UNIVERSITY OF KWAZULU-NATAL

Effects of climate and management on biomass, species composition and phenology and their regenerative responses in a mesic grassland

by

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ABSTRACT

Increasing temperatures, attributed mainly to increased greenhouse gas emissions, are a leading cause of climate change. Evidence shows that changing climatic conditions significantly affect terrestrial ecosystem structure and function. Fire, grazing, and recurrent drought are some of the more common disturbances that impact many grasslands. Two ongoing experiments (Ukulinga Grassland Fire Experiment (UGFE) and Drought-Net experiment at the Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal) were used to investigate the impacts of these disturbances on grassland community dynamics. This research assessed the effects of rainfall variation and warming and management factors (defoliation and fire) on phenology of grass species *vis-a-vis* their regenerative responses from bud bank**s,** soil seed bank, and seed rain and aboveground species composition and biomass in the mesic grasslands of South Africa over two years. The Drought-Net experiment treatments include the combined effect of rainfall variation (drought (50%), ambient (100%), and wet (150%)) and temperature (warmed and ambient) manipulation. The warming treatment was applied using open-topped warming chambers, and the rainfall treatment was applied using rainout shelters to intercept 50% of the ambient rainfall. The intercepted rainfall was piped onto the neighboring plot to increase rainfall by 50%. In the first objective (Chapter 3), the combined effect of rainfall variation and temperature manipulation on the phenology of grass species *vis-a-vis* their regenerative responses from bud bank**s** was conducted. Drought delayed the timing of budding and flowering and shortened the duration. There was no effect on the total number of buds per vegetative tiller per tuft compared to the reproductive tillers. Warming advanced the budding timing and extended the budding duration. This shows that the response of timing and duration of budding and flowering of these studied grass species was sensitive to the short-term effects of drought and warming. In the second objective (Chapter 4), the effect of burning frequency, winter defoliation type (fire/mow), summer defoliation with differing winter defoliation (defoliation time) applied over ~70 years and temperature manipulation on the phenology of grass species *vis-à-vis* their regenerative responses from bud banks was conducted. Across the two years of warming treatment application, the sensitivity and timing of species phenological responses and bud bank density relative to resource allocation to vegetative versus sexual reproduction were examined. Warming delayed the time of budding and flowering and increased duration slightly ($p < 0.005$). Annual winter mow delayed timing and extended duration of budding and flowering as compared to annual winter fire ($p < 0.005$). Summer defoliation frequency quickened the timing and shortened the duration of budding and flowering compared to winter defoliation frequency ($p < 0.005$). The flowering duration for

Themeda triandra was shortened under annual burning and lengthened under the triennial burn plots ($p < 0.005$). In ambient plots, vegetative status had more buds per tiller and number of tillers per tuft compared to warmed plots. Annual winter defoliation by fire had the greatest number of tillers per tuft for *Heteropogon contortus* and the lowest recorded in the annual winter defoliation by mow plots. A greater number of buds per tiller was recorded under the summer defoliation plots as against the winter defoliation plots. Summer defoliation plots had a greater number of tillers per tuft for *H. contortus* than the winter defoliation plots. The results of this study indicate that the type, time, and frequency of defoliation and their interaction with the effect of warming have a notable influence on the budding and flowering periods of the species studied, ultimately impacting the length of their reproductive cycle and altering the ratio of vegetative to flowering reproductive status. The reason for the contrasting results where warming advanced the time of budding in chapter 3 and delayed in chapter 4 could be as a result of the insurance hypothesis whereby the variation of species responses to changes in environmental condition of an ecosystem can insure the system against reduction in its functioning. The third objective (Chapter 5), combined effect of management factors (defoliation and fire), and temperature manipulation on the species composition, soil seed bank, and seed rain in the Drought-Net experiment and UGFE. Plant community composition was examined to determine sensitivity to climate and management. On the Drought-Net experiment, the main and interacting effects of warming and the various rainfall regimes did not impact the soil seed bank and seed rain ($p > 0.05$). On the UGFE, the main effect of warming and its interactions with the burning and defoliation treatments had no significant effect on soil seed bank and seed rain ($p > 0.05$). The seed rain composition was only affected by defoliation frequency, while the main effects of fire and defoliation frequencies affected the soil seed bank ($p < 0.05$). The result of the study showed that the responses of the seedlings that germinated from the seed bank and seed rain were species-specific towards the effects of the management factors. The lack of effect of drought and warming shows that mesic grasslands are resilient to fluctuations in moisture and temperature regimes in the short term. The fourth objective (Chapter 6), examined the effect of different rainfall regimes and temperature manipulation on the species composition and biomass of a mesic grassland in the Drought-Net experiment. The results showed that the main effect of rainfall variation and their interactions with warming had an impact on the grass species composition, with just the main effect of warming being observed in the following year. No impact on the forb composition was seen in either year. While there was no evidence of an interaction impact, the main effects of rainfall variation and warming on biomass production were significant. Drought and warming reduced biomass production. This demonstrated how quickly drought reduced the grass community composition, which resulted in changes in productivity. Objective five (Chapter 7), this study examined combined effect of warming and management factors (defoliation and fire) on the aboveground species composition and biomass at UGFE. Plant community composition was examined to determine sensitivity to the impact of long-term burning and defoliation frequency under ambient and warmed conditions and whether shifts in plant community composition resulted in changes in productivity. The study showed that the main effect of warming, burning, and defoliation regimes resulted in a shift in plant community composition, which altered productivity. The overall conclusion of this study is that under different defoliation frequencies, types and timing, the species-specific seasonal patterns of species composition, phenological development and bud bank production were strongly influenced by the resultant effect of these disturbances on the availability of soil moisture and light intensity. This resulted in a reduced productivity of the grass community in our mesic grassland.

PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Grassland Sciences, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The research was financially supported by National Research Foundation (NRF) (Reference number: SFH180511328259, grant number: 116115).

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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Signed: Theresa Abosede Ojo

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DECLARATION 1 – PLAGIARISM

I, Theresa Abosede Ojo, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original work.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs, or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a. Their words have been re-written, but the general information attributed to them has been referenced

b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks and referenced.

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

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Signed: Theresa Abosede Ojo

Date: 7 February 2024

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DECLARATION 2 – PUBLICATIONS

*Indicates the corresponding author

Chapter 7

Publication 1 – Under Review: African Journal of Range and Forage Science

Ojo, T*., Kirkman, K., Tedder, M., 2024. Effects of climatic (warming) and management factors (fire and mowing) on plant community composition and biomass in a mesic grassland, South Africa.

The data for this chapter was collected at the Ukulinga Grassland Fire Experiment, Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal. The research was conceived by Dr Michelle Tedder, Prof. Kevin Kirkman and I. I wrote the manuscript and performed the data analyses. Dr Michelle Tedder, and Prof. Kevin Kirkman both contributed greatly to the organisation, structuring, data analyses and final manuscript of the paper.

Signed: Theresa Abosede Ojo

…[redacted]……………………………………

Date: 7 February 2024

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DEDICATION

I dedicate this thesis to my Lord Jesus Christ, in whom I live, move, and exist.

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Chapter 1: Rationale and justification

1.1 Introduction

Global warming is causing changes in the volume and distribution of rainfall and extremes in temperature globally (IPCC, 2021). These more extreme climatic events are occurring more frequently and with greater intensity, influencing grassland systems (Hoover et al., 2014; Jentsch et al., 2011). Climatic factors significantly influence the structure and function of grassland systems worldwide (Fay et al., 2003). The timing and amount of precipitation in grassland systems are predicted to shift significantly under climate change, which may affect the plant productivity (Robertson et al., 2009). Regarding grassland ecosystems, the relationship between average annual rainfall and grassland productivity is well recognized (Chou et al., 2008; Knapp et al., 2015; Knapp & Smith, 2001; Smith, 2011a). In grassland systems worldwide, fluctuation in the timing of precipitation (rather than total rainfall) has recently been suggested to be a significant influence on plant productivity (Carroll et al., 2021; Nippert, Knapp, & Briggs, 2006), with other factors like grazing and fire impacting productivity within the limitations imposed by the prevailing moisture conditions (Beier et al., 2012; Koerner et al., 2014; Kraaij & Ward, 2006). One of the main factors constraining ecosystem productivity globally is soil moisture, which can be exacerbated by warming (Liu et al., 2021; Ma et al., 2021; Zhu et al., 2016). Increased soil evaporation and intensified drought stress on physiological processes in plants are two ways that rising temperatures might reduce productivity (Dangal et al., 2016; Xu & Zhou, 2011). These factors influence grasslands worldwide, along with inherent variations in the soil (Felton et al., 2020a; Wang et al., 2022a).

Worldwide, rangelands are actively managed, and these management strategies are based on different philosophies and practices (Harris, 2010). Ecological disturbance (such as fire and grazing) is employed in managing and maintaining the biodiversity of grasslands. Fire and grazing both remove litter and influence community structure and composition (Khoza et al., 2023), which minimize the effects of plant species' competition (Hartnett et al., 1996; Larson et al., 2020). Community species diversity and vegetation structure can be enhanced by the combined effect of grazing and fire (Koerner & Collins, 2013). Hence, based on the type, time and frequency: when the disturbances are applied inappropriately, it results in the degradation of the grassland (Gordijn et al., 2018; Scott-Shaw & Morris, 2015). For instance, grasslands exposed to excessive regular or irregular fire regimes can lead to changes in species composition, and reduced community stability and diversity (Scott-Shaw & Morris, 2015). Grazing has its own effects by being selective of palatable species along with trampling and defecation (Khoza et al., 2023). Mowing or hay cutting is also a source of litter removal which modifies the community composition and structure (Khoza et al., 2023), mowing is used in the production of biofuel feedstock (Kitchen et al., 2009a).

The response of grasslands to the type, time and frequency of fire, grazing/mowing and climate varies with mean yearly rainfall (Oesterheld et al., 1999). This is because in grasslands, rainfall is directly linked to biomass production which partly affects grazing frequency based on forage availability, and the production of litter as flammable fuel, which partly determines fire frequency. Thus, there is a gradient of mean yearly rainfall which may make the response of grasslands to climate change, grazing/mowing and fire vary (Ferraro & Oesterheld, 2002; Lyons et al., 2023; Russell et al., 2019). Plants' responses to the effect of rainfall combined with grazing and fire have been found to differ depending on the species' functional traits, climate and ecosystem type (Hyvärinen et al., 2019; McSherry & Ritchie, 2013; O'Connor et al., 2014). For instance, in burned areas, soils are often drier throughout the whole season, and disparities in soil moisture are highlighted in years with low rainfall (Koerner et al., 2014; Neary & Leonard, 2021). The same is true for grazed sites, which are often dryer and more susceptible to variations in precipitation than ungrazed sites (Blair et al., 2014a; Oesterheld et al., 1999).

Within the large body of literature on climate and management in grasslands, there has been a lack of experimental studies looking at the combined effect of climate change and management in South Africa and Africa, as a whole. In addition, the combined impact of climate change (rainfall variation and warming) and management (defoliation and fire) on phenology of grass species *vis-a-vis* their regenerative responses from bud bank**s,** soil seed bank, and seed rain and aboveground species composition and biomass in mesic grasslands has not been examined. There is limited research about how precisely increased climatic variations affect biodiversity, ecosystem functioning, and their regenerative responses (Jentsch & Beierkuhnlein, 2008).

CHAPTER TWO: LITERATURE REVIEW

2.1 Grasslands

Non-woody grassland constitutes about 8.3% of the global land area excluding Antarctica; Savannah about 13.8 %; open and closed shrubs take about 12.7%; and Tundra about 5.7%. Grassland (non-woody) may be described as terrestrial systems that is grass-dominated and has < 10% tree and shrub cover, while the wooded grasslands are regarded to have between 10 – 40 % tree and shrub cover (Suttie et al., 2005; White et al., 2000). Grasslands supply a host of critical ecosystem services ranging from direct (medicinal plants and grazing) to indirect (carbon storage and sequestration and water yield) (Hönigová et al., 2012). Grasslands, in their broadest sense, can be found in a variety of climates, from the tropics to the Arctic, at sea level to the peaks of mountains, in arid and wet regions, and in soil types ranging from shallow, deficient in nutrients to deep, rich in nutrients (Leys et al., 2018; Veldman et al., 2015). They occupy areas that has sufficient soil moisture for the growth of grass where both climatic (rainfall intensity) and anthropogenic conditions (fire and grazing used for maintenance) would prevent the growth of trees (Suttie et al., 2005).

Grasslands are essential to the Earth's ecosystem because they cycle carbon, water, and nutrients while preserving biodiversity, and providing forage for livestock and wildlife (Kemp & Michalk, 2007). Despite their significance, the biome is endangered and threatened by land use change, fire suppression and agricultural intensification. Additionally, anthropogenic climate change harms grasslands, causing warming, altered rainfall patterns, and other issues (Gibson & Newman, 2019). In many areas of the world, problems related to socioeconomic development and environmental degradation are closely related to the quality and quantity of grasslands (Bardgett et al., 2021). Shifts in plant community composition, loss of vegetation diversity and cover, increased soil erosion, and a decline in wildlife species abundance are all results of land-use alterations in grasslands (Wang et al., 2022b). Researchers in many regions of the world are concerned about a decline in grassland community cover owing to poor management, climatic changes, and extreme events (Tramblay et al., 2020; Zuazo & Pleguezuelo, 2009). Grasslands are endangered by changes in climatic conditions, improper management, and human-induced alterations despite their important role in carbon storage and nutrient recycling (Cojoc et al., 2016; Graux et al., 2013; Zuazo & Pleguezuelo, 2009).

2.2 Grasslands in South Africa

In South Africa, the grassland biome is primarily found in the country's central, high-lying areas. It spans through the highveld (often known as the " high central plateau "), to Lesotho's mountainous regions, connecting to the sub-escarpment of KwaZulu-Natal, Eastern Cape, and Mpumalanga (Carbutt et al., 2011) and occupies 360,589 km^2 (Palmer & Ainslie, 2006). The grassland biome makes up 28% of South Africa's terrestrial surface area and is the country's second-largest biome after the savanna biome (Mucina & Rutherford, 2006a). This grassland is defined based on vegetation structure and environmental factors, which include average summer precipitation and minimum winter temperatures (Mucina & Rutherford, 2006a; Müller et al., 2022). The grassland biome exists across a spectrum of soil types, from humic clays to poorly structured sands, found at elevations from sea level to >3 300 m, covers a variation in temperature from frost-free to snow-bound in winter and spans a range in rainfall from 400 to >1 200 mm/yr (Palmer & Ainslie, 2006). The growing season lasts nearly half of the year, and precipitation is primarily seasonal, falling in summer (Mucina & Rutherford, 2006a). The highly diverse ancient ecosystems, habitats, and communities in grasslands maintain many endemic and endangered species (Müller et al., 2022) and offer an immense array of ecosystem services and ecological infrastructure, which contribute significantly to livelihoods and economic growth. The Midlands Putative Center, Drakensberg Alpine Centre, and Wolkberg Center are the three centres of plant endemism in the grassland biome that are shared with the savanna biome (Soutpansberg, Centres Barberton, and Sekhukhune). From these three centres, an endemic suite of *c*. 310 taxa combined have been comprehensively estimated (Clark et al., 2022). Recent research of the Limpopo-Mpumalanga-Eswatini Escarpment (LMEE) has added another estimated endemic suite of *c*. 186 taxa to the already existed knowledge of local endemism. The LMEE has been ranked as the most important part of the Escarpment for high summer rainfall which encourages local endemism and other conservation practices (Clark et al., 2022). The biome also contains three World Heritage Sites (Vredefort Dome, Cradle of Humankind, and uKhahlamba Drakensberg) (Mucina & Rutherford, 2006a).

The grassland biome generally has a very homogeneous structure, yet it has diverse species composition, climates, dynamics, and management. The Poaceae family’s Hemicryptophytes predominate in terms of biomass in the region significantly (Palmer & Ainslie, 2006). The grassland biome comprises rich species composition and diversity, which provides essential services for the country’s economic growth and development. The biome supports other land uses such as forestry, urbanization, and agricultural activities such as crops and livestock, yet it remains improperly conserved O’Connor & Kuyler, 2009). Across the world, major threats to grassland biodiversity loss are habitat degradation and land use changes (urbanization and agriculture). These modifications cause habitat fragmentation and alteration in the community processes and resilience, climatic conditions, and biogeochemical cycles (Török et al., 2018a). The Southern African grassland biome is also facing these threats whereby twenty-three percent is used for cultivation, sixty percent has been transformed irreversibly and just about two percent is under protection (O’Connor & Kuyler, 2009). The remaining natural part is used as rangeland for livestock production (O’Connor & Kuyler, 2009). The impact of land transformation and fragmentation leads to biodiversity losses and shifts, which impedes proper conservation of the grassland systems as seen today (O’Connor & Kuyler, 2009). Previous studies suggested that the knowledge of the relative impacts and processes of the different land uses and other agents, such as climate change, is needed for effective planning for adequate conservation of this grassland (Jewitt et al., 2015; Mogonong et al., 2023; O’Connor & Kuyler, 2009).

Mesic grasslands in South Africa comprise simple, short-statured, single-layered plant communities of tussock (or bunch/tufted) perennial grasses and long-lived perennial forbs with large belowground storage reserves (Carbutt & Kirkman, 2022b). Since grasslands are predominantly herbaceous systems, it is not unexpected that grasses (Family: Poaceae) are the most significant contributor to grassland biomass and often dominate restoration efforts (Carbutt & Kirkman, 2022b). At the same time, the presence and abundance of forb species are primarily responsible for the species richness. A species' traits, including its photosynthetic pathway, secondary chemicals, and phenological events, as well as the composition of the community, primary production, foliage nutrient content, and nutrient cycling, are determined by rainfall regimes (Carbutt et al., 2011). The distribution of the grassland biomes does appear to be influenced by the rainfall gradient through the direct effect of water balance and the indirect effect of fire and grazing regimes. (Palmer & Ainslie, 2006). Defoliation intensity and type, season and intensity of the burn, and minimum temperature all impact canopy cover (Carbutt & Kirkman, 2022b).

2.3 Response of vegetation to climate change

Plant species' ability to acclimate by changing their physiology and seasonal behaviour or to track the changing environmental conditions by moving to new regions determines how the plant community will respond to changing climatic conditions (Jump & Peñuelas, 2005). As a result of the interaction of the various factors contributing to climate change (such as rising temperatures, shifting rainfall regimes, increase in the severity and frequency of harsh climatic occurrences, increased concentration of carbon dioxide in the atmosphere, and a modified nitrogen cycle) as well as changes in land use and cover all affect the ecosystem structure and functioning (Beier et al., 2012). Global ecosystems are already facing the consequences of changing climatic conditions on a large scale (Chong, 2014). Precipitation variability could cause tissue die-back and decreases in ANPP of individual plants in mesic grasslands over an extended period but due to the resistance of the plants, the total community biomass could still be remarkably steady (Backhaus et al., 2014). Effects on the plant population are evident at all levels, from genetic and elemental to specific performance of plant species, ecosystem functions, and dynamics (Jeyasingh et al., 2014; Weisser et al., 2017). With these ongoing global environmental impacts, changes such as biodiversity loss (Oliver & Morecroft, 2014), increased plant community extinction (Bradshaw et al., 2009; Traill et al., 2010a), increased invasions of alien species (Diagne et al., 2021), changes in the species composition, interactions and ranges (Boucek & Rehage, 2014), along with changes in phenological events and plant biomass are expected (Ernakovich et al., 2014a; Wolf et al., 2017). Yet, there is limited research about how precisely increased climatic variations affect biodiversity, ecosystem functioning, and their regenerative responses (Jentsch & Beierkuhnlein, 2008).

2.4 Climate change globally

Carbon dioxide, methane, and nitrous oxide concentrations in the atmosphere have increased due to human activities such as burning fossil fuels, making cement, and deforestation. Due to this, global radiative forcing has increased compared to pre-industrial levels, resulting in undeniable global warming (Tian et al., 2016). From 1880 to 2012, the mean surface temperatures on land and in the oceans increased by 0.85°C globally. As a result, today, there are more warm days and nights than cold days and nights (Sen Roy, 2018). In addition, the rate of warming varies seasonally, where summer and autumn experience slower increases in land-surface air temperature than in spring and winter globally (Song et al., 2021). Due to changes in plant growth, photosynthesis, and soil respiration, global warming is anticipated to impact the carbon budget (Melillo et al., 2011). Terrestrial ecosystems' ability to serve as carbon sources or sinks may be affected by changes in carbon cycling brought on by global warming due to changes in net primary production and heterotrophic respiration (Chuai et al., 2018). Another anticipated effect of rising temperatures is greater evaporative cooling in the leaves, leading to water stress in some plant species and impacting ecosystem hydrology (Lian et al., 2021). It is predicted that changing climatic conditions will affect both the timing and amount of annual precipitation (Feng et al., 2013; Shriver, 2016). Climate change increases extreme rainfall events worldwide, leading to more extreme drought periods and a rise in the occurrence and intensity of severe rainfall incidents (Beniston et al., 2007; Wilhite, 2016).

The effects of global warming of 1.5 °C, 2 °C and 3 °C have been studied in many parts of the world (Jacob et al., 2018). More severe effects on rainfall, evapotranspiration, runoff, and snow are expected across the majority of Europe at increasing levels of global warming. As warming progresses, impacts become more severe and widespread (Donnelly et al., 2017). Under a 2 °C global warming scenario, it is also predicted that during winter, the average precipitation would rise significantly (almost 20%) over Central and Northern Europe for example (Nikulin et al., 2011). Under a 3 °C global warming scenario, the increase is expected to be greater, whereas under a 1.5 °C scenario, average precipitation is projected to be less than that recorded for the 2 ºC and 3 ºC (Donnelly et al., 2017).

Previous studies on climate change have shown that under 1 ºC, 2 ºC, 3 ºC and 4 ºC global warming scenarios in the African continent, the resultant effect would have large impact on every sector (James & Washington, 2013; Weber et al., 2018). Some regions in this continent are expected to experience high interannual variations in precipitation leading to a substantial impact on human livelihood in relation to agriculture (James & Washington, 2013). It was projected that if global temperature is still kept below 2 ºC, the regions between 15 ºS and 15 ºN would still experience an increased and more frequent heat waves, and that exceeding the threshold of 2 ºC would intensify the resultant effects (Weber et al., 2018). An example of such intensified effects of increased global warming is an increase in the intensity of daily rainfall particularly in the African sub-Saharan coastal region (Weber et al., 2018). In the arid regions, temperatures are expected to increase higher than the global average, while precipitation is expected to vary in the amplitude and direction of temperature change. These precipitation changes are driven by increased global temperature and the magnitude of response to these changes are region-specific (James & Washington, 2013). The projections at 1 °C showed that the changes were not significant for most parts of Africa, except for the Mediterranean and East Africa with dry signal and wet signal respectively (James & Washington, 2013). More regions are projected to show significant changes at 2 °C especially in the southern Africa, Guinea Coast and Sahel (west coast) with dry signals. The projections at 2 °C and beyond showed strong and increased changes with delayed seasons in precipitation (James & Washington, 2013). At 2 °C, 3 °C, and 4 °C, the degree of change projected is expected to greatly impact African continent especially in the Sahel and East Africa regions. It was also projected that with these increasing levels of global warming, there are risks linked with them (James & Washington, 2013).

At 1.5 – 2.0 °C warming levels, the productivity of South African grassland is predicted to increase but could be altered at an increase above 1.5 – 2.0 ºC warming levels (Lawal et al., 2019). If global temperatures increase more than 2 - 3 °C above pre-industrial levels, the IPCC predicts that 20 – 30% of species would face an extremely high risk of extinction (Warren et al., 2013). The region's rainfall is predicted to decrease by 30% by 2100, while temperatures are predicted to climb by more than 3 °C (Rochdane et al., 2012; Thomas & Büntgen, 2019). Dry conditions are expected to worsen, particularly in the region's Southwestern areas, towards the end of the twenty-first century. A rise in evapotranspiration has been primarily blamed for this increase in aridity (Serdeczny et al., 2017). The drought intensity in this region is predicted to worsen by more than 40% before the end of the century due to regional warming (Gizaw & Gan, 2017). The streamflow of rivers and groundwater recharge rates in soil moisture is predicted to drop significantly due to changing climatic conditions (García-Ruiz et al., 2011).

2.5 Impact of climate change on grasslands

Climate variability is rising due to the Earth's water cycle accelerating due to global warming. Hence, variability in precipitation patterns is high, resulting in more severe and frequent weather events like extreme drought and floods (Allan et al., 2020; Trenberth, 2005, 2011). Concentration of water vapour in the atmosphere and water holding capacity of the air rises due to elevated temperatures and changing vertical velocities, leading to more intense precipitation occurrences (Liang & Ding, 2017; Westra et al., 2014).

In addition, rising temperatures enhance evaporation, lowering soil water content and increasing ecosystem vulnerability to extreme summer droughts (Vicente-Serrano et al., 2014). The alteration in severe climatic event frequency, intensity, spatial extent, duration, and timing is increasingly important for ecological research (Urbina et al., 2015). Climate policies are necessary because of climate change and the cumulative effects of these changes are greater than the sum of the individual effects such as changes in average rainfall conditions and overall trends (Thornton et al., 2009). At both a regional and global level, spatial patterns of rainfall and temperature are important regulating factors for plant community distribution (Hutley et al., 2011). Some species' geographic ranges and abundances increase, and others have their ranges constrained or are driven to extinction due to alterations in temperature and rainfall regimes (Walther et al., 2002a). A critical issue in global change science is how sensitive plant biogeography is to climate dynamics and how this affects ecosystem function (Franklin et al., 2017).

Research from the past decades indicates that the grassland plant community cover has been negatively impacted by changing climatic conditions (Ebrahimi-Khusfi et al., 2020; Zarei et al., 2020, 2021). Changing climatic conditions have through various anthropogenic activities, impacted many components of grassland systems (Parton et al., 1994; Thornton et al., 2014a; Wang et al., 2022a). These effects range from changes in the life cycle events of grassland plants, community composition, net primary production (NPP), grazing capacity, and soil water availability to effects on plant community cover (Dong et al., 2020; Wang et al., 2022a).

2.5.1 Elevated temperatures in grasslands

Rising temperatures are predicted to have several consequences on grassland vegetation worldwide (De Long et al., 2019). More biomass allocated to roots, longer growing duration, enhanced fertility, and potential shift of biomes toward those dominated by trees are all anticipated effects of this temperature rise in Africa (Scheiter & Higgins, 2009; te Beest et al., 2021). With grasslands' high biodiversity (Carbutt et al., 2017), especially in the tropics, where they make up 20% of the land cover, the consequences of increased grassland temperatures are crucial to consider (Parr et al., 2014). Rising temperatures can modify fire regimes, which are essential to the ecology of grasslands, and change the standing biomass (De Deyn et al., 2008). The physiological state of plants varies due to higher temperatures, including changing carbon absorption rates (Andersen, 2003; Dusenge et al., 2019). Temperature increases may not negatively impact all species equally; for example, C_3 and C_4 plants respond physiologically differently to warming (dos Santos et al., 2022; Sage & Kubien, 2007). C_4 plants' carbon fixation pathways are much less responsive to temperature increases than those of C_3 plants (Ducat & Silver, 2012).

In warm grasslands of low-latitude, greater NPP in C_4 species relative to C_3 species is expected to be produced because, in C_4 species, the process of photosynthesis has greater efficiency under higher temperatures (Buhrmann et al., 2016; Havrilla et al., 2023). (Pendall et al., 2011). Alternatively, a temperature rise may be followed by an increasing water deficit, which inhibits plant development and photosynthesis and has varying consequences in different ecosystems (Chaudhry & Sidhu, 2022). This indicates that while evaluating plant responses to elevated temperature, the effect of temperature and its interaction with either decreased or increased soil moisture must be considered (Raza et al., 2020).

