they have severe consequences for the overall biodiversity of these grasslands (Short et al. 2003).

In May 2016, an unplanned arson fire swept through most of the Cathedral Peak catchments, including all the Brotherton fire experimental trials, removing all biomass and effectively setting the time since last burn to zero in all fire treatments. This provided the ideal opportunity to examine the legacy effects of long-term burning on the productivity (in terms of aboveground biomass, basal cover and species composition) of a montane grassland. We used this arson fire to evaluate the hypothesis that legacy fire effects influence the magnitude of the production response to fire in this high-altitude mesic grassland.

This study aimed to answer the following questions:

1. Are there significant differences in the aboveground biomass between the different fire regimes, after the arson fire has invalidated the effects of time-since-burn?
2. How does 38-years of consistent burning management affect basal cover and species composition within the different fire regimes?

2.3. Methods

2.3.1. Study site

This study was carried out on a long-term fire manipulation experiment on the Brotherton plateau established by the Department of Forestry near Cathedral Peak State Forest (now Cathedral Peak Nature Reserve). This was established in 1981 with the objective to evaluate short and long-term effects of different burning regimes on the Drakensberg grasslands in the absence of grazing (Morris et al. 1999; Short et al. 2003; Uys et al. 2004). The experiment is located near Cathedral Peak Nature Reserve in the uKhahlamba-Drakensberg Park (29°00' S, 29°15' E, 1890 m asl.). The Brotherton trials have a flat to mildly rolling slope, with average annual precipitation of 1380 mm which mostly falls in summer (October to March) (Morris et al. 1999). This area has mild to humid summers, and dry, cool winters with occasional snow during winter (May to August) (Uys et al. 2004). Frost is common from May to August (winter), causing the grass to become dry and dormant (Everson and Everson 2016).

The vegetation is a dense short grassland with *Themeda triandra* Forssk. and *Tristachya leucothrix* Trin. ex Ness as common species (Short et al. 2003). The vegetation was classified by Acocks (1953) as Highland Sourveld, as Moist Upland Grassland by Bredenkamp et al. (1996) and as High-altitude Grassland by Mucina and Rutherford (2006). The experiment was set up in a randomized block design with a total of forty-five 25×25 m plots. Of the forty-five plots, only thirty-two were surveyed, with the remaining thirteen serving as non-replicated demonstration plots (also called redundant plots) (Figure 2.1). The surveyed plots consisted of ten maintained fire treatments which varied in both season and frequency. There was an uneven number of replicates per fire treatment, i.e., biennial spring had six replicates; annual spring, annual autumn, quinquennial spring, biennial winter, and no burn all had four replicates.. The following treatments were sampled for this study: annual autumn, annual spring, biennial autumn, biennial spring, biennial winter, quinquennial spring and no burn (fire protection),.

1

							MAIN GATE					
ANNUAL SPRING 45	BIENNIAL SPRING 40	ANNUAL AUTUMN 36	BIENNIAL SPRING 31	TRIENNIAL SPRING 27	NO BURNS 24	ANNUAL SPRING 21	BIENNIAL WINTER 18	BIENNIAL SPRING 15	ANNUAL SPRING 12	REDUNDANT 9 -> change to Triennial Spring	5 YEAR ROTATION 6	ANNUAL SPRING 3
NO BURN 44	ROCK NO TREATMENT 0 burn in winter	NO BURN 35	REDUNDANT 30 -> Biennial Alternate Spring Autumn	8 YEAR ROTATION SPRING 26	BIENNIAL WINTER 23	BIENNIAL AUTUMN 20	5 YEAR ROTATION 17	ALTERNATE SPRING AUTUMN 14	NO BURNS 11	REDUNDANT (annual winter) 8	ANNUAL AUTUMN 5	BIENNIAL SPRING 2
REDUNDANT 43 -> change to Annual Winter	REDUNDANT 39 -> change to Triennial Spring	ANNUAL AUTUMN 34	REDUNDANT (annual winter) 29	REDUNDANT 25 -> change to Biennial Winter	ANNUAL AUTUMN 22	BIENNIAL SPRING 19	REDUNDANT (annual winter) 16	5 YEAR ROTATION 13	ALTERNATE SPRING/ AUTUMN 10	BIENNIAL WINTER 7	BIENNIAL SPRING 4	BIENNIAL AUTUMN 1
REDUNDANT 42 -> change to 8 Yr rotation	REDUNDANT 38 -> change to 8 Yr rotation Spring	BIENNIAL AUTUMN 33	BIENNIAL WINTER 28									
REDUNDANT 41 -> change to Triennial Spring	5 YEAR ROTATION 37	ALTERNATE SPRING/ AUTUMN 32	NO TREATMENT - burn in winter									

2

- 3 Figure 2.1: Layout of plots sampled in the Brotherton fire trials. Each plot is 25 × 25 m. The spacing between the plots is 5 m. Redundant plots
 4 (shown in white) were not sampled as they were either not replicated or appropriate for the aims of this study.

2.3.2. Data collection

2.3.2.1. Aboveground biomass

Comparative yield method

For the comparative yield method, the observer first harvests five reference quadrats that represent the range of aboveground biomass seen across all the plots (Haydock and Shaw 1975). For this study, two 0.5×0.5 m quadrats were placed in a low and high (1 and 5) biomass areas respectively and another was placed in an area with biomass half-way between 1 and 5 which was regarded as a medium (3). Quadrats 2 and 4 were low-medium and medium-high, which were half-way between 1 and 3 and 3 and 5 respectively. The biomass in these reference plots was then clipped to 5 cm above the soil level, oven-dried for 48 hours at 60 °C and weighed. This method was performed by a single observer, to minimize subjectivity. The data then was calibrated using a linear regression to estimate the above ground biomass, in kg/ha (Haydock and Shaw 1975). Both the Disc Pasture Meter and the comparative yield method were used in this study for the estimation of aboveground biomass. Biomass sampling was conducted at the end of the growing season in April 2017.

Dry-weight rank method

The dry weight rank technique was established by 't Mannetje and Haydock (1963) as a simple method that uses ranks to quantify the biomass contributed by dominant species in a site. This method is complementary to the comparative yield method (Haydock and Shaw 1975). After ranking the area, the three most dominant species within that quadrat were identified and categorized according to their contribution to biomass (based on comparative yield estimation). The species that contributed the most was ranked 1, species that contributed second was ranked 2, and the least contributing species was ranked 3, any other species in the quadrat were ignored. A series of multipliers were used to calculate the composition percentage from the rankings, these multipliers were: Rank 1= 70; rank 2= 21; and rank 3= 9. This is intended to determine the proportion of species composition by providing a measure of the influence of the dominant species to the total biomass (dependent on dry matter) ('t Mannetje and Haydock 1963). In cases where there was only one species in a quadrat, it was given ranks 1, 2 and 3. Similarly, when there were two species, one was ranked 1 and 2, 1 and 3, or 2 and 3, depending on the biomass contributions of the two species in that particular quadrat, with the other species receiving

the outstanding rank. This method is meant for studies where measures of rare species are not necessary, therefore ignoring rare species in the quadrat is justified (‘t Mannetje and Haydock 1963; Gillen and Smith 1986). Species composition data was collected twice in this study. First in April 2017, and then again in February 2018. Disc-pasture meter

Standing grass biomass for all sampled fire treatments was measured using a standard disc pasture meter (Bransby and Tainton 1977). The disc-pasture meter (DPM) is a simple, inexpensive, and non-destructive tool that measures grass height (Bransby and Tainton 1977). A total of thirty random measurements were taken per plot at approximately one-meter intervals. Readings were only taken a meter away from the plot boundary to account for edge effects.

2.3.2.2. Basal cover

A quadrat of 0.5 x 0.5 m with a 10 cm grid of stainless-steel wire was used to estimate basal cover (Figure 2.2). This gave a total of 25 sub quadrats each representing 4 % of the quadrat area (Figure 2.2). Each 10 x 10 cm sub quadrat could easily be visualized as four quarters representing 1% cover each. Therefore, basal cover in the 25 sub quadrats was scored from 0 – 4 % in increments of one and the total was summed to give percentage basal cover. Before estimating the basal cover in each plot, quadrats were clipped to improve the visibility of basal cover and the clippings were then oven-dried at 60°C for 48 hours and later weighed for estimation of herbaceous biomass. A pilot study indicated that between six to eight quadrats per treatment plot were required so a total of six quadrats per treatment plot were sampled. Clippings were also collected to estimate herbaceous biomass. Basal cover sampling was conducted at the peak of the summer in January 2018.

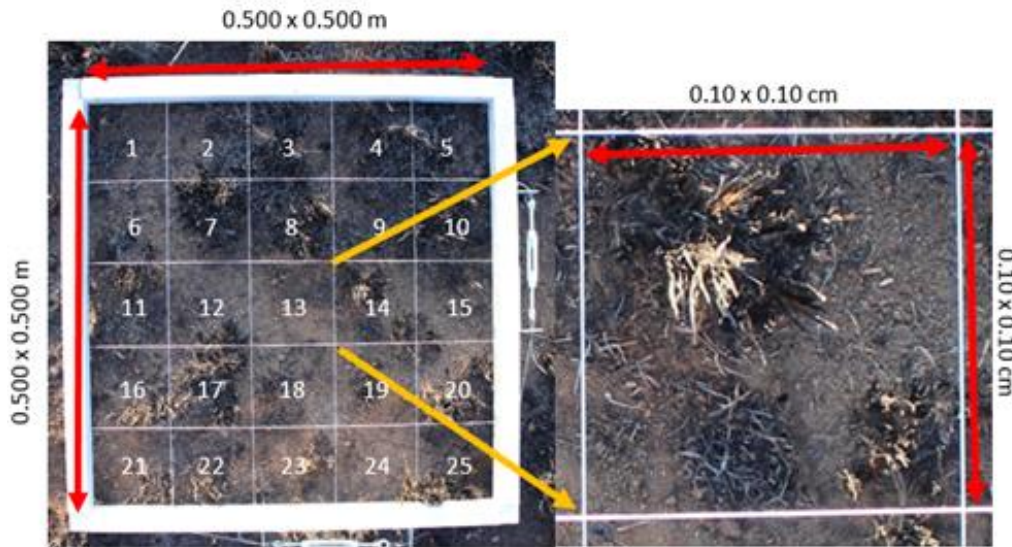


Figure 2.2: 0.50×0.50 m quadrat placed on a burnt grassland at the Brotherton fire trials, Cathedral Peak to estimate basal cover. The 25 0.10×0.10 cm sub-quadrats are numbered (Gordjin 2018 unpublished).

2.3.1. Data analyses

2.3.1.1. Biomass and basal cover

Biomass analyses used the DPM data and the DPM values were converted to kilograms per hectare using the linear equation ($Y = mx + c$) from the calibration, where: biomass (kg/ha) = $m \cdot \text{DPM} + c$. The linear equation was:

$$Y = 290.85x - 3509.80 \text{ and } R^2 = 0.8249.$$

To determine if burning frequency and seasonality had any effect on aboveground biomass and basal cover respectively, generalized linear models (GZLM) were used. This was because both biomass and basal cover data did not meet the assumptions of an analysis of variance (ANOVA) even after transformations. GZLM used a normal probability distribution with an identity link. The Consistent Akaike's Information Criterion (CAIC) for frequency and seasonality effects on biomass was 477.379 and 487.95; and 210.091 and 192.091 on basal cover respectively. Biomass and basal cover were the dependent variables and fire frequency, and season were both predictor variables in the respective analyses. All biomass and basal cover analyses used a linear model with a significance level of 0.05. Where the model showed significance, a Sequential Sidak *post hoc* test was

used for multiple comparisons. GZLMs were run using SPSS Version 25 (IBM SPSS 2017).

In order to determine the influence of different fire treatments on the dominant species composition, the data obtained via the dry-weight rank method was examined using ordination techniques. This data was first converted into percentages and arranged in an excel spreadsheet. There was minimal species turnover in the dataset, therefore a Principal Correspondence Analysis (PCA) was used (ter Braak and Smiluaer 1997). Early and late season data were analysed separately, both using PCA.

2.4. Results

2.4.1. *Effects of frequency and season of burn on aboveground biomass*

There was a significant difference in aboveground biomass between the different burning frequencies (Table 2.1). The unburned treatment had the greatest biomass ($474.2 \text{ g/m}^2 \pm 16.14$), followed by quinquennial burn ($376.4 \text{ g/m}^2 \pm 47.55$), with the biennial and annual burns having the least biomass ($352.9 \text{ g/m}^2 \pm 10.56$ and 331.67 ± 12.55) respectively (Figure 2.3). There was, however, no significant effect of season of burn on aboveground biomass (Table 2.2: $\chi^2 = 0.241$; $df = 2$; $p=0.624$).

Table 2.1: The effect of burning frequency on aboveground biomass on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa using a generalized liner model with a normal distribution and an identity link function. Degrees of freedom (df), Wald Chi-square (χ^2) and p-value are shown. Significant effects ($p < 0.05$) are shown in **bold**.

Source of variation	Df	χ^2	p-value
Block	2	0.876	0.645
Fire frequency	3	31.384	< 0.001
Residual	1	1765.933	

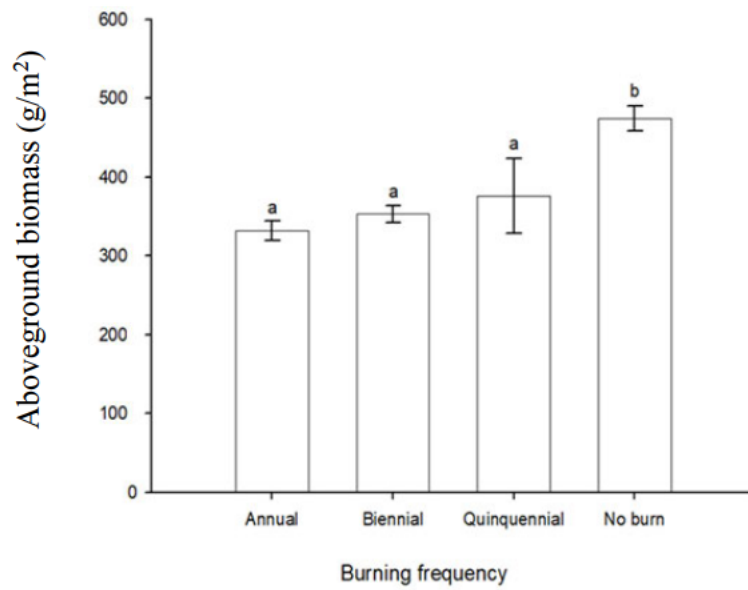


Figure 2.3: Mean aboveground biomass (\pm SE) between different burning frequencies on the Brotherton fire trials Cathedral Peak, Drakensberg, South Africa. Letters in common indicate non-significance ($P > 0.05$).

Table 2.2: The effect of season of burn on aboveground biomass on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa using a generalized liner model with a normal distribution and an identity link function. Degrees of freedom (df, Wald Chi-square (χ^2) and p-value are shown. Significant effects ($p < 0.05$) are shown in bold

Source of variation	Df	χ^2	p-value
Block	2	0.672	0.412
Season of burn	3	0.241	0.624
Residual	1	931.656	

2.4.2. *Effects of frequency and season of burn on basal cover*

The GLZM showed no significant burning frequency effect on basal cover ($\chi^2 = 5.857$; df= 3; $p = 0.119$). The effects of frequency on basal cover are shown on Table 3. Season of burn, however, did have a significant effect on basal cover. The spring burn showed the highest basal cover ($24.63 \% \pm 1.37$; Figure 2.4), and winter had the second highest basal cover, but was not significantly different to autumn burn, which had the lowest basal cover (16.95 ± 1.945 and 17.61 ± 1.716) respectively (Figure 2.4).

Table 2.3: The effect burning frequency on basal cover on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa using a generalized liner model with a normal distribution and an identity link function. Degrees of freedom (df), Wald Chi-square (χ^2) and p-value are shown. Significant effects ($p < 0.05$) are shown in **bold**.

Source of variation	Df	χ^2	p-value
Block	2	37.717	< 0.001
Fire frequency	3	5.857	0.119

Table 2.4: The effect of season of burn on basal cover on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa using a generalized liner model with a normal distribution and an identity link function. Degrees of freedom (df), Wald Chi-square (χ^2) and p-value are shown. Significant effects ($p < 0.05$) are shown in **bold**.

Source of variation	Df	χ^2	p-value
Block	2	25.364	< 0.001
Season of burn	2	15.131	0.001

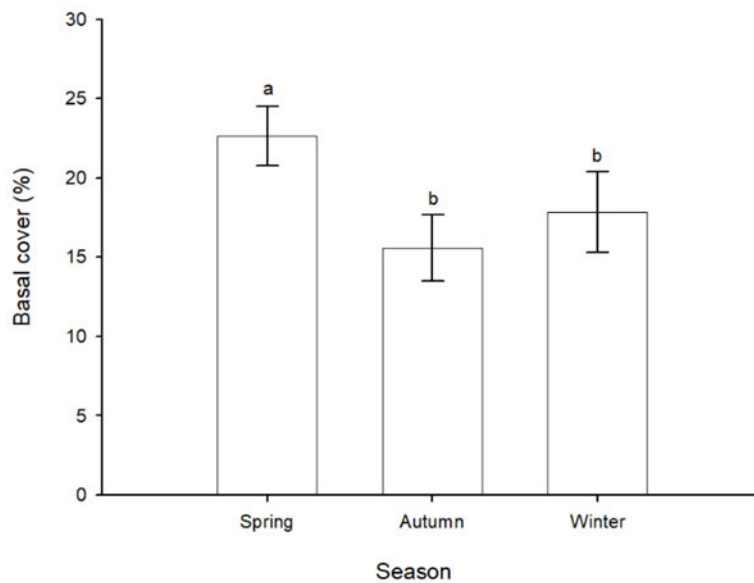


Figure 2.4: Mean basal cover (\pm SE) between different burning seasons on the Brotherton fire trials Cathedral Peak, Drakensberg, South Africa. Letters in common indicate non-significance ($P > 0.05$).