It is projected that rising temperatures and shifting precipitation patterns would impact the response of the ecosystem structure to the processes of biogeochemical cycling and different land use transformations of grassland ecosystems (Petrie et al., 2018). In temperate grasslands, the length of the growing season is increasing, and as a consequence increases in productivity have been measured (Grant et al., 2017a). Increasing temperatures are the likely cause of these changes (Wu et al., 2021a), and changes in the precipitation patterns can also significantly impact the aboveground net primary production of this grassland (Guo et al., 2012). Temperature might affect plant growth directly through impacts on metabolic rates, respiration, photosynthesis, resource utilization, and uptake of water and nutrients (Morison & Lawlor, 1999). High temperatures have been shown to speed up the rates at which organs initiate and expand since temperature is a significant driver of the rate at which ontogenetic growth occurs (Badeck et al., 2004). The timing of the start and end of growth is anticipated to be impacted by changing climatic conditions, given that temperature is one of the key components regulating the phenological events of plants (Ernakovich et al., 2014a).

The study on the impact of changing climatic conditions on flowering phenology of both individual and the whole plant community in an alpine meadow of a Tibetan Plateau was examined (Chen et al., 2023). Their studies showed how temperature controls flowering phenology at all scales, from the individual to the whole plant community. However, the degree to which species altered their timing and duration of flowering in response to higher temperatures differed. The flowering phenology in this community of alpine plants may change due to this species-level difference. Another study on the diverse responses of vegetation phenology to climate change was carried out in grasslands of meadow steppe, typical steppe and desert steppe in the Inner Mongolian grassland of Northern China during 2000–2016. Their findings also showed different responses to temperature and precipitation not in terms of species but according to the grassland type and the timing of phenology (Ren et al., 2017). Another study on how experimental warming changes phenology and shortens growing season of the dominant invasive species a cheatgrass (*Bromus tectorum*) was carried out in a desert grassland of the USA (Howell et al., 2020). Their results showed that the warming effects were lower as compared to the multiple environmental factor effects (altered rainfall regimes combined with warming). This shows how the interactive effect of multiple climatic factors is greater on the cheatgrass phenology than an individual climatic factor would. The study of differential effects of temperature and precipitation on early-versus late flowering species in water-limited shortgrass steppe showed that increased temperatures significantly accelerated the time of flowering. Increased precipitation lengthened the duration of flowering in late-season species, which suggested that the effect of climate change on flowering phenology in their study was controlled by higher temperatures in the early growing season and precipitation in the late growing season (Moore & Lauenroth, 2017). The diversity of responses and changes of plant phenology to several environmental changes, help explain and show that increases in temperature is just one of the multiple climatic factors which reshapes the timing of ecosystem processes (Cleland et al., 2006). These multiple environmental changes affect plant phenology and productivity (Cleland et al., 2006).

In a Chinese desert grassland, the impact of warming on the function and stability of vegetation under mild and severe warming treatments was examined (Liu et al., 2021). They discovered that aboveground net primary production (ANPP) declined significantly with rising temperatures, particularly in the drier and warmer periods. The decline in soil moisture brought on by increased temperatures was the main factor contributing to the reduction in ANPP. Another study of the effects of increased air (0.3 ºC-2.4 ºC) and soil temperatures (0.5 ºC-1.2 ºC) on the KwaZulu-Natal Sandstone Sourveld, a subtropical grassland, showed that only in the summer, increased temperature (using Open top chambers (OTCs)) greatly reduced forb density and significantly enhanced the combination of grass and shrub aboveground productivity. At the same time, increased temperatures had no impact on the production of belowground biomass. Forbs appear to be negatively impacted by elevated temperatures, while grasses and shrubs seem to benefit from them. This may be because of competition or because high temperatures have direct physiological impacts on forbs (Buhrmann et al 2016). Temperature is positively associated with the rates of evapotranspiration, and as such, increased temperatures are likely linked to an increase in moisture loss rates (Durán et al., 2016). Hence, in water-limited ecosystems, if the temperature rises without a proportional increase in moisture, plants are likely to become water-stressed, which can decrease their growth rate (Knapp et al., 2008; Lian et al., 2021). The observed differences in plant phenology responses to increases in temperature and altered precipitation expected with climate change in these studies could be concluded as based on the differences in their sensitivity to climate change in terms of their species type, age of plant, ecosystem type and time of event (Munson & Long, 2017).

2.5.2 Effect of different precipitation regimes on grasslands

Signs of an increase in the rate of occurrence and severity of droughts and severe precipitation incidents have risen across many regions in recent decades (Dash et al., 2007; Wilhite, 2016). Over the past few years, rainfall patterns have become more unpredictable, with extended dry seasons and increased extreme rainfall events (Felton et al., 2020b; Knapp et al., 2002). These patterns are expected to worsen as atmospheric carbon dioxide concentrations increase (Koerner & Collins, 2013; Lavergne et al., 2019). Rainfall patterns are predicted to become considerably more varied and more severe and extended droughts throughout the seasons are expected (Trenberth et al., 2014). Under global future climate scenarios, the responses of grasslands to precipitation variations will substantially affect plant diversity patterns and their productivity (Fay et al., 2003; Heisler-White et al., 2009). This is supported by a study stating that changes in the quantity and timing of precipitation alter the plant communities' composition and reduce their productivity (Cleland et al., 2013; Dangal et al., 2016).

Experimentally induced increases in precipitation alterations in mesic grasslands result in more variations in the patterns of soil water content, which lower aboveground net primary production (ANPP), regardless of fluctuations in total yearly rainfall (Heisler-White et al., 2008, 2009;

Koerner et al., 2014; Nippert, Knapp, & Briggs, 2006). Changes in precipitation regimes can lower ANPP by 10 – 22% in North American tallgrass prairie, according to studies there (Fay et al., 2003). The quantitative components such as biomass, species composition, plant life cycles, radiation-use efficiency, and phenology, are significantly impacted by changes in rainfall and drought (Batbaatar et al., 2022; Bat-Oyun et al., 2016; Nanzad et al., 2021).

The terrestrial net primary production (NPP) has generally decrease during large-scale droughts (Potter et al., 2012; M. Zhao & Running, 2010). In mesic temperate grassland systems, decreases in the total aboveground biomass following a drought episode compared to ambient circumstances were discovered (Chelli et al., 2016a). Intense droughts are anticipated to occur more frequently and last longer as climate change intensifies, reducing soil water availability for protracted periods (Jaman et al., 2022). For plant community production, the interplay between temperature rise and rainfall variation may be challenging (Thornton et al., 2014a). When temperature increases result in more soil water stress throughout already warm or water-stressed times of the year, negative consequences on ANPP can occur (Munson et al., 2021). As a result of the experimental temperature increase (+3°C) and drought stress in the summer, ANPP fell by 29 % in a mesic system. There is evidence for the interaction effect between rainfall variability and temperature rise, i.e., rises in yearly totals or years with droughts, on ANPP (Wilcox et al., 2017).

This study artificially decreased growing season precipitation by 45% in 7 temperate grasslands in North America for four years running (Batbaatar et al., 2022). Initially, aboveground net primary production (ANPP) decreased in response to drought compared to the ambient treatment, but in the fourth year, drought ANPP was greater than the ambient treatment. Similarly, the grass cover dropped at first but increased by the experiment's final year, which was correlated with observed variations in community composition between treatments across locations. According to their findings, the grass species are reasonably resilient to a four-year drought in their study area. Another study investigated how a mesic grassland responded to changing intra-annual rainfall and temperature increases over five years (Grant et al., 2017a). A late drought reduced biomass by 18 % compared to regular rainfall regimes during the growing season, while higher rainfall variation with spring drought caused aboveground productivity to decline by 17 %. Summer temperature rise had no discernible impact on ANPP but did reduce species richness, winter temperature increases enhanced biomass by 12 %. Forbs benefitted more than grasses during winter under both temperature rise and increased rainfall variation with spring drought episodes. Less erratic rainfall patterns during hotter summers favoured a balanced distribution of both grasses and forbs. Conversely, hotter summers accompanied by spring or summer drought resulted in less species diversity and probably encouraged the emergence of specialists and species that can tolerate drought. Seasonally changing climatic factors should be given more consideration in global warming studies since they may indirectly alter processes and interactions between species in an ecosystem.

Some of the effects of drought on plant communities are species-specific, where it either hinders their growth or influences the dynamics of the community; responses of the belowground bud bank may explain these effects. For example, in mesic grasslands of central North America recruitment is largely from bud banks and not from the seed bank (Carter et al., 2012; Finch & Runyon, 2016). According to previous studies (Simpson et al., 2021; van der Weide et al., 2014), maintenance of the belowground populations of bud banks enable the resprouting of vegetation after being exposed to disturbances. More recently, research suggests that bud banks may also be crucial for the response of plants in herbaceous plant communities to disturbances such as drought, fire, and grazing (Carter et al., 2012; Pausas et al., 2018).

Examples can be found in a study in two semi-arid systems that have different dominant grass growth forms (rhizomatous versus bunchgrass species), (Qian et al., 2022a). They examined the impacts of a four-year experimental drought (using a 66% decrease in growing season rainfall) on both bud and shoot density, and the meristem limitation index (MLI); the ratio of belowground bud to aboveground shoot density. Drought decreased both the stem and bud density while not affecting MLI at the community level. The buds, stems, and MLI were unaffected by drought on the dominant plant growth form in each community. The vegetation type and growth form were significant determinants of the impact of the long-term effects of drought. Specifically, communities dominated by bunchgrasses exhibit higher meristem limitation than those dominated by rhizomatous grass species, probably due to the cluster/phalanx clonal type of growth. The study hypothesized that bud banks may be susceptible to long-term dry periods depending on plant growth form and community features. Another study worked on the drought-mediated dynamics of stems and buds in a newly restored system. For one growing season, severe drought was imposed using experimental rain-out shelters. Results showed a decrease in both the stem and bud bank density in response to drought. Still, in the year after, bud bank density regenerated, and bud output was greater on the former subplots subjected to drought relative to ambient subplots. According to functional groups of C_3 grass, C_4 grass, and forbs, the bud and stem density response to drought varied, with forbs having the least resistance to drought but the most significant ability to recover from it. Although the bud and stem density in the restored grasslands was generally resilient, the impacts of drought on the bud banks could have a long-term influence on the vegetation structure. After the drought, the observed decrease in the densities of buds and stems, which occur during the growing season, may allow for the survival of plants substantially more dependent on seed bank recruitment in favourable open spaces (Carter et al., 2012). As a result of climate change, altered precipitation regimes may directly influence the persistence of seeds in the seed bank (Basto et al., 2018); making it difficult to predict how alterations in precipitation regimes will affect the longevity of seeds and seed banks. This occurs due to the intricate associations between the water content of the soil and seed longevity (Hudson et al., 2015).

A study investigated whether prolonged dry conditions in late summer or early spring impact the community abundance and composition of reproductive stems and seed rain, and whether these impacts correlate with species' varying rooting depths. The research was done in Negrentino, Switzerland, in a semi-natural grassland with high species richness. The findings revealed that the risk of recurrence and length of two arid periods in late summer and spring were comparable. The timing of these two extreme dry spells altered the community composition throughout the season, while they separately decreased the successive reproductive production of the plant community. In comparison to the spring drought, the summer drought decreased soil moisture, although the consequences of drought in late summer subsided as the plant rooting depth increased. Grasses with shallow roots exhibited a constant sensitivity to summer drought, but legumes as well as forbs displayed more variable responses to drought both in spring and summer. The density of the community seed rain (-53%) and species richness (-43%) were significantly decreased by the drought in spring, with the grass seed density (-44%) also affected by drought in late summer. The effects of drought were differentiated according to the timing throughout the season, with reduced changes in the number of seeds per stem against reproductive stem density. The detrimental effect of drought occurrences in various seasons on reproductive production suggests that more recurrent droughts may accelerate the loss of plant community diversity by exacerbating seed deficits in species-rich systems (Zeiter et al., 2016).

Fire and grazing impact ANPP and significantly alter the composition of plant communities, but rainfall is the primary factor influencing grassland production (Collins et al., 2017; Li et al., 2018). Climate-induced alterations, such as drought, in the phenology of plants might lead to changes in the timing of when seed germinates and when plants flower and mature (Iler et al., 2021). Also, the scarcity of water may have an impact on plant growth by affecting photosynthetic rates directly, mainly because of the closure of stomata (Farooq et al., 2009), or indirectly, mainly due to the reduction in nutrients supplied to the plant's roots (Zia et al., 2021). Water stress may accelerate the process of ageing in leaves. As a result, even after this phase of moisture stress, and gas exchange rates are restored, the development of the whole plant may still be delayed due to a reduction in the specific leaf area (Chaves et al., 2003; Munne-Bosch & Alegre, 2004).

2.6 Management regimes in grasslands

2.6.1 Use of fire in grasslands

Fire may affect grassland function by reducing or removing biomass, decreasing belowground physical, chemical, and microbial-mediated processes, or changing the soil seed bank size and species composition (Neary et al., 1999; Pressler et al., 2019; Snyman, 2005). Fire is an essential component in the maintenance of grassland diversity (Blair et al., 2014a; Uys et al., 2004). It is a significant factor in determining the dynamics of the plant community; without it, major compositional shifts in the community can occur quickly (Bond et al., 2003b; Mishra & Young, 2020). Fire is frequently used to alter plant species composition, reduce the cover of woody vegetation, and stimulate the growth of desirable forage grass (Collins et al., 2021). The removal of concentrated plant litter on the soil surface and the reduction in moribund standing biomass, which results in increased optimal conditions (availability of energy and light) for the effective growth of the vegetation, is one of the essential benefits of fire (Bonanomi et al., 2022; Kitchen et al., 2009a).

In addition, fire can increase the productivity of the vegetation in deep soils where soil moisture content is adequately available (Buis et al., 2009). Forbs, C_3 grasses, and woody plants are increased both in abundance and productivity under irregular burning relative to regular fire, while C_4 (perennial) grasses dominate in the overall species (grasses and forbs) both in abundance and productivity under regular fire (Collins & Calabrese, 2012; Wragg et al., 2018). Burning is a widely utilized management tool that can be used for removing moribund plant material and inhibiting the spread of unwanted plant species (Carbutt & Kirkman, 2022b). Fire can also control shrub and tree invasion (Davies et al., 2019). In grasslands, fire and removal of aboveground biomass by either animals or mowing impact the structure and functioning of the ecosystem (Kitchen et al., 2009a; O'Connor et al., 2020).

The long-term impacts of the burning regime on aboveground biomass were examined in the montane grasslands of the KwaZulu-Natal Drakensberg, South Africa (Everson & Everson, 2016). There were no discernible variations in the average aboveground biomass between plots burned annually in winter and plots burned biennially in spring for 30 years. Yet, primary production in unburned areas was 20% lower than in areas burned frequently. According to the study, to increase long-term production, the system should be burned annually or every two years during the dormant period. In the same vein, the long-term Ukulinga Grassland Fire Experiment (UGFE) in KwaZulu-Natal, South Africa, (Fynn et al., 2004) investigated the impact of the type, timing, and frequency of disturbance on the richness of grass and forb species. Grass species richness significantly decreased in undisturbed grassland, although forb species richness was unaltered. Maximum grass species richness is reported to require disturbance, perhaps through removing litter and moribund material, and increasing light availability. The interplay between early versus late summer defoliation and spring against winter burning during the dormant season greatly impacted species richness.

Similarly, another study investigated whether the structure and composition of mesic grassland plant communities are affected by fire frequency similarly in South Africa and North America. Across the two grasslands, there was a general difference in how the plant communities responded to fire frequency. Due to regular burning, few deeply rooted rhizomatous graminoids became dominant in North American grasslands. Some rhizomatous grasses remained dominant in unburned areas, although smaller, shade-tolerant species became more prevalent. Species richness increased in North American grasslands as burning frequency decreased. *Themeda triandra*, *Tristachya leucothrix*, and *Hyparrhenia hirta* are only a few of the grasses that are weakly dominant in the short, diverse system in South African grassland as a result of recurrent fire.

Aristida junciformis and a few other rather tall caespitose grasses came to dominate the grassland as a result of irregular burning frequency, which also decreased species richness. It was determined that the differences in South Africa and North America's responses to burning frequency are probably related to the dominant species and their distinctive features, such as height and clonal reproduction (Kirkman et al., 2014b).

To better understand how forbs, respond to various fire regimes, this study sampled three long-term burning experiments in South Africa's mesic, montane, and semi-arid grasslands. Season and fire frequency significantly influenced the dominant grasses, but there were no clear changes in forb diversity. The composition of forbs differed less with burning regimes than with local site climatic conditions. In all three systems, forbs appear to be very fire-resistant. In contrast, all three sites displayed significant alterations in the species composition if unburned for 10 years or longer, where woody species replaced these herbaceous species. Their results showed slightly different patterns, with species turnover rising with the open space created between plants by fires. This indicates that most forbs can withstand a broader range of burning regimes than the predominant grasses (Uys et al., 2004). Another study examined how grazing and burning alter the structure of the plant community of mountainous systems in Argentina. Tussock grasses and shrubs contributed most of the live biomass in all treatments. In assessing plot-to-plot similarities in plant community composition, fire was shown to be more significant than grazing. Fire decreased all biomass groups, i.e., litter, aboveground biomass, standing dead biomass, and live biomass, which was also decreased by grazing. Burning increased the contribution of live biomass, which was more noticeable in the plots grazed. All biomass groups' proportional contributions to total biomass were significantly influenced by fire, season of burn, and growing season. It was concluded that, under fire and grazing treatment, fire has a more significant influence on the dynamics of these grasslands than grazing (Carilla et al., 2011).

Despite long-standing knowledge of the significance of belowground buds that allow aboveground plant communities to survive and resprout after a fire (Ott et al., 2019a; Pausas et al., 2018), plants can also reproduce by recruiting from the soil seed bank (Tangney et al., 2020). This means that species must produce a seed bank that is resistant to fire, which would enhance the influx of species to be recruited from the soil seed bank (Cuello et al., 2020). In an experimental semiarid savanna in Texas, they investigated the initial bud response of two dominant grasses, a C_3 caespitose grass, *Nassella leucotricha*, and a C_4 stoloniferous grass, *Hilaria belangeri*, after fires of varied intensity (Hiers et al., 2021). An unburned treatment was also used in addition to both low and high-intensity burns. The availability of fuel load determined the intensity of burns. To ascertain the immediate impacts of burning energy on bud activity, dormancy, and death, belowground axillary buds were numbered and their activities were categorized. In summer, *N. leucotricha* and *H. belangeri* buds died instantly after being subjected to high-energy fires. Following both low-energy and high-energy fires on both species, active buds were reduced. In contrast, bud activity, dormancy, and mortality stayed the same in the unburned plots. These findings imply that, for these two species, soil heating caused by fire energy influences the activity and mortality of buds. To predict grass response to greater usage of intense controlled fire in land management, it is crucial to understand how fire energy affects the belowground bud banks.

Another study was carried out by choosing 6 pairs of widely controlled (*Festuco-Brometea*) and intensively managed (*Arrhenatheretalia*) grasslands with conventional late mowing regimes from across Switzerland, measured the seed rain and soil seed bank size and composition in 12 permanent systems. It was determined that the density and species richness of the seed rain increased with community productivity. In contrast, the average seed size decreased, and fewer species had persistent seeds in the topsoil and the sward. The reason the widely controlled semi-natural systems (unmowed areas) have reduced species diversity than intensively managed areas (systems that undergo late mowing regimes) can be explained by a stronger seed limitation in the unmowed areas (Zeiter et al., 2013).

2.6.2 Use of defoliation regimes in grasslands

Long term heavy grazing in grasslands could directly modify the stability and functioning of ecosystem, and indirectly alter species composition, diversity and functional traits. Mowing increased species diversity in grasslands by reducing competition between dominant grasses (Maalouf et al., 2012). In grasslands, mowing can be termed a management strategy, which affects leaf litter quality by increasing leaf N content and also impacts biomass production. So, regardless of an increase in mowing, the intensity of mowing, that is, its history, and cutting height, all remain critical factors in determining grassland productivity (Mayel et al., 2021; Vogel et al., 2012). Mowing and removing aboveground biomass can boost vegetation productivity and decrease both forb and woody plant cover in the burned and unburned sites (Fynn et al., 2004; Turner et al., 1993; Yang et al., 2020).

Defoliation by mowing reduces litter inputs and alters root structure. It can also alter micro-climatic conditions such as temperature, water content, and the availability of soil nutrients (De Deyn et al., 2008). The removal of litter by mowing increases evaporation, which enables more radiation to reach the soil while also aiding in the conservation of the soil moisture content by reducing transpiration due to the reduction of the surface area of the leaf (Bremer et al., 1998). In grasslands with poor soil nutrients, heavy grazing has significantly increased plant mortality with species richness reported to be low (Cheng et al., 2011; Davis et al., 2000; Dorrough et al., 2007; Olff & Ritchie, 1998). Grazing decreases the biomass and abundance of palatable species while increasing the fraction of unpalatable species resistant to grazing (Boavista et al., 2019; Tessema et al., 2011). Several studies have shown that excessive grazing can degrade grasslands, while moderate grazing can enhance the growth and diversity of the herbaceous plant community (Fedrigo et al., 2018; Scott-Shaw & Morris, 2015; Zhang et al., 2015).

A meta-analysis was conducted on grasslands in different parts of China (wet and dry regions) to examine the effects of grazing on community diversity and biomass. The study also estimated the differences in these responses based on the climate, the type of livestock involved in grazing, and the intensity and time of grazing. The result of their study showed that grazing in dry areas reduced belowground, aboveground, and total biomass, while in wet areas, there are no obvious changes in the vegetation richness, evenness, and root-to-shoot ratio. It was reported that heavy grazing reduced productivity, while light and moderate grazing had no effects. The study concluded that the resultant effects of grazing on species richness, evenness and biomass was based on grazing patterns and type of climate (Cao et al., 2024). According to another study, a 30-year experiment was set up across six semi-arid grassland in China to investigate a long-term effect of mowing on the species composition, diversity and biomass compared between the mowed and unmowed plots. Their results showed that mowing did not affect biomass and species richness, but species evenness increased. The lack of effect on biomass in the mowed plots was linked to the trade-off between grass and forb biomass: where grass biomass was reduced significantly and forb biomass increased in the mowed plots. This is evident from how mowing reduced the biomass of the dominant grass, *Leymus chinensis*. The study concluded that the limited effects of mowing on community richness and biomass led to increased species evenness enhancing the production of forage and increasing community diversity for effective conservation of the ecosystem (Hassan et al., 2023).

In South Africa, which grazing management practices are of the most appropriate for the maintenance of grassland biodiversity was investigated (O'Connor et al., 2010). Their findings showed the importance of how plant diversity in relation with veld condition must be brought to fore before using veld condition as a management tool in the maintenance of grassland biodiversity. Another study in South Africa focused on how fire and grazing influence the structure and species diversity of the vegetation. Their findings showed how detrimental the effect of intensive fire and grazing was on the structure and plant species diversity (Little et al., 2015). In the same vein, a study looked at the interactive effects of fire, grazing and climate manipulations on grassland plant species in North America and South America. Their results show that the two grasslands responded in the same way to the treatments even with their different evolutionary history. On both sites, grazing reduced grass cover and production and belowground biomass with increased diversity and drought slightly influenced the vegetation structure (Koerner & Collins, 2014). In a study where it was examined if grazing depletes forb species diversity in the mesic grasslands of South Africa (Scott-Shaw & Morris, 2015). Their findings showed that overgrazing caused a reduction in the abundance of perennial local forb species and their replacement by exoctic ones. Their study advised moderate grazing in this mesic grassland.

2.7 OUTLINE OF DISSERTATION STRUCTURE

Knowledge of plant species' response to disturbances provides insights into the effective conservation strategies upon which the threatened mesic grasslands depend (Kirkman et al., 2014b). This is illustrated by plant responses' effect on ecosystems and their services, affecting entire food webs, hydrological cycles, carbon and nutrient cycling and storage (Abdalla et al., 2018; Wolkovich & Cleland, 2011). This study aims to investigate how mesic grasslands' phenology *vis-a-vis* their regenerative responses from bud bank**s,** soil seed bank, and seed rain and aboveground species composition and biomass respond to increased climate change.

AIMS, OBJECTIVES AND RESEACH HYPOTHESIS

Chapter three: Effects of warming and different rainfall regimes on grass phenology and regenerative responses in mesic grassland

The aim of this study was to assess both the single and combined effects of warming and rainfall variation on grass phenology and their regenerative responses from bud banks in a mesic grassland in South Africa.

Objectives:

(i) To assess how warming altered belowground bud bank densities and the phenological development of three locally common grass species, namely *Tristachya leucothrix*, *Themeda triandra* and *Heteropogon contortus*,

(ii) To examine how rainfall variation altered belowground bud bank densities and the phenological development of Tristachya leucothrix, Themeda triandra and Heteropogon contortus and

(iii) To evaluate how warming interacts with rainfall variation to affect the phenological events of these species and their belowground bud bank densities in allocating resources to vegetative versus reproductive tillers in the mesic grassland of South Africa

Research hypothesis:

It was hypothesized that within each of the rainfall treatments, warming combined with drought (50% reduction of rainfall) would delay the timing and lengthen the duration of phenological events and reduce the number of buds per vegetative tiller, but ambient rainfall and 50% rainfall addition would offset the negative effects of warming on the phenological stages and plants relative resource allocation from the bud banks.

Chapter four: Effects of climate (warming) and long-term management regimes (fire and defoliation) on grass phenology and regenerative responses in mesic grassland

The aim of this study was to investigate the effects of warming under different defoliation types, frequencies and timing on grass phenology and regenerative responses from bud banks in the mesic grasslands of South Africa. Here, the sensitivity and timing of species phenological responses and bud bank density relative to resource allocation to vegetative versus sexual reproduction were examined.

Objectives:

(i) To examine the effect of warming on belowground bud bank densities and the phenological development of three locally common grass species; *Tristachya leucothrix, Themeda triandra* and *Heteropogon contortus,*

(ii) To assess the influence of burning frequency (with and without warming) on belowground bud bank densities and the phenological development,

(iii) To examine the effect of winter defoliation type (fire/mow) (with and without warming) on belowground bud bank densities and phenological development,

(iv) To evaluate how summer defoliation with differing winter defoliation (with and without warming) affect the phenological events and belowground bud bank densities in allocating resources to vegetative versus reproductive tillers in the mesic grasslands of South Africa.

Research hypothesis:

It was hypothesized that the main effects of warming, winter defoliation and annual winter mowing would delay the timing and lengthen the duration of phenological events and reduce the number of buds per vegetative tiller than for unwarmed, summer defoliation and annual winter burning. These effects were predicted to vary depending on the species type, age of plant, type and time of disturbance.

Chapter 5: The interactive effect of climate change (drought and warming) and management factors (defoliation by fire and/or mowing) on species composition, soil seed bank and seed rain in a mesic grassland.

The aim of this study was that the plant community composition of the soil seed bank and seed rain was examined to determine sensitivity to climate and management.

Objectives:

(i) To examine if there was a correlation between the species composition of the sward, and the seed banks and seed rain under the impacts of climate change and management factors,

(ii) To determine the effect of rainfall variation and warming on the species composition, richness, diversity, and evenness of the soil seed bank, and seed rain, and

(iii) To examine the impact of warming under different fire conditions, and mowing treatments on the species composition, richness, diversity, and evenness of the seed bank, and seed rain

Research hypothesis:

(i) It was hypothesized that within each of the rainfall treatments, warming combined with drought (50% reduction of rainfall) would cause more reduction of the abundance of seedling emergence in the seed bank and seed rain than it would on the sward, but ambient rainfall and 50% rainfall addition would offset the negative effects of warming.

(ii) It was also hypothesized that the effects of warming, winter defoliation and annual winter mowing would cause more reduction of the abundance of seedling emergence in the seed bank and seed rain than it would on the sward for the unwarmed, summer defoliation and annual winter burning.

(iii) Species richness in the species functional groups was also predicted to be lower under the effects of warming combined with drought and under the effects of warming, winter defoliation and annual winter mowing in the seed bank and seed rain as compared to the sward. These effects are predicted to vary depending on the species type, frequency, type and time of the disturbance.

Chapter 6: Effects of warming and different rainfall regimes on plant community composition and biomass in a mesic grassland

The aim of this study was to examine a multi-year manipulative experiment of combined precipitation and temperature manipulation on the mesic grassland plant community composition and biomass production. In this chapter, pant community composition was examined to determine sensitivity to experimental warming and drought and whether shifts in plant community composition resulted in changes in productivity.

Objectives:

(i) To assess how warming altered species composition and productivity,

(ii) To examine how rainfall variation altered species composition and productivity, and

(iii) To evaluate how warming interacts with rainfall variation to affect the species composition and biomass production in the mesic grasslands of South Africa

Research hypothesis:

It was hypothesized that species composition would be sensitive to the main and interactive effects of warming and drought, leading to productivity shifts relative to unmanipulated control treatments.

Chapter 7: Effects of climatic (warming) and management factors (defoliation by fire and/or mowing) on plant community composition and biomass in a mesic grassland

The aim of this study was to investigate the impacts of warming on aboveground biomass, species composition, richness, diversity and evenness of grassland under various defoliation types, timing, and frequencies. The study examined plant community composition to determine sensitivity to the impact of long-term defoliation type, timing, and frequency under ambient and warmed conditions and whether shifts in plant community composition resulted in changes in productivity.

Objectives:

(i) To assess how burning frequency altered plant community composition and productivity,
(ii) To examine how summer mowing under different burning frequency affects aboveground biomass and species composition,
(iii) To determine how summer defoliation with differing winter defoliation altered aboveground biomass, species composition, richness, diversity, and evenness of grasses and forbs under warmed and ambient conditions, in the mesic grasslands of South Africa.

Research hypothesis:

It was hypothesized that species composition would be sensitive to the effects of warming, winter defoliation and annual winter mowing, leading to reduced productivity relative to summer defoliation, annual winter burning and unmanipulated control treatments.

KNOWLEDGE GAP

There have been few studies carried out in South Africa on the effect of climate change on phenology (Chidumayo, 2001; Currier & Sala, 2022), bud banks (Dalgleish et al., 2012; Hartnett et al., 2006), seed banks and/or seed rain (Snyman et al., 2013), species composition and biomass production (Fynn et al., 2005; Jewitt et al., 2023; Wilcox et al., 2020). The same can be explained for the effect of defoliation by fire and/or mowing on phenology (none at the moment), bud banks (Morris et al., 2021; Morris, 2021), seed banks and/or seed rains (Snyman, 2013), plant community composition and biomass (Morris et al., 2021; H. Snyman, 2015; Venter et al., 2020). These studies have focused mostly on their individual impacts with not much consideration given to their combined effects. Studies carried out in the past in Southern African mesic grasslands have not shown much detailed analysis of the combined effects of warming and different rainfall regimes and /or defoliation by fire and/or mowing on the vegetation structure in terms of the plant phenology, bud banks, seed banks and seed rain, species composition and biomass production (figure 2.1). This may have a great influence on the functioning of the grassland system. Therefore, the objective of this study was to assess how mesic grasslands' phenology *vis-a-vis* their regenerative responses from bud bank**s,** soil seed bank, and seed rain and aboveground species composition and biomass respond to increased climate change under different defoliation types, frequencies and timing.

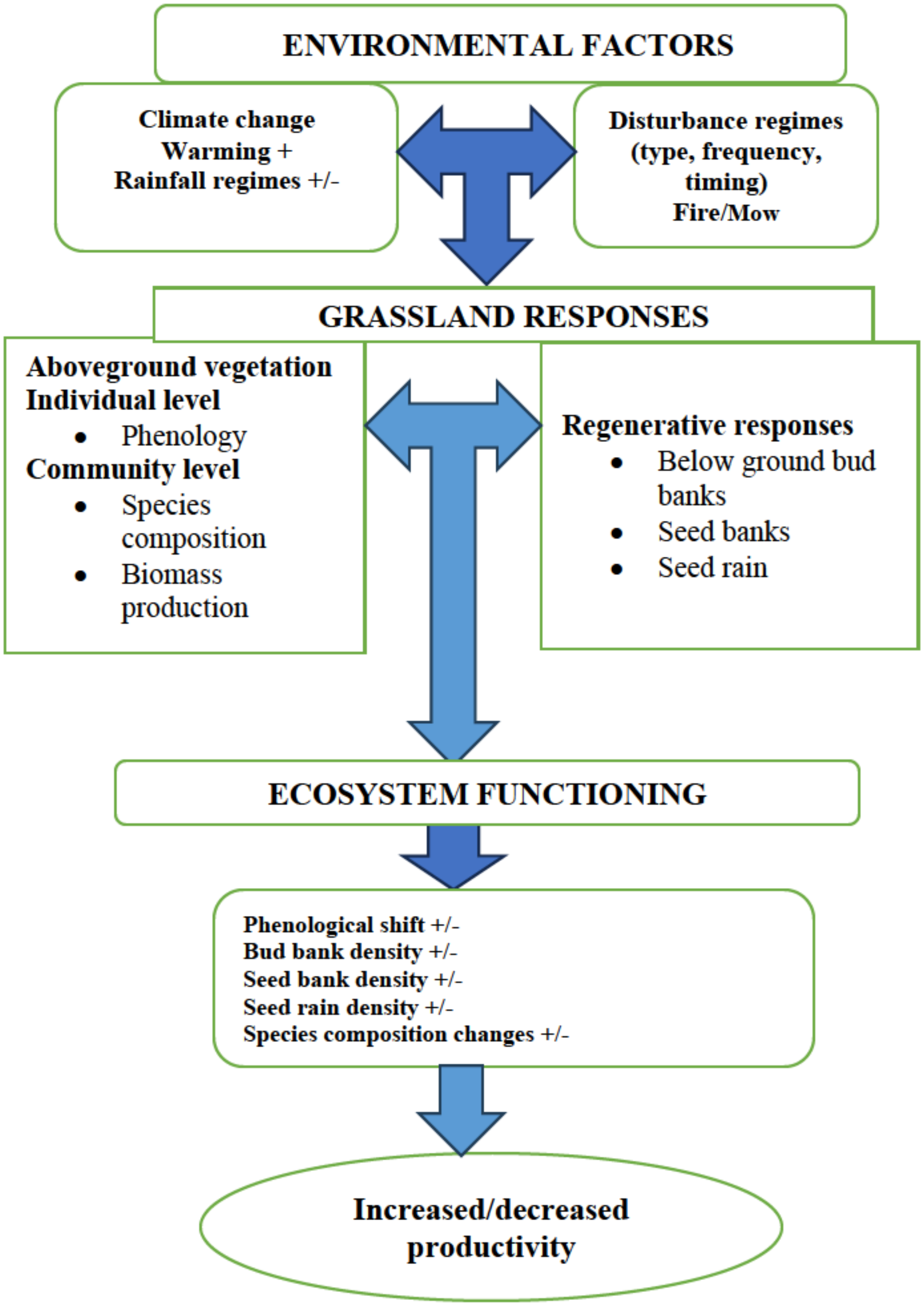

Figure 2.1: A flow chart showing the interactive effect of climate change and management factors on the grassland species composition, biomass, phenology and their regenerative responses.

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CHAPTER 3: Effects of warming and different rainfall regimes on grass phenology and regenerative responses in mesic grassland

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Abstract

Phenological changes can alter grassland community structures by influencing interspecific interactions, population dynamics, individual species migration or extinction, and the fitness of those species on a local scale. In this study, the combined effect of rainfall variation (drought (50%), ambient rainfall (100%), and wet (150%)) and temperature (warmed and ambient) manipulation on the phenology of grass species vis-a-vis their regenerative responses from bud bank**s** in a mesic grassland was conducted at the Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal. The warming treatment was applied using open-topped warming chambers, and the rainfall treatment was applied using rainout shelters to intercept 50% of the ambient rainfall. The intercepted rainfall was piped onto the neighbouring plot to increase rainfall by 50%. This resulted in six treatment combinations, replicated three times and arranged in a split-plot randomized block design. Across the two years of treatment application, the study examined species phenological responses and bud bank density per vegetative and reproductive tiller per tuft. The phenological events were examined to determine the sensitivity of timing and duration of budding and flowering to experimental warming and rainfall manipulation. Generalized linear models were used to analyze whether shifts in these phenological events intensified or stabilized changes in the density of buds per tiller and their relative allocation to either vegetative or sexual reproduction. Drought delayed the timing of budding and flowering and shortened the duration ($p < 0.05$). There was no effect on the total number of buds per vegetative tiller per tuft compared to the reproductive tillers. Warming advanced the budding timing and extended the budding duration ($p < 0.05$). Thus, the response of timing and duration of budding and flowering of these studied grass species was sensitive to short-term effects under the ambient and manipulated temperature and moisture regimes in this study. There were apparent shifts in the phenological events but no changes in the density of buds per tiller and their relative allocation to either vegetative or sexual reproduction. These findings show that grass bud banks are adaptable and can modify their regenerative responses according to the timing of climatic events. The study also suggests that some aspects of grass species phenology in South African mesic grasslands are sensitive to climate change effects in the short term.

Keywords: **Warming chamber; Phenological Events; Vegetative Reproduction; Plant sexual reproduction; Ukulinga Research Farm.**

3.1. Introduction

The phenology of plants in many ecosystems is aligned with climatic factors such as temperature and precipitation (Workie & Debella, 2018; Yuan et al., 2007). Soil moisture can promote germination and delay senescence in wetter soils (Munson & Long, 2017; Xu et al., 2004). The growing season length regulates when seeds are produced and dispersed. This can influence how plants interact and compete within the ecosystem (Price, 2012; Raymundo et al., 2021). The timing and magnitude of rainfall events in drylands are vital in defining the phenological stages through the growing season, such as when the plant flowers, seeds are produced, and plants senesce (Lamichaney et al., 2021; Prevéy & Seastedt, 2014). Changes in plant phenology can alter vegetation structure and composition by influencing interspecific interactions, population dynamics, individual species migration or extinction, and the fitness of those species on a local scale (Kudo & Cooper, 2019). There is a mix of plant functional groups including shrubs, forbs and grasses in all grasslands, and they all respond to climatic alterations differently (Grant et al., 2017b; Prevéy & Seastedt, 2014). Grass species which can adjust how they grow and reproduce by responding to optimal or unfavourable conditions, may have a greater chance of surviving under the effect of climate change in the future (Munson & Long, 2017; Scheiter et al., 2013). In the short term, these plants can exhibit significant responses through acclimation to elevated warming (Milcu et al., 2013; Morgan et al., 2011). Evidence of the potential response of plant feedback resulting from the relationship between phenology and climate is seen in altered rates of photosynthesis and respiration which may affect both the emissions, and uptake of carbon and ecosystem functioning (Dusenge et al., 2019; Peñuelas et al., 2013; Richardson et al., 2013). Determining how much a grass species changes its phenology in response to changing climate can provide insight into the potential response as either adaptive or nonadaptive. Divergent phenological responses to climatic conditions may also indicate significant changes in species composition that may affect ecosystem services (Jiang et al. 2021; Hopping et al. 2018; Lavorel 2013).

Temperature variations significantly affect the rate at which plants grow and develop and will cause a shift in the phenology of individual species, altering population dynamics and ecosystem productivity (Ganjurjav et al., 2020). Reduced and erratic rainfall which leads to drought, decreases plant species growth individually and modifies community structure (Bloor et al., 2010). It has a significant impact on grassland plant communities and some of these resultant effects may be ascribed to both the above- or belowground bud bank responses (Carter & Schindler, 2012). When above- or belowground bud density reduces after a drought, the seedbank becomes more critical for reproduction (Carter & Schindler, 2012). Consequently, tiller recruitment is reduced under decreased precipitation and elevated temperatures following defoliation where a large dormant bud bank is preserved and made ready for improved future climatic conditions (Male et al., 2022; Ott et al., 2019b; Snyman et al., 2013).

Globally, studies showed that dominant grasses in perennial grasslands reproduce via vegetative reproduction while sexual reproduction is generally low (Dalgleish & Hartnett, 2006; Ottaviani et al., 2021). Sexual reproduction is nonetheless important because seeds play a vital role in dispersal and are a key factor in re-establishing vegetation after soil disturbance (Walck et al., 2011a). Belowground bud-bearing organs in perennial grasslands are crucial for the structure, persistence, and dynamics of the local plant community (Ottaviani et al., 2021). Belowground bud banks may affect net primary production patterns in grasslands where meristem constraints may limit primary output and intrinsic temporal variability (Nippert et al., 2006). In the belowground bud banks or seed populations, the relative abundance of their species may be different from those of the aboveground community, affecting the community structure, dynamics and disturbance response (Benson et al., 2004; Qian et al., 2017). A few studies conducted outside of Africa have looked at how bud outgrowth was sensitive to high temperature, watering frequency, and clipping (Bam et al., 2022; Garcia Favre, 2022; Ponsens et al., 2010) and showed a reduced bud bank as a result of reduced disturbance. This was also found in several studies conducted across different African Savannas where reduced bud banks were associated with reduced disturbance (Bombo et al., 2022; Hartnett et al., 2006).

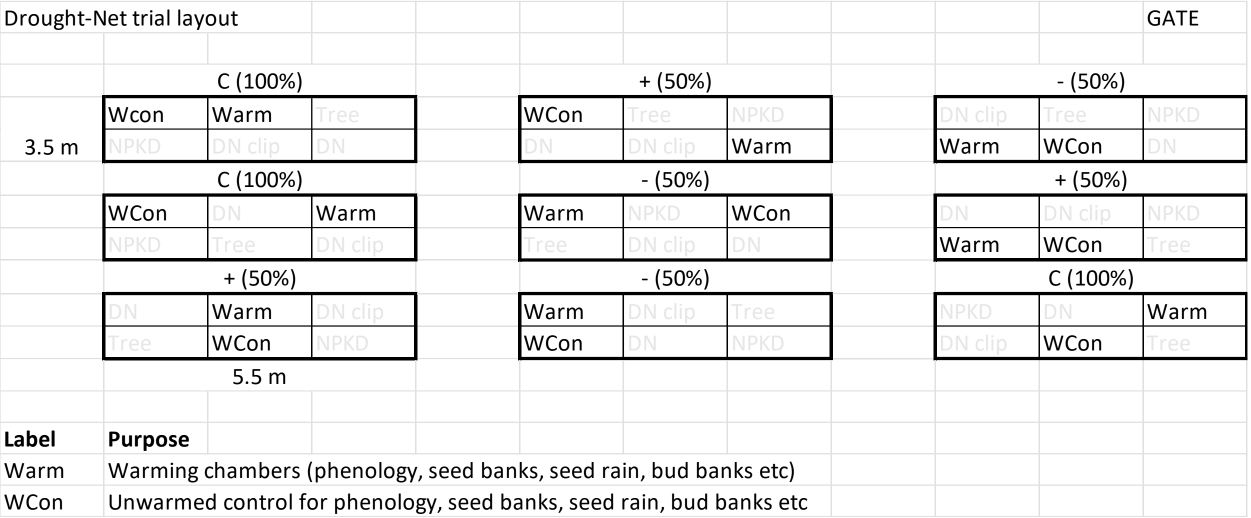
Concerning the large body of literature available for both phenology and bud banks in grasslands, there has been a lack of experimental studies investigating the combined effect of warming and drought in South Africa and Africa. The objectives of this study were to (i) assess how warming altered belowground bud bank densities and the phenological development of three locally common grass species, namely *Tristachya leucothrix*, *Themeda triandra* and *Heteropogon contortus*, (ii) examine how rainfall variation altered belowground bud bank densities and the phenological development of *Tristachya leucothrix*, *Themeda triandra* and *Heteropogon contortus* and (iii) evaluate how warming interacts with rainfall variation to affect the phenological events of these species and their belowground bud bank densities in allocating resources to vegetative versus reproductive tillers in the mesic grassland of South Africa. Therefore, this research sought to look at both the single and combined effects of warming and rainfall variation on grass phenology and their regenerative responses from bud banks in a mesic grassland in South Africa. This study also sought to investigate the variations in the timing and duration of grass reproductive stages to determine the relative contribution of sexual versus vegetative reproduction to the regeneration of grass communities under warming and different rainfall regimes. Whilst looking at how these changes in the phenological events affect grass species regenerative response from bud banks, we also observed how the resources were allocated to either vegetative or sexual reproduction. It was hypothesized that within each of the rainfall treatments, warming combined with drought (50% reduction of rainfall) would delay the timing of phenological events and reduce the number of buds per vegetative tiller, but ambient rainfall and 50% rainfall addition combined with warming could advance these phenological stages and increase plants relative resource allocation from the bud banks.

3.2 Materials and methods

3.2.1 Study area

The experiment was carried out at the Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa (30°24′ S, 29°24′ E), a region with summer rainfall that receives an average of 838 mm of precipitation annually (Ward et al., 2020b). Winters are mild with some frost and an average monthly minimum temperature of 8.8°C in July, while summer months are hot with an average monthly maximum of 26.4°C in February (Ward et al., 2020b). These climatic variables work together resulting in a growing season from October to April. The vegetation is grassland, classified as KwaZulu-Natal Hinterland Thornveld (Mucina & Rutherford, 2006c) where *Vachellia sieberiana* is dominant alongside *Hyparrhenia hirta*, *Themeda triandra,* and other herbaceous plants. In the absence of fire, the dominant grass species is *Aristida junciformis,* while *Themeda triandra*, *Tristachya leucothrix* and *Heteropogon contortus,* underlying a sparse woody canopy, are common with regular burning (Morris & Fynn, 2001a). A C4 photosynthetic pathway is being used by all grass species (Ward et al., 2020b).

3.2.2 Experimental design



Drought-Net trial layout											GATE
		C (100%)				+ (50%)				- (50%)	
	Wcon	Warm	Tree		WCon	Tree	NPKD		DN clip	Tree	NPKD
3.5 m	NPKD	DN clip	DN		DN	DN clip	Warm		Warm	WCon	DN
		C (100%)				- (50%)				+ (50%)	
	WCon	DN	Warm		Warm	NPKD	WCon		DN	DN clip	NPKD
	NPKD	Tree	DN clip		Tree	DN clip	DN		Warm	WCon	Tree
		+ (50%)				- (50%)				C (100%)	
	DN	Warm	DN clip		Warm	DN clip	Tree		NPKD	DN	Warm
	Tree	WCon	NPKD		WCon	DN	NPKD		DN clip	WCon	Tree
		5.5 m									
Label	**Purpose**										
Warm	Warming chambers (phenology, seed banks, seed rain, bud banks etc)										
WCon	Unwarmed control for phenology, seed banks, seed rain, bud banks etc										

Figure 3.1: Drought-Net experimental plot plan at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Light grey subplots were used for other projects.

The experimental plots are part of the Drought-net Research Coordination Network (https://droughtnet.weebly.com/) and were established at the beginning of October 2019, where treatment application was initiated using a split-plot randomized block design across the slight slope gradient of the site. This slight slope makes the changes along the gradient negligible. A weather station was established and started functioning towards the end of January 2020, collecting temperature, precipitation, relative humidity, solar irradiance, wind speed, wind direction, and saturated water vapour pressure data. The site was mowed at the end of each growing season to remove moribund biomass and prevent woody encroachment. The plot size was 5.5m by 3.5m divided into six subplots of 1m each, and these subplots have a corridor that is ½m wide between the subplots for easy movement. Moreover, each plot was trenched around the edges to a depth of 0.5 m and lined with thick plastic to isolate each plot hydrologically. The experimental site consisted of three blocks, and in each of these blocks were three plots with different levels of precipitation: drought (50%), ambient rainfall (100%), and wet (150%). The warming treatment was applied at a subplot level with warmed and ambient subplots, which were 1m by 1m in size, and replicated in each plot and block (figure 3.1). Warming was applied using hexagonal open-topped warming chambers constructed from 2mm thick clear polycarbonate sheeting (Mu et al., 2017a; Wu et al., 2011a).

Rainout shelters were established following the Drought-Net protocol to control the incoming precipitation in the experimental plots (https://droughtnet.weebly.com/). Transparent corrugated plastic roofing sheets were mounted on wooden frames to reduce 50% of the incoming precipitation. The intercepted rainfall from the drought plots was collected in gutters along the edge of the rainout shelters and piped onto the addition (wet) plot to increase precipitation by 50%.

Figure 3.2: Drought-Net experimental plot at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Study Species

For this study, three perennial C4 grass species of *Themeda triandra* Forssk, *Heteropogon contortus* Beauv. ex Roemer and J. A. Schultes and *Tristachya leucothrix* Trin. ex Nees, were chosen as being amongst the most common and widely distributed species occurring locally (H. M. Ghebrehiwot et al., 2014). These C4 grass species (Poaceae) are characterised by meristematic growth forms which are at different locations at or immediately below the soil surface (Nelson & Moore, 2020). The positioning of these growth zones makes the grass species resistant and varying in their responses to biomass loss through defoliation by fire or mowing frequency (Bredenkamp et al., 2002). These grasses are short and palatable. *Themeda triandra* and *H. contortus* are fire tolerant and in the absence of regular burning, are replaced by species such as *T. leucothrix* and *Aristida junciformis* (Kirkman et al., 2014b)**.** *Themeda triandra* and *H. contortus* are decreaser species which decrease with over- or under-utilized grasslands, while *Tristachya leucothrix* is an increaser I species which increases with under-utilized grasslands (Everson et al., 2021).

3.2.3 Phenological measurement

At the beginning of the 2019/2020 and 2020/2021 growing seasons, three tufts of each study species were randomly selected in warmed and ambient subplots under each rainfall variation level. Once a week the marked grass tufts were examined and scored according to their phenological stage. Following a modified scoring method from where tuft phenology was categorised into six stages: the greening stage, stage 0 for sprout-out leaves, stage 1 for the plant booting stage, stage 2 for the presence of spikelet, stage 3 for exerted anthers or styles, and, stage 4 for the absence of anther and styles where they have served their functions and fallen off (Dunne et al., 2003a; Xia & Wan, 2013) Every marked tuft with buds was examined and given a phenological score. Data collection ended when all the tagged tufts of the three study species reached phenological stage 4.

3.2.4. Bud bank sampling

3.2.4.1 Field and laboratory methods

Bud bank sampling was carried out in the second year of treatment application in September 2020. Past work on belowground bud banks indicates that 90% or more of the belowground, overwintering buds emerge into vegetative tillers at the beginning of the growing season (Zhai et al., 2022). Two complete tufts of reproductive tillers (those with mature inflorescences and dispersed seed) and two complete tufts of vegetative (nonflowering) tillers were randomly selected for each species. Under each level of rainfall variation, we examined the aboveground shoots and belowground bud bank in the warmed and ambient subplots. In this grassland, the majority of the buds are in shallow soil profiles (0-30mm). Thus, all belowground components were excavated within a depth of 0-30mm (Qian et al., 2017) while keeping intact the aboveground plant parts to accurately identify the buds and tillers according to the different study species. The samples were rinsed to remove soil, placed in plastic bags, taken to the laboratory, and stored at 4°C for subsequent analysis. The tufts were separated into tillers for easy dissection and a thorough examination of the axillary buds, located at the shoot base of each tiller, was conducted (Qian et al., 2017, 2021). Buds and tillers from each tuft were examined under a dissecting microscope while the roots were trimmed to allow a detailed investigation of the belowground structures. Each reproductive and vegetative tuft was separated into tiller segments, and buds were counted as either reproductive or vegetative buds per tiller.

3.2.4 Data analysis

3.2.4.1. Statistical analysis

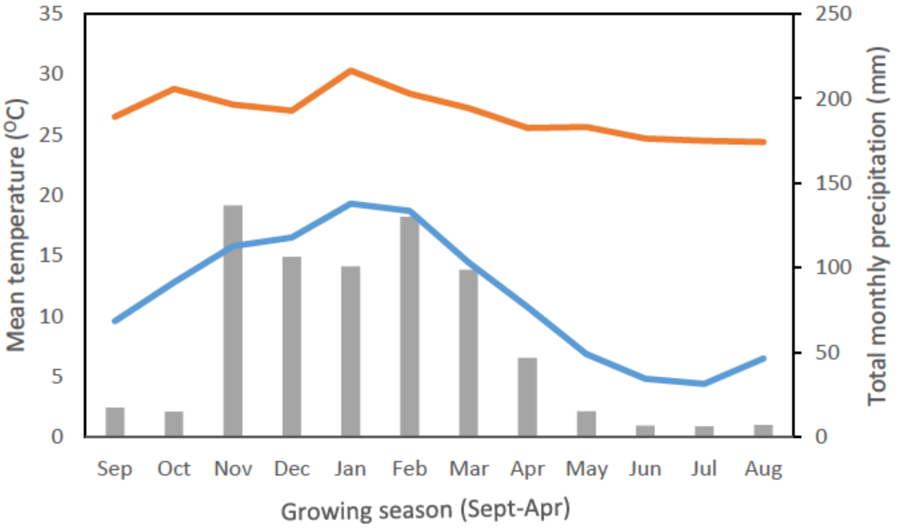
In examining the effects of warming (warm), rainfall variation (rain) and year on the time of budding (TB), time of flowering (TF), duration of budding (DB) and duration of flowering (DF) of the three study species, linear mixed-effects models (LMMs) was used. The three study species were not pooled together during the analysis but was analysed separately for each species. The TB, TF, DB and DF for each species were treated as response variables and rain, warm and year as fixed factors. We have included only the rain*warm interactions as part of the fixed factors so as to address the questions we were interested in which is to observe how grassland phenology responds to warming under different rainfall regimes. In fitting the LMMs, block was regarded as a random effect. The LMMs fitting was conducted using lmer function in lme4 package in R and the corresponding *F*- and *P*-values were obtained from the ANOVA function. We decided to use this LMMs because it was a better fit with a lower AIC value = 273.30 than GLMMs (AIC = 277.87). The model residuals were checked for normality and variance homogeneity assumptions, where *p*-values > 0 .05 indicate no violation of homogeneity and normality assumptions. Where the model showed significance, post-hoc comparisons were performed by emmeans and multicomp. For the effect of rainfall variation (rain), warming (warm) and year on the number of buds per tiller and tillers per tuft for each species, the same analysis was used. Although, this data (number of buds per tiller and tillers per tuft) is in the form of a count data which would be fit for a Poisson distribution. Poisson distribution is often used when data is skewed. it was stated that Poisson distribution can be used when data is not normal, is highly skewed and has outliers (Green, 2021). Our data was not skewed, thus, the use of the Gaussian method because the data fitted a normal distribution. This made our analysis appropriate. Data distribution was checked prior to analysis and was found to meet the requirements of a Gaussian distribution. Thus, the analysis used was appropriate. All analysis was carried out in R Studio (version 4.2.3). The LMMs were performed using the package "lme4" (Bates et al., 2015) and "lmerTest", respectively (Kuznetsova et al., 2017). For plotting, 'ggplot2' was used.