2.4.3. Burning effects on species composition

The Principal Component Analysis (PCA) results from the 2017 dataset (Figure 2.5 A) and the 2018 dataset (Figure 2.5 B) in the Brotherton fire trials give an indication of the species composition associated with the different burning treatments. The axes represent the summed abundance of all species across all fire treatments in Brotherton. The species that are clustered together with the burning treatment are the species that were recorded in that burning treatment. Species that had longer arrows were species that were most abundant species across burning treatments. The overall dominant species in the early and late growing seasons were *Themeda triandra* Forssk. (Thetri), *Tristachya leucothrix* Trin. ex Ness (Trileu), *Koeleria capensis* Ness (Koecap), *Harpochloa falx* (L.f.) Kunztze (Harfal), *Rubus cuneifolius* Pursh (Rubcun) and *Helichrysum aureonitens* Sch.Bip. (Heliaur). In the early growing season, the spring burns showed the greatest variation, with the replicates being scattered in ordination space (Figure 2.5A). Autumn and winter burns were mostly clustered on axis 1, and were dominated by *T. triandra*, *Panicum ecklonii* Nees (Paneck), *K. capensis*, and *Heteropogon contortus* Schult. (Hetcon) (Figure 2.5A). With regards to

species response to fire frequency, treatments that were frequently burned were much variable in their composition while the less frequent burns were more distinct. The quinquennial burns were dominated by *T. leucothrix*, *Stiburus alopecuroides* Hack. Stapf (Stibalo) and *Andropogon appendiculatus* Ness (Andapp), while the no burn plots were quite distinct and dominated by *H. falx*, *R. cuneifolius* and *H. auronitens* along the first axes.

There was no clear trend of species composition response to frequency and seasonality in the late growing season, where a wider variation was observed, and species scattered in all treatments. This is with the exception of the no burn treatment which still had a consistent trend as the early growing season and was dominated by *H. falx*, *H. auronitens* and *R. cuneifolius*.

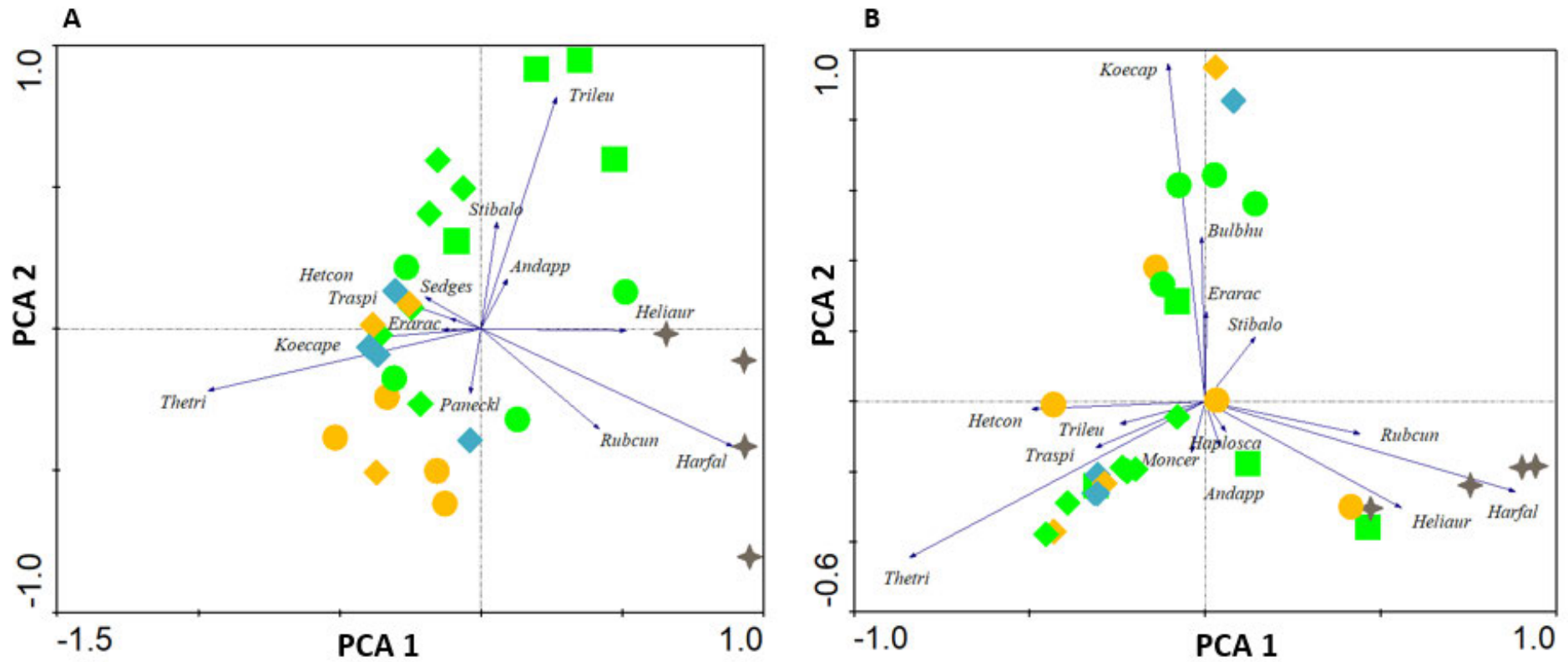


Figure 2.5: Principal Components Analysis (PCA) of dominant species composition from different fire treatments in Brotherton fire trials, Cathedral Peak in the 2017 dataset (A) and the 2018 dataset (B). The eigenvalues for axis 1 and axis 2 in A are 0.661 and 0.156, and 0.394 and 0.253 for B, respectively. Green= spring; yellow= autumn; blue= winter; grey= no burn. Circle= annual, diamond= biennial; square= quinquennial; star=no burn. See appendix 1 for full species names.

2.5. Discussion

2.5.1. *Legacy effects of fire treatment on aboveground biomass*

This study investigated the legacy effects of long-term burning on aboveground production of a high-altitude grassland in South Africa. This study's main findings revealed significant differences in aboveground production even though the time since last fire was the same in all plots.

This suggests that the long-term application of a fire regime has more impact on productivity and composition than the time since the last fire. This is in line with previous research in similar grasslands that has shown that fire is not only an essential factor in driving the aboveground productivity in these systems (Everson and Everson 2016), but also that fire will have significantly different effects on sites with different burning histories in terms of the frequency and season of burning (Knapp et al. 1998). This was also observed in this study, where the no burn treatment had significantly higher aboveground biomass compared to the other treatments. According to Briggs et al. (1992), fire in an infrequently burned site may result in a considerably greater biomass production than frequently burned sites due to the accumulation of nitrogen in unburned sites (Briggs et al. 1992). According to Fynn et al. (2004), plots with infrequent burns and fire protection are high in soil nitrogen, promoting tall grasses and leading to high aboveground net productivity. These results were different from those of Little et al. (2015), who found that annual and biennial burning resulted in increased vegetation biomass while unburnt plots had the lowest biomass in a long-term study on fire impacts in moist highland grassland in Mpumalanga, South Africa. The low biomass in the unburnt treatments were due to that long-term fire exclusion results in shading of smaller tufts and an increase in bare ground in between tufts as tufts become moribund and die, therefore decreasing the overall aboveground biomass in these unburnt plots (Little et al. 2015).

However, Uys (2000) found an increase in aboveground biomass with decreased fire frequency in long-term mowing and burning experiment at Ukulinga farm, KZN. Another study which investigated the long-term effects of burning frequencies on biomass production found that biomass was reduced with increased burning frequency (Oluwole et al. 2008). According to Snyman (2004), the low aboveground biomass associated with frequent burning could be consequent to reduced plant cover, destruction of seed banks, and reductions in species diversity.

Although South African grasslands are naturally maintained by spring and winter fires, there are concerns over the detrimental effects of wild and arson fires on plant diversity and aboveground biomass (Everson 1985; Little et al. 2015). It has been suggested that the natural fire frequency in moist highland grassland would have been only every four years or more, depending on the amount of litter present (Manry and Knight 1986), amount of rainfall that season, the rainfall the past season, herbivory, and the type of species growing in a site (Archibald et al. 2019). More recent studies in Hungary and Europe also agree with this notion, maintaining that burning annually results in the reduction of biodiversity, vegetation coverage and biomass production in grassland systems and is therefore not recommended (Deák et al. 2014). According to Kahmen et al. (2002), annual burning does not allow for enough time for grassland regeneration and can therefore lead to undesired states of succession. This however is contrary to a recent study in the mesic Drakensberg by Morris et al. 2000 who found that annual burning maintained a stable grassland close to the original composition.

Our results show no significant effects of season of burn on aboveground biomass. These results are consistent with those of Uys (2000) in the same study site. Uys (2000) mentions that the narrow range of burn seasons in the Brotherton trials prevents any clear trends from being determined for biomass response to the burning season. Similar conclusions were drawn by Morris et al. (1999) from work also previously done on the Brotherton trials.

2.5.2. Legacy effects of fire treatment on basal cover

Basal cover is often considered a measurable characteristic of grassland vegetation and productivity (Hardy and Tainton 1993). In South Africa, basal cover is frequently used as a measure of assessing the long-term effects of disturbances like fire on natural grassland vegetation (Hardy and Tainton 1993), with the hypothesis that changes in basal cover will mirror the impacts of the treatment applied to the grassland (Morris and Müller 1970).

Some studies have shown that frequent prescribed fires have both positive and negative consequences on basal cover, depending on slope, rainfall, wind, and other environmental factors (Guevara et al. 1999; Engle and Bidwell 2001; Oluwole et al. 2008). A study by Oluwole et al. (2008) reported a reduction in basal cover with frequent burning, which makes the grassland more susceptible to soil erosion and land degradation (Oluwole et al.

2008). Robinett (1994) also found a significant decline in both basal cover and biomass production with an increase in fire frequency. A study in the Drakensberg by Gordjin et al. (2018) however found greater grass basal cover in areas that experienced frequent fires. By contrast, our study found no frequency effects on basal cover, and therefore opposes findings by Everson et al. (1989), Robinett (1994), Short (2001), and Oluwole et al. (2008). They all (respectively) found higher basal cover in sites that were frequently burned. According to Everson et al. (1989), this is due to the capability of grasses to quickly recuperate after burns, together with the removal of aboveground biomass (which would shade tillers), which encourages good maintenance basal cover. Manson et al. (2007) similarly found that 20 years of fire protection significantly reduced basal cover in a moist montane grassland. Our results rather show a significant effect of season of burn on basal cover (Figure 2.4), where the spring burns had higher cover than the autumn and winter burns.

2.5.3. Legacy effects of fire treatment on species composition

As with other studies worldwide, species composition in this study was significantly influenced by frequency and season of burn (Everson and Tainton 1984; Everson 1985; Uys 2000; Fynn et al. 2005; Gordjin et al. 2018). Our results show that frequently burned sites and less frequently burned sites differ in their composition. These results are similar to Short (2004), who also found that high-frequency burning and low-frequency burning has different effects on species composition. In the early growing season, our results reveal that species such as *T. triandra*, *K. capensis*, *T. spicatus*, and *H. contortus* all increase with increasing burning frequency, while *H. aureonitens*, and *R. cuneifolius* all increase in abundance with a decrease in burn frequency. Also, in the early growing season, the two tufted species, *H. falx* and *T. leucothrix* both increased as burn frequency decreased, the former being the dominant species in the fire protection treatments in both early and late season sampling. These results are consistent with those of Everson and Tainton (1984), who also found a high abundance of species such as *T. triandra* and *H. contortus* in frequently burnt sites, and high abundance of *H. falx* and *T. leucothrix* in less frequently burnt sites in a study done in the Drakensberg. In a long-term study conducted in the Ukulinga trials, Fynn et al. (2005) also found that short grasses such as *H. contortus* and *T. triandra* were common in annually and biennially burned plots. This was because, according to Fynn et al. (2004), short grasses such as *H. contortus* and *T. triandra* thrive in low soil nitrogen and low aboveground productivity plots (Snyman 2004). These species also do well in plots with low litter and improved light availability, which is promoted by

frequent burning (Osem et al. 2004). Species composition in the 2018 dataset did not show a clear pattern of fire treatment influence; this is with exception of the no burn treatment which ordinated to the far right, a trend also observed in the early growing season. According to Archibald et al. (2019) the contrasting patterns in species composition (in the two datasets) could be explained by two things. Firstly, the level or degree of fire (or herbivory) have a huge influence on the type of species that dominate an area at any time (Archibald et al. 2019). Secondly, other environmental constraints such as nutrient availability and/or soil moisture content also determine how species are affected by a disturbance (Coley et al. 1985; Archibald et al. 2019), therefore could explain why there were different patterns in species composition in 2017 and 2018 respectfully.

Studies conducted in the Drakensberg grasslands by Everson (1985) and Uys (2000) independently found no significant effects of frequency and season of burn on species composition, with differences observed between the burning and no burn treatments. This demonstrated directional changes in species composition with fire protection (Uys 2000). Uys (2000) further concluded that sward structure was more determined by changes in post-burn treatments rather than the long-term effects of fire frequency, even though no conclusions of species response to season of burn were made. To maintain species diversity in grasslands, less frequent burning (3-5 years) was recommended (Deák et al. 2014). Morris et al. (1999) also came to the same conclusions in a study done on the Brotherton trials.

Forbs and sedges were poorly represented in this study and showed no clear response to burning treatments. This is because the comparative yield and DWR methods used in this study are not suitable for measuring the abundance of rare species as they are not detailed analyses (Everson and Clarke 1987; Gordjin et al. 2018). Therefore, species composition was primarily limited to changes in common species, and grasses rather than forbs and sedges. Consequently, small subtle compositional fluctuations may have been hidden (Gordjin et al. 2018). Species such as *Rubus cuneifolius*, an invasive shrub, and *Helichrysum aureonitens* were common in the no burn treatments. Uys (2000) also reported the dominance of these species in non-disturbed treatments in a study conducted in the same trials. Comparisons of species composition between treatments also indicated that the burn treatments were more similar to each other than to the fire protection treatments, this was the case in both the 2017 and the 2018 dataset (Figure 3).

2.6. Conclusions

A general conclusion that can be drawn from this study is that time since the last fire has no noticeable impact on the overall productivity in the Brotherton trials. However, the legacy effects of the long-term fire regime had significance in the overall aboveground productivity and species community of this montane grassland. This study unexpectedly revealed that the no burn treatment yielded the highest aboveground biomass ($474.2 \text{ g/m}^2 \pm 16.14$), with annual burning producing the least biomass ($331.67 \text{ g/m}^2 \pm 12.55$), which was unexpected as studies have shown that frequent burning increases productivity in grasslands (e.g., Little et al. 2015). Though we could determine no significant effects of fire frequency on basal cover, basal cover appeared to respond to the season of burn, where a substantial increase in basal cover was observed in the spring burns. Species composition in Brotherton showed a clear trend of species response to frequency and season of burn, with the evident dominance of *Themeda triandra* with increase in fire frequency and dominance of *Harpochloa falx* with decreasing frequency. Findings of this study support the need to further investigate the interactive impacts of fire and other environmental (e.g., slope, rainfall, temperature), vegetation (e.g., species diversity) and soil variables (soil nutrients, soil carbon), on mesic grassland vegetation similar to the Brotherton trials. These will allow for a broader range of analysis and understanding of the long-term effects of different treatments and variables on the ecology of montane grasslands, which will ultimately help understand impacts and aid in better management.

CHAPTER 3: EFFECTS OF ELEVATED AIR AND SOIL TEMPERATURE ON ABOVEGROUND PRODUCTIVITY OF HIGH-ALTITUDE GRASSLAND IN SOUTH AFRICA

(Prepared according to the format guidelines of the African Journal of Range and Forage Science)

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3.1. Abstract

Climate change, which is evidenced through temperature increase, sea-level rise, extreme weather, and varied rainfall, has greatly affected natural systems and the processes that occur within them. Temperature is one of the primary driving factors of biochemical processes in terrestrial biomes. Climate change factors, such as temperature increase, are most likely to interact with grassland processes, such as biomass production, and disturbances, such as the fire regime. The aim of this study was to determine how elevated temperature affects vegetation dynamics, in terms of aboveground biomass, soil moisture content, and species composition in a fire-climax high-altitude grassland. Experimental open-top chambers (OTCs) were used to simulate temperature increase. OTCs were placed in four burning treatments (annual spring, biennial spring, quinquennial, and no burn). Each of these treatments was replicated four times, resulting in sixteen (16) OTCs in total. Each OTC was paired with a non-warmed control positioned 2 m from the chamber. Our results showed that OTCs increased mean daily air temperatures by 1 °C and soil temperature by 0.7 °C. Midday air temperatures were increased by up to 4°C and midday soil temperatures by up to 2°C. Warming had no effect on aboveground biomass in late spring ($331.67 \text{ g/m}^2 \pm 12.5$; $\chi^2 = 0.802$; $\text{df} = 1$; $p = 0.370$) or late summer ($507.91 \text{ g/m}^2 \pm 70.6$; $\chi^2 = 1.533$; $\text{df} = 1$; $p = 0.216$), however, in mid-winter, was significantly higher in the warming treatment ($\chi^2 = 19.535$; $\text{df} = 1$; $p < 0.001$). Fire frequency, as expected, had a significant effect on aboveground biomass in all sampling seasons ($\chi^2 = 214.012$; $\text{df} = 3$; $p < 0.001$; $\chi^2 = 7.833$; $\text{df} = 3$; $p = 0.050$; and $\chi^2 = 40.060$; $\text{df} = 3$; $p < 0.001$ respectively).

Warming significantly reduced soil moisture in the late spring and late summer ($\chi^2=39.762$; $df=1$; $p < 0.001$ and $\chi^2=10.188$; $df=1$; $p < 0.001$, respectively), while it had no significant impact on moisture in mid-summer and early autumn. Warming also did not influence species composition, which was most likely due to the short timeframe the OTCs had been set up in the Brotherton trials. Instead, species composition was found to be driven by fire treatment.

Keywords: *grasslands, open-top chambers; warming; climate change; productivity.*

3.2. Introduction

Climate change, which is evidenced through temperature increase, sea-level rise, extreme weather, and varied rainfall, has greatly affected natural systems and the processes that occur within them (Gunn and Farral 1999; Saleska et al. 1999; Lemmens et al. 2006; Joyce et al. 2016). This phenomenon, which is a result of increased atmospheric carbon dioxide and other greenhouse gases (Wang et al. 2019), is predicted to become one of the primary drivers of biodiversity loss in the next century (Levy 2004; Dukes et al. 2005; Lemmens et al. 2006; Jewitt et al. 2015). Temperature, precipitation, and carbon dioxide, which are the main controlling factors of plant growth, have been greatly modified since preindustrial times (Sheiter and Higgings 2009; Wu et al. 2012). As climate change progresses, there is a growing concern about the changing disturbance-climate interactions and their potential impacts on biodiversity and ecosystem function (Dukes et al. 2005; Slingsby et al. 2019).