3.3 Results

3.3.1. Climatic conditions

The growing season in 2019/2020 (651.95 mm total from September to April) (Fig. 2 A) was drier than in 2020/2021 (785.2 mm total) (Fig. 2 B). In contrast to the long-term mean annual rainfall of 838 mm, the total annual rainfall (September to August) in 2019/2020 was 686.99 mm (Fig. 2 A), and 826 mm in 2020/2021 (Fig. 2 B). In 2019/2020, the growing season maximum and minimum temperatures were 27.6 °C and 14.7 °C, and the annual maximum and minimum temperatures were 26.7 °C and 11.7 °C, (Fig. 2 A). For 2020/2021, the growing season and annual maximum and minimum temperatures were 27.4 °C and 15.1 °C and 26.2 °C and 12.4 °C, respectively (Fig. 2 B).

A)



B)

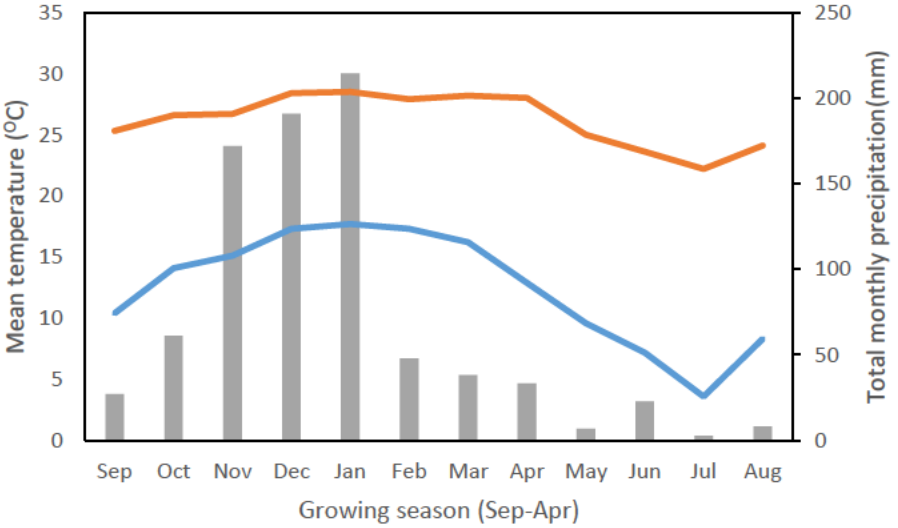


Figure 3.3: Growing season rainfall and temperature at Ukulinga Research Farm, KwaZulu-Natal, South Africa for the (A) 2019/2020 and (B) 2020/2021 growing seasons. Shown are mean monthly precipitation as bars and annual maximum temperature (orange), and minimum temperature (blue) as lines.

3.3.2. Phenology

Ambient conditions in 2019/2020 were dry and warm, with the first rains starting on July 31 (Day of year (DOY): 212, Fig. 4 A), the greening of the plots was observed on November 9 (DOY: 313, Fig. 4 A) and the growing season ended on April 30 (DOY: 121, Fig. 4 A) 2020. While in 2020/2021 it was wetter and relatively cooler during the period when phenological measurements were made, with the first rains starting on July 8 (DOY: 190, Fig. 4 B), the greening of the plots was observed on October 1 (DOY: 275, Fig. 4 B) and the growing season ended on May 3 (DOY: 124, Fig. 4 B) 2021. Rain started approximately a month earlier and greening took place a month earlier in 2020/2021 as compared to 2019/2020.

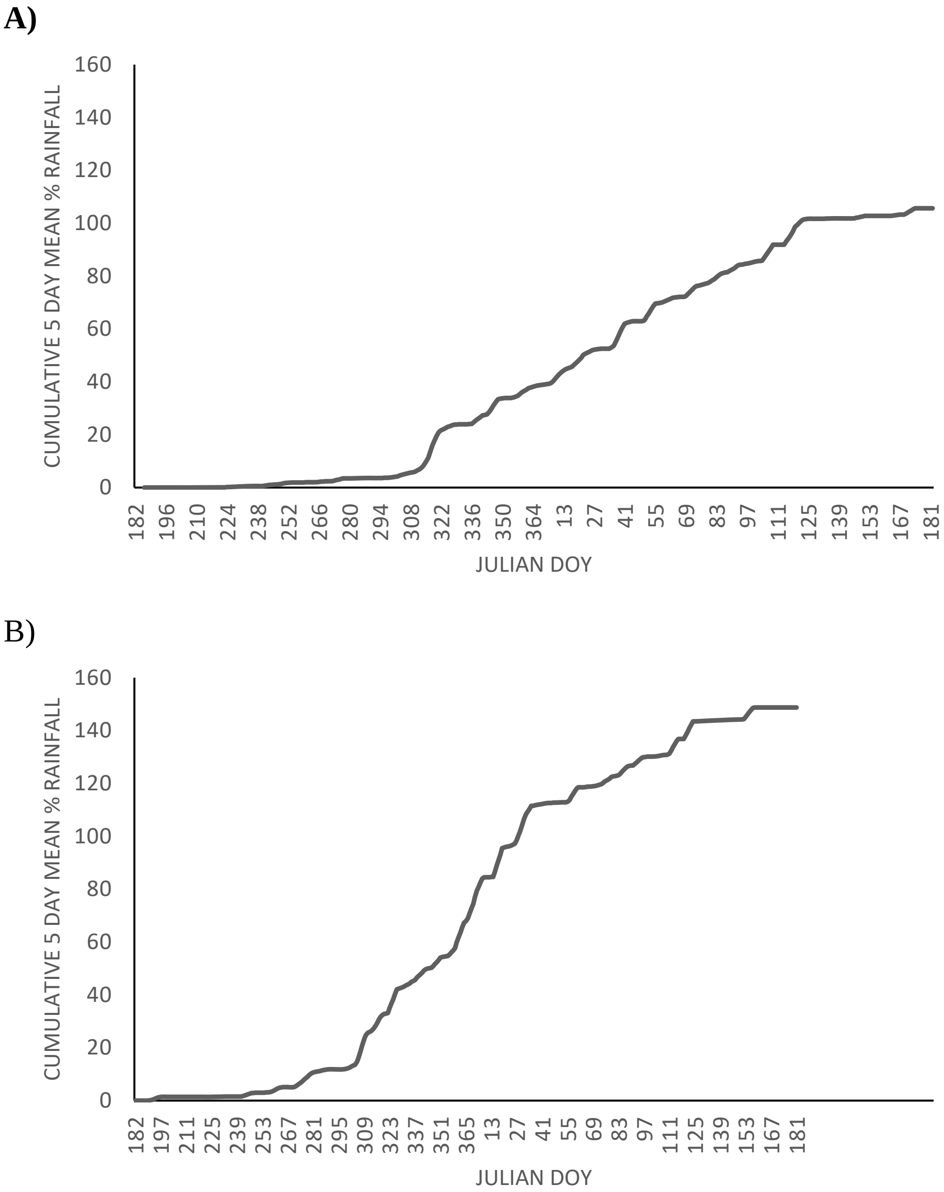


Figure 3.4: Rainfall onset and retreat periods and the length of the growing season at Ukulinga Research Farm, KwaZulu-Natal, South Africa with the use of a relative definition method for the (A) 2019/2020 and (B) 2020/2021 growing season.

The late onset of rains delayed the time of budding by 15 days in *Tristachya leucothrix*, 11 days in *Themeda triandra* and 10 days in *Heteropogon contortus* and delayed flowering by 18 days in both *T. leucothrix* and *T. triandra* and 17 days in *H. contortus*. The duration of budding was extended by 7 days in all the study species and no obvious effect on the duration of flowering.

For all three study species, rainfall variability significantly affected the time and duration of budding and flowering over the two years ($p < 0.05$, Table 3.1, 3.2, 3.3 & 3.4). Drought delayed the timing of budding and flowering while it shortened the duration of budding (i.e., the number of days from the occurrence of emergence to the date of flower set) and flowering as compared to ambient and rainfall addition plots.

Warming advanced the time of budding for *T. leucothrix* by 6 days but did not affect *T. triandra* and *H. contortus* ($p < 0.05$, Table 3.1 & Fig. 3.5 (D-F)). Warming did not affect the timing of flowering ($p > 0.05$, Table3. 2). The duration of budding for the three study species was lengthened by 1 and 2 days (Table 3.3 & Fig. 3.7 (D-F)) while the duration of flowering for *T. leucothrix* and *T. triandra* was extended by 1 day under warming over the two years (Table 3.4 & Fig. 3.8 (D-F)). There was no interactive effect of rainfall variation and warming on the timing and duration of budding and flowering in either year (Tables 3.1, 3.2, 3.3 & 3.4). All the treatment effects were grouped to observe their effects on each of the response variables. The statistical part of this result is reported below (Table 3.1). The time and duration of budding and flowering are represented on the y-axis as DOY (Day of Year).

Table 3.1: The results of LMMs showing the main effect of rainfall variation (R), warming (W) and year and interactions of R*W on the time of budding for the study species

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
RAIN(R)	2	8.304	**0.001**	12.316	**<0.001**	11.156	**<0.001**
WARM(W)	1	4.649	**0.041**	1.996	0.169	1.760	0.195
YEAR(Y)	1	37.813	**<0.001**	17.418	**<0.001**	8.428	**0.007**
R*W	2	0.002	0.998	0.008	0.991	0.013	0.987

It shows the degrees of freedom (df), F, and p-value with significant values in bold

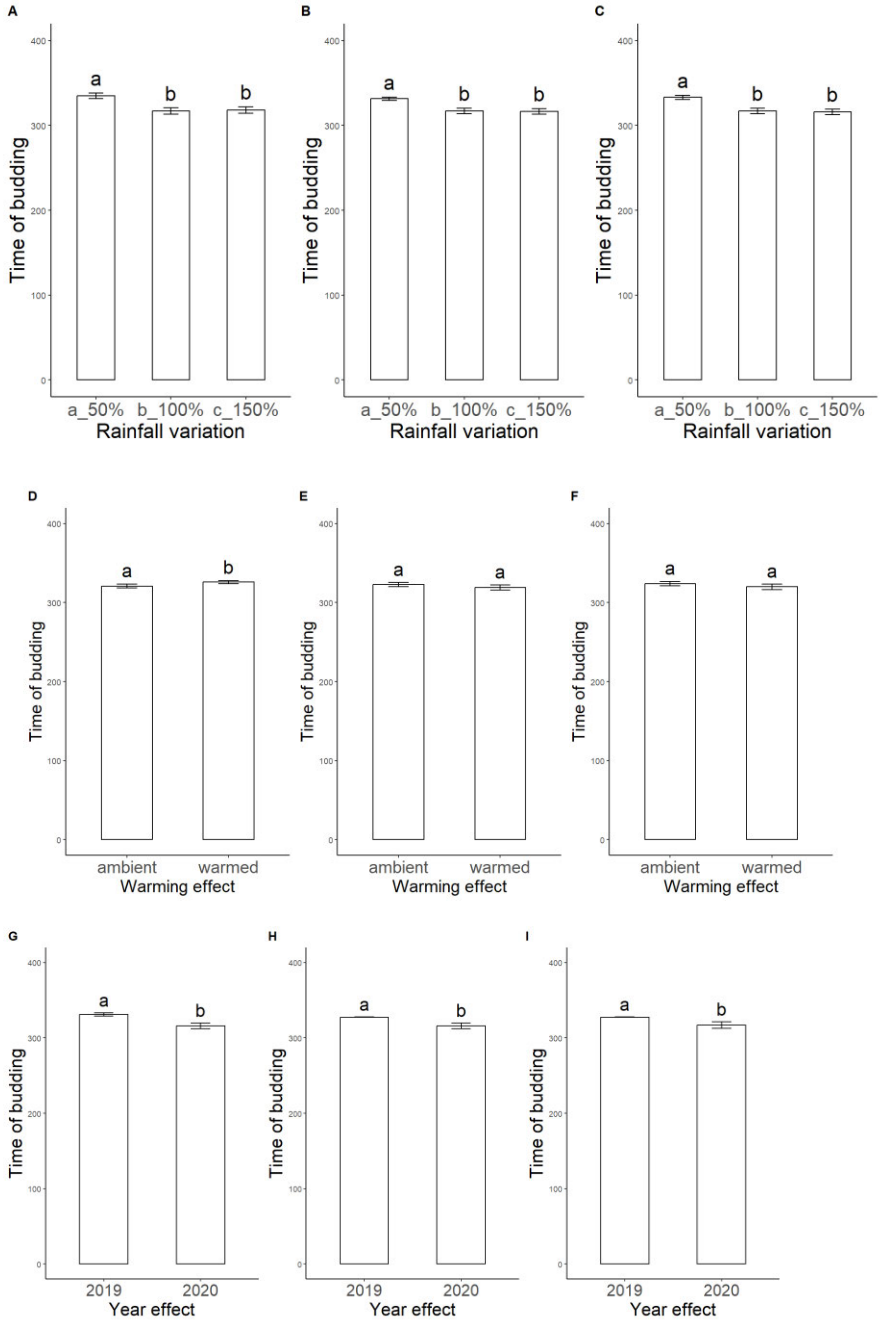


Figure 3.5: Main effect of rainfall variation (A-C) , warming (D-F), and year (G-I) on time of budding for *T. leucothrix* (a+d+g), *T. triandra* (b + e +h) and *H. contortus* (c + f + i) on the Drought-Net trials, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Letters in common indicate non-significance (*p* > 0.05). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 3.2: The results of LMMs showing the main effect of rainfall variation (R), warming (W) and year and interactions of R*W on the time of flowering for the three study species

		T. leucothrix		*T. triandra*		*H. contortus*	
	Df	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
RAIN(R)	2	11.556	**<0.001**	11.030	**<0.001**	10.198	**<0.001**
WARM(W)	1	1.674	0.207	1.421	0.244	0.849	0.365
YEAR(Y)	1	51.561	**<0.001**	52.598	**<0.001**	36.933	**<0.001**
R*W	2	0.061	0.941	0.064	0.938	0.011	0.989

It shows the degrees of freedom (df), F, and p-value with significant values in bold.

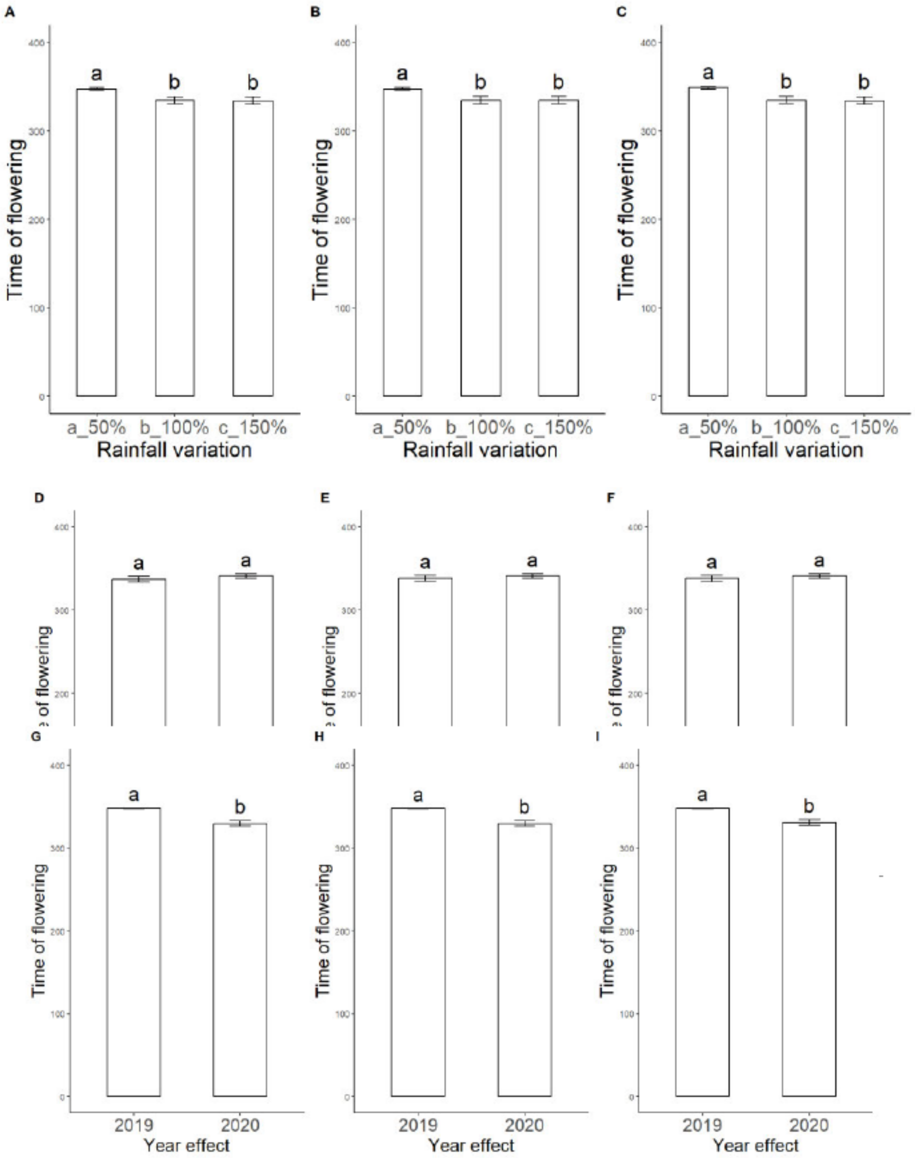


Figure 3.6: Main effect of rainfall variation (A-C), warm (D-F) and year (G-I) on time of flowering for *T. leucothrix* (a + d + g)*, T. triandra* (b + e + h) and *H. contortus* (c + f + i) on the Drought-Net trials, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Letters in common indicate non-significance ($p > 0.05$). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 3.3: The results of LMMs showing the main effect of rainfall variation (R), warming (W) and year and interactions of R*W on duration of budding for the study species

		T. leucothrix		*T. triandra*		*H. contortus*	
	Df	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
RAIN(R)	2	15.083	**<0.001**	3.358	**0.049**	15.441	**<0.001**
WARM(W)	1	10.975	**0.003**	3.932	**0.010**	16.294	**0.000**
YEAR(Y)	1	348.672	**<0.001**	205.8540	**<0.001**	329.1797	**0.000**
R*W	2	1.905	0.168	0.903	0.417	0.0885	0.916

It shows the degrees of freedom (df), F, and p-value with significant values in bold.

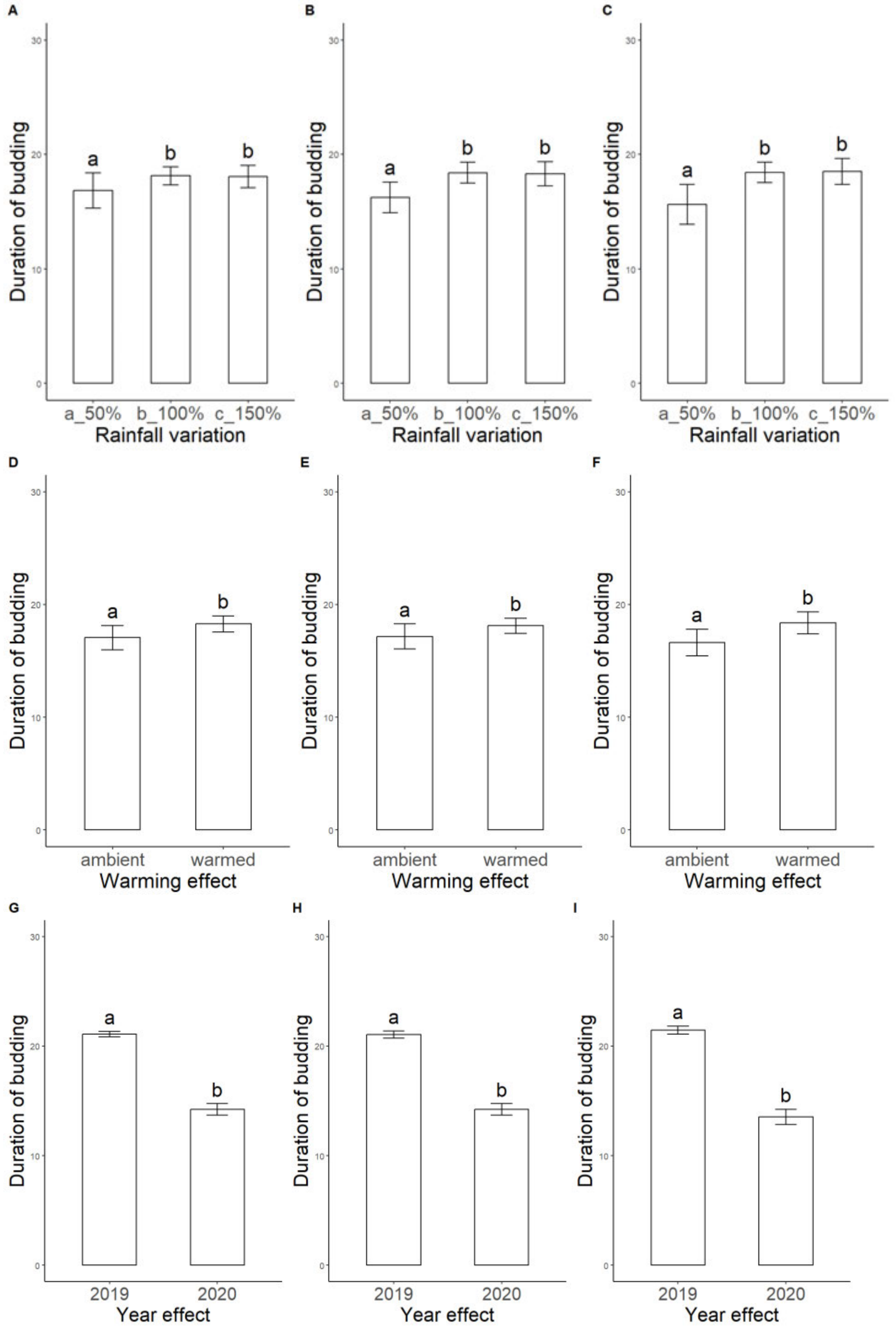


Figure 3.7: Main effect of rainfall variation (A-C), warming (D-F), and year (G-I) on duration of budding for *T. leucothrix* (a + d + g), *T. triandra* (b + e + h), and H. contortus (c + f + i) on the Drought-Net trials, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Letters in common indicate non-significance (*p* > 0.05).

Table 3.4: The results of LMMs showing the main effect of rainfall variation (R), warming (W) and year and interactions of R*W on duration of flowering for the study species

		T. leucothrix		*T. triandra*		*H. contortus*	
	Df	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
RAIN(R)	2	14.648	**<0.001**	7.338	**0.003**	10.303	**0.000**
WARM(W)	1	6.097	**0.020**	6.834	**0.014**	3.552	0.069
YEAR(Y)	1	0.002	0.964	0.293	0.593	0.073	0.789
W*R	2	0.183	0.833	0.057	0.945	0.077	0.926

It shows the degrees of freedom (df), F, and p-value with significant values in bold.

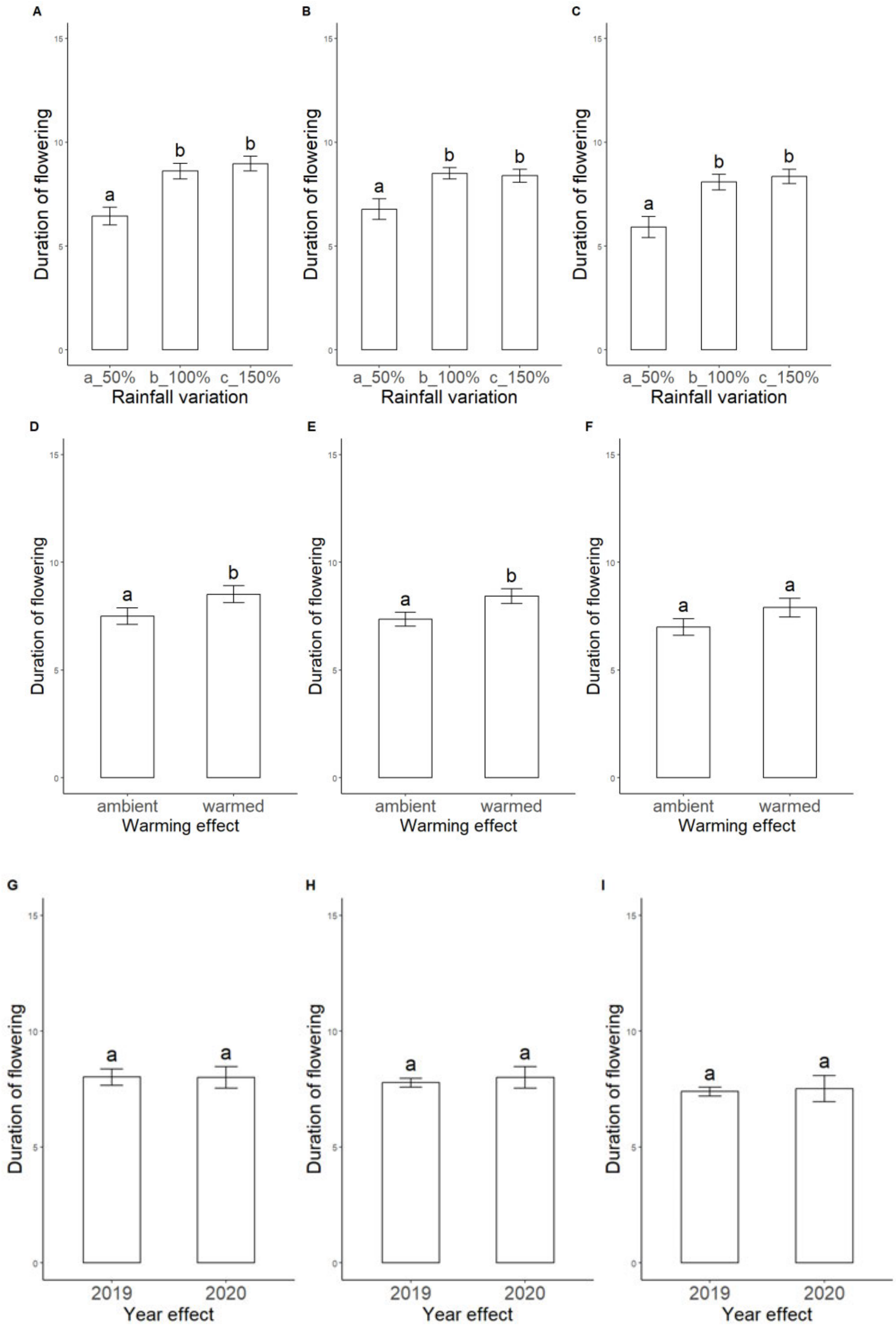


Figure 3.8: Main effect of rainfall variation (A-C), warming (D-F) and year (G-I) on duration of flowering for *T. leucothrix* (a + d + g), *T. triandra* (b + e + h), and H. contortus (c + f + i) on the Drought-Net trials, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Letters in common indicate non-significance (*p* > 0.05).

3.3. Bud bank density

Table 3.5 The results of LMMs showing the main effect of rainfall variation (R), warming (W) and status (S) and interactions of R*W*S on the number of buds per tiller and number of tillers per tuft for a) *Tristachya leucothrix*, b) *Themeda triandra* and c) *Heteropogon contortus*

a)

		Number of buds per tiller		Number of tillers per tuft	
	df	*F*-value	*p*-value	*F*-value	*p*-value
RAIN(R)	2	0.802	0.426	-0.051	0.960
WARM(W)	1	0.496	0.622	-0.471	0.639
STATUS(S)	1	0.009	0.992	-0.048	0.962
BLOCK(B)	2	0.702	0.486	-0.106	0.916
R*W	2	-0.571	0.570	0.213	0.832
R*S	2	0.001	0.976	0.000	0.988
W*S	1	0.013	0.989	0.093	0.927
R*W*S	2	0.000	0.992	0.000	0.897

b)		Number of buds per tiller		Number of tillers per tuft	
	df	*F*-value	*p*-value	*F*-value	*p*-value
RAIN(R)	2	0.990	0.326	0.068	0.946
WARM(W)	1	0.917	0.363	-0.387	0.700
STATUS(S)	1	0.008	0.993	-0.041	0.967
BLOCK(B)	2	1.171	0.247	-0.063	0.950
R*W	2	-0.800	0.427	0.094	0.926
R*S	2	0.001	0.999	0.002	0.998
W*S	1	0.083	0.934	0.093	0.926
R*W*S	2	0.002	0.999	0.002	0.998

c)		Number of buds per tiller		Number of tillers per tuft	
	df	*F*-value	*p*-value	*F*-value	*p*-value
RAIN(R)	2	0.662	0.511	0.115	0.909
WARM(W)	1	0.456	0.650	-0.347	0.730
STATUS(S)	1	0.016	0.988	-0.038	0.970
BLOCK(B)	2	0.614	0.542	0.095	0.924
R*W	2	-0.455	0.651	0.067	0.947
R*S	2	0.006	0.995	0.001	0.999
W*S	1	0.072	0.943	0.094	0.925
R*W*S	2	0.004	0.997	0.004	0.996

It shows the degrees of freedom (df), F-value *and p-value with no significant effects*

The total number of buds per tiller for the three study species was not significantly affected under the main and interactive treatments of warming, rainfall variation, reproductive and vegetative status and their interactions ($p > 0.05$ Table 3.5). Similarly, the number of tillers per tuft under the main effect of warming, rainfall variation and status with their interactions were not statistically significant. Similarly, the single and combined effects of warming and rainfall variation had no significant effect on the number of buds produced per tiller and on the number of tillers produced per tuft. Hence, buds per tiller did not vary by warming or drought treatment ($p > 0.05$ Table 3.5).

3.4. Discussion

Fluctuations in climatic factors, including precipitation, temperature, the timing of photoperiod and snowmelt, are the main causes of differences in interannual patterns in the timing of phenological phases in plants (Post & Stenseth, 1999). In this study, the late onset of rains experienced in 2019 caused the time of budding and flowering for the three study species to be delayed, and the duration of budding was also lengthened. The study found that each year, the time of budding began a few weeks after the start of the rainy season which could have caused the delayed responses in the phenological phases seen in 2019. These patterns provide evidence that the regulation of the vegetation dynamics of South African mesic grassland under climatic perturbations is critically dependent on soil moisture (Bond et al., 2003a; Chidumayo, 2001; Dabengwa et al., 2022; Scholtz et al., 2022).

Drought (rainfall reduction (50%)) delayed the timing of budding and flowering, while the duration of budding and flowering was shortened for the three study species as compared to the ambient rainfall (100%), and rainfall addition (150%) plots. This shows that the phenology of grass species in our study area mainly depends on variations in rainfall (Currier & Sala, 2022). Similarly, higher variations in rainfall amounts are believed to lead to greater variability in soil water. This results in increased drought stress, which alters the growth of plants by delaying their phenological phases. A drought may have detrimental effects on grass phenology since it can reduce the length of the growing season by either causing a delay in the greening, speeding up senescence, or both. This makes grass phenology sensitive to variations in rainfall amounts due to drought, leading to shifts in their phenological phases (Currier & Sala, 2022). This might have caused the varied responses observed in both the timing and duration of budding and flowering in our study. In a moisture-limited system in the USA, the study species displayed a similar pattern where reduced precipitation shifts phenology and changes the production of flowers and fruits. It also showed that the extent and way in which the plant community respond to drought, relies on the functional type and species (Castillioni et al., 2022).

Warming caused *Tristachya leucothrix* to bud earlier while the other two species, *Themeda triandra* and *Heteropogon contortus* were unaffected. This shows that budding responses to warming appear to be species-specific. Warming only makes the soil and air dry by not removing the litter. This could have caused *T. leucothrix* a shade loving plant to bud earlier than *T. triandra* a shade intolerant plant, and due to the difference in their growth zones. The dried soil (reduced moisture) could deter growth in *T. triandra* due to its shallow root systems as against the deep root systems of *T. leucothrix* which allow them access to water deep down in the soil. Warming also lengthened the duration of budding in all the species and the duration of flowering was extended in *T. leucothrix* and *T. triandra* with no effect on *H. contortus*. Future rises in global temperatures are likely to alter the timing of the phenological phases of plants like flowering and senescence (Cerlini et al., 2022; Parmesan & Hanley, 2015).

The responses of plant phenology to warming contrast with what was observed for drought in this study, as more delayed plant growth has been observed for drought. This is because warming results in drier soil and air conditions which affects plant growth differently than reduced rainfall (Dai, 2011). Increased temperatures make the environment more conducive for growth, allowing plants to develop earlier, whereas drought makes the environment unfavourable. In this respect, a phenological response to warming which is the opposite of what was observed for drought may be expected.

Grassland ecosystems are made up of different functional groups of plants (graminoids (C3), grasses (C4), and herbaceous dicots) with various phenological patterns, growth rates, water-use efficiency, and root traits, making them an ideal system to study links between physiology and phenological processes (Briske & Richards, 1995; Ocheltree et al., 2020). Even though soil moisture gradually decreases over the growing season in many temperate grassland ecosystems, some plants have varying degrees of tolerance and survival when soil water is low resulting in varied responses (Delzon, 2015; Ocheltree et al., 2020).

In a dry alpine meadow of the Qinghai-Tibetan Plateau, under a 4-year manipulation of warming and rainfall (Ganjurjav et al., 2020) and also over two years of study in a grassland (alpine meadow), China (Zhu et al., 2016), warming was reported to delay reproductive phenology (budding, and flowering). These two grasslands are drier than our mesic grassland with the latter recording a lower mean annual precipitation of 430 mm compared to ours of 838 mm. This implies that despite the same duration of study as ours, the amount of rainfall over the long term and during the growing season of the study was a determining factor in aiding the warming effect aggravating water stress or offsetting its negative effects on the plant communities. As a result of higher rainfall in our study area, the warming effect was still well pronounced in our study compared to theirs.

These results concurred with the studies performed in steppes, prairies, and alpine meadows where experimental warming lengthened the duration of flowering (Ganjurjav et al., 2020; Ma et al., 2022; Zhu et al., 2016; Zhu et al., 2017). The warming chambers used in this study warmed to between 1.5 to 2 degrees during the day only, which is in line with other studies which recorded that warming advanced phenological events (Augspurger & Zaya, 2020; Hughes, 2000; Jiang et al., 2016; Post et al., 2008; Suonan et al., 2017; Wolkovich et al., 2012). The main effect of different rainfall regimes and their interaction with warming had no significant effect on the total number of buds per tiller, where the number of buds per vegetative tiller and the number of buds per flowering tiller also did not differ significantly across the treatments. The synergistic effect expected from warming and drought to reduce the bud bank to an extent greater than when either disturbance is applied singly was not observed. Similar responses were observed in the tallgrass prairie of North America where the number of buds per grass tiller was constant under a multi-year drought (Qian et al., 2021). In opposition, the study carried out in the Songnen Grassland of China over a twelve-year period discovered a significant increase in the density of buds in the belowground bud bank as a result of nocturnal warming (Li et al., 2014). The result of this research is in tandem with the study of two semiarid grasslands in China, which discovered that below-ground buds were not significantly affected by a four-year experimental drought (Qian et al., 2022b).

Additionally, in a tallgrass prairie in the United States, the density of the belowground bud bank was unresponsive in the two years after a severe drought (van der Weide et al., 2014). The study location (van der Weide et al., 2014) has a mean annual precipitation of 880mm, comparable to our mesic grasslands' mean annual precipitation of 838mm. This suggests that bud bank density is a result of long-term selective pressures caused by water availability (Ott & Hartnett, 2012a). Therefore, it is anticipated that the buds found at the tiller bases will act as a buffer against short-term variations in precipitation and temperature in the presence of disturbances like drought and high temperatures for bud banks.

Since graminoid tillers are produced intravaginally (i.e., they form tillers from within the persistent leaf sheath of the present tiller, which makes it easy to connect buds with an individual tiller), buds found at these tiller bases (initiated aboveground rhizomes) (Klimeš & Klimešová, 2002) are shielded by leaf sheaths and are adapted to moisture-limited ecosystems (Qian et al., 2017). Bud number and other bud bank traits influence how plant community bud banks respond to dry periods. Plants with bud-bearing organs are better suited to dry habitats than those that do not reproduce vegetatively. Large buds such as bulbs are an example where the apical meristems are shielded by leaf bases, retain moisture, and are particularly adapted to seasonally dry habitats (Qian et al., 2017). Likewise, tiller bases as found in our study are adapted to aridity, which makes them insensitive to short-term drought. Through regulating the population regeneration patterns, ecosystem functioning, and community dynamics, research in recent years has suggested that below-ground bud banks could play a vital role in determining the response of vegetation to the effect of drought and other disturbances (van der Weide et al., 2014). As the main source of tiller production, bud banks in grasslands aid in the ecosystem's recovery after severe disturbances such as drought (Ott et al., 2019b; Qian et al., 2022b). Drought can change structural attributes, like the number of buds and tillers, decrease ecosystem functioning, and aboveground net primary productivity (ANPP), and alter patterns of biomass allocation in most dry habitats. These changes can have long-term post-drought effects on ecosystem function (Wang et al., 2019).

The results of this study could be attributed to the fact that in the energy allocation strategy of these grasses, energy is being transported to both aboveground parts and belowground parts resulting in a balanced growth strategy (Dalgleish et al., 2012). This agrees with and indirectly supports previous studies. That is, perennial grasses can stimulate how their belowground bud-bearing organs grow by increasing the biological activities of the roots, where energy is passed on to the belowground bud-bearing organs and stored in rhizomes for the viability of the preserved meristems for adverse seasons (Ott et al., 2019b). Perennial grasses can endure harsh climates through the senescence of aboveground tissues and persist through unfavourable conditions with belowground bud banks in their dormant states (Pérez-Llorca & Munné-Bosch, 2021). These clonal growth patterns might be a form of adaptation, that enables plants to persist in adverse seasons (Qian et al., 2023). The belowground bud banks in these perennial herb-dominated ecosystems act as a buffer to efficiently withstand short-term seasonal fluctuations (Ma et al., 2022).

The similarity in the proportion of buds per flowering tiller and buds per vegetative tiller observed in this study collectively suggests a double allocation strategy to recruit from seeds and belowground buds which has been demonstrated to increase the maintenance, persistence, and stability of some species populations (Chen et al., 2015; Kingsolver, 1986). This study contradicts studies carried out in Botswana, where the reproductive strategy of grasses showed more allocation of resources to reproduction by seed than to reproduction by vegetative means in comparison with species in North American semiarid grasslands where a lower percentage of buds per flowering tiller and higher belowground bud densities per vegetative tiller were observed suggesting that in the North American ecosystems, grasses maintain their bud banks as an important form of adaptive strategy (Hartnett et al., 2006; Tuomi et al., 1994). The relative allocation to seed reproduction versus vegetative reproduction varies depending on the species' life history, where perennial (longer-lived) grasses showed higher numbers of buds per vegetative tiller as compared to flowering tillers relative to shorter-lived annual grasses (Dalgleish et al., 2012).

Sward density is affected by disturbances like grazing and drought through enhanced bud mortality (Flemmer et al., 2003) or by a reduction in the production of rhizomes (van der Weide & Hartnett, 2015). Therefore, repeated exposure of the aboveground vegetation to these disturbances tends to make plant communities allocate more resources to belowground structures which are used for recruitment of the aboveground shoot population (Qian et al., 2023). Bud banks differ from soil seed banks in that they are formed through the vegetative growth of plants with an interconnection to the aboveground parent plant parts. Seed bank size and composition are determined by the corresponding aboveground vegetation (Wellstein et al., 2007).

In the present study, the total number of buds per tiller and number of tillers did not change significantly with the single effect of rainfall variations and their combination with warming. This indicates that both the aboveground and belowground structures work pari passu for an effective functioning of the vegetation where the belowground bud bank might be functioning as a buffer for the effects of warming and drought and could help to regenerate the population and restore vegetation following the effect of these disturbances. These results could be traceable to the variations in rainfall and temperature, growing season length and species composition. Since perennial grasses predominate in the mesic grassland where our study area is located, it is possible that the perennial grasslands responses to drought may be aided by the belowground bud bank stability, with changes in individual species abundance maintaining the overall density of the bud bank and ecosystem function (van der Weide & Hartnett, 2015).

Although many perennial grass species allocate most of their resources to vegetative reproduction, seed production is crucial for long-distance dispersal, maintaining genetic diversity and lowering intraspecific competition (Benson & Hartnett, 2006; Hartnett et al., 2006; Ott & Hartnett, 2011). The functional traits of grass species, specifically their life history and photosynthetic pathways (C_3 and C_4), influence how they respond phenologically to climate change such as warming and rainfall fluctuation (Munson & Long, 2017). In C_4 grass species, high temperatures can enhance photosynthesis, and increasing precipitation allows these grasses to invest more in growth and belowground structures, which may lead to a delay in their time of flowering, whereas C_3 species often have their time of flowering advanced under increasing temperatures (Munson & Long, 2017; Sherry et al., 2011). C_4 grass species are late-season species and require an optimum temperature for growth and other phenological processes, which causes their responses to reduced precipitation as a result of increased temperature to differ. Increased temperature leads to reduced soil moisture available to C_4 species resulting in earlier or withheld phenological processes, while the response of early-season C_3 grass species to combined warming and reduced water availability causes a delay in the plant phenological events (Munson & Long, 2017; Sherry et al., 2011).

Based on the ecoregions, phenological responses can also differ. For example, grasses growing in relatively cold regions like the northern latitudes advance phenophases under warmer conditions, whereas those growing in relatively warmer regions such as the southern latitudes delay phenology under warm temperatures (Munson & Long, 2017). This is to say that apart from photosynthetic pathways and life history, ecoregions play an important role in determining plant phenological responses. In water-limited ecoregions, precipitation interacts with temperature and acts as a major factor in phenological development (Gerst et al., 2017).

3.5. Conclusion

Overall, studies that combine altered rainfall with warming are needed to enhance our understanding of the grass phenological shifts and their regenerative responses from bud banks. The need for understanding the mechanisms behind plant phenology and their regenerative responses from bud banks under the effects of increased warming and altered rainfall which may occur in Africa, especially in the mesic grassland of South Africa, where this kind of data is deficient, is of great importance.

Findings from this study demonstrate that drought delayed both budding and flowering times in the short term, leading to a reduced reproductive duration. Warming significantly lengthened the reproductive duration, it advanced the time of budding in *Tristachya leucothrix*. This means that the response of grass phenology to the warming effect was species-specific in our study. The budding and flowering times and reproductive duration of these species were significantly different across years where it differed with the timing of rainfall onset in the growing seasons.

The effect of timing of rainfall onset resulted in no significant difference in the number of buds per vegetative and reproductive tiller, with no significant difference in the total number of tillers per tuft under warming and drought as compared with control. These findings show that grass bud banks are adaptable and can modify their regenerative responses according to the timing of climatic events and that the temperature and rainfall conditions imposed by the treatments may not have driven the vegetation beyond the variability in precipitation and warming to which it is adapted. Our study has shown that the effects of modified rainfall regimes and warming on grass phenology were apparent in the short term. This suggests that some aspects of grass species phenology in South African mesic grasslands are sensitive to climate change effects in the short term.

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CHAPTER 4: Effects of climate (warming) and long-term management regimes (fire and defoliation) on grass phenology and regenerative responses in mesic grassland

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Abstract

Plant phenology responses to environmental change can alter community structure, inter-species interactions, and ecosystem carbon exchange. In this study, the effect of burning frequency, winter defoliation type (fire/mow), summer defoliation with differing winter defoliation (defoliation time) applied over ~70 years and temperature (warmed and ambient) manipulation on the phenology of grass species vis-à-vis their regenerative responses from bud banks was conducted in a mesic grassland at the Ukulinga Grassland Fire Experiment, Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal. The warming treatment was applied using open-topped warming chambers. Across the two years of warming treatment application, the sensitivity and timing of species phenological responses and bud bank density relative to resource allocation to vegetative versus sexual reproduction were examined. Year, warming, winter defoliation type and defoliation time affected both the timing and duration of budding and flowering. Meanwhile, warming, reproductive status, winter defoliation type, and defoliation time altered the total number of buds per vegetative tiller per tuft compared to the flowering tillers. The late onset of rains (2019/2020) delayed the initiation of buds and shortened duration of budding and flowering ($p < 0.005$). Warming delayed the time of budding and flowering and increased duration slightly ($p<0.005$). Annual winter mow delayed timing and extended duration of budding and flowering as compared to annual winter fire ($p < 0.005$). Summer defoliation frequency quickened the timing and shortened the duration of budding and flowering compared to winter defoliation frequency ($p < 0.005$). The flowering duration for *Themeda triandra* was shortened under annual burning and lengthened under the triennial burn plots ($p < 0.005$). In ambient plots, vegetative status had more buds per tiller and number of tillers per tuft compared to warmed plots. Annual winter defoliation by fire had the greatest number of tillers per tuft for *Heteropogon contortus* and the lowest recorded in the annual winter defoliation by mow plots. A greater number of buds per tiller was recorded under the summer defoliation plots as against the winter defoliation plots. Summer defoliation plots had a greater number of tillers per tuft for *H. contortus* than the winter defoliation plots. The results of this study indicate that the type, time, and frequency of defoliation and their interaction with the effect of climate change have a notable influence on the budding and flowering periods of the species studied, ultimately impacting the length of their reproductive cycle and altering the ratio of vegetative to flowering reproductive status.

Keywords: **Warming chamber; Phenological Events; Plant Vegetative Reproduction; Plant Sexual reproduction; Ukulinga Research Farm.**

4.1 Introduction

Plant phenology refers to the timing of life cycle events in plants, influenced by biotic factors like competition, diseases, and pests, and abiotic factors such as soil properties, slope, and topography (Badeck et al., 2004; Inouye, 2008; Richardson et al., 2013). Plant phenology varies within communities, and the individual plant's phenology significantly influences the structure and functioning of the ecosystem (Richardson et al., 2013). Changes in environmental conditions can cause plant phenological responses, leading to shifts in competitive interactions, carbon cycling, water relations, and nutrient uptake among species in the ecosystem (Piao et al., 2019; Reyer et al., 2013). Plant phenology is widely recognized as an indicator of climate change because it involves changes in growth and developmental events (Garonna et al., 2014; Zhao et al., 2022).

Global warming can alter plant phenological events, such as budding, flowering, fruiting, seed dispersal, and senescence. This can affect the fitness and functioning of ecosystems (Buonaiuto & Wolkovich, 2021; Khorsand Rosa et al., 2015). Warming can lead to an earlier onset of the phenological sequence and directly enhance growth by accelerating metabolic reactions; however, it can also hinder growth by reducing soil moisture availability (Ernakovich et al., 2014b; Walck et al., 2011b). The amount of water lost through transpiration can affect a flower's blooming period (Wullschleger et al., 2002). Since flowering plant species rely heavily on the timing of their phenological phases, any changes caused by global warming are expected to impact ecological interactions significantly. These changes may affect when seeds are dispersed, how pollinators compete, and the pollination process (Traill et al., 2010b). Changes in the interactions between plants and dependent organisms can affect their survival. Such changes can impact the ecosystem's productivity and carbon sequestration capability (Catovsky et al., 2002; Hopkinson et al., 2012; Hovenden et al., 2008; Molnár et al., 2012).

Long-term temperature increases can affect the timing of plant phenological processes in different ecosystems (Diez et al., 2012; Prevéy, 2020; Samplonius et al., 2020; Walther et al., 2002b). When temperatures increase, they can exceed the species flowering heat accumulation threshold, which can induce earlier flowering.

Grasses can regenerate through asexual or sexual means by growing from belowground meristems or producing seeds (Ding et al., 2021). In perennial mesic grasslands, the primary driver of grass community dynamics and productivity is asexual reproduction through belowground bud banks (Qian et al., 2022b). When disturbances such as fire or herbivory occur, changes in soil water and nutrient availability can affect population regeneration patterns, dynamics, and overall ecosystem function, all of which are regulated by belowground bud banks (Ott et al., 2019b; van der Weide et al., 2014). As important as bud bank is, it can be reduced or limited when disturbances aboveground occur too frequently and at an early stage of the plant growth. The depletion of these buds may have resultant effects on the vegetation growth as the timing of these disturbances (fire and grazing) may occur at the same time with the early growth stage of the buds leading to an inhibition of their production and maintenance (Russell et al., 2015). Belowground buds are the primary source of tiller and ramet production, and they may assist in ecosystem recovery after severe events such as drought and warming (Ding et al., 2021). At the nodes of each parent tiller, lateral buds emerge to create new tillers, ensuring the continued growth and survival of the grasslands (Everson et al., 2021; Zhai et al., 2022). For perennial grasslands to persist under extreme climate conditions, the survival of the community of meristems above and below ground is crucial.

During severe weather conditions, most herbaceous flowering plants survive by allowing their aboveground tissues to atrophy while relying on dormant bud-bearing structures belowground to regenerate (Lubbe, 2019; Qian et al., 2017). These communities can rapidly adapt to variations in weather conditions with associated environmental changes, such as fluctuations in soil moisture and nutrient availability (Clarke et al., 2013; Qian et al., 2017; van der Weide et al., 2014), however, long-term changes in environmental conditions may negatively influence these plants (Eckardt et al., 2023; Iler et al., 2019).

Numerous studies worldwide have explored the impact of warming on plant species using open-topped chambers (Chen et al., 2023; Lyons et al., 2020; Peng et al., 2020). In several International Tundra Experiment (ITEX) studies, plant lifecycle events, including budding and flowering, occurred earlier with warming (Kelsey et al., 2021; Liu et al., 2021; Ma et al., 2021; Myers-Smith et al., 2019; Roslin et al., 2021; Staudinger et al., 2019; Stuble et al., 2021). Recent research indicates that plant species exhibit individual responses to warming, with some showing advanced and others delayed phenophases (Bjorkman et al., 2015; Jarrad et al., 2008; Winkler, Grossiord, et al., 2019).

Despite the extensive literature available on phenology and bud banks in grasslands, there is a lack of experimental studies investigating the combined impact of warming under different types, timing and frequencies of defoliation. The combined effect of warming, fire, and mowing frequency on grass phenology and their regenerative responses from bud banks in mesic grasslands has not been quantified.

Therefore, this research sought to assess the effects of warming under different defoliation types, frequencies and timing on grass phenology and regenerative responses from bud banks in the mesic grasslands of South Africa. The objectives of this study were to (i) examine the effect of warming on belowground bud bank densities and the phenological development of three locally common grass species; *Tristachya leucothrix*, *Themeda triandra* and *Heteropogon contortus*, (ii) assess the influence of burning frequency (with and without warming) on belowground bud bank densities and the phenological development (iii) examine the effect of winter defoliation type (fire/mow) (with and without warming) on belowground bud bank densities and phenological development (iv) evaluate how summer defoliation with differing winter defoliation (with and without warming) affect the phenological events and belowground bud bank densities in allocating resources to vegetative versus reproductive tillers in the mesic grasslands of South Africa.

4.2 Materials and Methods

4.2.1 Study area

The experiment was conducted at the Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa (30°24′ S, 29°24′ E), a region with summer rainfall that receives an average of 838 mm of precipitation annually (Ward et al., 2020a). The average annual lowest temperature is 8.8 °C and occurs in July during the mild winters, while the average annual maximum temperature of 26.4 °C occurs in February during the hot summers (Ward et al., 2020a). These climatic variables result in a growing season spanning October to April. The vegetation is grassland classified as KwaZulu-Natal Hinterland Thornveld where *Vachellia sieberiana* is dominant alongside *Hyparrhenia hirta*, *Themeda triandra* and other herbaceous plants (Mucina & Rutherford, 2006c). In the absence of fire, the dominant grass species is *Aristida junciformis*, while *Themeda triandra*, *Tristachya leucothrix* and *Heteropogon* *contortus*, with sparse tree cover, is common with regular burning (Morris & Fynn, 2001b). A C4 photosynthetic pathway is used by all grass species at this site (Ward et al., 2020a).

4.2.2 Experimental design

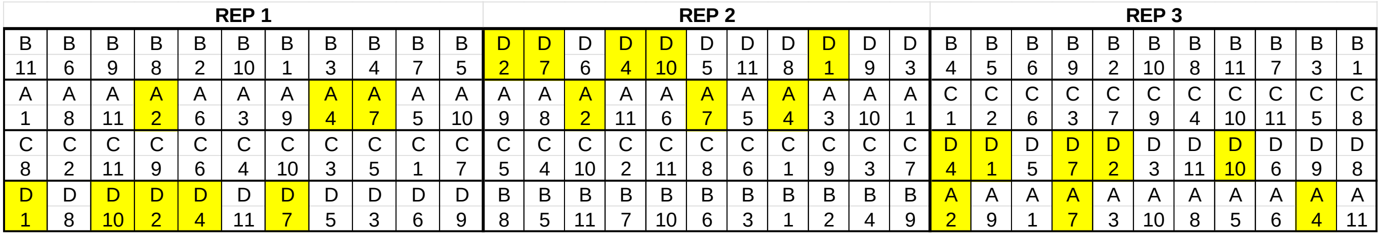
The Ukulinga Grassland Fire Experiment (UGFE), which was started in 1950, used a split-plot, full-factorial design with randomized blocks (three replicates). Within each block, four whole-plot treatments, and eleven subplot treatments were applied, separated by 4-m pathways. As a result, each whole-plot treatment in each block was made up of a row of 11 subplots (13.7 x 18.3 m in size), to which subplot treatments were allocated at random. The selected sub-plots were sampled in the whole plots of A (burned with no summer mowing defoliation) and D (burned with mowing in December and February). The subplots sampled in this study were annual (A2), biennial (A4), and triennial winter burning (A7), biannual mowing (D1), biannual mowing with an annual winter burn (D2), biannual mowing with a biennial winter burn (D4), biannual mowing with a triennial winter burn (D7), and biannual mowing with an additional annual winter mow as a substitute for burning (D10) (Table 4.1 and Fig. 4.1) (R. Fynn et al., 2004).