Temperature increases, the primary focus of this study, are expected to greatly affect plant communities worldwide (Wu et al. 2012; Buhrmann et al. 2016; Wang et al. 2019). Since the late 19th century, there has been a global air temperature increase of 0.3°C – 0.6°C, with a further increase of 0.6°C – 2.5°C predicted over the next 50 years, and 1.4°C – 5.8°C over the next century (IPCC 2001; Dhillon and Wuenhlish 2013). In the past five decades, South Africa has experienced an increase in average annual temperatures by over 1.5 times the global average of 0.6°C, with associated increases in the occurrence of extreme rainfall events (Dhillon and Wuenhlish 2013; Ziervogel et al. 2014). Temperature is one of the primary driving factors of biochemical processes in terrestrial biomes (Rustad et al. 2001; Dukes et al. 2005). These include soil respiration, litter decomposition, plant nutrient uptake, and plant productivity (Rustad et al. 2001; Lemmens et al. 2006). Drought induced by warming can also reduce both gross primary production and ecosystem respiration in semi-arid grasslands (Wang et al. 2019). Longer growing seasons, increased aboveground productivity, increased root biomass, and a shift from grasslands to savanna,

are all possible consequences of temperature increase in grasslands and similar biomes (Lemmens et al. 2006; Buhrmann et al. 2016).

Grasslands comprise approximately 40% of the world's total land area (Bond et al. 2005; Egoh et al. 2011; Boval and Dixon 2012; Blair et al. 2014) and can be found on every continent apart from Antarctica (Egoh et al. 2011). Grasslands are home to approximately one billion people worldwide and provide many ecosystem services that are vital to human wellbeing in and outside the biome (Egoh et al. 2011; Everson and Everson 2016; Gordjin et al. 2018; Morris et al. 2020). Water provision is one of the most important of these ecosystem services (Everson et al. 1990; Egoh et al. 2011; Ziervogel et al. 2014), particularly in South Africa, where most of the major catchments for water resources are covered by natural grasslands (Everson et al. 1990; Ziervogel et al. 2014). Grasslands have the second-highest level of plant species endemism and diversity, after the fynbos biome in South Africa (Egoh et al. 2011; Buhrmann et al. 2016), with several endemic-rich areas dominated by C_3 grasslands at higher altitudes (Egoh et al. 2011). The grassland biome is also rich in faunal endemism and biodiversity, hosting 52 of South Africa's 122 important bird species, 107 threatened butterfly species and 15 of endemic mammals (Cadman et al. 2013; Buhrmann et al. 2016). The grassland biome, unfortunately, is also the most threatened in South Africa, with over 35% being permanently transformed, mostly by forestry and agriculture, and over 7% severely degraded (Matsika 2007; Egoh et al. 2011; Cadman et al. 2013; Little et al. 2015). Only a small fraction (2%) of this biome is formally protected in this country (Everson et al. 1990; Egoh et al. 2011; Ziervogel et al. 2014). Understanding the impacts of climate change, predominantly temperature increase, on grassland vegetation can, therefore, aid in better management and conservation of this biome, especially given its high biodiversity value and overall importance to human livelihoods (Thuiller et al. 2008; Buhrmann et al. 2016).

One of the predicted outcomes of temperature increase in grasslands and other similar biomes is a shift in plant production by either shifting or increasing niche availability on plant communities (Duke et al. 2005; Komatsu et al. 2019). A large portion of organic matter is consumed by microbes, animals, and humans, therefore changes in productivity will most likely have an impact on the quality and quantity of forage available for both animal and human use (Potter et al. 2012; Buhrmann et al. 2016). There is evidence that in colder climates, warming increases plant aboveground productivity (Sage 2000; Duke et al. 2005; Wang et al. 2019). However, other studies in warmer climates found drastic declines in plant productivity with increased temperature, especially in the long-term (Wu et al. 2012). In changing the aboveground biomass and plant productivity, warming

inevitably also changes fire regimes, which are a vital driver in South African grassland ecosystems (Trollope 1978; Trollope et al. 2002). Loss of soil moisture is often another consequence of increased temperature (Xu et al. 2013), thereby restraining photosynthesis and plant growth (Buhrmann et al. 2016). It is therefore of fundamental importance that the interactive effects of both temperature and soil moisture be taken into account and measured when evaluating the effects of elevated temperatures in grassland vegetation productivity (Buhrmann et al. 2016).

The use of open-top chambers (OTCs) to simulate temperature increase has received a lot of attention in recent decades (Flanagan and Johnson, 2005; Buhrmann et al. 2016), specifically in colder regions like the Arctic. However, OTCs have not been used extensively in southern hemisphere ecosystems, particularly in high altitude natural grasslands. This is partly due to the concerns associated with the use of OTCs such as overheating of vegetation as shown in the succulent Karoo (Musil et al. 2004; 2009). The interactive impacts of climate warming and disturbances, such as fire, in grassland systems are understudied, particularly for southern African grasslands. Since fire is such an important management tool in grassland systems, climate warming is expected to interact with or affect the fire regime, thereby altering ecosystem function and overall production (Carlyle et al. 2014; Buhrmann et al. 2016). Understanding the interactive effects of climate change and fire is therefore important for the long-term sustainability and maintenance of these ecosystems (Carlyle et al. 2014). The fact that South Africa, and Africa at large, is predicted to experience one of the greatest temperature increases (IPCC 2007; Ziervogel et al. 2014) is what motivated the current study, which aimed at determining aboveground growth and species compositional responses to elevated temperatures in a mesic high-altitude grassland under four different fire regimes. Grassland responses to different fire regimes, particularly in the Drakensberg, has been studied extensively (e.g.: Everson 1985; Short 2001; Everson et al. 2009; Gordjin et al. 2018; Morris et al. 2020). Grassland responses to climate change have also been greatly researched at global scale (e.g., Riedo et al. 2000; Shaw et al. 2002; Zavaleta et al. 2003; Fay et al. 2008; Yang et al. 2011; Carlyle et al. 2014; Buhrmann et al. 2016). However, what has not yet been investigated, which is the aim of this current study, is the effect of warming and long-term fire, including their interactive effect, on grassland aboveground productivity.

We asked the following questions:

1. Can OTCs imitate temperature increases that are accurate and realistic (i.e. increases that are consistent with the predictions for this century in southern Africa) in a high-altitude grassland?
2. How does temperature increase affect aboveground biomass in interaction with different fire regimes?
3. How does temperature increase in interaction with different fire regimes affect soil moisture content?
4. Does an increase in temperature affect species compositional structure within the different fire regimes?

3.3. Methods

3.3.1. Study site

This experiment was carried out in a long-term fire manipulation experiment, on the Brotherton plateau, Cathedral Peak, South Africa (29°00'S, 29°15'E, 1890 m asl). This experiment was set up in 1980 to evaluate short and long-term effects of different burning regimes on the Drakensberg grasslands (Uys et al. 2004). The experimental area has a flat to gently rolling slope, with a mean annual rainfall of 1380 mm, most of which falls in the summer season (November - March). Summers are mild and humid, and the winters are dry and cool with occasional snow. Frosts are common from May to August (winter), which in conjunction with reduced rainfall, causes the grass to become dry and dormant (Everson and Everson 2016). The vegetation was classified by Acocks (1953) as Highland Sourveld, Moist Upland Grassland by Bredenkamp et al. (1996) and as uKhahlamba Basalt Grassland, dominated by the grass *Themeda triandra* Forssk by Mucina and Rutherford (2006).

3.3.2. Experimental design

For this study, experimental open-top chambers (OTCs) were used to simulate temperature increase. These OTCs were set up in January 2017 within the Brotherton trial, a long-term fire-manipulation experiment that has been ongoing since 1980 to examine effects of different fire regimes on plant community dynamics in montane grasslands. These are non-permanent structures made of six pieces of trapezoidal shaped Perspex with an inside diameter of 1.5 m and a height of 58 cm, modelled according to the International Tundra Experiment (ITEX) (Molau and Mølgaard 1996; Marion et al. 1997). Three holes, about 15

cm apart were drilled along the vertical axes of each panel. The first two holes were used to hold the sheets together using cable ties, while the bottom hole was used to attach the chambers to the ground using string and steel tent pegs. OTCs were attached to the ground to ensure they were not blown away by strong winds, and tent pegs were used to allow for their easy removal when the plots were due to be burnt. In the winters of 2000, 2007 and 2016 respectively, unplanned arson fires burned through the experiment. The 2016 arson fire removed all the standing biomass on all fire treatments just four months prior to the initiation of the warming treatment. However, we assumed that the long-term soil legacy effect of the different fire treatments would still be present, and biomass quickly recovered (Chapter 2). OTCs and control plots were placed in the periphery of the fire plots across all fire frequencies (annual, biennial, quinquennial and fire exclusion), for only the spring burns. This resulted in a full-factorial randomised-block experiment with two main treatments: warming and fire frequency. Each of these treatments was replicated four times, resulting in sixteen (16) OTCs in total. Each OTC was paired with a non-warmed control of the same size and positioned 2 m from the chamber. All OTCs together with other aboveground equipment, were removed before burning in all the plots.



Figure 3.1: Open-top chamber in the Brotherton fire trials.

Image: Mariska Te Beest

3.3.3. Measurements of environmental variables

Air and soil temperatures were monitored continuously across all sixteen plots, both in the OTCs and their paired controls, using iButtons (Maxim Integrated). For soil temperature, these were put inside small plastic bags and buried 10 cm below the soil surface. Air temperature was measured 20 cm above the ground, and the iButtons were attached to a 15 cm pencil-like rod to ensure they stayed aboveground. The iButtons were set to measure temperatures on an hourly basis during the entire study period from January 2017 to July 2018. Soil moisture content was sampled in January 2017 (mid-summer), March 2017 (early autumn), November 2017 (late spring), and February 2018 (late summer). The January and March measurements were taken using an HH2 Moisture Meter (Delta-T Devices Ltd). For the November and February soil moisture measurements, an HS2P Hydro Sense II (Campbell Scientific) was used.

3.3.4. Measurements of plant growth

To measure aboveground biomass, a standard disc-pasture meter (DPM) was used (Bransby and Tainton, 1977) ([See Chapter 2.3.2.3](#)). Three replicate readings were taken in each OTC plot and the paired controls. OTCs were removed temporarily when the DPM readings were done. Aboveground biomass was sampled in November 2017 (late spring), February 2018 (late summer), and July 2018 (winter). DPM values were converted to grams per square meter. This was done by using the linear equation ($Y = mx + c$) from the calibration, where: $\text{biomass (g/m}^2\text{)} = \text{DPM} \times m + c$. Linear equations for the 2017 and 2018 calibrations are:

$$Y = 1272x + 1208; \text{ and } Y = 2424x - 1416 \text{ respectively}$$

Species composition was sampled via the point intercept method, using a Levy bridge (Levy and Madden, 1933). This bridge had seven pins which were 10 cm apart. The length of the bridge was reduced in order to fit within the footprint of the chamber. The bridge was moved seven times, resulting in 49 hits per plot. OTCs were removed temporarily when the Levy Bridge was used". For each pin, the species (both grasses and forbs) at the tip of the pin was recorded. When there was no plant species within a 5cm the radius of the pin, bare soil was recorded. This was done in both the OTCs and their paired controls in April 2017 and February 2018, respectively.

3.3.5. Statistical analysis

3.3.5.1. Biomass

Generalized linear models (GZLM) performed in SPSS 25 (IBM SPSS 2015) were used to assess the effects of fire frequency and warming on aboveground biomass. This was because biomass data did not meet the assumptions of an analysis of variance (ANOVA) even after transformations. This was done for all biomass data collected in November 2017 (late spring), February 2018 (late summer), and July 2018 (winter). The Consistent Akaike's Information Criterion (CAIC) values for warming and fire frequency effects on aboveground biomass for the late spring, late summer, and winter sampling seasons were 492.773; 552.799 and 503.641, respectively. These analyses used a linear model with a significance level of 0.05. Where the model showed significance, a Sequential Sidak post hoc test was used for multiple comparisons.

3.3.5.2. Soil moisture

To determine the effects of warming and fire frequency, as well as their interactions on soil moisture content, a generalized linear model (GZLM) was used. This was because soil moisture did not meet the assumptions of an analysis of variance (ANOVA). All analyses used a significance level of 0.05. The GZLM used a linear model. Where the model showed significance, a Sequential Sidak post hoc test was used for multiple comparisons. GZLMs were run using SPSS Version 25 (IBM SPSS 2015).

3.3.5.3. Species composition

To directly examine the influence of warming and fire treatment on species composition, a principal correspondence analysis (PCA) was done for both April 2017 and February 2018 data. The output was displayed using CanoDraw (Smilauer 1993; ter Braak and Smilauer 1997).

3.4. Results

3.4.1. Temperature

Can OTCs imitate temperature increases that are accurate and realistic (i.e. increases that are consistent with the predictions for this century in southern Africa) in a high-altitude grassland?

Temperature results showed that OTCs do indeed increase above- and belowground temperature. The OTCs increased ambient midday air temperature by up to 4° C, and by 2° C during the night, while they also increased midday soil temperature by up to 1.5°C and by 0.5°C during the night.

In summer, air temperature was maximum at 11:00 am, while soil temperature was highest between 1:00 - 2:00 pm. Minimum temperatures were observed at 4:00 am for air temperature, and at 7:00 am for soil temperature. This was for both OTCs and control plots. In winter, air temperature was highest between 12:00 – 1:00 pm and soil temperature between 4:00 pm – 5:00 pm, for both the chambers and their paired controls. The minimum air temperatures were observed at 7:00 am for the OTCs and between 11pm – 12am for the paired controls. Minimum soil temperatures were observed between 7am – 8:00 am for both chambers and the controls (Figure 3.1).

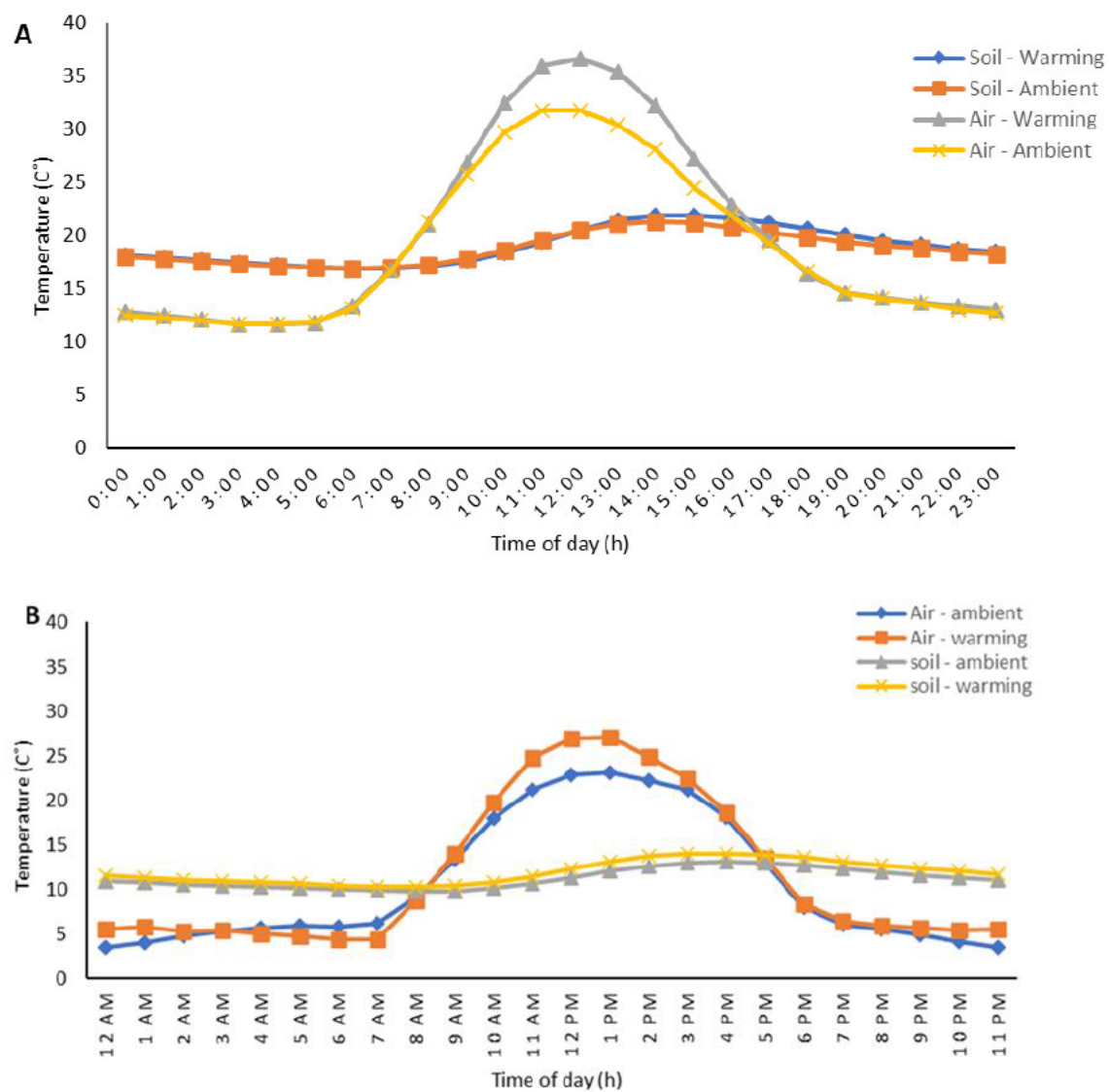


Figure 3.1: Variations in air and soil temperature in OTC and control plots in summer (January) (A) and winter (June) (B) on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa.

3.4.2. Biomass

How does the increase in temperature affect aboveground biomass in interaction with different fire regimes?

Aboveground biomass production in the late spring (Nov 2017) sampling period was not significantly different in OTC and control plots ($\chi^2 = 0.802$; $P = 0.370$; Table 3.1A). However, there were significant differences between fire regimes ($\chi^2 = 214.012$; $P < 0.001$; Table 3.1A; Figure 3.2A). The quinquennial burn treatment had significantly greater biomass ($423.46 \text{ g/m}^2 \pm 23.169$), the no burn treatment had the second greatest biomass ($408.41 \text{ g/m}^2 \pm 22.609$), while the biennial and annual fire treatments had the least aboveground biomass ($344.11 \text{ g/m}^2 \pm 11.063$ and $158.05 \text{ g/m}^2 \pm 6.894$). A similar trend was found in the early summer sampling (Feb 2018), where warming did not have any significant effect on aboveground biomass ($\chi^2 = 1.488$; $P = 0.223$; Table 3.1B), whereas biomass significantly differed between fire treatment ($\chi^2 = 7.883$; $P = 0.050$; Table 3.1B; Figure 3.2B). In this sampling season, the no burn treatment had the greatest biomass ($604.54 \text{ g/m}^2 \pm 116.675$), and the annual treatment had the least biomass ($349.86 \text{ g/m}^2 \pm 78.713$). Both the quinquennial and biennial treatments had intermediate biomass ($444.57 \text{ g/m}^2 \pm 88.371$ and $453.52 \text{ g/m}^2 \pm 65.758$, respectively). The winter (July 2018) sampling, which was the last biomass sampling done in this study, revealed a significant effect of both warming and fire frequency (respectively) on aboveground biomass production ($\chi^2 = 19.533$; $P < 0.001$; $\chi^2 = 40.060$; $P < 0.001$ Table 3.1C; Figure 3.3). The OTC treatments had significantly greater biomass when compared to the control treatments ($497.73 \text{ g/m}^2 \pm 41.105$ and $369.06 \text{ g/m}^2 \pm 28.951$ respectively). With regards to fire frequency effects on biomass, the biennial burn treatments had the greatest biomass ($540.55 \text{ g/m}^2 \pm 50.307$), followed by the no burn and quinquennial treatments ($439.56 \text{ g/m}^2 \pm 49.592$ and $436.89 \text{ g/m}^2 \pm 63.423$ respectively). The annual burn treatment had the least aboveground biomass ($316.59 \text{ g/m}^2 \pm 24.278$). There were no interactive effects of warming and fire treatment in all three sampling seasons ($p > 0.05$; Table 3.1A, 3.1B, and 3.1C).

Table 3.1: The effect of burning frequency, warming, and their interaction on aboveground biomass in the (A) late spring (November), (B) late summer (February) and (C) mid-winter (July) sampling season on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa using a generalized linear model with a normal distribution and an identity link function. Degrees of freedom (d.f.), Wald Chi-square (χ^2), and p-value are shown. Significant effects ($P < 0.05$) are shown in **bold**.

A)

Source of variation	d.f.	χ^2	p-value
Block	2	6.465	0.039
Warming (W)	1	0.802	0.370
Fire frequency (FF)	3	214.012	<0.001
W * FF	3	0.878	0.831

B)

Source of variation	d.f.	χ^2	p-value
Block	2	4.397	0.111
Warming (W)	1	1.488	0.223
Fire frequency (FF)	3	7.833	0.050
W * FF	3	2.673	0.445

C)

Source of variation	d.f.	χ^2	p-value
Block	2	5.196	0.074
Warming (W)	1	19.535	<0.001
Fire frequency (FF)	3	40.060	<0.001
W * FF	3	3.922	0.270

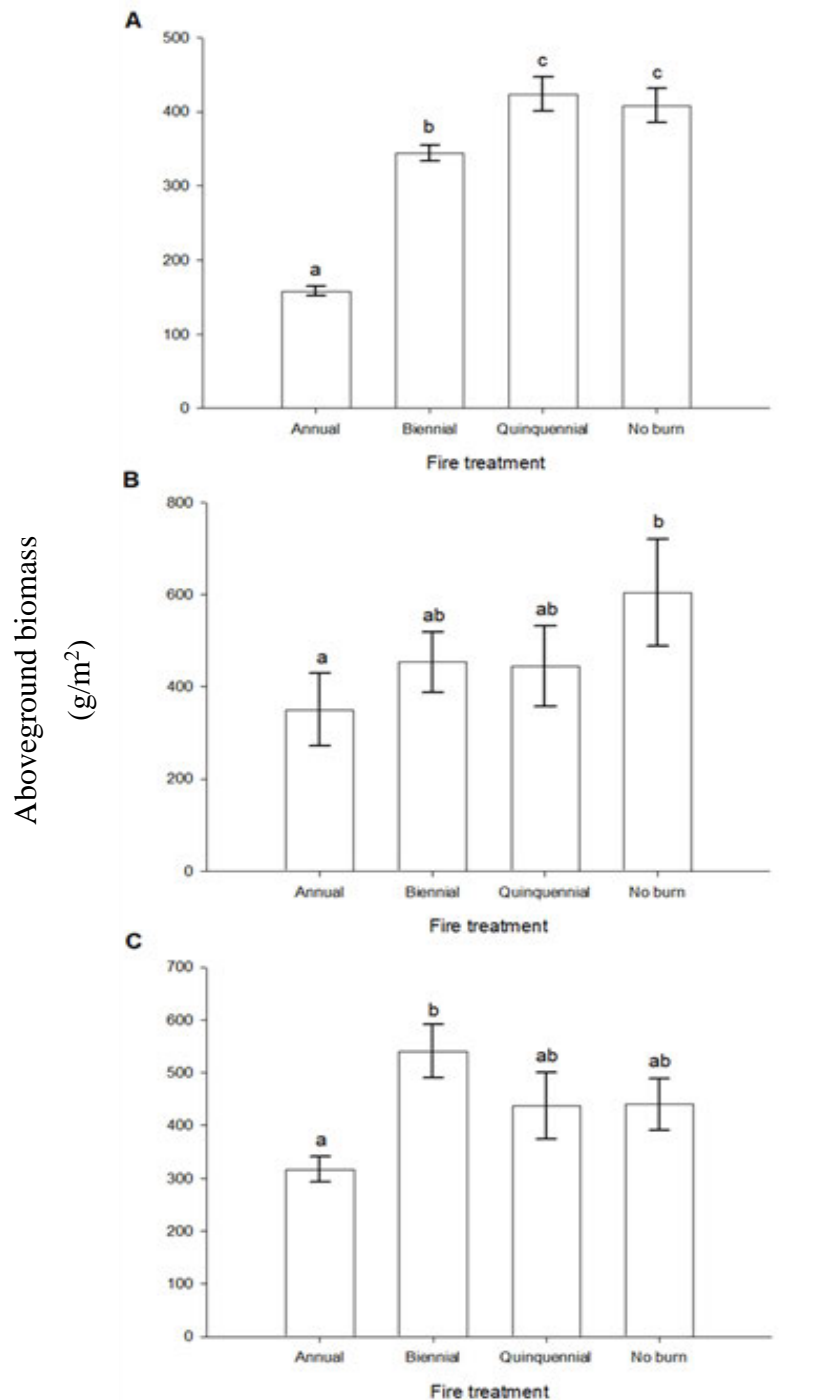


Figure 3.2: Mean aboveground biomass (\pm SE) between different burning frequencies in the late spring (A), late summer (B), and mid-winter (C) sampling seasons on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa. Letters in common indicate non-significance ($P > 0.05$).

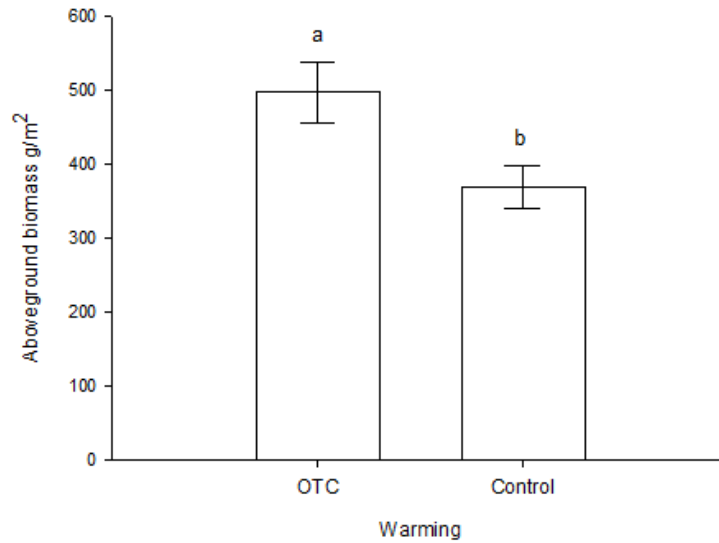


Figure 3.3: Mean aboveground biomass (\pm SE) between OTC and control plots in the mid-winter sampling season on the Brotherton fire trials Cathedral Peak, Drakensberg, South Africa. Letters in common indicate non-significance ($P > 0.05$).

3.4.3. Soil moisture

How does an increase in temperature affect soil moisture in interaction with different fire regimes?

The mid-summer (January) sampling showed no significant impacts of warming on soil moisture ($\chi^2 = 0.225$; $P = 0.635$; Table 3.2A). Warming also did not have any significant impact on soil moisture content in the early autumn sampling (March) ($\chi^2 = 0.706$; $P = 0.401$; Table 3.2B). The late spring (November) sampling however did have significant impacts of warming on soil moisture content ($\chi^2 = 39.762$; $P < 0.001$; Table 3.2C), where the OTCs had significantly lower soil moisture content ($20.99 \% \pm 1.83$) than the control plots ($29.89 \% \pm 1.25$) (Figure 3.4A). The late summer (February) sampling also revealed significant impacts of warming on soil moisture content ($\chi^2 = 10.188$; $p < 0.001$; Table 3.2D), with the OTC plots showing slightly less soil moisture content ($45.73 \% \pm 0.601$) compared to the control plots ($47.89 \% \pm 0.591$) (Figure 3.4B). The effects of fire frequency on soil moisture content were significant in all sampling seasons (Table 3.2A, 3.2B, 3.2C and 3.2D). In the mid-summer sampling season, quinquennial burns had the greatest soil moisture content ($61.67 \% \pm 3.538$), followed by the no burn treatment ($55.82 \% \pm 3.531$), and the biennial ($78.27 \% \pm 1.772$) and annual ($43.94 \% \pm 0.954$) fire treatments having the least soil moisture content (Figure 3.5A). The early autumn (March)

sampling followed a similar trend, where the quinquennial treatment had the greatest soil moisture content ($35.95 \% \pm 1.671$), and the annual treatment had the least soil moisture content ($26.52 \% \pm 1.212$; Figure 3.5B). In the late spring sampling season, the no burn fire treatment had the greatest soil moisture content ($30.07 \% \pm 2.182$), followed by the quinquennial treatments ($28.49 \% \pm 2.269$), with the biennial and the annual treatments having the least soil moisture content ($24.09 \% \pm 2.602$ and $19.10 \% \pm 2.309$ respectively) (Figure 3.5C). A similar pattern was found in the late summer sampling season where quinquennial and the no burn treatments had the greatest soil moisture content ($48.08 \% \pm 0.678$ and $47.70 \% \pm 1.263$ respectively), and the biennial and the annual treatments had the least soil moisture content ($45.98 \% \pm 0.919$ and $45.50 \% \pm 0.347$ respectively) (Figure 3.5D). There were no significant interactive effects of warming and fire frequency in all the different sampling seasons (Table 3.2).

Table 3.2: The effect of warming, fire treatment, and their interaction on soil moisture in (A) mid-summer (January 2017), (B) early autumn (March 2017), (C) late spring (November 2017) and (D) late summer (February 2018) on the Brotherton fire trials, Cathedral Peak, Drakensberg, South Africa using a generalized linear model with a normal distribution and an identity link function. Degrees of freedom (d.f.), Wald Chi-square (χ^2), and p-value are shown. Significant effects ($p < 0.05$) are shown in **bold**.

A)

Source of variation	d.f.	χ^2	p-value
Block	2	6.873	0.032
Warming (W)	1	0.225	0.635
Fire frequency (FF)	3	40.180	<0.001
W * FF	3	2.381	0.497

B)

Source of variation	d.f.	χ^2	p-value
Block	2	1.765	0.414
Warming (W)	1	0.706	0.401
Fire frequency (FF)	3	13.407	0.004
W * FF	3	0.555	0.907

C)

Source of variation	d.f.	χ^2	p-value
Block	2	5.196	0.074
Warming (W)	1	19.535	<0.001
Fire frequency (FF)	3	40.060	<0.001
W * FF	3	3.922	0.270

D)

Source of variation	d.f.	χ^2	p-value
Block	2	0.785	0.675
Warming (W)	1	10.188	< 0.001
Fire frequency (FF)	3	10.700	0.013
W * FF	3	3.498	0.332

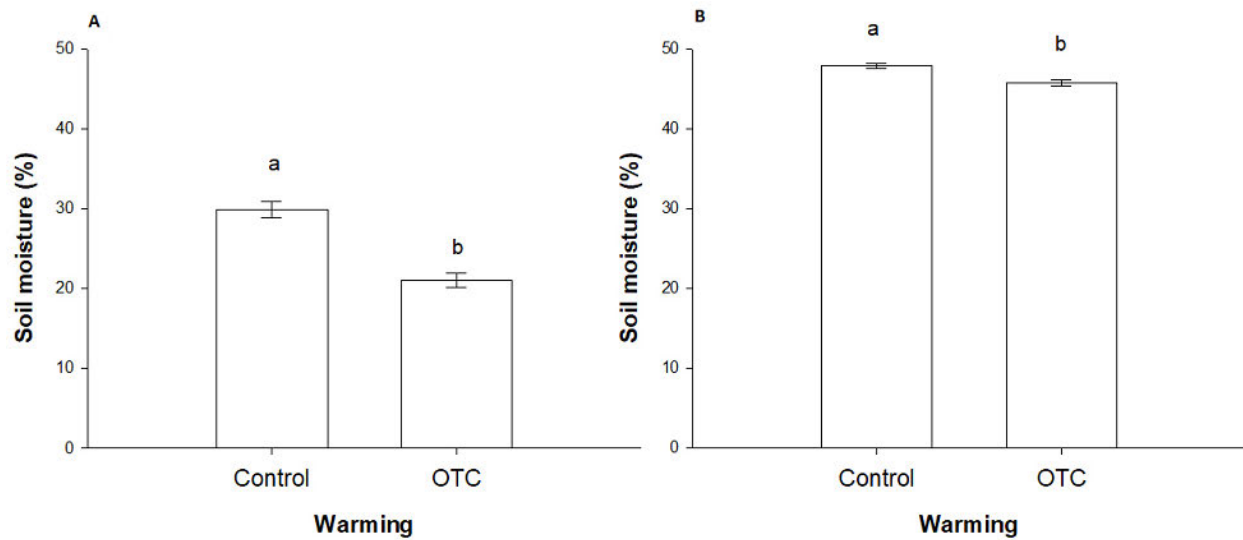


Figure 3.4 Effects of warming on soil moisture content for the late spring (A) and late summer (B) sampling period in the Brotherton fire trials Cathedral Peak, Drakensberg, South Africa. Letters in common indicate non-significance ($P > 0.05$).

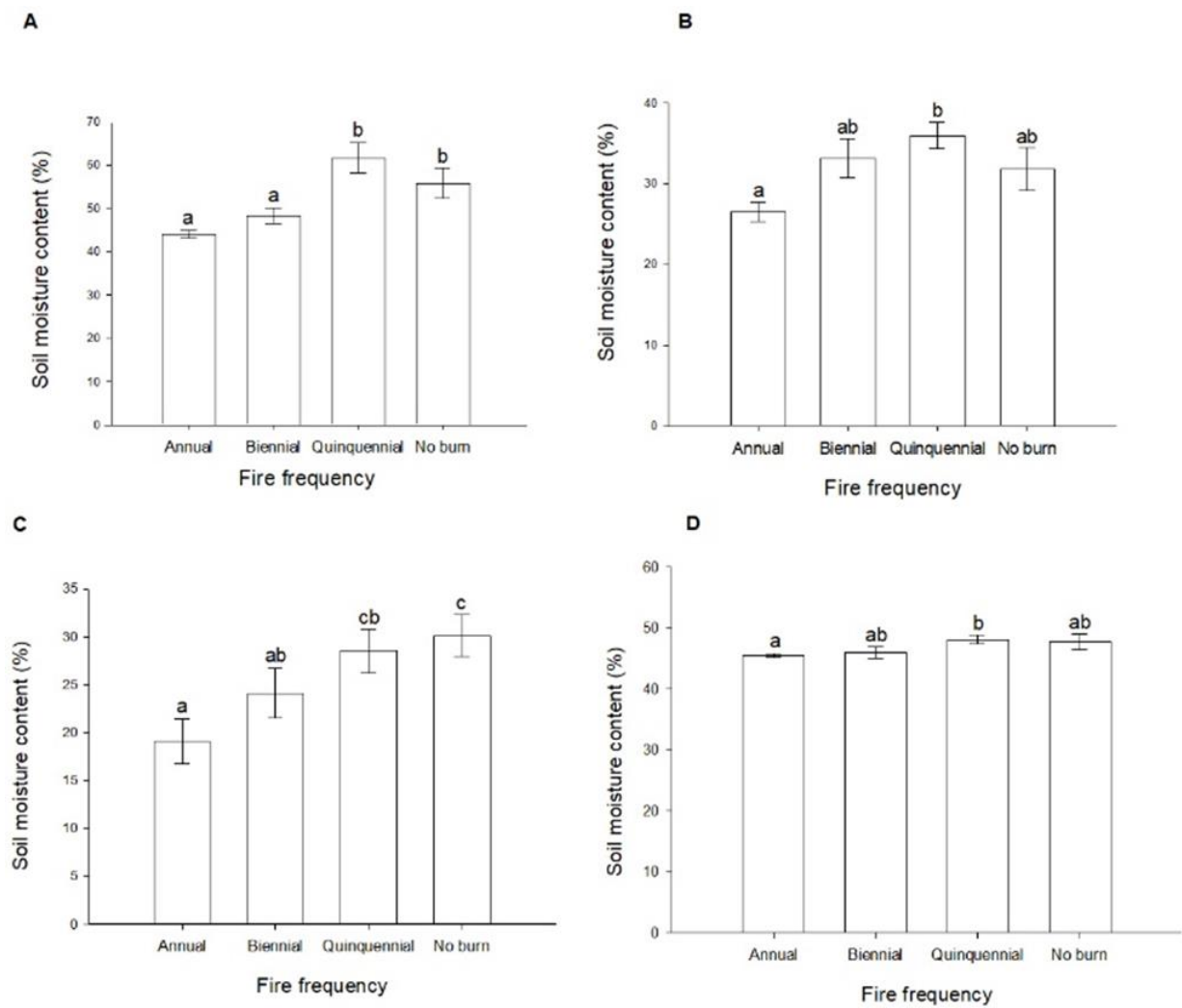


Figure 3.5: Effects of fire frequency on soil moisture content for the mid-summer (A), early autumn (B), late spring (C), and late summer (D) sampling in the Brotherton fire trials Cathedral Peak, Drakensberg, South Africa. Letters in common indicate non-significance ($P > 0.05$).