Table 4.1: The treatment plan of the UGFE showing the treatment codes (TC) against their description and time of application

TC	Time executed			Treatment groups		
	August	December	February	Burning frequency	Defoliation time/type	Defoliation frequency
A2	Annual burn			Annual burn	Winter fire	6 times per 6 year cycle
A4	Biennial burn			Biennial burn	Winter fire	3 times per 6 year cycle
A7	Triennial burn			Triennial burn	Winter fire	2 times per 6 year cycle
D1		Mowing	Mowing	Unburned	Summer mow	12 times per 6 year cycle
D2	Annual burn	Mowing	Mowing	Annual burn	Summer mow & winter fire	18 times per 6 year cycle
D4	Biennial burn	Mowing	Mowing	Biennial burn	Summer mow & winter fire	15 times per 6 year cycle
D7	Triennial burn	Mowing	Mowing	Triennial burn	Summer mow & winter fire	14 times per 6 year cycle
D10	Annual winter mow	Mowing	Mowing	Unburned	Summer mow & winter mow	18 times per 6 year cycle

Whole-plot	
A	**No mowing**
B	**One cut early in season (December)**
C	**One cut end of February**
D	**Two cuts, one at B (December) and one at C (February)**
Sub-plot	
1	**Control**
2	**Annual burn in the first week of August**
3	**Annual burn after the first 12.5 mm of spring rain**
4	**Biennial burn in the first week of August**
5	**Biennial burn after the first 12.5 mm of spring rain**
6	**Biennial burn in autumn**
7	**Triennial burn in the first week of August**
8	**Triennial burn after the first 12.5 mm spring rain**
9	**Triennial burn in autumn**
10	**Annual mowing in the first week of August**

11	**Annual mowing after the first 12.5 mm spring rain**



REP 1											REP 2											REP 3										
B 11	B 6	B 9	B 8	B 2	B 10	B 1	B 3	B 4	B 7	B 5	D 2	D 7	D 6	D 4	D 10	D 5	D 11	D 8	D 1	D 9	D 3	B 4	B 5	B 6	B 9	B 2	B 10	B 8	B 11	B 7	B 3	B 1
A 1	A 8	A 11	A 2	A 6	A 3	A 9	A 4	A 7	A 5	A 10	A 9	A 8	A 2	A 11	A 6	A 7	A 5	A 4	A 3	A 10	A 1	C 1	C 2	C 6	C 3	C 7	C 9	C 4	C 10	C 11	C 5	C 8
C 8	C 2	C 11	C 9	C 6	C 4	C 10	C 3	C 5	C 1	C 7	C 5	C 4	C 10	C 2	C 11	C 8	C 6	C 1	C 9	C 3	C 7	D 4	D 1	D 5	D 7	D 2	D 3	D 11	D 10	D 6	D 9	D 8
D 1	D 8	D 10	D 2	D 4	D 11	D 7	D 5	D 3	D 6	D 9	B 8	B 5	B 11	B 7	B 10	B 6	B 3	B 1	B 2	B 4	B 9	A 2	A 9	A 1	A 7	A 3	A 10	A 8	A 5	A 6	A 4	A 11

Figure 4.1: The plot plan of the UGFE at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The plots used for this study are highlighted. Letters are described in Table 4.1.

The warming treatment was applied at a sub-subplot level with warmed and ambient sub-subplots, which were 2m by 2m in size, and replicated in each plot and block. Warming was applied using hexagonal open-topped warming chambers constructed from 2mm thick clear polycarbonate sheeting (Mu et al., 2017b; Wu et al., 2011b).

4.2.3 Study Species

Three dominant grass species; *Tristachya leucothrix, Themeda triandra* and *Heteropogon contortus* were used for this study. Three perennial C4 grass species of *Themeda triandra* Forssk, *Heteropogon contortus* Beauv. ex Roemer and J. A. Schultes and *Tristachya leucothrix* Trin. ex Nees, were chosen as being amongst the most common and widely distributed species naturally occurring locally (Ghebrehiwot et al., 2014). These C4 grass species (Poaceae) are characterised by meristematic growth forms which are at different locations at or immediately below the soil surface (Nelson & Moore, 2020). The positioning of these growth zones makes the grass species resistant and varying in their responses to biomass loss through defoliation by fire or mowing frequency (Bredenkamp et al., 2002). These grasses are short and palatable. *Themeda triandra* and *H. contortus* are fire tolerant and in the absence of regular burning, are replaced by species such as *T. leucothrix* and *Aristida junciformis* (Kirkman et al., 2014b). *Themeda triandra* and *H. contortus* are decreaser species which decrease with over- or under-utilized grasslands, while *Tristachya leucothrix* is an increaser I species which increases with under-utilized grasslands (Everson et al., 2021).

4.2.4 Phenological measurement

At the beginning of the 2019/2020 and 2020/2021 growing seasons, three tufts of each study species were randomly selected in the warmed and ambient sub-subplots under different burning and mowing frequencies. Once a week the marked grass tufts were examined and scored according to their phenological stage. Tuft phenology was categorised into six stages: the greening stage, stage 0 for sprout-out leaves, stage 1 for the plant booting stage, stage 2 for the presence of spikelets, stage 3 for exerted anthers or styles, and stage 4 for the absence of anther and styles where they have served their functions and fallen off (Dunne et al., 2003b; Xia & Wan, 2013). Every marked tuft with buds was counted and given a phenological score. Data collection ended when all the tagged tufts of the three study species reached phenological stage 4.

4.2.5 Bud bank sampling

4.2.5.1 Field and laboratory methods

Bud bank sampling was carried out in September 2020, the second year of treatment application. Past work indicates that 90% and more of the belowground, overwintering buds emerge into vegetative tillers at the beginning of the growing season (Zhai et al., 2022). Two complete tufts of reproductive tillers (those with mature inflorescences and dispersed seed) and two complete tufts of vegetative (nonflowering) tillers were randomly selected for each study species. In this grassland, most of the buds are immediately below the soil surface (0-30 mm). Thus, all belowground components were excavated to a depth of 30 mm (Qian et al., 2017) while keeping the aboveground plant parts intact. The samples were rinsed to remove soil, placed in plastic bags, taken to the laboratory, and stored at 4 °C for subsequent analysis. The tufts were separated into tillers for easy dissection and a thorough examination of the axillary buds located at the shoot base of each tiller (Qian et al., 2017, 2021). Buds and tillers from each tuft were examined under a dissecting microscope while the roots were trimmed to allow a detailed investigation of the belowground structures. Each reproductive and vegetative tuft was separated into tiller segments, and buds were counted as either reproductive or vegetative buds per tiller.

4.2.6 Statistical analysis

In examining the effects of warming, winter defoliation type, defoliation time (summer/winter), burning frequency and year and their interactions on the time of budding (TB), time of flowering (TF), duration of budding (DB) and duration of flowering (DF) of the three study species, linear mixed-effects models (LMMs) was used. The three study species were not pooled together during the analysis but was analysed separately for each species. The TB, TF, DB and DF for each species were treated as response variables and warming, winter defoliation type, defoliation time (summer/winter), burning frequency and year as fixed factors. The same analysis was used for the effect of warming, winter defoliation type, defoliation time (summer/winter), burning frequency and status and their interactions on the number of buds per tiller and tillers per tuft for each species. Although, this data (number of buds per tiller and tillers per tuft) is in the form of a count data which would be fit for a Poisson distribution.

Poisson distribution is often used when data is skewed. it was stated that Poisson distribution can be used when data is not normal, is highly skewed and has outliers (Green, 2021).
Our data was not skewed, thus, the use of the Gaussian method because the data fitted a normal distribution. This made our analysis appropriate. Data distribution was checked prior to analysis and was found to meet the requirements of a Gaussian distribution. Thus, the analysis used was appropriate. We included some interactions as part of the fixed factors in order to address the questions we were interested in which is to assess the effect of warming under different defoliation types, frequencies and timing on grass phenology and regenerative responses from bud banks. We looked at the winter defoliation type (DEFO) effect with and without warming (WARM) on the timing and duration of budding and flowering and on the number of tillers per tuft and number of buds per tiller of the study species with their vegetative or reproductive status (STATUS) over two years (YEAR). For this reason, we have included only the DEFO*WARM, DEFO*YEAR, WARM*YEAR and DEFO*WARM*YEAR interactions for phenology and DEFO*WARM, DEFO*STATUS, WARM*STATUS and DEFO*WARM*STATUS for the bud banks. Also, on defoliation time (summer/winter) (DEFO) and burning frequency (BURN) with and without warming (WARM) on the timing and duration of budding and flowering and the number of tillers per tuft and number of buds per tiller of the study species with their vegetative/reproductive status (STATUS) over two years (YEAR). For this reason, we have included only the DEFO*WARM, DEFO*YEAR, WARM*YEAR, DEFO*WARM*YEAR, BURN*WARM, BURN*YEAR and BURN*WARM*YEAR interactions for phenology and DEFO*WARM, DEFO*STATUS, WARM*STATUS, DEFO*WARM*STATUS, BURN*WARM, BURN*STATUS and BURN*WARM*STATUS for the bud banks. In fitting the LMMs, block was regarded as a random effect. The LMMs fitting was conducted using lmer function in lme4 package in R and the corresponding *F*- and *P*-values were obtained from the ANOVA function. We decided to use this LMMs because it was a better fit with a lower AIC than GLMMs. The model residuals were checked for normality and variance homogeneity assumptions, where *p*-values > 0 .05 indicate no violation of homogeneity and normality assumptions. Where the model showed significance, post-hoc comparisons were performed by emmeans and multicomp. All analysis

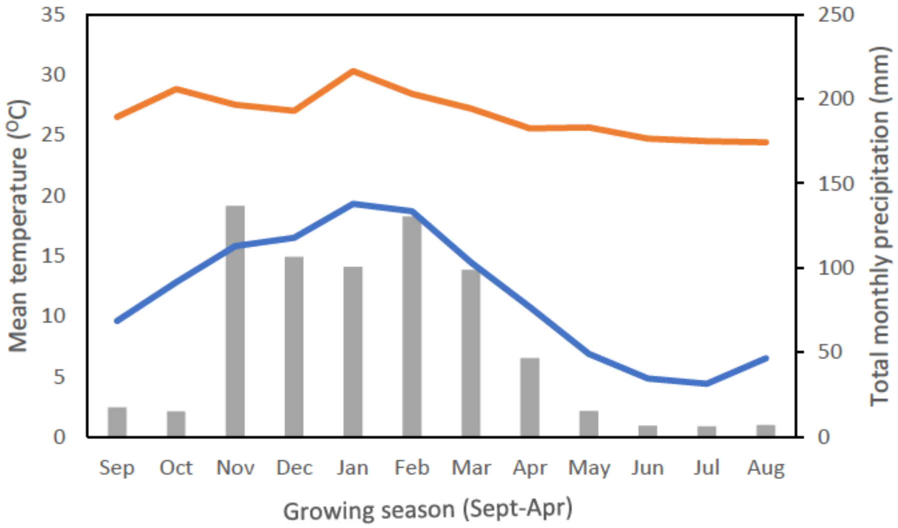
was carried out in R Studio (version 4.2.3). The LMMs were performed using the package "lme4" (Bates et al., 2015) and "lmerTest", respectively (Kuznetsova et al., 2017) . For plotting, 'ggplot2' was used.

4.3 Results

4.3.1 Climate conditions

The description of the figures (4.2 A & 4.2 B) can be found under the results section of chapter three of this thesis.

A)



B)

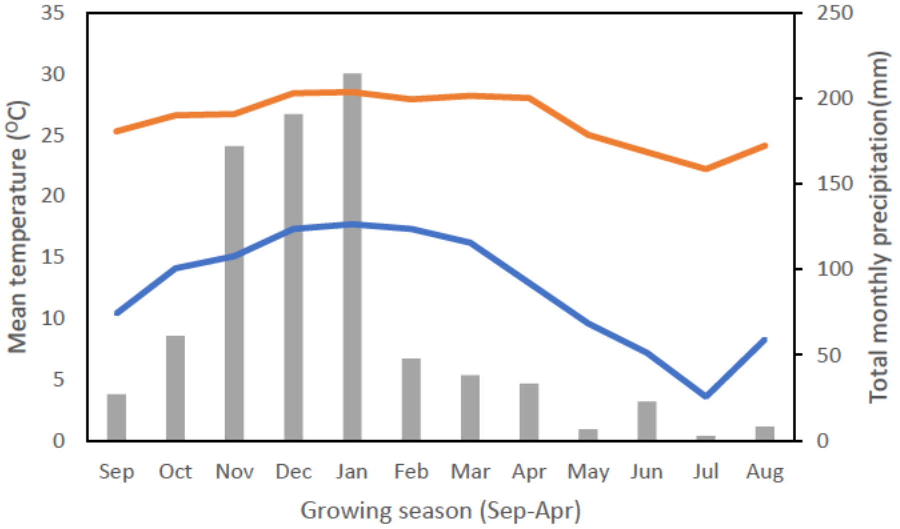
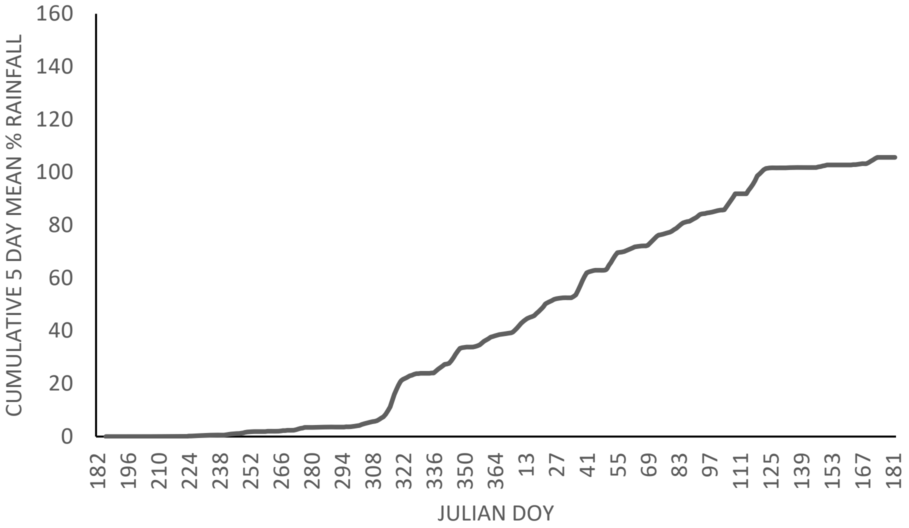


Figure 4.2: Growing season rainfall and temperature at Ukulinga Research Farm, KwaZulu-Natal, South Africa for the (A) 2019/2020 and (B) 2020/2021 growing seasons. Mean monthly precipitation as bars and annual maximum temperature (orange) are shown, and minimum temperature (blue) as lines.

4.3.2 Phenology

The description of the figures (4.3 A & 4.3 B) can be found under the results section of chapter three of this thesis.

A)



B)

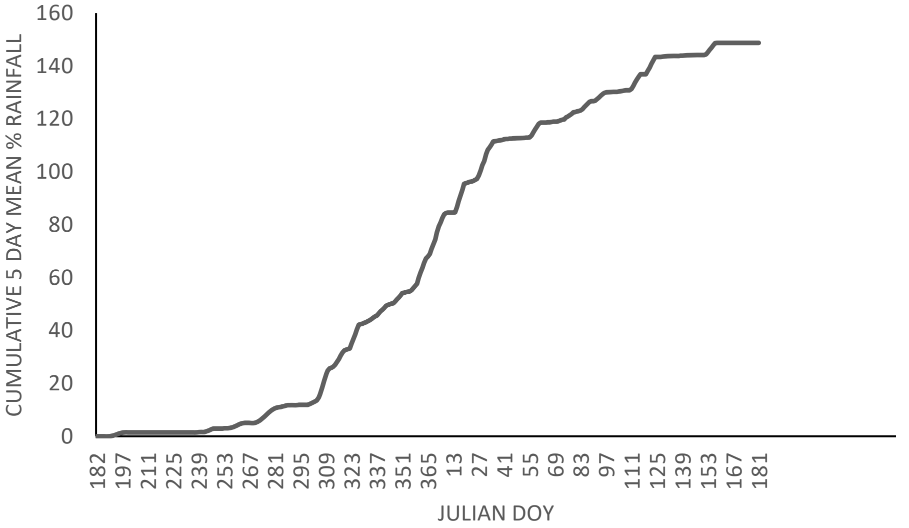


Figure 4.3: Rainfall onset and retreat periods and the length of the growing season at Ukulinga Research Farm, KwaZulu-Natal, South Africa with the use of a relative definition method for the (a) 2019/2020 and (b) 2020/2021 growing season.

4.3.3 Winter defoliation type effect on the timing and duration of budding and flowering

There was a later onset of budding in the first year, but then a report of different times/delays for annual winter mowing (which was delayed more) than for annual winter burning and defoliation (which were delayed less by later onset of rain).

The late onset of rains in the 2019/2020 growing season delayed the time of budding by 38 days in both *Tristachya leucothrix*, by 35 days in *Heteropogon contortus* and by 34 days in *Themeda triandra* and delayed flowering by 33 days in *T. leucothrix*, 28 days in *T. triandra* and 26 days in *H. contortus* as compared to the early onset of rains in the 2020/2021 growing season. Duration of budding responded similarly, being shorter by 5, 6 and 8 days in *T. leucothrix*, *T. triandra* and *H. contortus* respectively, while the duration of flowering was shortened by 8 days in both *Tristachya leucothrix* and *Heteropogon contortus* and by 10 days in *T. triandra* in 2019/2020 as compared to 2020/2021.

For all three study species, warming delayed the time of budding and flowering by 1 and 2 days and increased their duration slightly. The winter defoliation type significantly affected the time and duration of budding and flowering over the two years ($p < 0.05$, Table 4.2, 4.3, 4.4 & 4.5). Annual winter burning budded and flowered first while annual winter mowing budded 3 to 7 days and flowered 8 to 13 days later. The duration of budding and flowering was shortened under the annual winter burning and annual winter mowing extended budding by 3 to 6 days and flowering by 1 to 3 days.

There was a significant interactive effect of year and winter defoliation type on the time and duration of budding and flowering. For all the study species, the pattern of response for the timing of budding and flowering under the interactive effect of year and winter defoliation type differed between 2019/2020 and 2020/2021. Annual winter mowing budded later by 2 to 9 days than the annual winter burning and no defoliation plots in 2019/2020 with no difference amongst the three levels of winter defoliation type in 2020/2021. Time of flowering for *T. leucothrix, T. triandra* and *H. contortus* was delayed by 17, 9 and 5 days in 2019/2020 and 9, 6 and 10 days in 2020/2021 respectively, under the annual winter mowing as compared to the annual winter burning and no defoliation plots.

The pattern of response for the duration of flowering under winter defoliation type differed amongst the study species over the years. In 2020/2021, the duration of flowering for *T. triandra* was extended by 3 days under the annual winter mowing with no differences observed amongst the three levels of winter defoliation in 2019/2020. For *H. contortus* duration of flowering was different between both years where in 2019/2020, it was lengthened by a day and was shortened by a day in 2020/2021 under the annual winter mowing as compared to the annual winter burning and no defoliation. Interactive effects of year, winter defoliation type and warming were significant on the duration of budding for the study species.

Duration of budding for the three study species responded differently to winter defoliation type under different warming levels across the years. Duration of budding for the three study species was extended by 3 to 7 days under the annual winter mowing as compared to the annual winter burning and no defoliation across the years. For *Tristachya leucothrix* the warmed plots differed in their responses by an extension of 1 day under the annual winter burning and no defoliation but annual winter mowing showed no differences in 2019/2020, while in 2020/2021, warmed plots differed from ambient plots under three levels of winter defoliation. For *Themeda triandra*, the warmed plots differed in their responses by an extension of 1 day under the annual winter burning and no defoliation but annual winter mowing showed no differences in 2020/2021, while in 2019/2020, warmed plots differed from ambient plots. For *Heteropogon contortus*, the warmed plots differed from ambient plots in their responses by lengthening the duration of flowering by 1 to 2 days under the three levels of winter defoliation type over the two years. (Table 4.2, 4.3, 4.4 & 4.5).

Table 4.2: The results of linear mixed models showing the main effect and interactions of winter defoliation type (DEFO), warming and year on the time of budding for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	18382.656	**<0.001**	6566.406	**<0.001**	1985.537	**<0.001**
WARM(W)	1	22.500	**<0.001**	7.656	**0.011**	1.673	0.210
DEFO(D)	2	269.101	**<0.001**	26.406	**<0.001**	16.198	**<0.001**
Y*W	1	1.406	0.249	0.156	0.696	0.000	1.000
Y*D	2	165.039	**<0.001**	7.656	**0.003**	10.000	**<0.001**
W*D	2	0.351	0.707	0.156	0.856	0.000	1.000
Y*W*D	2	0.351	0.707	0.156	0.856	0.000	1.000

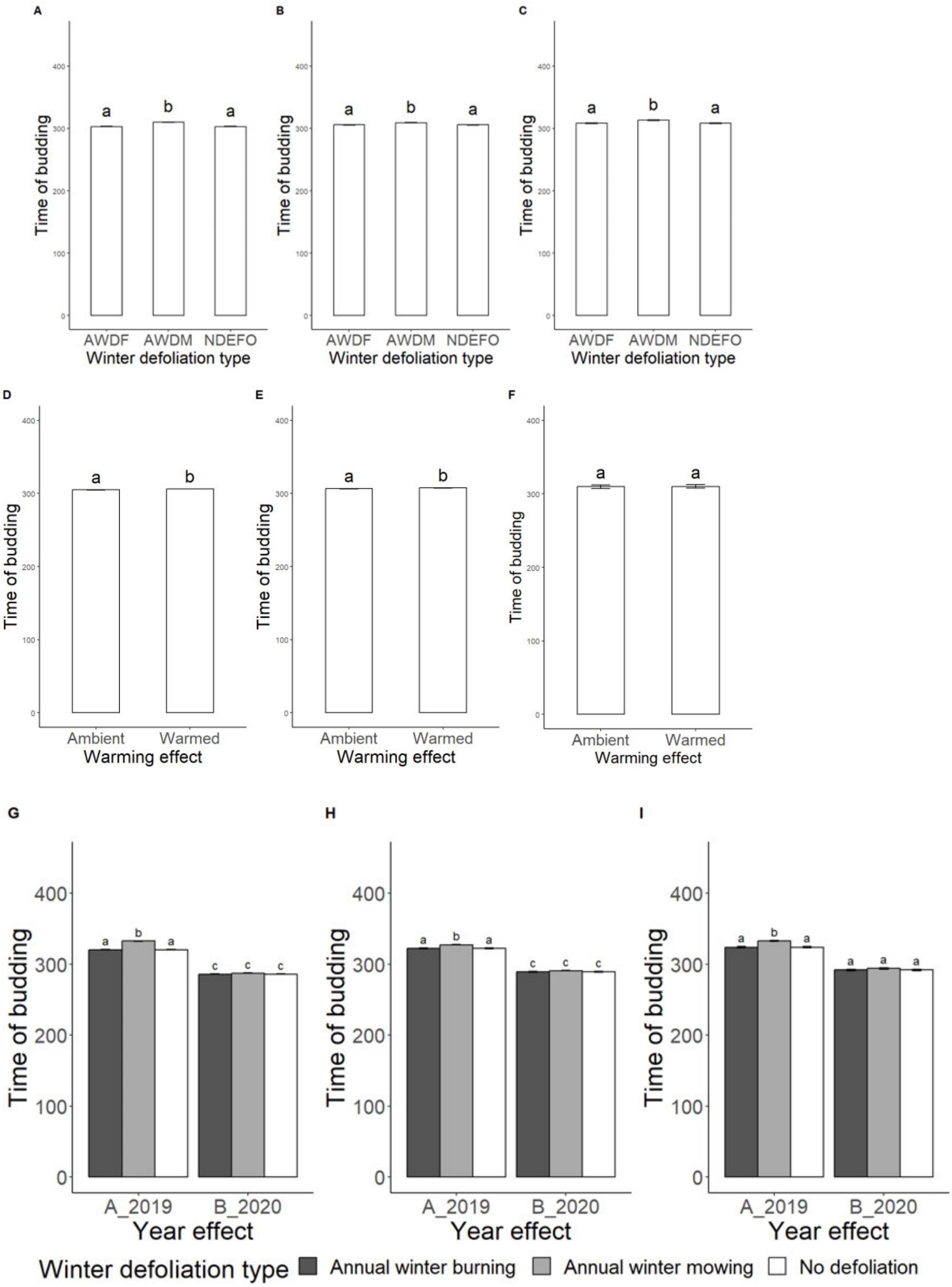


Figure 4.4: Main effect of winter defoliation type (annual winter burning (AWDF), annual winter mowing (AWDM) and no defoliation (NDEFO)) (A-C), warm (D-F) and Y*D (G-I) on time of budding for *T. leucothrix* (a+d+g), ***T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance ($p > 0.05$). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.**

Table 4.3: The results of linear mixed models showing the main effect and interactions of winter defoliation type (DEFO), warming and year on the time of flowering for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	18060.198	**<0.001**	3265.765	**<0.001**	1428.025	**<0.001**
WARM(W)	1	79.207	**<0.001**	16.531	**<0.001**	11.025	**0.003**
DEFO(D)	2	1220.247	**<0.001**	107.959	**<0.001**	51.756	**<0.001**
Y*W	1	3.168	0.090	0.000	1.000	0.225	0.640
Y*D	2	149.752	**<0.001**	5.102	**0.016**	8.556	**0.002**
W*D	2	1.237	0.311	0.000	1.000	0.056	0.945
Y*W*D	2	0.049	0.951	0.000	1.000	0.056	0.945

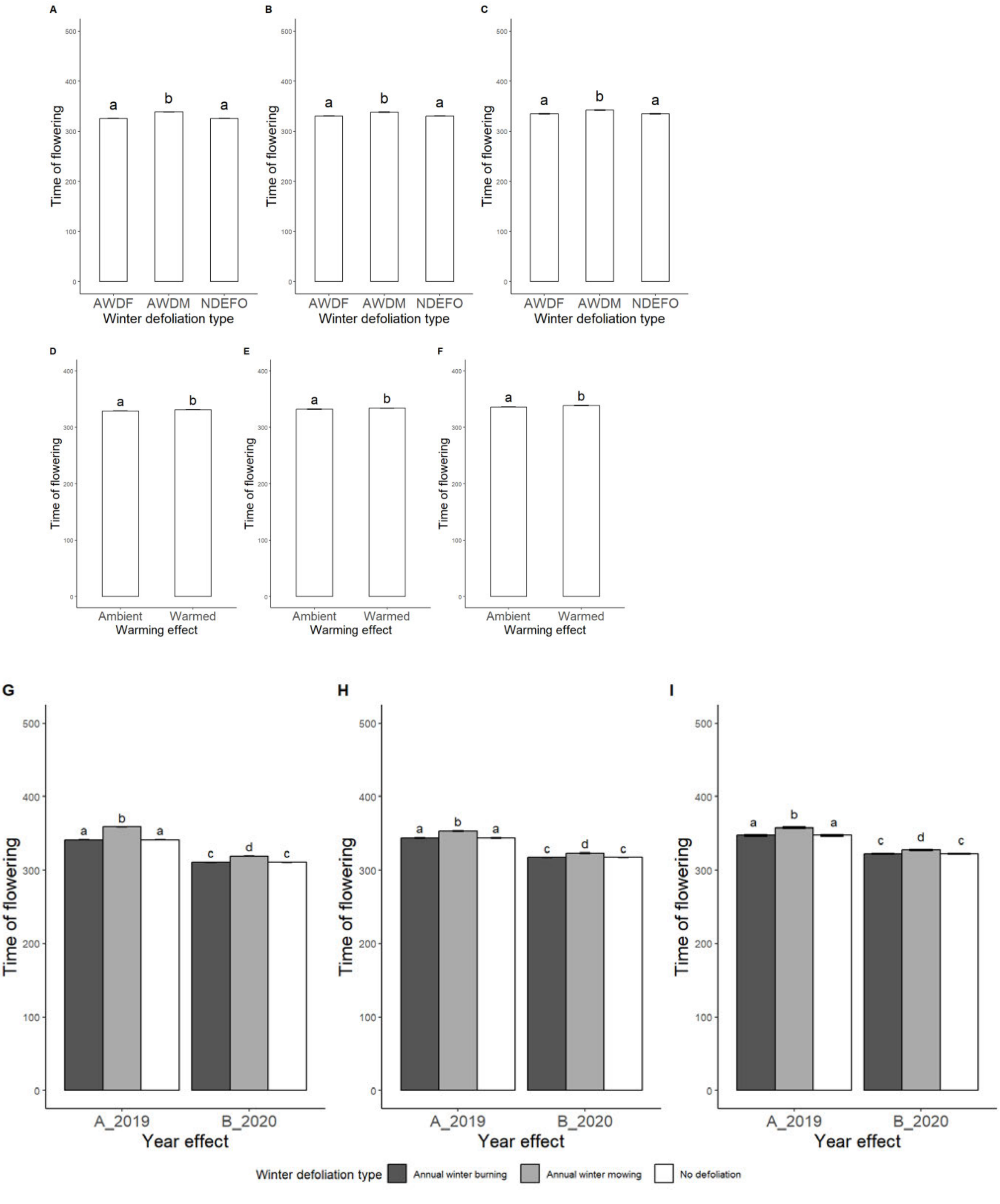


Figure 4.5: Main effect of winter defoliation type (annual winter burning, annual winter mowing and no defoliation) (A-C), warm (D-F) and Y*D (G-I) on time of flowering for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance (p > 0.05). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 4.4: The results of linear mixed models showing the main effect and interactions of winter defoliation type (DEFO), warming and year on the duration of budding for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	6724	**<0.001**	7425.625	**<0.001**	12602.500	**<0.001**
WARM(W)	1	256	**<0.001**	140.625	**<0.001**	360.000	**<0.001**
DEFO(D)	2	5476	**<0.001**	1755.625	**<0.001**	765.625	**<0.001**
Y*W	1	4	0.059	5.625	0.027	22.500	**<0.001**
Y*D	2	100	**<0.001**	0.625	0.545	30.625	**<0.001**
W*D	2	4	**0.034**	5.625	**0.011**	5.625	**0.011**
Y*W*D	2	2	**0.034**	5.625	**0.011**	5.625	**0.011**