3.4.4. Species composition

Does an increase in temperature affect species compositional structure within the different fire regimes?

There was no apparent effect of warming on species composition (Figure 3.6). The April 2017 data shows that most of the annual and biennial burns cluster together towards the left side of the ordination and were characterized by *Themeda triandra*, *Koeleria capensis* Ness, *Trachypogon spicatus*, *Heteropogon contortus*, and *Oxalis obliquifolia*. Quinquennial burns cluster to the top right of the ordination plot and were characterized by *Tristachya leucothrix*, *Richardia brasiliensis*, and *Stiburus alopecuroides*. The no-burn treatment, which stands out on the far right of the ordination was characterized by *Harpochloa falx*, *Andropogon appendiculatus*, *Alloteropsis semialata*, *Helichrysum pallidum*, *Rubus rigidus*, and a substantial amount of bare soil. A similar trend was observed in the February 2018 dataset, where the frequently burnt treatments (annual and biennial) ordinated to the left of the plot and was characterized by *T. triandra*, *A. semialata*, *A. appendiculatus*, *H. contortus* and *K. capensis*. Plots that were burnt quinquennially ordinated towards the top right of the plot and were characterized by *T. leucothrix*, *Bulbostylis humilis* (Kunth) C.B.Clarke. and *Tolpis capensis* (L.) Sch.Bip. The no-burn treatment in 2018, similar to the 2017 data, ordinated to the bottom right of the plot and was characterized by species such as *H. falx*, *Helichrysum aureonitens*, *Senecio harveianus* DC., *Helichrysum appendiculatum*, (L.f.) Less. and bare soil.

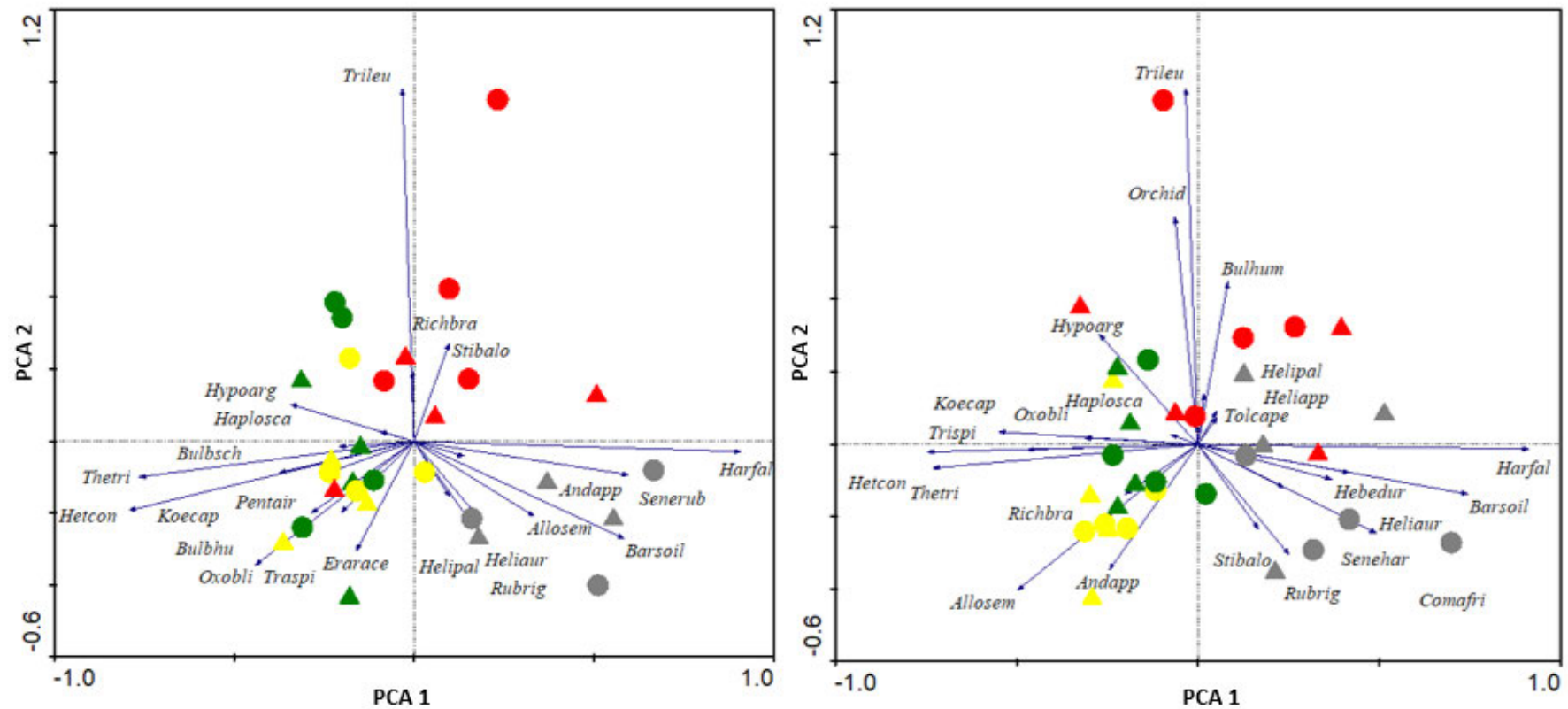


Figure 5: Figure 3.6: Principal Components Analysis (PCA) of dominant species composition from different fire treatments in Brotherton fire trials, Cathedral Peak in April 2017 (A), and February 2018 (B). The eigenvalues for axis 1 and axis 2 in A are 0.377 and 0.140, and 0.332 and 0.183 for B, respectively. Green = annual; yellow = biennial; red = quinquennial; grey = no burn, triangle = OTC, circle = control. See appendix for full species names.

3.5. Discussion

This study sought to determine how warming, in interaction with the fire regime, affected the aboveground biomass, soil moisture, and species composition in a high-altitude grassland in the KwaZulu-Natal Drakensberg mountains. OTCs have been shown to simulate realistic increases in temperature as predicted by climate warming studies (e.g., Kruger and Shongwe 2004; IPCC 2007; Ziervogel et al. 2014). The effectiveness of OTCs is based on their ability to simulate realistic elevated temperatures, i.e., temperatures that are in line within predictions for the near future.

3.5.1. *Effectiveness of OTCs*

This study used OTCs which rely only on solar radiation, which is trapped on the chamber, therefore not using any heaters to manipulate temperature (Marion et al. 1997). The efficiency of these chambers is centred around their ability to elevate air and soil temperatures within the range that is consistent with future predictions of warming in the region. OTCs in this study increased maximum midday air temperature by ± 4 °C and soil temperatures by up to 1.5 °C (Figure 3.1). Mean daily air temperatures were increased by 1 °C and soil temperature by 0.7 °C. A study by Godfree et al. (2011) which investigated the use of OTCs in elevating temperature and manipulating carbon dioxide in an Australian grassland reported similar increases in maximum air temperature in their hexagon chambers, with about 4.1 °C temperature increase in the spring/summer season. Their soil temperatures were 0.4 - 0.5 °C warmer than controls in all seasons (Godfree et al. 2011), results which are also consistent to results found in this study. Since projections have shown that temperatures in southern Africa are expected to increase by 3 °C to 4 °C within the century (IPCC 2007; Ziervogel et al. 2014; Hummel 2016), results from this study suggest that the OTCs can indeed simulate consistent and realistic temperature warming when installed in mesic high-altitude grasslands.

3.5.2. *Effects of warming on aboveground biomass*

In the present study, the biomass sampling period was divided into three seasons, late spring, late summer, and mid-winter. We found no significant impact of warming on aboveground biomass for the late spring and late summer sampling period. The non-significant differences between OTC and control treatments in late spring and late summer periods respectively were

likely since the chambers in this study were only deployed in the previous year (December 2016), and therefore had limited time to have any significant biomass effects. Similar results were reported by Rustad et al. (2001) in a meta-analysis, where they reported no significant responses of warming on productivity in the first five years of warming on some of the sites (e.g., high altitude tundra and the short grass steppe in North America) reviewed in the analysis. The lack of response of biomass to warming has also been commonly explained as a result of the decline in soil moisture associated with warming (Lukac et al. 2010).

In mid-winter, our results showed significant increases in biomass in the warmed plots when compared to the control plots, with the greatest biomass observed in the biennial treatments. These results are consistent with that of Arft et al. (1999), who found that warming significantly enhances aboveground plant growth in the ITEX experiments conducted in the arctic and alpine vegetation. Our results are also consistent with other studies that investigated the response of grassland biomass to warming (Rustad et al. 2001; De Boeck et al. 2007; Lin et al. 2010). In a South African context, a study by Buhrmann et al. (2016) which investigated the response of a subtropical grassland to elevated temperatures also found that warming using OTCs (similar to the ones used in this study) increased aboveground biomass by at least 19%. The positive effect of warming on aboveground biomass has been suggested to be a direct result of enhanced photosynthetic rates that are consequent to warming, or an indirect effect of increased nutrient availability, which is a consequence of increased rates of litter decomposition (Rustad et al. 2001). The increase in aboveground biomass in OTCs in the middle of winter in this present study suggests that elevated temperatures may have a positive effect on biomass production even in periods where productivity and precipitation are generally low (Buhrmann et al. 2016). However, biomass was not actively growing in mid-winter, but there was early winter growth due to an extended growing season from the warming. This increased the total biomass produced over the season causing higher midwinter biomass in the chambers as seen in this study.

Although warming has been reported to have a greater effect on plant growth in spring and winter (Walther 2003) other studies have produced contrasting results. A study in North Belgium in an arid artificially simulated grassland on the effects of climate change on species richness and above- and belowground productivity by De Boeck et al. (2007), found that elevating temperature by at least 3°C resulted in a massive decline of up to 18% in aboveground biomass. They explained that this could have been due to the increase in drought

stress, which is a direct result of the lowered soil moisture caused by elevated temperature (De Boeck et al. 2007; Prieto et al. 2009; Lukac et al. 2010). Similarly, Carlyle et al. (2014) found similar outcomes in a study conducted in a semi-arid grassland in Canada. They found that aboveground biomass was significantly reduced by warming, and they attributed this decline to water stress, triggered by the increase in temperature (Carlyle et al. 2014).

There were no interactions of warming and fire in all sampling seasons, indicating that warming effects did not vary with fire treatment. A study by Jarrad et al (2009) found that the increased soil temperature which was consequent to burning encouraged early post-fire flowering in both grasses and forbs. There is therefore great potential for fire to amplify climate change impacts by accelerating the occurrence of important phenological events such as flowering (Jarrad et al. 2009). However, when this research was conducted, there had not been any studies on the interactive effects of fire and warming, particularly in a South African context.

3.5.3. Effects of warming on soil moisture

Temperature and moisture are major drivers of plant and ecosystem processes (Melillo et al. 1990; Rustad et al. 2001). A reduction in moisture supply will, in many cases, reduce plant growth and consequently reduce all respiration associated with growth (Melillo et al. 1990). The consistent increase in global temperatures has been found to have significant impacts on soil moisture and has therefore received increasing interest in recent years (Wan et al. 2007; Seager et al. 2013; Subin et al. 2013; Xia et al 2014).

Our present study found that elevated temperature did not have any significant impact on soil moisture in the mid-summer and early autumn seasons. This was not expected as warming has been previously found to significantly lower soil moisture in experimental warming throughout seasons (Melillo et al.1990; Rustad et al. 2001; De Boeck et al. 2007; Xu et al. 2013). However, we predict this could have been due to the fact the chambers in this study had only been installed the previous year and therefore had limited time to cause any substantial impact on soil moisture in these two seasons.

In the late spring and late summer seasons, however, warming was found, as predicted, to cause significant declines in soil moisture (up to 8.9% and 2.16% declines in soil moisture in late spring and summer respectively). A study by Xu et al. (2013) found that warming decreased soil moisture by up to 8.5% in grasslands. Other similar studies on the impact of

warming on soil moisture content have also found similar results (Rustad et al. 2001; Chapin et al. 2002; Xia, 2010; Wu et al. 2011). According to Chapin et al. (2002), this is a result of increased evaporation from the soil surface and heightened transpiration by plants caused by warming which leads to water loss from the soil. The negative soil moisture responses associated with warming could also be due to the enhanced plant aboveground biomass (also observed in this study; see [Chapter 3.5.2](#)) and transpiration processes (Xia et al. 2010; Xu et al. 2013). In contrast, a short-term experiment in the Mediterranean California grassland found that simulated warming led to a 5- 10 % increase in soil moisture (Zavaleta et al. 2003). They concluded that increasing temperature fast-tracked the decline of canopy greenness, and therefore increased soil moisture availability by reducing seasonal transpiration losses (Zavaleta et al. 2003).

It has also been reported that ecosystem management tools (e.g., fire) can influence soil moisture responses to warming (Henry et al. 2006). For example, a fire may indirectly enhance soil water evaporation by reducing the shading of the soil surface, which may consequently result in significant declines in soil moisture (Xu et al. 2013). In this study, we also found significant fire treatment effects on soil moisture content in all sampling seasons. These results were consistent with those of Henry et al. (2006) who also found that the removal of aboveground litter through burning in an annual grassland resulted in declined soil moisture. This was because the removal of litter encouraged more light into the soil surface (Briggs and Knapp 1995), which in turn increases surface temperatures which ultimately decreases soil moisture (Li and Herbert 2004). The findings of this study, however, did not reveal any significant interactions of warming and fire on soil moisture content throughout all the sampling season.

3.5.4. Warming effects on species composition

There is convincing evidence that for many plant communities around the world, species composition will change drastically in different terrestrial ecosystems in response to increased temperature (Harte and Shaw 1995; Kudernatsch et al. 2008; Thuiller et al. 2008; Yang et al. 2011; Wu et al. 2012; Ganjurjav et al. 2018). In high-altitude ecosystems, such changes are predicted to be dramatic due to the general susceptibility of high-altitude regions to snow and ice cover, coupled with the sensitivity of plant production and nutrient availability to timing of snow, length of growing season, and air and soil temperatures (Harte and Shaw 1995).

There were no apparent effects of warming on species composition, which was expected since the chambers in this study had only been up for two years, which is considered too short to adequately determine warming impacts on any compositional changes. According to Marion et al. (1997), reliable experimental manipulation studies should be carried out over longer periods, as it may take years for disturbances to have a significant detectable effect, especially on species composition. Similar to our findings, some studies have also found no changes in species composition after warming in an arctic grassland experiment (Grime et al. 2008) and a semi-natural temperate grassland (Harmens et al. 2004). Ganjurjav et al. (2016) has also reported no significant impacts of warming on species composition in a short-term study (2-5 years) in the alpine meadow, China. Inconsistently however, a study by Wu et al. (2012) found that plant communities in warmed plots were significantly distinct to those in the ambient plots in grassland system in North Arizona. Another 10-year experiment in a meadow grassland showed a shift from forbs to a shrubbier composition in warmed treatments (Saleska et al. 1999). Liu et al. (2018) also reported a change in species composition in an experiment in the Tibetan Plateau grasslands, where grasses were favoured by warming over sedges and forbs.

Shifts in temperature (and precipitation) are known to have significant impact on the fire regime, particularly the frequency and intensity in fire-driven systems (Polley et al. 2017). The intensity and frequency of grassland fires is expected to increase in a warmer and drier world (Pechony and Shindell 2010). Warmer and drier conditions are conducive to more frequent fires, but sufficient fuels will be required to sustain grassland fires (Polley et al. 2017). Our study did not however find any species compositional changes due to warming, nor did we find any interaction of fire and warming. The time frame for this study was perhaps too short for any meaningful compositional changes to have occurred. We instead, as expected, found that species composition was due to the fire regime.

Species composition was related to fire regime in both the 2017 and 2018 dataset, this was expected, and is similar to what was found in chapter [2.4.3.](#) Frequently burned sites were mostly characterized by perennial grasses such as *T. triandra*, *H. contortus* and *K. capensis*. It has been previously reported that species such as the ones mentioned above generally increased with increasing fire frequency (Everson 1985; Uys 2000; Gordijn et al. 2018). The fire protection plots differed greatly from the burning treatments and was characterized mostly by *H. falx*, and forbs such as *H. aureonitens*, *Senecio harveianus*, and the alien

invasive *Rubus rigidus*. Everson and Tainton (1984) also found similar species in less frequently burnt plots in a study done in the Drakensberg grasslands. There was also substantial bare soil in fire protection treatments, which was expected as fire protection has been found to result in decreased basal cover and erosion (Gordijn et al. 2018, Morris 2020).

3.6. Conclusions

Experimental warming studies have been conducted for over a decade, in different terrestrial ecosystems all over the world. These studies are vital as they test the hypothesis that plant responses to experimental warming are consistent and realistic to long-term climate warming impacts on a variety of plant communities (Wolkovich et al. 2012). Predicting grassland responses to climate warming is of great importance since their responses can affect food webs, disturbance regimes such as fire and important ecosystem services such as water and food provision and nutrient cycling (Wolkovich et al., 2012).

This study has shown that *in situ* OTCs can be effectively used in high-altitude grasslands to investigate warming effects on the productivity of these systems. OTCs used in this study have shown to elevate air and soil temperatures at rates that are consistent with future predictions in this region. Results from this study suggest that aboveground biomass in fire-climax grassland might be favoured by warming, especially in the short term. Soil moisture content however, depicted a negative impact of warming, which are results consistent with most warming studies across most terrestrial biomes globally (e.g., Rustad 2001; Xia et al 2014). The chambers in this study had only been set up in December 2016, only two years from last sampling, therefore there were no warming impacts on species composition, as these often take years to be visible. We also did not find any interactive impacts of warming and fire in aboveground biomass or soil moisture content, and we suspect this might be due to the short duration of this study. While direct warming effects such as higher photosynthesis may have instantaneous effects on vegetation (Kudernatsch et al. 2008), indirect warming effects such as reduction in soil moisture content and shifts in species composition need a lengthier time span to be visible (Kudernatsch et al. 2008). This further emphasizes the importance of long-term warming experiments, in order for well-informed decisions to be made.

The warming chambers in the Brotherton trials are still kept on site and the experiment is continuing. As a result, we recommend that a similar study be conducted after 10 years (or

longer) as some ecological responses to warming can only be observed through long-term monitoring.

CHAPTER 4: SYNTHESIS AND RECOMMENDATIONS

Grasslands are one of the largest biomes globally, covering over 40% of the Earth's terrestrial surface (White et al. 2000; Kirkman et al. 2013). Even though this biome is widespread worldwide, it is also one of the most threatened biomes due to land-use change, global climate change, alien plant invasion, and altered disturbance regimes (Gibson 2009; Kirkman et al. 2013). One of the most common grassland ecosystem drivers, particularly in the Drakensberg montane grasslands, is fire, which affects vegetation production, structure, and diversity. Fire has proven to significantly affect the structuring and regulation of grassland ecosystems, both spatially and temporally (Coyle et al. 2017). With the climate rapidly changing, it is expected that ecosystem drivers, such as the fire regime, will be significantly impacted (Carlyle et al. 2014; Buhrmann et al. 2016). Understanding how grassland communities will respond to climate change and associated changes in the fire regime is essential to protect these ecosystems' unique biodiversity and functional properties. Climate change manipulation experiments such as the one reported in this dissertation provide a powerful way of testing how grassland communities respond to climate change drivers such as increasing temperatures, especially in fire-climax grasslands.

Historically, long-term experiments have generally evaluated the effects of fire treatments on grassland structure (Uys 2000), species composition (Everson 1985; Gordjin et al. 2018), and species diversity (Uys et al. 2004), but not the legacy effect of these regimes. Even more scarce are studies on the combined impacts of fire history and warming on grassland systems. This study gave insights into the legacy effects of fire regime on grassland productivity and the combined impacts of fire history and elevated temperature on grassland productivity in montane mesic grasslands.

4.1. Synthesis

The second chapter of this study investigated legacy effects of long-term fire regimes on aboveground biomass, basal cover, and species composition after an arson fire burnt through all the Brotherton fire-manipulation experiment plots. The main results of this study indicated that fire history (+35 years of burning) affects grassland productivity more than the time since the last fire. We found that the less frequently burnt treatments (no burn and quinquennial treatment) produced the greatest aboveground biomass compared to the more regularly burnt

treatments (annual and biennial). We found no effects of fire frequency on basal cover, which was unexpected as previous studies in the Drakensberg have found greater basal cover in more frequently burnt areas (Gordijin et al. 2018). According to Short et al. (2014), less frequent burning (e.g., no burn and 5-year rotation) reduces basal cover and may be harmful to soil conservation in the Drakensberg.

Ordination results on the impacts of fire treatment on species composition are in line with results from Uys (2001), which showed that fire frequency was the primary determinant of community composition. PCA ordination indicated that species composition between the burn treatments and the no-burn treatment differed significantly. This study showed a clear trend of species response to frequency and season of burn, with the evident increase of *Themeda triandra* with increased fire frequency and an increase of *Harpochloa falx* with decreasing fire frequency. Contrasts between fire treatments also showed that the species composition of the burn treatments was more similar to each other than to the unburned fire protection plots. These results were consistent with other studies previously conducted on the Brotherton trials (Everson 1985; Uys 2001; Gordijin et al. 2018; Morris et al. 2020).

Global climate change impacts are becoming more and more prominent, and the need to predict ecosystem responses to these impacts, particularly increased temperatures, is of great importance. This is especially true for the grassland biome, which is already under significant threat with over 35% being permanently transformed for agriculture, and over 7% affected by land degradation (Mucina and Rutherford 2006; Egoh et al. 2011; Cadman et al. 2013; Little et al. 2015). Only as little as 2% of the grassland biome is formally protected in South Africa (Egoh et al. 2011; Ziervogel et al. 2014). The third chapter, which was the first of its kind in southern African grasslands, investigated the impacts of elevated air and soil temperatures, in combination with a long-term fire regime, on aboveground productivity in a high-altitude mesic grassland. Our results showed that warming effects on high-altitude grasslands can be successfully examined *in situ* using open-top chambers (OTCs). In this study, OTCs increased air temperature by an average of 2°C and soil temperature by up to 1°C, which are increases consistent with warming projections for the next century. This study suggests that enhanced temperatures also enhance aboveground biomass production in montane grassland, where we recorded higher aboveground biomass (497.73 g/m²) in OTCs compared to control plots (369.06 g/m²). This was consistent with similar studies of warming impacts on aboveground biomass (De Boeck et al. 2007; Lin et al. 2010; Buhrmann et al.

2016). We also found that warming decreases soil moisture, which was expected since higher temperatures have been shown to increase evapotranspiration in grasslands (Chapin et al. 2002; Xia et al. 2010). This study found no combined effects of warming and fire on neither aboveground biomass nor soil moisture content. A possible explanation for this could be that the chambers had only been deployed for a relatively short time during this study. According to Marion et al. (1997), more consistent and long-term studies on experimental warming ought to be carried out as it may take a few years for climate change variables (such as warming) to have significant visible effects on species composition, as evidenced in this study where we recorded no compositional changes in response to warming. Over the longer term, however, impacts of warming (together with the fire regime) are likely to determine community structure and composition to a great extent (Harte and Shaw 1995; Marion et al. 1997; Yung et al. 2011).

4.2. Recommendations and future research

This research provided data on legacy effects of fire and climate warming on grassland productivity in montane grasslands. One of the important recommendations is the prevention of frequent arson fires in the Drakensberg. This needs to be prioritized in order to allow for a proper and consistent burning regime that is beneficial to biodiversity and conservation of these mountains. This study's results are an essential benchmark for the long-term monitoring of climate change impacts on high-altitude grasslands. This will be vital to future research and decisions for developing updated and reliable South African policy around the adaptation and mitigation of global warming and climate change impacts (Everson and Everson 2016). Historically, climate change research in southern Africa has focused on carbon dioxide impacts rather than temperature impacts on the natural ecosystem. Our understanding of the effect of a changing fire regime due to climate change is still limited. Therefore, there is an urgent need for studies that incorporate fire in assessing ecosystem response to climate change. The findings of this study support the need to further investigate the interactive impacts of fire and other environmental (e.g., slope and rainfall), vegetation (e.g., species diversity), and soil variables (soil nutrients, soil carbon), on grassland vegetation. These will allow for a broader range of analysis and understanding of the long-term effects of different treatments and variables on the ecology of montane grasslands, which will ultimately help understand impacts and aid in better management of similar systems. Though this study was

not examining the effects of elevated temperatures on the phenology of grassland communities, data on these characteristics would have provided additional information on the possible mechanisms governing the productivity and floristic responses observed (Buhrmann et al. 2016).

I also highly recommend that warming effects in the Brotherton trials continue being monitored, which is currently occurring since the chambers have been left on site to remain operational. Ecosystem responses to elevated temperature have provided more informative results on community responses when continued over several years (Shaver et al. 2000). The size and direction of warming responses have been shown to evolve over more extended periods due to ever-changing resource availability and changes in competitive interactions (Shaver et al. 2000). Therefore, it is imperative to continue climate change studies beyond the 2-year academic cycle to differentiate between short- and long-term impacts and trends.

REFERENCES

- Acocks JPH. 1953. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* No. 28.
- Adams RM. 1989. Global climate change and agriculture: an economic perspective. *American Journal of Agricultural Economics* 71(5): 1272-1279.
- Al-Ghussain L. 2019. Global warming: review on driving forces and mitigation. *Environmental Progress & Sustainable Energy* 38(1): 13-21.
- Allen MS, Palmer MW. 2011. Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie. *Journal of Vegetation Science* 22(3): 436-444.
- Alvarado ST, Silva TSF, Archibald S. 2018. Management impacts on fire occurrence: A comparison of fire regimes of African and South American tropical savannas in different protected areas. *Journal of environmental management* 218: 79-87.
- Anderson RC. 2012. Ecology and management of prairie division. *Southern Research Station*.
- Anderson TR, Hawkins E, Jones PD. 2016. CO₂, the greenhouse effect and global warming: from the pioneering work of Arrhenius and Callendar to today's Earth System Models. *Endeavour* 40(3): 178-187.
- Anguyi AG. 2010. Effects of fire frequency on plant species diversity and composition in queen Elizabeth national park, southwestern Uganda. *Unpublished Master of Science Dissertation. Makerere University, Uganda*.
- Archibald S, Hempson, GP, Lehmann C. 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist* 224(4): 1490-1503.
- Archibald S, Lehmann CE, Gómez-Dans JL, Bradstock RA. 2013. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences* 110(16): 6442-6447.
- Archibald S, Roy DP, van Wilgen BW, Scholes RJ. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology* 15(3): 613-630.

- Archibald S. 2016. Managing the human component of fire regimes: lessons from Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1696): 20150346.
- Arft AM, Walker MD, Gurevitch JEA, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* 69(4): 491-511.
- Aronson EL, McNulty SG. 2009. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology* 149(11): 1791-1799.
- Bachinger LM, Brown LR, van Rooyen MW. 2016. The effects of firebreaks on plant diversity and species composition in the grasslands of the Loskop Dam Nature Reserve, South Africa. *African Journal of Range & Forage Science* 30(1): 21-32.
- Beaumont PB, de Villiers H, Vogel JC, 1978. Modern man in sub-Saharan Africa prior to 49 000 years BP: a review and evaluation with particular reference to Border Cave. *South African Journal of Science* 74(11): 409-419.
- Berger LR. 1998. The dawn of humans, redrawing our family tree. *National Geographic* 194(2): 90-99.
- Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Rüger N, Beck PS, Blach-Overgaard A, Blok D, Cornelissen JHC, Forbes BC, Georges D. 2018. Plant functional trait change across a warming tundra biome. *Nature* 562(7725): 57-62.
- Blair J, Nippert J, Briggs J. 2014. Grassland ecology. *Ecology and the Environment*. Springer, New York pp. 389-423.
- Blair JM. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology* 78: 2359-2368.
- Bokhorst S, Huiskes A, Aerts R, Convey P, Cooper EJ, Dalen L, Erschbamer B, Gudmundsson J, Hofgaard A, Hollister RD, Johnstone J. 2013. Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. *Global Change Biology* 19(1): 64-74.

- Boko M, Niang I, Nyong A, Vogel C, Githeko A, Medany M, Osman-Elasha B, TaboR, Yanda P. 2007: Africa. In: Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 433-467.
- Bond WJ, Keeley JE. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20(7): 387-394.
- Bond WJ, Midgley GF, Woodward FI, Hoffman MT, Cowling RM. 2003. What controls South African vegetation—climate or fire? *South African Journal of Botany* 69(1): 79-91.
- Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525-537.
- Bond WJ. 1997. Fire. In: *Vegetation of Southern Africa* by Cowling RM, Richardson DM, Pierce SM (eds). Cambridge University Press London. Chap. 18.
- Boval M, Dixon RM. 2012. The importance of grasslands for animal production and other functions: a review on management and methodological progress in the tropics. *Animal* 6(5): 748-762.
- Brain CK, Sillent A. 1988. Evidence from the Swartkrans cave for the earliest use of fire. *Nature* 336(6198): 464-466.
- Bransby D, Tainton NM. 1977. The disc pasture meter: possible applications in grazing management. *Proceedings of the Grassland Society of South Africa* 12: 115-118
- Bredenkamp GJ, Granger JE, Lubke RA, van Rooyen N. 1996. Moist Upland Grassland. In: *Vegetation of South Africa, Lesotho and Swaziland* by Low AB, Rebelo AG (eds). Department of Environmental Affairs and Tourism, Pretoria
- Briggs JM, Fahnestock J, Fisher LE, Knapp AK. 1992. Aboveground biomass in tallgrass prairie: effect of time since fire. In *Spirit of the Land: Our Prairie Legacy. Proceedings of the Thirteenth North American Prairie Conference. Preney Print and Litho Inc., Windsor, Ontario, Canada*:165-169.

- Briggs JM, Knapp AK, Blair JM, Heisler JL, Hoch GA, Lett MS, McCarron JK. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55(3): 243-254.
- Briggs JM, Knapp AK. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82(8): 1024-1030.
- Buhrmann RD, Ramdhani S, Pammenter NW, Naidoo S. 2016. Grasslands feeling the heat: The effects of elevated temperatures on a subtropical grassland. *Bothalia-African Biodiversity & Conservation* 46(2): 1-12.
- Cadman M, de Villiers C, Lechmere-Oertel R, McCulloch D, South African National Biodiversity Institute. 2013. Grasslands Ecosystem Guidelines: Landscape interpretation for planners and managers. *South African National Biodiversity Institute, Pretoria*.
- Callaway JM. 2004. Adaptation benefits and costs: are they important in the global policy picture and how can we estimate them? *Global Environmental Change* 14 (3): 273-282.
- Campbell BD, Stafford-Smith DM, McKeon GM. 1997. Elevated CO₂ and water supply interactions in grasslands: A pastures and rangelands management perspective. *Global Change Biology* 3(3):177-187.
- Carbutt C, Tau M, Stephens A, Escott B. 2011. The conservation status of temperate grasslands in southern Africa. *Grassroots* 11(1): 17-23.
- Ceballos G, Davidson A, List R, Pacheco J, Manzano-Fischer P, Santos-Barrera G, Cruzado J. 2010. Rapid decline of a grassland system and its ecological and conservation implications. *PLoS One* 5(1): 8562.
- Chapin FS, Matson P, Mooney HA, Vitousek PM. 2002. Principles of Terrestrial Ecosystem Ecology (New York: Springer)
- Chapin III FS, Shaver GR. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66(2): 564-576.

- Chapin, F. S., Matson, P. A., Mooney, H. A., & Vitousek PM. (2002). Principles of terrestrial ecosystem ecology.
- Charles H, Dukes JS. 2009. Effects of warming and altered precipitation on plant and nutrient dynamics of a New England salt marsh. *Ecological Applications* 19(7): 1758-1773.
- Christensen JH., Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli, RK, Kwon WT, Laprise R, Magaña-Rueda V. 2007. Regional climate projections. Chapter 11.
- Coley PD, Bryant JP, Chapin FS. 1985. Resource availability and plant antiherbivore defence. *Science* 230: 895–899.
- Coppens Y. 2013. Hominid evolution and the emergence of the genus Homo. *Neurosciences and the Human Person: New Perspectives on Human Activities* 121: 320.
- Cowling RM, Hilton-Taylor C. 1994. Patterns of plant diversity and endemism in southern Africa: an overview. *Strelitzia* 1:31-52.
- Daniau AL, Bartlein PJ, Harrison SP, Prentice IC, Brewer S, Friedlingstein P, Harrison-Prentice TI, Inoue J, Izumi K, Marlon JR, Mooney S. 2012. Predictability of biomass burning in response to climate changes. *Global Biogeochemical Cycles* 26(4): 1-12
- Daniau AL, Goñi MFS, Martinez P, Urrego DH, Bout-Roumazelles V, Desprat S, Marlon JR. 2013. Orbital-scale climate forcing of grassland burning in southern Africa. *Proceedings of the National Academy of Sciences* 110(13): 5069-5073.
- De Boeck HJ, De Groote T, Nijs I. 2012. Leaf temperatures in glasshouses and open-top chambers. *New Phytologist* 194(4): 1155-1164.
- De Boeck HJ, Lemmens CMHM, Gielen B, Bossuyt H, Malchair S, Carnol M, Merckx R, Ceulemans R, Nijs I. 2007. Combined effects of climate warming and plant diversity loss on above-and below-ground grassland productivity. *Environmental and Experimental Botany* 60(1): 95-104.
- De Frenne P, De Schrijver A, Graae BJ, Gruwez R, Tack W, Vandeloock F, Hermy M, Verheyen K. 2010. The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. *Ecological research* 25(1): 163-171.

- De Villiers AD, O'connor T. 2011. Effect of a single fire on woody vegetation in Catchment IX, Cathedral Peak, KwaZulu-Natal Drakensberg, following extended partial exclusion of fire. *African Journal of Range & Forage Science* 28(3): 111-120.
- Deák B, Valkó O, Török P, Végvári Z, Hartel T, Schmotzer A, Kapocsi I, Tóthmérész B. 2014. Grassland fires in Hungary—experiences of nature conservationists on the effects of fire on biodiversity. *Applied ecology and Environmental Research*. 267-83.
- Dhillon RS, von Wuehlich G. 2013. Mitigation of global warming through renewable biomass. *Biomass and Bioenergy* 48: 75-89.
- Dukes JS, Chiariello NR, Cleland EE, Moore LA, Shaw MR, Thayer S, Tobeck T, Mooney HA, Field CB. 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS biology* 3(10): 319.
- Dzerefos CM, Witkowski ETF. 2001. Density and potential utilisation of medicinal grassland plants from Abe Bailey Nature Reserve, South Africa. *Biodiversity & Conservation* 10(11): 875-1896.
- Edwards D. 1984. Fire regimes in the biomes of South Africa. In *Ecological effects of fire in South African ecosystems*. Springer, Berlin, pp. 19-37
- Egoh BN, Reyers B, Rouget M, Richardson DM. 2011. Identifying priority areas for ecosystem service management in South African grasslands. *Journal of Environmental Management* 92(6): 1642-1650.
- Ellery WN, Mentis MT. 1992. How old are South Africa's grasslands? In: *Forest-Savanna Boundaries* by Furley PA, Proctor J, Ratter JA (eds). Chapman & Hall, London.
- Evans EW, Briggs JM, Finck EJ, Gibson DJ, James SW, Kaufman DW, Seastedt TR .1989. Is Fire a Disturbance in Grasslands? *Proceedings of the North American Prairie Conferences* 37: 151-169
- Everson CS, Clarke GPY. 1987. A comparison of six methods of botanical analysis in the montane grasslands of Natal. *Vegetation* 73(1): 47-51.
- Everson CS, Dye PJ, Gush MB, Everson TM. 2011. Water use of grasslands, agroforestry systems and indigenous forests. *Water SA* 37(5): 781-788.