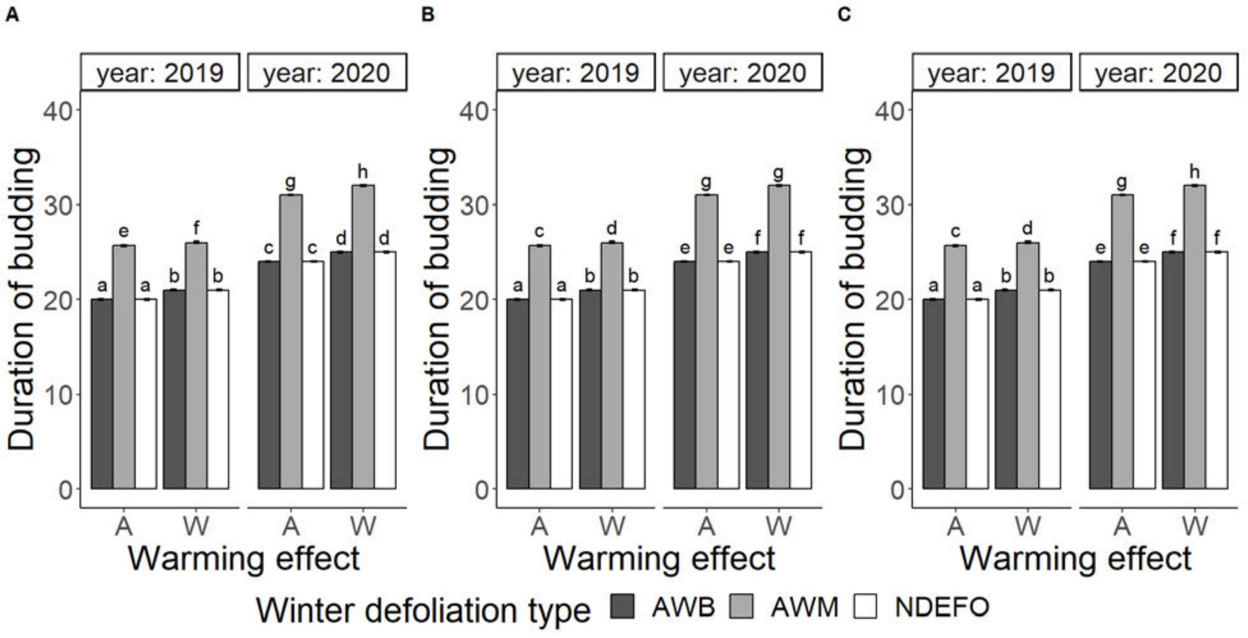


Figure 4.6: Interactive effect of winter defoliation type (annual winter burning (AWB), annual winter mowing (AWM) and no defoliation (NDEFO)), warm and year on duration of budding for a) *T. leucothrix* b) *T. triandra* and c) *H. contortus* on the UGFE. Letters in common indicate non-significance (p > 0.05). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 4.5: The results of linear mixed models showing the main effect and interactions of winter defoliation type (DEFO), warming and year on the duration of flowering for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	787.656	**<0.001**	936.202	**<0.001**	8326.545	**<0.001**
WARM(W)	1	22.500	**<0.001**	8.101	**0.009**	122.909	**<0.001**
DEFO(D)	2	47.851	**<0.001**	12.653	**<0.001**	6.045	**0.008**
Y*W	1	1.406	0.249	0.506	0.484	0.000	1.000
Y*D	2	1.914	0.173	4.208	**0.029**	72.863	**<0.001**
W*D	2	0.351	0.707	0.031	0.968	0.045	0.955
Y*W*D	2	0.351	0.707	0.031	0.968	0.136	0.873

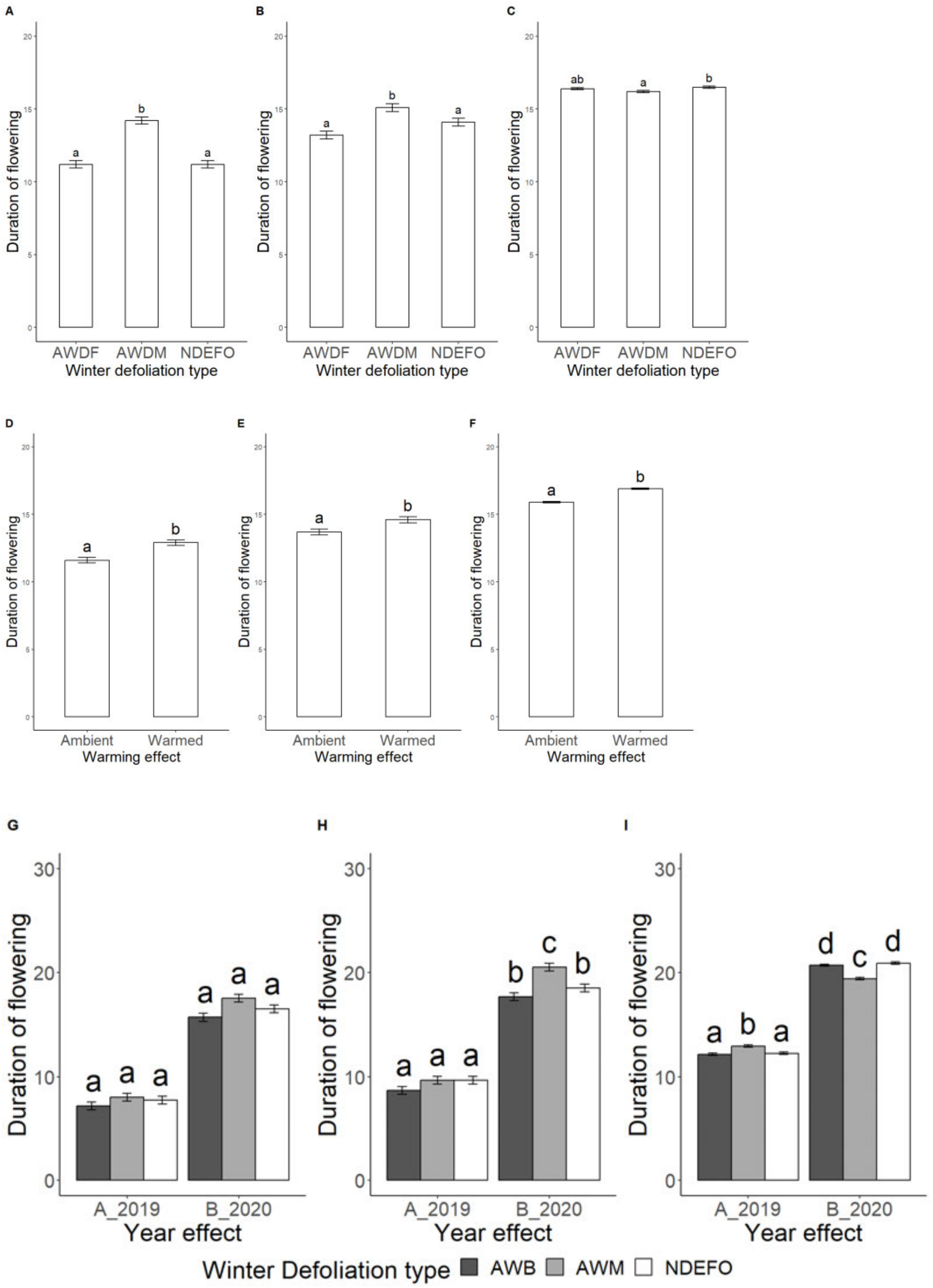


Figure 4.7: Main effect of winter defoliation type, annual winter burning (AWB), annual winter mowing (AWM) and no defoliation (NDEFO) (A-C), warm (D-F) and D*Y (G-I) on duration of flowering for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance (p > 0.05). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

4.3.4 Winter defoliation type effect on the number of tillers per tuft and number of buds per tiller

The total number of buds per tiller and the number of tillers per tuft for the three study species was significantly affected by warming, winter defoliation type, burning frequency, defoliation time (summer/winter) and status (vegetative/flowering). Vegetative status had more buds per tiller and number of tillers per tuft for the three study species as compared to the flowering status. Ambient plots had more buds per tiller and number of tillers per tuft for the three study species as compared to the warmed plots.

Interactive effects of warming and status were found in the number of tillers per tuft for *Tristachya leucothrix* only. The vegetative and flowering status differed significantly under the ambient plots and was not different in the warmed plots, the number of tillers per tuft was higher in the vegetative status under the ambient plots. Winter defoliation type affected only the number of tillers per tuft for *Heteropogon contortus*. Annual winter defoliation by fire had the highest and the lowest recorded in the annual winter defoliation by mow plots ($p < 0.005$, Table 4.6 & 4.7).

Table 4.6: The results of linear mixed models showing the main effect and interactions of winter defoliation type, warm and status on the a) number of tillers per tuft for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	Df	F-value	p-value	F-value	p-value	F-value	p-value
STATUS(S)	2	8.836	**0.007**	7.620	**0.012**	5.811	**0.025**
WARM(W)	1	44.732	**<0.001**	49.001	**<0.001**	45.774	**<0.001**
DEFO(D)	1	0.579	0.569	0.094	0.909	4.709	**0.021**
S*W	1	4.433	**0.048**	3.888	0.062	2.500	0.129
S*D	2	1.806	0.190	1.402	0.269	1.513	0.244
W*D	2	0.138	0.871	0.410	0.668	0.618	0.548
S*W*D	2	0.187	0.871	0.038	0.961	0.008	0.991

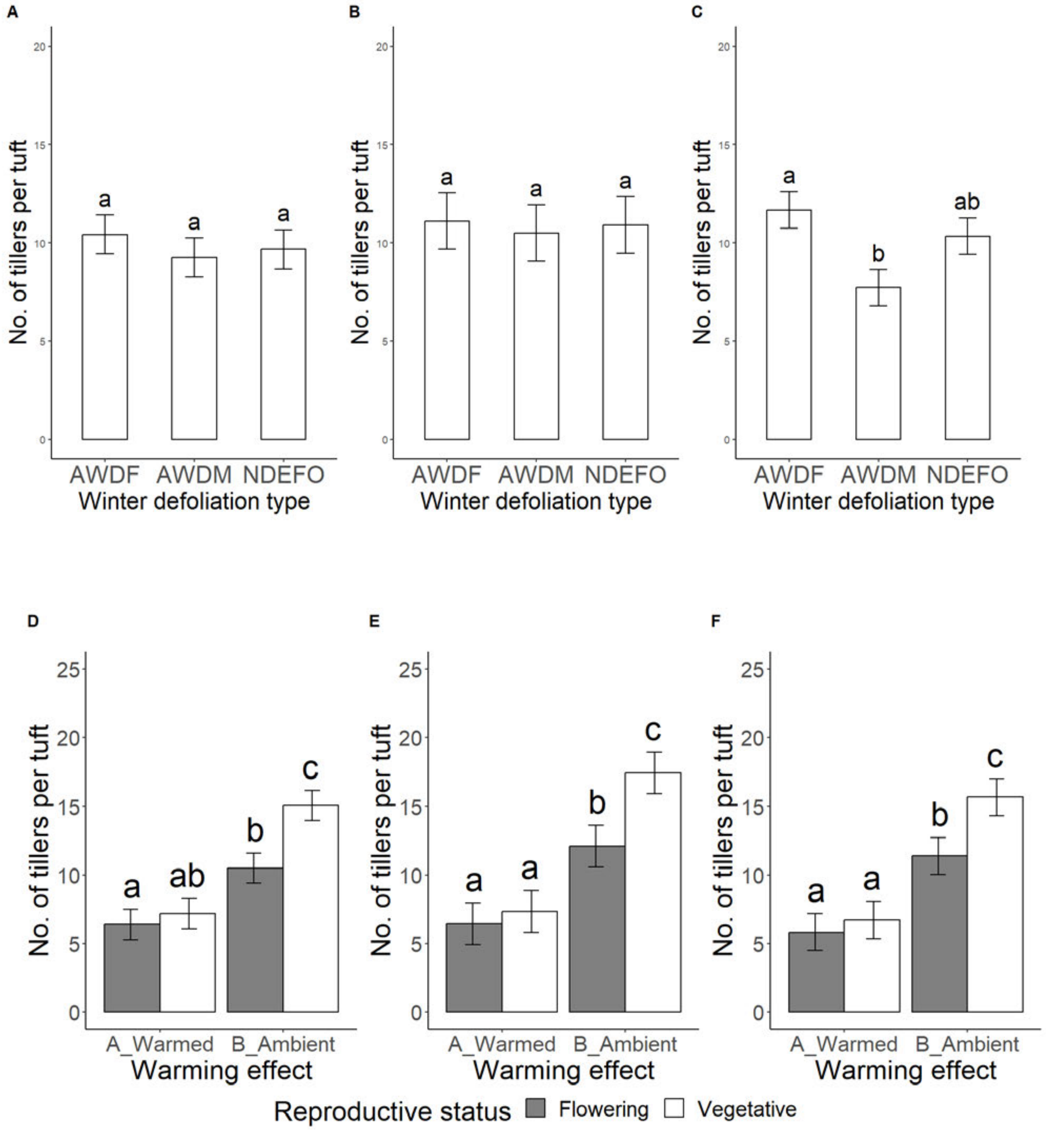


Figure 4.8: Main effect of winter defoliation type, annual winter burning (AWDF), annual winter mowing (AWDM) and no defoliation (NDEFO) (A-C) and interaction of warm*status (D-F) on number of tillers per tuft for *T. leucothrix* (a+d), *T. triandra* (b+e) and *H. contortus* (c+f) on the UGFE. Letters in common indicate non-significance (p > 0.05).

Table 4.7: The results of linear mixed models showing the main effect and interactions of winter defoliation type, warm and status on the number of buds per tiller for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	Df	F-value	p-value	F-value	p-value	F-value	p-value
STATUS(S)	2	5.429	**0.030**	7.637	**0.030**	6.078	**0.011**
WARM(W)	1	26.626	**<0.001**	31.059	**<0.001**	28.875	**<0.001**
DEFO(D)	1	2.435	0.113	3.200	0.113	2.016	0.062
S*W	1	3.689	0.069	3.817	0.069	2.785	0.064
S*D	2	1.278	0.300	1.060	0.300	0.181	0.365
W*D	2	0.505	0.610	0.938	0.610	2.182	0.407
S*W*D	2	0.153	0.858	0.098	0.858	0.328	0.906

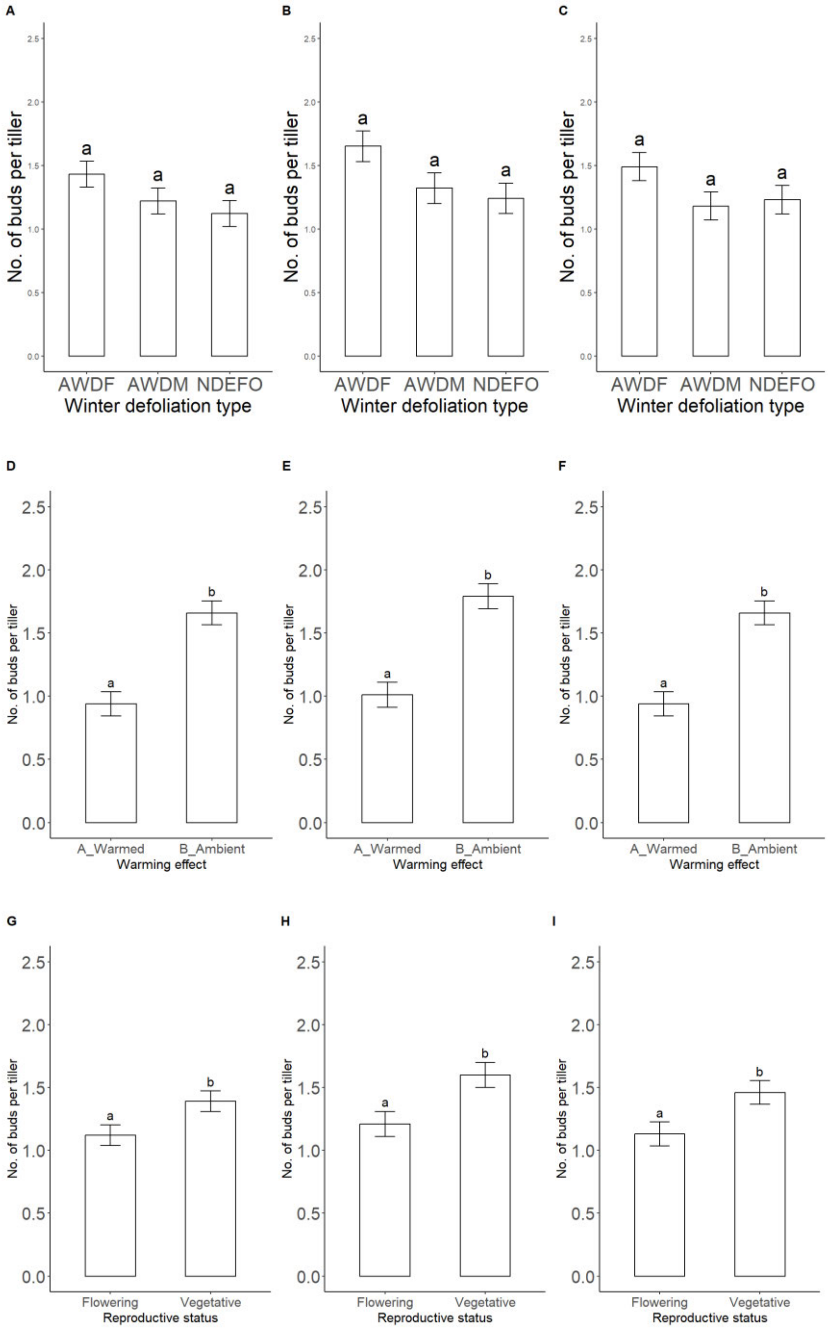


Figure 4.9: Main effect of winter defoliation type (A-C), warm (D-F) and year (G-I) on number buds per tiller for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance ($p > 0.05$).

4.3.5 Defoliation time (summer/winter) and burning frequency effect on the timing and duration of budding and flowering

Summer defoliation treatments budded and flowered first while winter defoliation treatments budded 2 to 6 days and flowered 6 to 10 days later. The duration of budding and flowering was shortened under summer defoliation and an extended budding of 2 to 5 days and flowering of 1 to 2 days under winter defoliation was observed. The pattern of response differed for the duration of flowering for *H. contortus* which was lengthened by a day under summer defoliation in comparison to winter defoliation ($p < 0.05$, Table 4.8, 4.9, 4.10 & 4.11). There were no significant interactions of warming under different levels of summer defoliation effect on the time and duration of budding and flowering. Burning frequency affected only the duration of flowering in *T. triandra*, where it was shortened under annual burning and extended by a day under triennial burning (Table 4.8, 4.9, 4.10 & 4.11). Time of defoliation (summer/winter) differed significantly in 2019/2020 but showed no difference for *Heteropogon contortus* only in 2020/2021. Warming effect differed under the different levels of defoliation time effect across the years. The duration of budding for *Themeda triandra* and *Heteropogon contortus* was extended under warming and winter defoliation by 1 to 2 days as compared to ambient temperature and summer defoliation across the years. There were no significant interactions of warming under different burning frequency on the time and duration of budding and flowering.

Table 4.8: The results of linear mixed models showing the main effect and interactions of defoliation time (summer/winter), burn, warm and year on the time of budding for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	11064.135	**<0.001**	10511.320	**<0.001**	28340.95	**<0.001**
WARM(W)	1	13.155	**<0.001**	12.379	**0.001**	19.80	**<0.001**
BURN(B)	2	0.291	0.748	0.729	0.487	2.200	0.122
DEFO(D)	1	245.424	**<0.001**	88.542	**<0.001**	752.950	**<0.001**
Y*W	1	0.720	0.400	0.328	0.569	0.000	1.000
Y*B	2	0.291	0.748	0.729	0.487	2.200	0.122
W*B	2	0.006	0.994	0.006	0.993	0.000	1.000
Y*D	1	87.196	**<0.001**	28.286	**<0.001**	673.750	**<0.001**
W*D	1	0.291	0.591	0.328	0.569	0.000	1.000
Y*W*B	2	0.006	0.999	0.006	0.993	0.000	1.000
Y*W*D	1	0.291	0.591	0.328	0.569	0.000	1.000

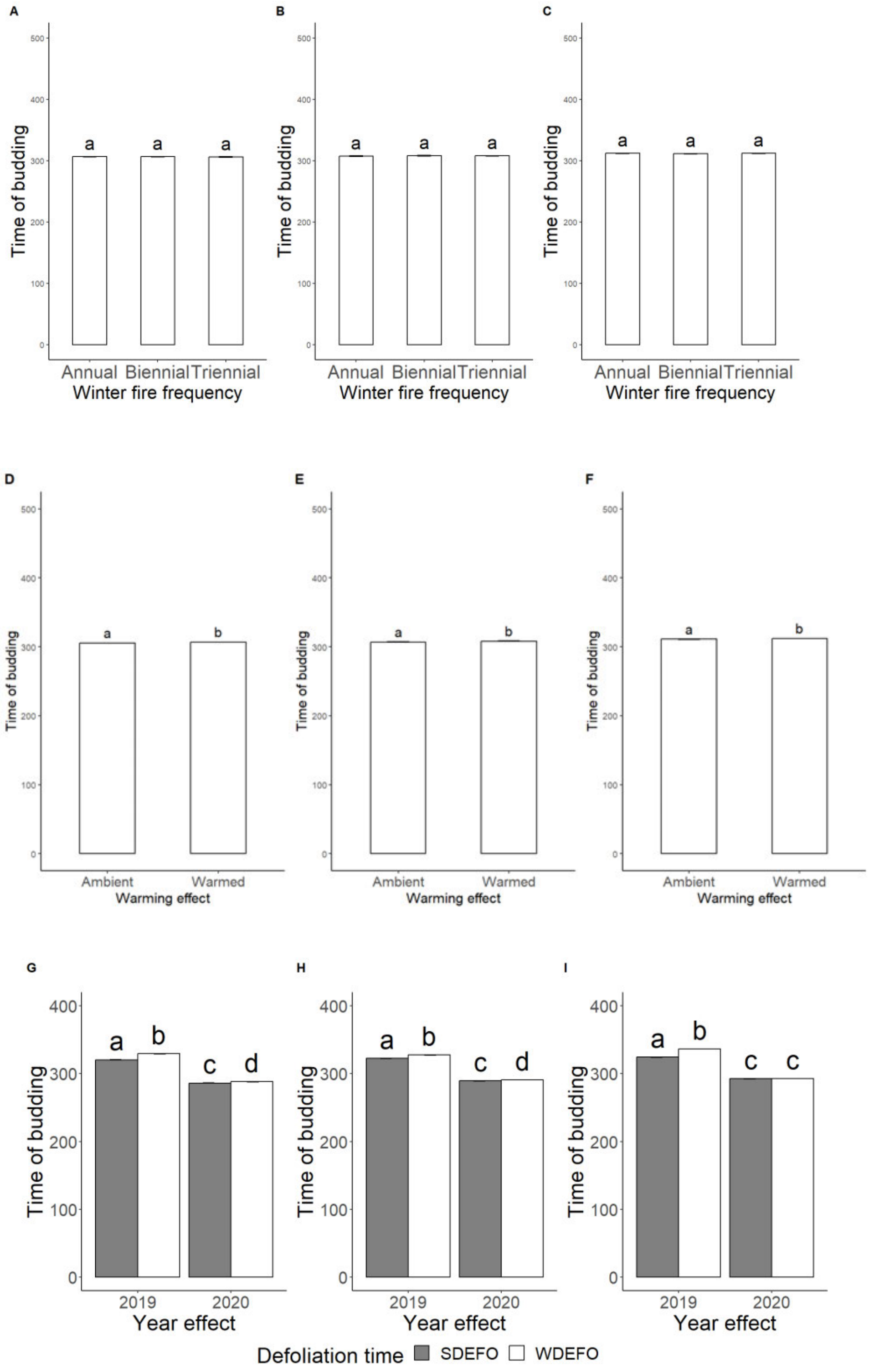


Figure 4.10: Main effect of burn (A-C), warming (D-F) and interaction of defoliation time, summer defoliation (SDEFO) and winter defoliation (WDEFO) and year (G-I) on time of budding for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance ($p > 0.05$). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 4.9: The results of linear mixed models showing the main effect and interactions of defoliation time (summer/winter), burn, warm and year on the time of flowering for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	Df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	6909.790	**<0.001**	5006.523	**<0.001**	9820.602	**<0.001**
WARM(W)	1	27.585	**<0.001**	24.369	**<0.001**	56.383	**<0.001**
BURN(B)	2	0.313	0.732	0.902	0.412	2.200	0.122
DEFO(D)	1	894.168	**<0.001**	358.092	**<0.001**	863.577	**<0.001**
Y*W	1	1.103	0.299	0.000	1.000	0.696	0.408
Y*B	2	0.313	0.732	0.902	0.412	2.200	0.122
W*B	2	0.000	1.000	0.000	1.000	0.000	1.000
Y*D	1	38.845	**<0.001**	16.923	**<0.001**	300.514	**<0.001**
W*D	1	1.103	0.299	0.000	1.000	0.696	0.408
Y*W*B	2	0.000	1.000	0.000	1.000	0.000	1.000
Y*W*D	1	0.044	0.834	0.000	1.000	0.696	0.408