- Everson CS, Everson T. 2016. The long-term effects of fire regime on primary production of montane grasslands in South Africa. *African Journal of Range & Forage Science* 33(1): 33-41.
- Everson CS, George WJ, Schulze RE. 1989. Fire regime effects on canopy cover and sediment yield in the montane grasslands of Natal. *South African Journal of Science* 85: 113-116.
- Everson CS, Tainton NM. 1984. The effect of thirty years of burning on the Highland sourveld of Natal. *Journal of the Grassland Society of South Africa* 1(3): 15-20.
- Everson CS. 1985. *Ecological effects of fire in the montane grasslands of Natal*. PhD thesis, University of Natal, Pietermaritzburg.
- Everson CS. 1999. Veld burning in different vegetation types. *Veld Management in South Africa. University of Natal Press, Pietermaritzburg, South Africa*, pp. 228-326.
- Everson CS. 2001. The water balance of a first order catchment in the montane grasslands of South Africa. *Journal of Hydrology* 241(1-2): 110-123.
- Everson TM, Clarke GPY, Everson CS. 1990. Precision in monitoring plant species composition in montane grasslands. *Vegetatio* 88(2): 135-141.
- Everson TM, Yeaton RI, Everson CS. 2009. Seed dynamics of *Themeda triandra* in the montane grasslands of South Africa. *African Journal of Range and Forage Science* 26(1): 19-26.
- Fay PA, Kaufman DM, Nippert JB, Carlisle JD, Harper CW. 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. *Global Change Biology* 14(7): 1600-1608.
- Flanagan LB, Johnson BG. 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology* 130(3): 237-253.
- Füssel HM. 2009. An updated assessment of the risks from climate change based on research published since the IPCC Fourth Assessment Report. *Climatic change* 97(3): 469-482.

- Fynn RW, Morris CD, Edwards TJ. 2005. Long-term compositional responses of a South African mesic grassland to burning and mowing. *Applied Vegetation Science* 8(1): 5-12.
- Gallego-Ayala, J. and Juárez, D., 2011. Strategic implementation of integrated water resources management in Mozambique: An A'WOT analysis. *Physics and Chemistry of the Earth, Parts A/B/C* 36(14-15): 1103-1111.
- Ganjurjav H, Gornish ES, Hu G, Wan Y, Li Y, Danjiu L, Gao Q. 2018. Temperature leads to annual changes of plant community composition in alpine grasslands on the Qinghai-Tibetan Plateau. *Environmental Monitoring and Assessment* 190(10): 1-12.
- Gedan KB, Bertness MD. 2009. Experimental warming causes rapid loss of plant diversity in New England salt marshes. *Ecology Letters* 12(8): 842-848.
- Gemeda DO, Sima AD. 2015. The impacts of climate change on African continent and the way forward. *Journal of Ecology and the Natural environment* 7(10): 256-262.
- Gill RA, Polley HW, Johnson HB, Anderson LJ, Maherali H, Jackson RB. 2002. Nonlinear grassland responses to past and future atmospheric CO₂. *Nature* 417(6886): 279-282.
- Godfree R, Robertson B, Bolger T, Carnegie M, Young A. 2011. An improved hexagon open-top chamber system for stable diurnal and nocturnal warming and atmospheric carbon dioxide enrichment. *Global Change Biology* 17(1): 439-451.
- Gordijn PJ, Everson TM, O'Connor TG. 2018. Resistance of Drakensberg grasslands to compositional change depends on the influence of fire-return interval and grassland structure on richness and spatial turnover. *Perspectives in Plant Ecology, Evolution and Systematics* 34: 26-36.
- Grimm EC, Donovan JJ, Brown KJ. 2011. A high-resolution record of climate variability and landscape response from Kettle Lake, northern Great Plains, North America. *Quaternary Science Reviews* 30(19-20): 2626-2650.
- Guevara JC, Stasi CR, Wuilloud CF, Estevez OR. 1999. Effects of fire on rangeland vegetation in south-western Mendoza plains (Argentina): composition, frequency,

- biomass, productivity and carrying capacity. *Journal of Arid Environments* 41(1): 27-35.
- Gunn S, Farrar JF. 1999. Effects of a 4 C increase in temperature on partitioning of leaf area and dry mass, root respiration and carbohydrates. *Functional Ecology* 13: 12-20.
- Haddad CR, Butler VP. 2018. Ground-dwelling spider assemblages in contrasting habitats in the central South African Grassland Biome, *Koedoe* 60(1): a1482.
- Hall M. 1984. Man's historical and traditional use of fire in southern Africa. In Ecological effects of fire in South African ecosystems (pp. 39-52). Springer, Berlin, Heidelberg.
- Harmens H, Williams PD, Peters SL, Bambrick MT, Hopkins A, Ashenden TW. 2004. Impacts of elevated atmospheric CO₂ and temperature on plant community structure of a temperate grassland are modulated by cutting frequency. *Grass and Forage Science* 59(2): 144-156.
- Harte J, Shaw R. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* 267(5199): 876-880.
- Henry GHR, Molau U. 1997. Tundra plants and climate change: The International Tundra Experiment (ITEX). *Global Change Biology* 3(S1): 1-9.
- Henry HA, Chiariello NR, Vitousek PM, Mooney HA, Field CB. 2006. Interactive effects of fire, elevated carbon dioxide, nitrogen deposition, and precipitation on a California annual grassland. *Ecosystems* 9(7): 1066-1075.
- Higgins SI, Bond WJ, Trollope WS. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213-229.
- Hoeppepner SS, Dukes JS. 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology* 18(5): 1754-1768.
- Hollister RD, Webber PJ, Nelson FE, Tweedie CE. 2006. Soil thaw and temperature response to air warming varies by plant community: results from an open-top chamber experiment in northern Alaska. *Arctic, Antarctic, and Alpine Research* 38(2): 206-215.

- Hollister RD, Webber PJ. 2000. Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology* 6(7): 835-842.
- Houghton J. 2009. *Global warming: the complete briefing*. Cambridge university press. (4th ed.).
- Househam S. 2017. The use of fire in the KwaZulu-Natal mistbelt and highland sourveld. Department of Agriculture and Rural Development. Agricultural Livestock Research Services Grass & Forage Scientific Research Services, Kokstad.
- Hughes WS, Balling Jr RC. 1996. Urban influences on South African temperature trends. *International Journal of Climatology: A Journal of the Royal Meteorological Society* 16(8): 935-940.
- Hulme M, Doherty R, Ngara T, New M, Lister D. 2001. African climate change: 1900-2100. *Climate research* 17(2): 145-168.
- Hummel D. 2016. Climate change, land degradation and migration in Mali and Senegal—some policy implications. *Migration and Development* 5(2): 211-233.
- Huntley BJ. 1984. Characteristics of South African biomes. In *Ecological effects of fire in South African ecosystems* (pp. 1-17). Springer, Berlin, Heidelberg.
- Huq S, Reid H, Konate M, Rahman A, Sokona Y, Crick F. 2004. Mainstreaming adaptation to climate change in least developed countries (LDCs). *Climate Policy* 4(1): 25-43.
- IPCC (Intergovernmental Panel on Climate Change). 2001. Climate Change 2001: the scientific basis. *Contribution of working group I to the third assessment report of the intergovernmental panel on climate change*, p.881.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, p. 996.
- IPCC 2014 Summary for policymakers In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate

Change ed C B Field et al (Cambridge)(Cambridge University Press)(Cambridge, United Kingdom and New York, NY, USA) pp 1–32

- James B. 2010. Ecosystem service and climate adaptation. *Resource for the Future, Issue brief*, pp. 10-16.
- Jarrad FC, Wahren CH, William RJ, Burgman MA. 2009. Impacts of experimental warming and fire on phenology of subalpine open-heath species. *Australian Journal of Botany* 56(8): 617-629.
- Jewitt D, Erasmus BF, Goodman PS, O'Connor TG, Hargrove WW, Maddalena DM, Witkowski ET. 2015. Climate-induced change of environmentally defined floristic domains: A conservation based vulnerability framework. *Applied Geography* 63: 33-42.
- Jian-Bin H, Shao-Wu W, Yong L, Zong-Ci Z, Xin-Yu W. 2012. Debates on the causes of global warming. *Advances in climate change research* 3(1): 38-44.
- Kahmen S, Poschlod P, Schreiber KF. 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation* 104(3): 319-328.
- Kennedy AD. 1995. Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology* 1(1): 29-42.
- Kimball BA. 2005. Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology* 11(11): 2041-2056.
- Klein JA, Harte J, Zhao XQ. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters* 7(12): 1170-1179.
- Knapp AK, Briggs JM, Blair JM, Turner CL. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. ppv193-221 In: *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA

- Komatsu KJ, Avolio ML, Lemoine NP, Isbell F, Grman E, Houseman GR, Koerner SE, Johnson DS, Wilcox KR, Alatalo JM, Anderson JP. 2019. Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proceedings of the National Academy of Sciences* 116(36): 17867-17873.
- Kozlowski TT, Ahlgren CE. 1974. Effects of fire on grasslands. *Fire and ecosystems*. 5: 139-145.
- Kruger AC, Sekele SS. 2013. Trends in extreme temperature indices in South Africa: 1962–2009. *International Journal of Climatology* 33(3): 661-676.
- Kruger AC, Shongwe S. 2004. Temperature trends in South Africa: 1960–2003. *International journal of Climatology* 24(15): 1929-1945.
- Kudernatsch T, Fischer A, Bernhardt-Römermann M, Abs C. 2008. Short-term effects of temperature enhancement on growth and reproduction of alpine grassland species. *Basic and Applied Ecology* 9(3): 263-274.
- Kusangaya S, Warburton ML, Van Garderen EA, Jewitt GP. 2014. Impacts of climate change on water resources in southern Africa: A review. *Physics and Chemistry of the Earth, Parts A/B/C* 67: 47-54.
- Levy PE, Cannell MGR, Friend AD. 2004. Modelling the impact of future changes in climate, CO₂ concentration and land use on natural ecosystems and the terrestrial carbon sink. *Global Environmental Change* 14(1): 21-30.
- Leys BA, Marlon JR, Umbanhowar C, Vanni  re B. 2018. Global fire history of grassland biomes. *Ecology and Evolution* 8(17): 8831-8852.
- Li J, Cui Y, Liu J, Shi W, Qin Y. 2013. Estimation and analysis of net primary productivity by integrating MODIS remote sensing data with a light use efficiency model. *Ecological Modelling* 252: 3-10.
- Li W, Li X, Zhao Y, Zheng S, Bai Y. 2018. Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. *Current Opinion in Environmental Sustainability* 33: 124-135.

- Li Y, Herbert, SJ. 2004. Influence of prescribed burning on nitrogen mineralization and nitrification in grassland. *Communications in Soil Science and Plant Analysis* 35(3-4): 571-581.
- Little IT, Hockey PA, Jansen R. 2015. Impacts of fire and grazing management on South Africa's moist highland grasslands: A case study of the Steenkampsberg Plateau, Mpumalanga, South Africa. *Bothalia-African Biodiversity & Conservation* 45(1): 1-15.
- Liu D, Peñuelas J, Ogaya R, Estiarte M, Tielbörger K, Slowik F, Yang X, Bilton MC. 2018. Species selection under long-term experimental warming and drought explained by climatic distributions. *New Phytologist* 217(4): 1494-1506.
- Lukac M, Calfapietra C, Lagomarsino A, Loreto F. 2010. Global climate change and tree nutrition: effects of elevated CO₂ and temperature. *Tree Physiology* 30(9): 1209-1220.
- Luo Y, Gerten D, Le Maire G, Parton WJ, Weng E, Zhou X, Keough C, Beier C, Ciais P, Cramer W, Dukes JS. 2008. Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14(9): 1986-1999.
- Lüthi D, Le Floch M, Bereiter B, Blunier T, Barnola JM, Siegenthaler U, Raynaud D, Jouzel J, Fischer H, Kawamura K, Stocker TF. 2008. High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* 453(7193): 379.
- Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah LEE. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation biology* 20(2): 538-548.
- Manase G. 2010. Impact of climate change on water in southern africa: research on climate change and water resources in Southern Africa. Council for Scientific and Industrial Research and Danish Water Forum.
- Mannetje LT, Haydock KP. 1963. The dry-weight-rank method for the botanical analysis of pasture. *Grass and Forage Science* 18(4): 268-275J.

- Manry D.E, Knight RS. 1986. Lightning density and burning frequency in South African vegetation. *Vegetatio* 66(2): 67-76.
- Manry DE. 1983. Ecology of the bald ibis *Geronticus Calvus* and fire in the South African grassland biome (Master's thesis, University of Cape Town).
- Marchand FL, Kockelbergh F, Van De Vijver B, Beyens L, Nijs I. 2006. Are heat and cold resistance of arctic species affected by successive extreme temperature events? *New Phytologist* 170(2): 291-300.
- Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Levesque E, Molau U, Mølgaard P, Parsons AN, Svoboda J. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* 3(S1): 20-32.
- Marion GM. 1996. Temperature enhancement experiments. *The ITEX Manual. Danish Polar Center, Copenhagen, Denmark* pp. 14-19.
- Melillo JM, Callaghan TV, Woodward FI, Salati E, Sinha S. 1990. Effects on ecosystems. *Climate change: The IPCC Scientific Assessment* pp. 283-310.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL. 1993. Global climate change and terrestrial net primary production. *Nature* 363(6426): 234.
- Mentis MT, Meiklejohn MJ, Scotcher JSB. 1974. Veld burning in Giant's Castle Game Reserve, Natal Drakensberg. *Proceedings of the Grassland Society of Southern Africa* 9: 26-31.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Desertification Synthesis*. World Resources Institute.
- Moncrieff GR, Scheiter S, Slingsby JA, Higgins SI. 2015. Understanding global change impacts on South African biomes using Dynamic Vegetation Models. *South African Journal of Botany* 101: 16-23.
- Morgan JA, LeCain DR, Pendall E, Blumenthal DM, Kimball BA, Carrillo Y, Williams DG, Heisler-White J, Dijkstra FA, West M. 2011. C 4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476(7359): 202-205.

- Morison JIL, Lawlor DW. 1999. Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant, Cell & Environment* 22(6): 659-682.
- Morris CD, Dicks HM, Everson TM, Everson CS. 1999. Brotherton Burning Trial: effect of treatment on species composition and diversity. Unpublished report. Pietermaritzburg, South Africa: Agricultural Research Council - Range and Forage Institute.
- Morris CD, Dicks HM, Everson TM, Everson CS. 1999. Brotherton Burning Trial: effect of treatment on species composition and diversity. Unpublished report. Pietermaritzburg, South Africa: Agricultural Research Council - Range and Forage Institute.
- Morris CD, Everson CS, Everson TM, Gordijn PJ. 2020. Frequent burning maintained a stable grassland over four decades in the Drakensberg, South Africa. *African Journal of Range & Forage Science* 38(1): 39-52.
- Mowll W, Blumenthal DM, Cherwin K, Smith A, Symstad AJ, Vermeire LT, Collins SL, Smith MD, Knapp AK. 2015. Climatic controls of aboveground net primary production in semi-arid grasslands along a latitudinal gradient portend low sensitivity to warming. *Oecologia* 177(4): 959-969.
- Mucina L, Rutherford MC. 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.
- Mueller KE, Blumenthal DM, Pendall E, Carrillo Y, Dijkstra FA, Williams DG, Follett RF, Morgan JA. 2016. Impacts of warming and elevated CO₂ on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. *Ecology Letters* 19(8): 956-966.
- Murray S, White R, Rohweder M. 2000. *Pilot Analysis of Global Ecosystems: Grasslands Ecosystems*. World Resources Institute, Washington D.C.
- Musil CF, Schmiedel U, Midgley GF. 2004. Lethal effects of experimental warming approximating a future climate scenario on southern African quartz-field succulents: a pilot study. *New Phytologist* 165(2): 539-547.

- Nänni UW. 1969. Veld management in the Natal Drakensberg. *South African Forestry Journal* 68(1): 5-15.
- New M, Hewitson B, Stephenson DB, Tsiga A, Kruger A, Manhique A, Gomez B, Coelho CAS, Masisi DN, Kululanga E, Mbambalala E, Adesina F, Saleh H, Kanyanga J, Adosi J, Bulane L, Fortunata L, Mdoka ML, Lajoie R. 2006. Evidence of trends in daily climate extremes over southern and west Africa. *Journal of Geophysical Research D: Atmospheres* 111(D14).
- Nicholson SE, Nash DJ, Chase BM, Grab SW, Shanahan TM, Verschuren D, Asrat A, Lézine AM, Umer M. 2013. Temperature variability over Africa during the last 2000 years. *Holocene* 23(8): 1085-1094.
- O'Connor TG, Kuyler P. 2009. Impact of land use on the biodiversity integrity of the moist sub-biome of the grassland biome, South Africa. *Journal of Environmental Management* 90(1): 384-395.
- Oosterheld M, Semmartin LM, Paruelo JM. 1999. Grazing, fire and climate effects on productivity of grasslands and savannas. *Ecosystems of the World*. Elsevier Science, pp. 287-306
- Ojima DS, Schimel DS, Parton WJ, Owensby CE. 1994. Long-and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* 24(2): 67-84.
- Olsson L, Opondo M, Tschakert P, Agrawal A, Eriksen SH, Ma S, Perch LN, Zakieldeen SA. 2014. Livelihoods and poverty. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 793-832.
- Oluwole FA, Sambo JM, Sikhalazo D. 2008. Long-term effects of different burning frequencies on the dry savannah grassland in South Africa. *African Journal of Agricultural Research* 3(2): 147-153.
- Osem Y, Perevolotsky A, Kigel J. 2004. Site productivity and plant size explain the response of annual species to grazing exclusion in a Mediterranean semi-arid rangeland. *Journal of Ecology* 92(2): 297-309.

- Palmer AR, Ainslie AM. 2005. Grasslands of South Africa. In: *Grasslands of the World* 34: 77.
- Parr CL, Lehmann CE, Bond WJ, Hoffmann WA, Andersen AN. 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends in Ecology & Evolution* 29(4): 205-213.
- Pechony O, Shindell DT. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences* 107(45): 19167-19170.
- Phillips JF. 1930. Fire: its influence on biotic communities and physical factors in South and East Africa. *South African Journal of Science* 27: 352-367.
- Polley HW, Bailey DW, Nowak RS, Stafford-Smith M. 2017. Ecological consequences of climate change on rangelands. In *Rangeland Systems*. Springer, pp. 229-260
- Polley HW, Briske DD, Morgan JA, Wolter K, Bailey DW, Brown JR. 2013. Climate change and North American rangelands: trends, projections, and implications. *Rangeland Ecology & Management* 66(5): 493-511.
- Potter C, Klooster S, Genovese V. 2012. Net primary production of terrestrial ecosystems from 2000 to 2009. *Climatic Change* 115(2): 365-378.
- Prieto P, Penuelas J, Llusia J, Asensio D, Estiarte M. 2009. Effects of experimental warming and drought on biomass accumulation in a Mediterranean shrubland. *Plant Ecology* 205(2): 179-191.
- Quante M. 2010. The changing climate: past, present, future. In *Relict Species*. Springer, Berlin, Heidelberg, pp. 9-56
- Reeves MC, Moreno AL, Bagne KE, Running SW. 2014. Estimating climate change effects on net primary production of rangelands in the United States. *Climatic Change* 126(3): 429-442.
- Reyers B, Tosh CA, 2003. National grasslands initiative: Concept document. *Johannesburg, South Africa: Gauteng Department of Agriculture, Conservation and Land Affairs*.
- Riedo M, Gyalistras D, Fuhrer J. 2000. Net primary production and carbon stocks in differently managed grasslands: simulation of site-specific sensitivity to an increase

- in atmospheric CO₂ and to climate change. *Ecological Modelling* 134(2-3): 207-227.
- Rind D. 1999. Complexity and climate. *Science* 284(5411): 105-107.
- Roe G. 2006. In defense of Milankovitch. *Geophysical Research Letters* 33(24).
- Rustad LEJL, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126(4): 543-562.
- Sage RF. 2000. C₃ versus C₄ photosynthesis in rice: ecophysiological perspectives. *Studies in Plant Science* 7:13-35.
- Sala OE, Paruelo JM. 1997. Ecosystem services in grasslands. In: *Nature's services: Societal dependence on natural ecosystems*. Island Press, Washington DC, pp. 237-251.
- Saleska SR, Harte J, Torn MS. 1999. The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Global Change Biology* 5(2): 125-141.
- Sanderson MG, DL Hemming, Betts RA. 2011. Regional temperature and precipitation changes under warming. *Philosophical Transactions of the Royal Society A* 369(1934): 85-98.
- Saxe H, Cannell MG, Johnsen Ø, Ryan MG, Vourlitis G. 2001. Tree and forest functioning in response to global warming. *New phytologist* 149(3): 369-399.
- Scheintaub MR, Derner JD, Kelly EF, Knapp AK. 2009. Response of the shortgrass steppe plant community to fire. *Journal of Arid Environments* 3:1136-1143.
- Scheiter S, Higgins SI. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology* 15(9): 2224-2246.
- Schulze RE. 2000. Modelling hydrological responses to land use and climate change: a southern African perspective. *AMBIO: A Journal of the Human Environment* 29(1): 12-23.

- Seager R, Ting M Li C, Naik N, Cook B, Nakamura J, Liu H. 2013. Projections of declining surface-water availability for the southwestern United States. *Nature Climate Change* 3(5): 482-486.
- Seddon AW, Macias-Fauria M, Long PR, Benz D, Willis KJ. 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531(7593): 229.
- Selleck GW. 1960. The climax concept. *The Botanical Review* 26(4): 534-545.
- Shaver GR, Canadell J, Chapin FS, Gurevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L, Rustad L. 2000. Global Warming and Terrestrial Ecosystems: A Conceptual Framework for Analysis. *Bioscience* 50(10): 871-882.
- Sheuyange A, Oba G, Weladji RB. 2005. Effects of anthropogenic fire history on savanna vegetation in northeastern Namibia. *Journal of Environmental management* 75(3): 189-198.
- Sheuyange J, Nippert J, Briggs J. 2014. Grassland ecology. *Ecology and the Environment* 14: 390-421.
- Short A. 2007. Revisiting the Brotherton Burning Trial. *African Journal of Range & Forage Science* 24: iii-v.
- Short AD, Everson TM, Everson CS. 2003. The effect of twenty years of burning on the species diversity and basal cover of a moist montane grassland in KwaZulu-Natal, South Africa. In *Proceedings of the VIIth International Rangelands Congress. Document Transformation Technologies, Durban, South Africa* pp. 399-401.
- Short AD, O'Connor TG, Hurt CR. 2003. Medium-term changes in grass composition and diversity of Highland Sourveld grassland in the southern Drakensberg in response to fire and grazing management. *African Journal of Range and Forage Science* 20(1): 1-10.
- Short AD. 2001. The influence of different burning treatments on the plant species diversity of the Highland Sourveld Grasslands. *BSc Agric thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa*.
- Short AD. 2004. Long-term burning experiments: revisiting the Brotherton Burning Trial. *Bulletin of the Grassland Society of Southern Africa* 4: 23-24.

- Short AD. 2010. Can we use the ordered-distance method to estimate basal cover in tufted grasslands? *The Grassland Society of Southern Africa. Grassroots* 10(1): 15 - 18
- Slingsby JA, Merow C, Aiello-Lammens M, Allsopp N, Hall S, Mollmann HK, Turner R, Wilson AM, Silander JA. 2017. Intensifying postfire weather and biological invasion drive species loss in a Mediterranean-type biodiversity hotspot. *Proceedings of the National Academy of Sciences* 114(18): 4697- 4702.
- Smith MD, van Wilgen BW, Burns CE, Govender N, Potgieter AL, Andelman S, Biggs HC, Botha J, Trollope WS. 2013. Long-term effects of fire frequency and season on herbaceous vegetation in savannas of the Kruger National Park, South Africa. *Journal of Plant Ecology* 6:71-83.
- Snyman HA. 2004. Estimating the short-term impact of fire on rangeland productivity in a semi-arid climate of South Africa. *Journal of arid environments* 59(4): 685-697.
- Snyman HA. 2004. Short-term response in productivity following an unplanned fire in a semi-arid rangeland of South Africa. *Journal of Arid Environments* 56: 465-485.
- Snyman HA. 2006. Estimating grassland production loss due to fire for a semi-arid climate. *South African Journal of Animal Science* 36: 38-41.
- Solomon S. Climate change 2007: The physical science basis: contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.
- Stephens GL, O'Brien D, Webster PJ, Pilewski P, Kato S, Li JL. 2015. The albedo of Earth. *Reviews of geophysics* 53(1): 141-163.
- Suliman M. 1990. *Greenhouse effect and its impact on Africa*. Institute for African Alternatives, London.
- Tainton N. 1999. *Veld management in South Africa*. University of Natal Press.
- Tainton NM, Mentis MT. 1984. Fire in grassland. In: *Ecological effects of fire in the South African ecosystems* by deVBooyesen P, Tainton NM (eds). Springer-Verlag, Berlin. Chap. 6.
- Taylor SJ, Ferguson JHW, Engelbrecht FA, Clark VR, Van Rensburg S, Barker N. 2016. The Drakensberg Escarpment as the great supplier of water to South Africa. In:

- Greenwood GB, Shroder JF (Eds). Mountain ice and water -investigations of the hydrologic cycle in alpine environments. Amsterdam: Elsevier, pp 1–46.
- Ter Braak C, Smilauer P. 1997. Canoco for Windows, Biometrics. Plant Research International, Wageningen, The Netherlands.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, De Siqueira MF, Grainger A, Hannah L, Hughes L. 2004. Extinction risk from climate change. *Nature* 427(6970): 145.
- Thuiller W, Albert C, Araujo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9(3-4): 137-152.
- Titshall LW, O'Connor TG, Morris CD. 2000. Effect of long-term exclusion of fire and herbivory on the soils and vegetation of sour grassland. *African Journal of Range and Forage Science* 17(1-3): 70-80.
- Tobias PV. 1981. The emergence of man in Africa and beyond. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 292(1057): 43-56.
- Trenberth KE, Jones PD, Ambenje P, Bojariu R, Easterling D, Klein Tank A, Parker D, Rahimzadeh F, Renwick JA, Rusticucci M, Soden B. 2007. Observations. Surface and Atmospheric Climate Change. Chapter 3, United Kingdom
- Trollope LA, Trollope LA. 2010. Fire effects and management in African grasslands and savannas. *Range and Animal Sciences and Resources Management* 2: 121-145.
- Trollope WSW, Trollope LA, Hartnett DC. 2002. Fire behaviour a key factor in the fire ecology of African grasslands and savannas. *Forest Fire Research and Wildland Fire Safety*, Millpress, Rotterdam
- Trollope WSW. 1978. Fire- a rangeland tool in southern Africa. *Proceedings of the First International Rangeland Congress* pp. 245-247.
- Unganai LS. 1996. Historic and future climatic change in Zimbabwe. *Climate research* 6(2): 137-145.

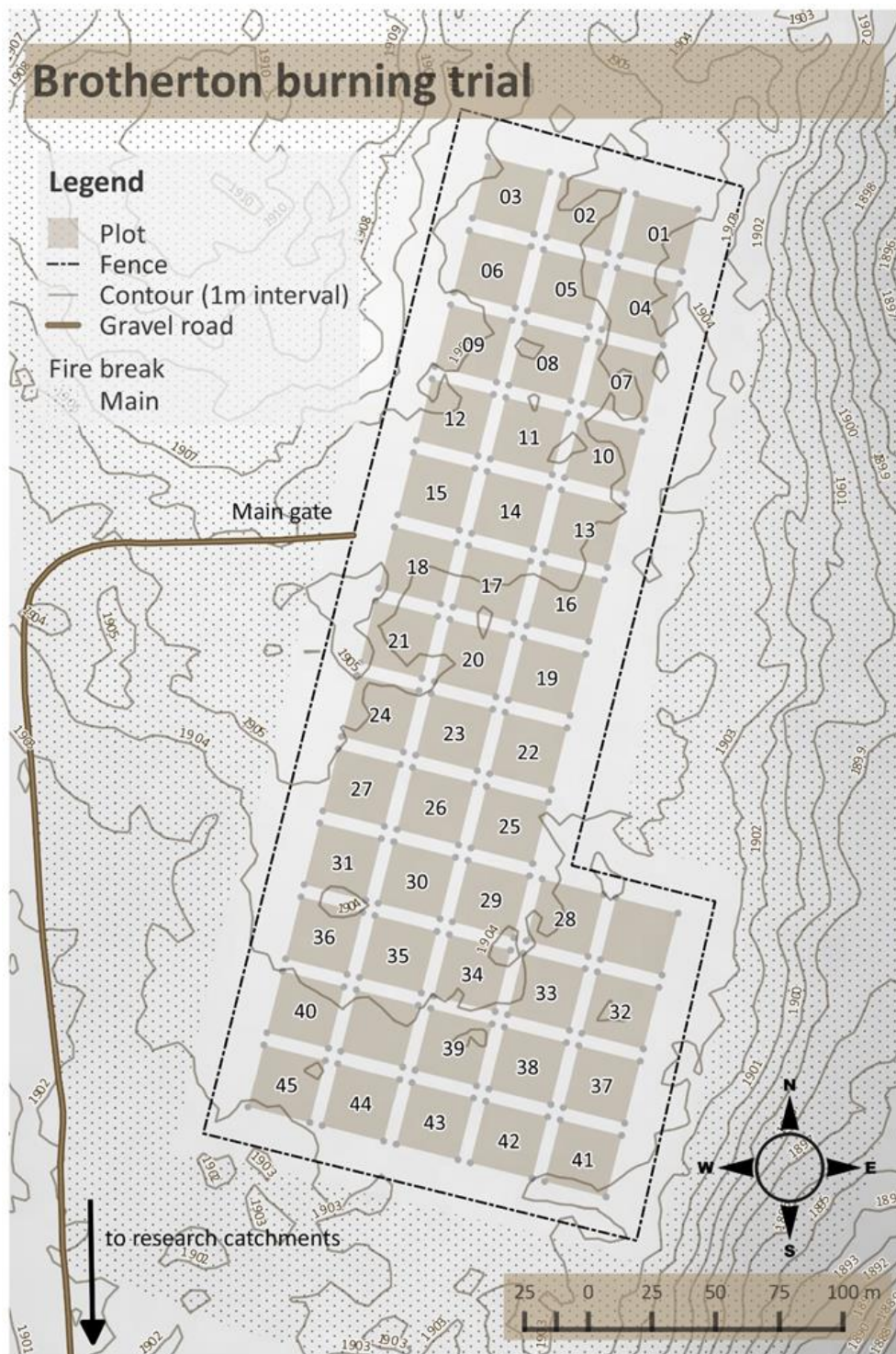
- Urama KC, Ozor N. 2010. Impacts of climate change on water resources in Africa: the role of adaptation. *African Technology Policy Studies Network* 29:1-29.
- Uys C, Hamer M, Slotow R. 2006. Effect of burn area on invertebrate recolonization in grasslands in the Drakensberg, South Africa. *African Zoology* 41(1): 51-65.
- Uys C, Hamer M. 2007. The effect of long-term fire treatments on invertebrates: results from experimental plots at Cathedral Peak, South Africa. *African Journal of Range & Forage Science* 24: 1–7.
- Uys RG, Bond WJ, Everson TM. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological conservation* 118(4): 489-499.
- Uys RG. 2000. The Effects of Different Burning Regimes on Grassland Phytodiversity. MSc thesis, Botany Department, University of Cape Town, South Africa.
- Van Staden J, Brown NAC, Jager AK, Johnson TA. 2000. Smoke as a germination cue. *Plant Species Biology* 15: 167-178.
- Van Wilgen BW, Scholes RJ. 1997. The vegetation and fire regimes of southern hemisphere Africa. In: *Fire in Southern African Savannas: Ecological and Atmospheric Perspectives*, Witwatersrand pp. 27–46.
- Venkataramanan M. 2011. Causes and effects of global warming. *Indian Journal of Science and Technology* 4(3): 226-229.
- Vogel C, Scholes R. 2015. Why Africa is particularly vulnerable to climate change. *The Conversation, Academic rigour, journalistic flair*.
- Volman TP. 1984. Early prehistory of southern Africa. *Southern African prehistory and palaeoenvironments*: 69-220.
- Walther GR. 2003. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6(3): 169-185.
- Wang N, Quesada B, Xia L, Butterbach-Bahl K, Goodale CL, Kiese R. 2019. Effects of climate warming on carbon fluxes in grasslands—A global meta-analysis. *Global Change Biology* 25(5): 1839-1851.

- Warburton ML, Schulze RE, Maharaj M, 2005. Is South Africa's temperature changing? An analysis of trends from daily records, 1950–2000. In: Schulze, R.E. (Ed.) *Climate Change and Water Resources in Southern Africa: Studies on Scenarios, Impacts, Vulnerabilities and Adaptation*. Water Research Commission, Pretoria, RSA, WRC Report 1430/1/05, pp. 275–295 (Chapter 16).
- Wertin TM, Belnap J, Reed SC. 2017. Experimental warming in a dryland community reduced plant photosynthesis and soil CO₂ efflux although the relationship between the fluxes remained unchanged. *Functional Ecology* 31(2): 297-305.
- Wertin TM, Reed SC, Belnap J. 2015. C 3 and C 4 plant responses to increased temperatures and altered monsoonal precipitation in a cool desert on the Colorado Plateau, USA. *Oecologia* 177(4): 997-1013.
- White RP, Murray S, Rohweder M, Prince SD, Thompson KM. 2000. *Grassland ecosystems*. Washington, DC, USA: World Resources Institute, pp. 81.
- Whittaker R. 1970. *Communities and Ecosystems* (No. 574.52 W624c). New York, US: Macmillan.
- Wu Z, Dijkstra P, Koch GW, Hungate BA. 2012. Biogeochemical and ecological feedbacks in grassland responses to warming. *Nature Climate Change* 2(6): 458-461.
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* 17(2): 927-942.
- Xia J, Chen J, Piao S, Ciais P, Luo Y, Wan S. 2014. Terrestrial carbon cycle affected by non-uniform climate warming. *Nature Geoscience* 7(3): 173.
- Xu W, Yuan W, Dong W, Xia J, Liu D, Chen Y. 2013. A meta-analysis of the response of soil moisture to experimental warming. *Environmental Research Letters* 8(4): 044027.
- Yang H, Wu M, Liu W, Zhang ZHE, Zhang N, Wan S. 2011. Community structure and composition in response to climate change in a temperate steppe. *Global Change Biology* 17(1): 452-465.

- Yang Z, Zhang Q, Su F, Zhang C, Pu Z, Xia J, Wan S, Jiang L. 2017. Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biology* 23(1): 154-163.
- Ziervogel G, New M, Archer van Garderen E, Midgley G, Taylor A, Hamann R, Stuart-Hill S, Myers J, Warburton M. 2014. Climate change impacts and adaptation in South Africa. *Wiley Interdisciplinary Reviews: Climate Change* 5(5): 605-620.

**APPENDIX 1.1: Species abbreviations and full names used in the PCA ordination plots
Figure 2.5 and Figure 3.6**

Abbreviation	Species name
Allosem	Alloteropsis semialata
Andapp	Andropogon appendiculatus
Barsoil	Bare soil
Bulbhu	Bulbostylis humilis
Bulbsch	Bulbostylis schoenoides
Comafri	Commelina africana
Erarac-	Eragrostis racemosa
Haplosca	Haplocarpha scaposa
Harfal	Harpochloa falx
Heliaur	Helichrysum aureonitens
Helipal	Helichrysum pallidum
Heliapp	Helichrysum appendiculatum
Hebedur	Hebenstretia dura
Hetcon	Heteropogon contortus
Hypoarg	Hypoxis argentea
Moncer	Monocymbium ceresiiforme
Oxobli	Oxalis obliquifolia
Paneckl	Panicum ecklonii
Pentair	Pentaschistis airoides
Richbra	Richardia brasiliensis
Rubrig	Rubus rigudus
Senehar	Senecio harveianus
Senerub	Senecio erubescens
Stibalo	Stiburus alopecuroides
Thetri	Themeda triandra
Traspi	Trachypogon spicatus
Trileu	Trystachya leucothrix
Tolcape	Tolpis capensis
Koecap	Koeleria capensis
Orchid	Orchid
Sedges	Sedges



Brotherton burning trial plot layout. Each plot is 25×25 m. The spacing between the plots is 5 m. Note that two plots are not part of the experiment design and are therefore not numbered.