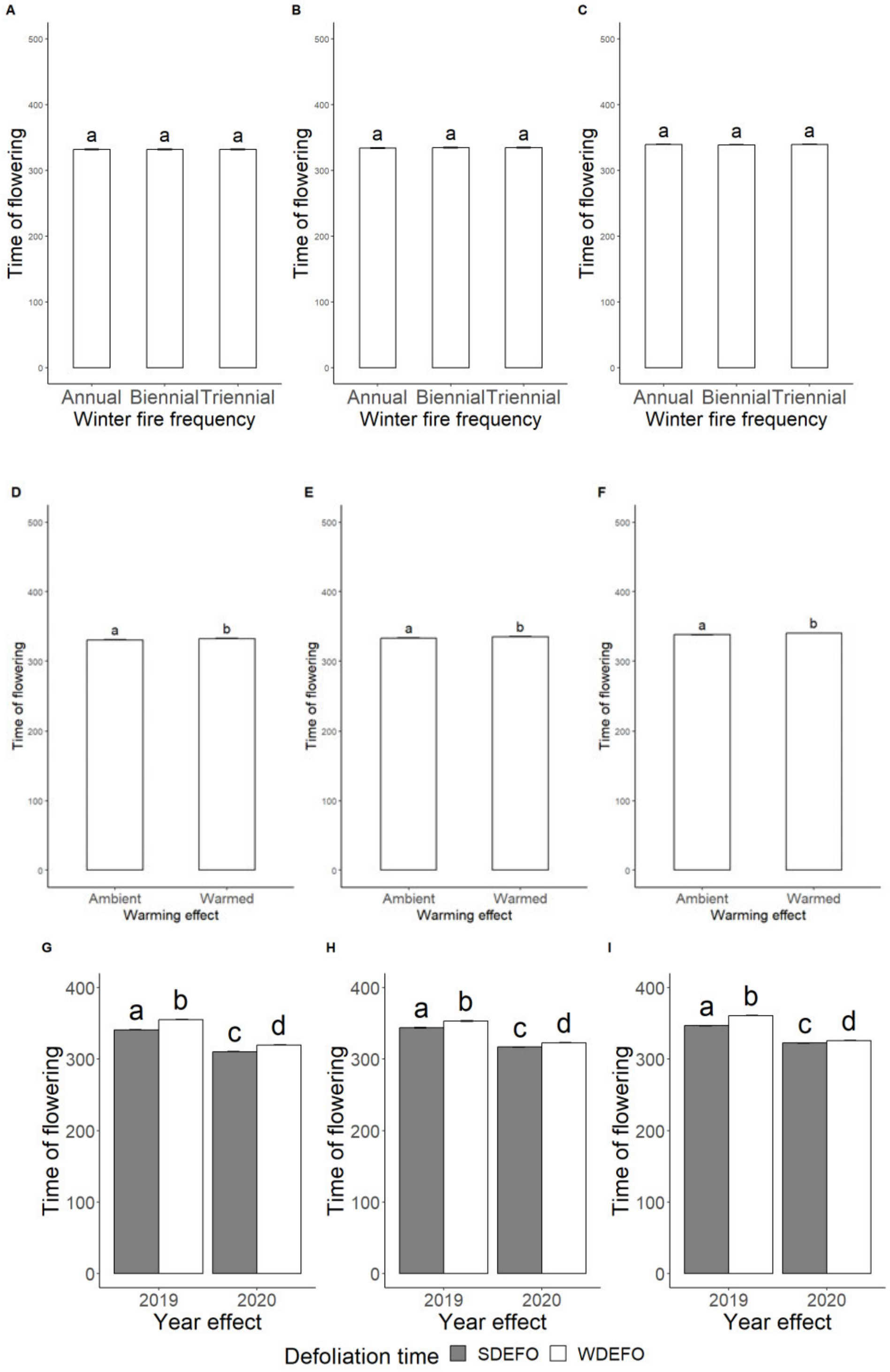


Figure 4.11: Main effect of burn (A-C), warm (D-F) and interaction of defo*year (G-I) on time of flowering for *T. leucothrix* (a+d+g) *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance ($p > 0.05$). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 4.10: The results of linear mixed models showing the main effect and interactions of defoliation time (summer/winter), burn, warm and year on the duration of budding for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	6814.720	**<0.001**	5655.273	**<0.001**	11804.237	**<0.001**
WARM(W)	1	172.480	**<0.001**	97.378	**<0.001**	278.438	**<0.001**
BURN(B)	2	0.220	0.083	1.505	0.233	2.200	0.122
DEFO(D)	1	11038.720	**<0.001**	3001.378	**<0.001**	1240.938	**<0.001**
Y*W	1	3.520	0.067	5.673	**0.021**	11.137	**0.001**
Y*B	2	0.220	0.803	1.505	0.233	2.200	0.122
W*B	2	0.220	0.803	0.115	0.890	0.000	1.000
Y*D	1	225.28	**<0.001**	2.894	0.095	72.737	**<0.001**
W*D	1	14.080	0.803	5.673	**0.021**	11.137	**0.001**
Y*W*B	2	0.22	0.803	0.115	0.890	0.000	1.000
Y*W*D	1	3.520	0.067	5.673	**0.021**	11.137	**0.001**

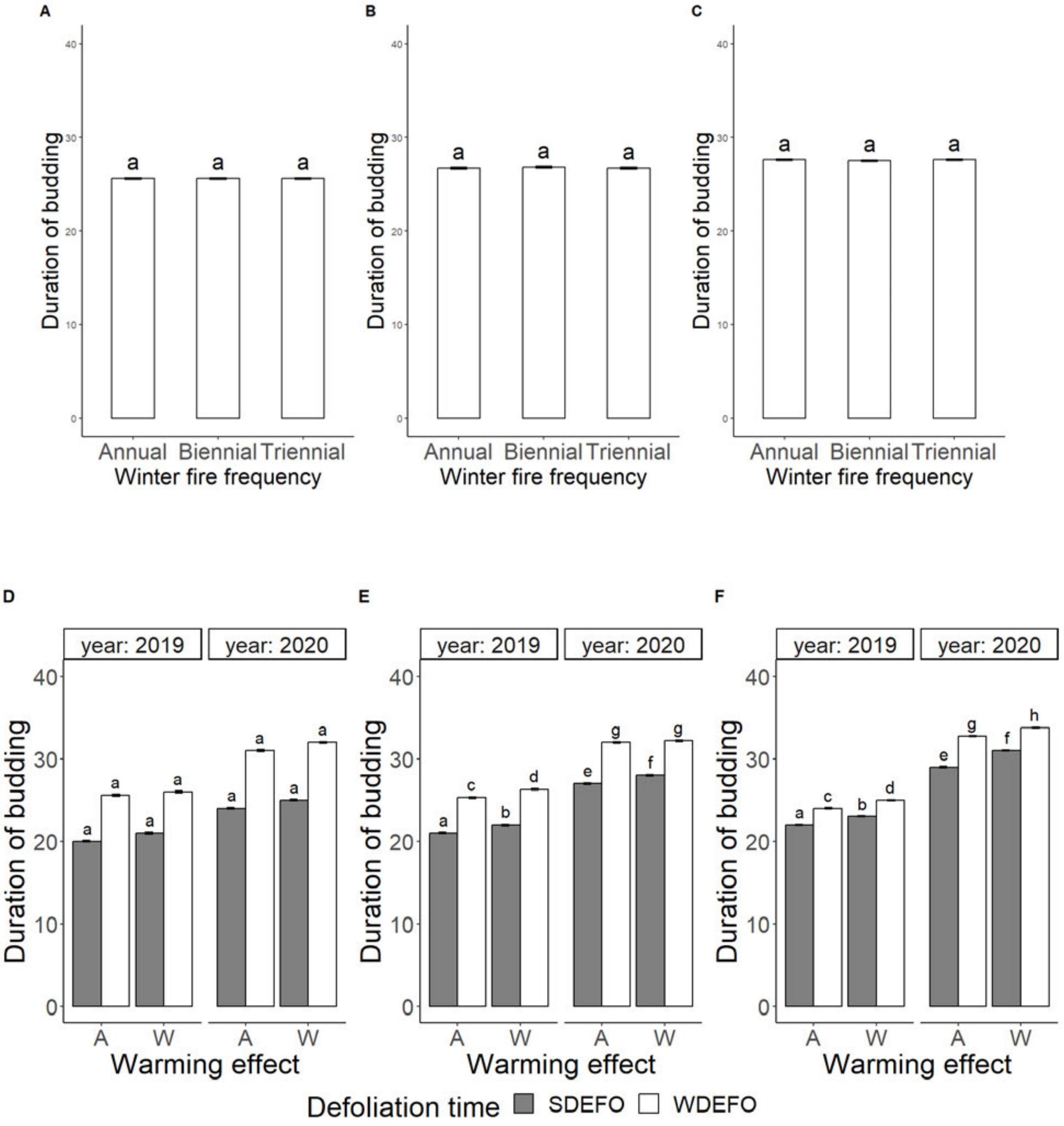


Figure 4.12: Main effect of burn (A-C) and interaction effect of defoliation time (summer defoliation (SDEFO) and winter defoliation (WDEFO)), warming and year (D-F) on duration of budding for *T. leucothrix* (a+d) *T. triandra* (b+e) and *H. contortus* (c+f) on the UGFE. Letters in common indicate non-significance ($p > 0.05$). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

Table 4.11: The results of linear mixed models showing the main effect and interactions of defoliation time (summer/winter), burn, warm and year on the duration of flowering for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
YEAR(Y)	1	3324.784	**<0.001**	3294.949	**<0.001**	16748.285	**<0.001**
WARM(W)	1	69.609	**<0.001**	25.411	**<0.001**	254.571	**<0.001**
BURN(B)	2	0.550	0.580	8.752	**<0.001**	0.785	0.462
DEFO(D)	1	350.659	**<0.001**	44.449	**<0.001**	12.571	**<0.001**
Y*W	1	2.784	0.102	0.661	0.420	0.000	1.000
Y*B	2	0.550	0.580	0.185	0.831	0.785	**<0.001**
W*B	2	0.000	1.000	0.026	0.973	0.000	1.000
Y*D	1	57.784	**<0.001**	25.411	**<0.001**	201.142	**<0.001**
W*D	1	2.784	0.102	1.295	0.261	0.000	1.000
Y*W*B	2	0.000	1.000	0.026	0.973	0.000	1.000
Y*W*D	1	2.784	0.102	0.661	0.420	0.000	1.000

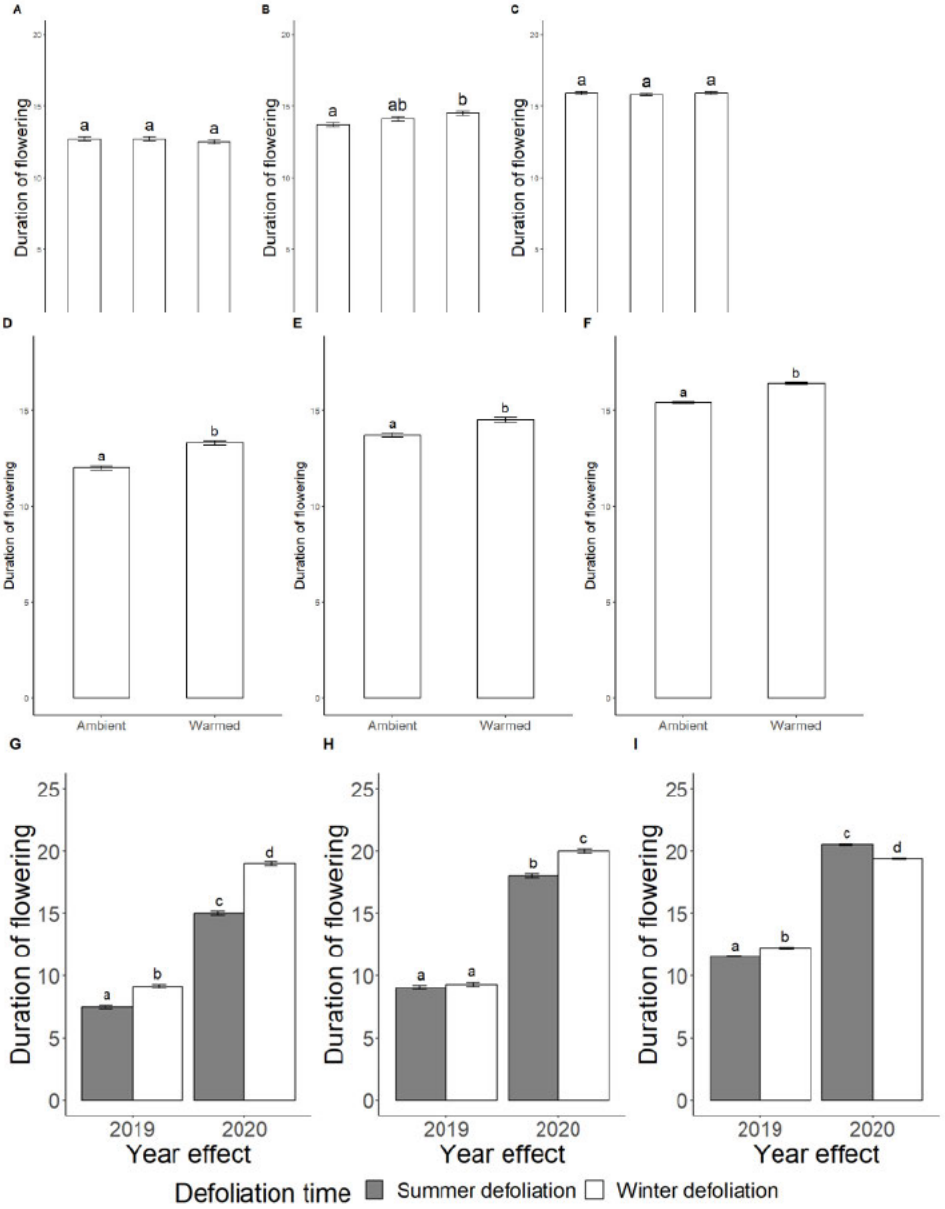


Figure 4.13: Main effect of burn (A-C), warm (D-F) and interaction effect of defo*year (G-I) on duration of flowering for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance (p > 0.05). Note: Variability in the data were low and as a consequence the error bars are not visible on the scale of the graph.

4.3.6 Defoliation time (summer/winter) and burning frequency effect on number of tillers per tuft and number of buds per tiller

Burning frequency had no significant effect on the number of buds per tiller and number of tillers per tuft for all the study species (p > 0.005, Table 4.12 & 4.13). Defoliation time (summer/winter) affected the number of buds per tiller for *Themeda triandra* and *Heteropogon contortus* with a higher number of buds per tiller recorded under summer defoliation as against winter defoliation ($p < 0.005$, Table 4.12 & 4.13). Defoliation time affected the number of tillers per tuft for *Heteropogon contortus* only, with summer defoliation having greater numbers of tillers than winter defoliation.

For all the study species, the interactive effect of warming and status showed that under warming, the reproductive status (vegetative and flowering) did not differ but was significantly different under ambient temperature. Greater number of buds per tiller and number of tillers per tuft was recorded for the vegetative status compared to flowering status under ambient temperature ($p < 0.005$, Table 4.12 & 4.13).

For *Heteropogon contortus*, the interactive effect of warming and defoliation time (summer/winter) on the number of buds per tiller and number of tillers per tuft showed that under warming there was no observed difference between the two seasons of defoliation, while a significant difference was seen under ambient temperature. Summer defoliation recorded greater number of buds per tiller and number of tillers per tuft for the vegetative status under ambient temperature than winter defoliation ($p < 0.005$, Table 4.12 & 4.13).

Table 4.12: The results of linear mixed models showing the main effect and interactions of defoliation time (Summer/Winter), burn, warm and status on the number of tillers per tuft for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
STATUS(S)	2	6.856	**0.012**	5.993	**0.018**	6.608	**0.013**
WARM(W)	1	70.209	**<0.001**	59.002	**<0.001**	85.565	**<0.001**
BURN(B)	2	0.681	0.511	1.694	0.195	0.221	0.802
DEFO(D)	1	0.035	0.852	1.896	0.175	23.012	**<0.001**
S*W	1	8.082	**0.006**	7.252	**0.009**	9.590	**0.003**
S*B	2	0.542	0.584	0.345	0.709	0.615	0.545
W*B	2	0.135	0.873	0.496	0.612	0.288	0.751
S*D	1	0.035	0.852	0.015	0.903	0.069	0.793
W*D	1	0.236	0.629	0.413	0.523	5.047	**0.029**
S*W*B	2	0.211	0.810	0.215	0.807	0.276	0.759
S*W*D	1	0.035	0.852	0.003	0.951	0.020	0.887

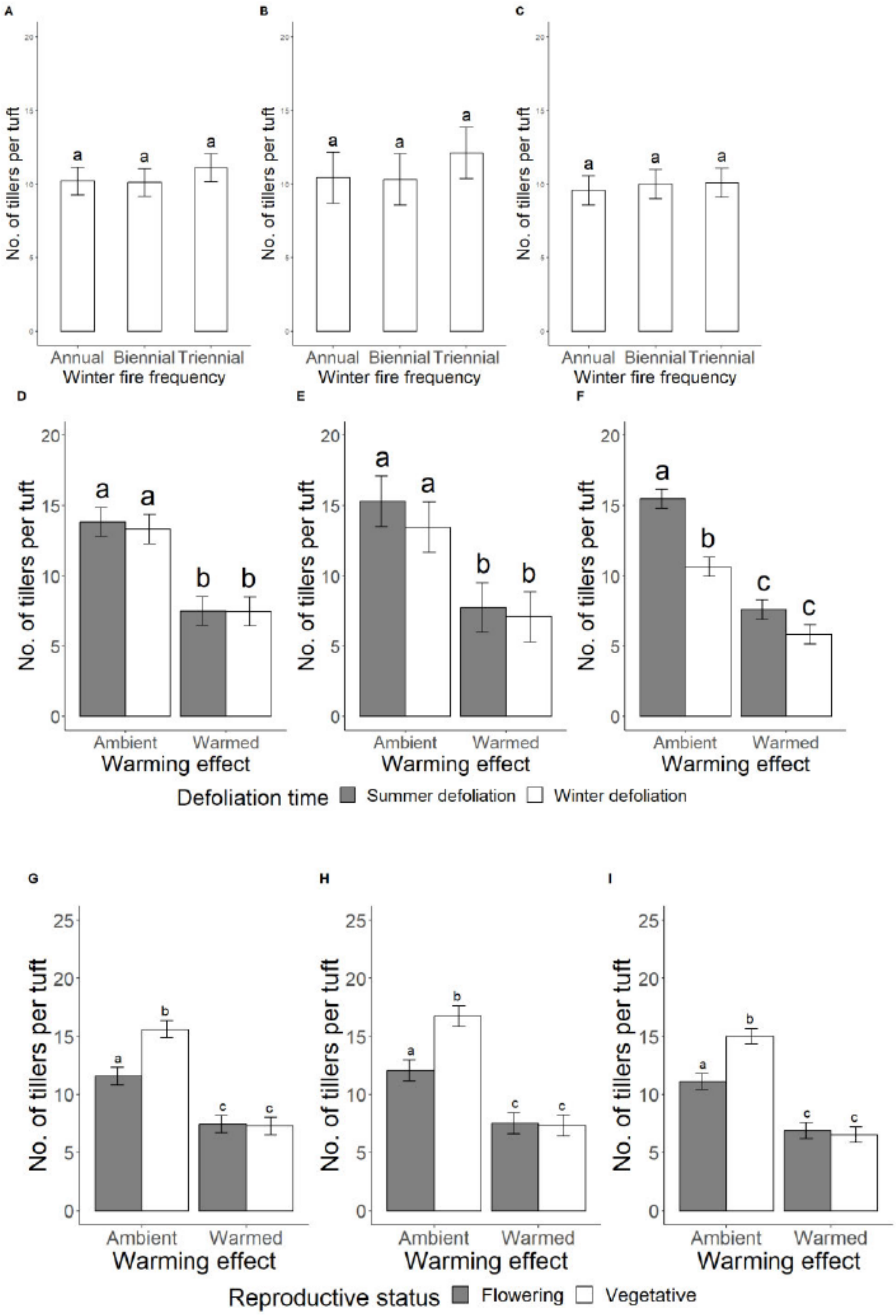


Figure 4.14: Main effect of burn (A-C) and interaction effects of defoliation time*warm (D-F) and warm*status (G-I) on number of tillers per tuft for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance ($p > 0.05$).

Table 4.13: The results of linear mixed models showing the main effect and interactions of defoliation time (Summer/Winter), burn, warm and status on the number of buds per tiller for the study species. It shows the degrees of freedom (df), F-value, and p-value with significant values in bold

		T. leucothrix		*T. triandra*		*H. contortus*	
	df	F-value	p-value	F-value	p-value	F-value	p-value
STATUS(S)	2	13.333	**<0.001**	13.049	**0.000**	14.997	**0.000**
WARM(W)	1	44.918	**<0.001**	46.273	**<0.001**	57.940	**<0.001**
BURN(B)	2	0.095	0.909	0.083	0.920	0.501	0.608
DEFO(D)	1	3.471	0.069	7.516	**0.008**	20.813	**<0.001**
S*W	1	13.714	**<0.001**	11.077	**0.001**	11.393	**0.001**
S*B	2	0.381	0.684	0.467	0.629	0.298	0.743
W*B	2	0.765	0.471	0.478	0.623	1.328	0.275
S*D	1	0.442	0.509	0.050	0.823	0.015	0.900
W*D	1	3.127	0.083	3.344	0.074	10.387	**0.002**
S*W*B	2	0.553	0.578	0.958	0.391	0.443	0.644
S*W*D	1	0.083	0.774	0.139	0.710	0.027	0.868

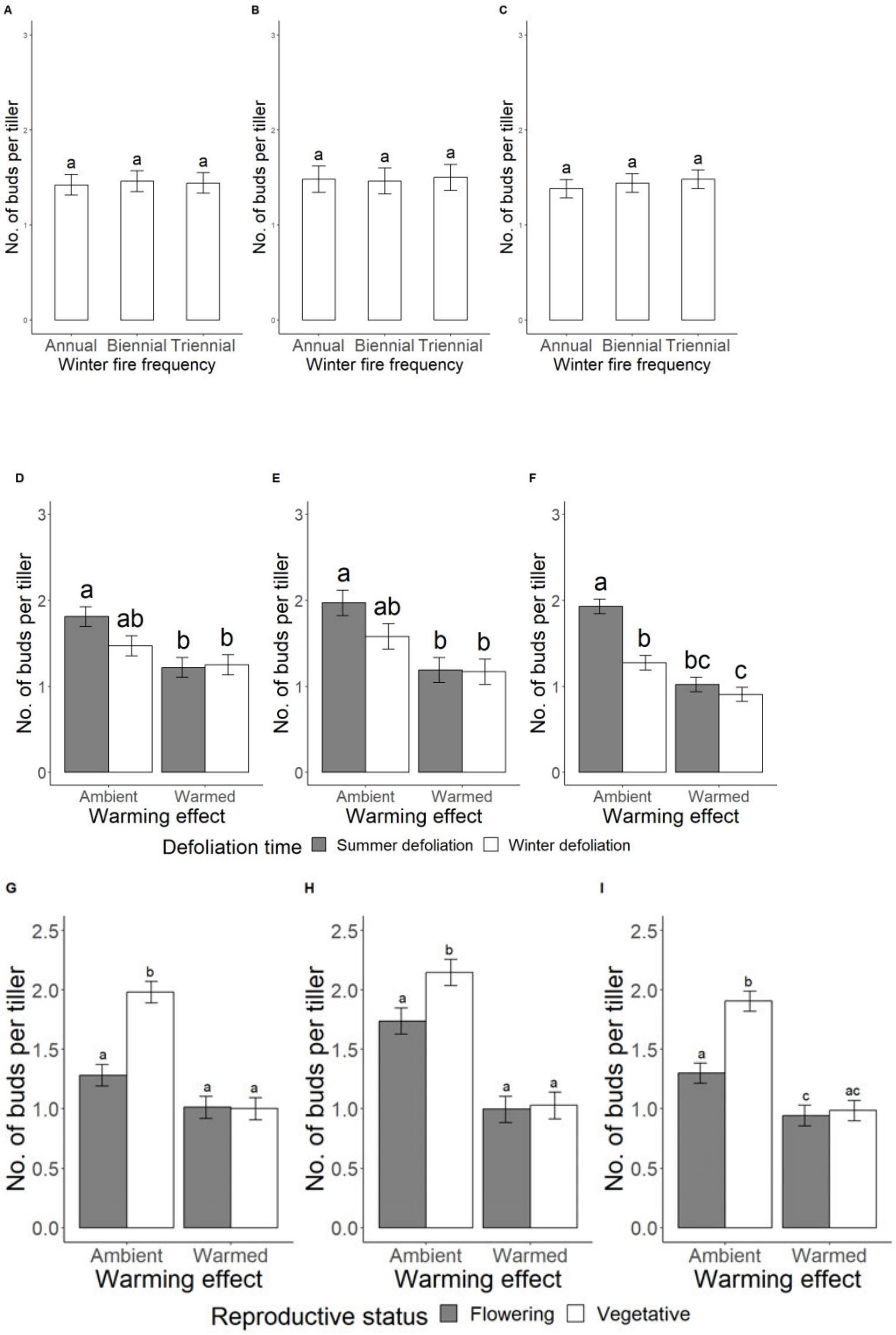


Figure 4.15: Main effect of burn (A-C) and interaction effects of defoliation time*warm (D-F) and warm*status (G-I) on number of buds per tiller for *T. leucothrix* (a+d+g), *T. triandra* (b+e+h) and *H. contortus* (c+f+i) on the UGFE. Letters in common indicate non-significance (p > 0.05).

4.4 Discussion

Interannual variability in the mesic grassland community is partly driven by changes in rainfall, making these grasslands inherently more dynamic (Knapp et al., 2006). Temperatures and precipitation at URF throughout the research period were remarkably close to the long-term averages. Total rainfall was lower than the long-term average in 2019/2020 and was similar to the long-term mean in 2020/2021 (Fig. 4.2 A and B). Changing environmental conditions, including photoperiod, precipitation, temperature, and time of snowmelt, are the main causes of interannual differences in the timing of plant phenophases (Shen et al., 2022; Tan et al., 2023; Yang et al., 2020; Zheng et al., 2022). One of the greatest responses of plant phenology to biological cues such as changing environmental conditions is the ability to alter their phenological events (Alilla et al., 2022; Bastian & Bayliss Hawitt, 2023; Caparros-Santiago et al., 2021; Qu et al., 2020).

According to this study, budding each year began a few weeks after the rainy season started (Figure 4.3), confirming the role that rainfall plays in regulating how community dynamics respond to changes in weather patterns in a mesic grassland in South Africa (Knapp et al., 2006). The timing of key plant phenological events can exhibit significant interannual variability (Jarrad et al., 2008), indicating that unfavourable environmental conditions could impact plant physiology (Feller & Vaseva, 2014).

Fire frequency did not significantly affect the timing and duration of budding and flowering in either of the two years for the studied species except for *Themeda triandra* which flowered for longer under the triennial winter burn and shorter under the annual winter burn. Other studies have shown that the effect of fire varies between species, where the time of flowering occurred earlier for some and was delayed for others (Mackenzie et al., 2016). This shows that the response of grass species to different burning frequencies differs. This is dependent on the complex interactions between the time of burning, plant phenology at the season of burn, differences in the severity of burn among seasons of burn, and change in weather conditions during the time of burning (Ruckman et al., 2012). In this study, burning occurred during winter, and it is believed that winter burns are of low intensity and has little or no effect on the grass community (Morris & Fynn, 2001b), which could be why burning had no effects on the other two study species. The different burning frequency leads to alterations in light intensity and canopy cover which are important factors for growth in perennial grasses (Everson et al., 2021). The response of these dominant grasses in mesic grassland to different burning frequencies depend on their tolerance of shade and the positioning of the growing zones (Everson et al., 2021). *Themeda triandra* is shade intolerant and its growing zones are at the soil surface which make them dominant and a vigorous competitor in grasslands burnt annually (Everson et al., 2021). The *T. triandra* dominance can be attributed to their high productivity as a result of highly efficient use of the available resources of nutrients, light and moisture after fire (Ghebrehiwot et al., 2009). The high productivity of *T. triandra* could have resulted in their fast regrowth after fire (Ghebrehiwot et al., 2009), this could partly be the reason for a shortened duration of flowering observed for *T. triandra* under annual winter burning, another reason could be that the total removal of accumulated litter increases evaporation and reduces soil moisture infiltration, which could shorten plant phenological events. This is relative to triennial winter burning, where the dead material accumulated in the previous season creates lower light intensities and canopy shading which does not favour the growth of *T. triandra*. Since soil moisture, temperature, and nutrients are crucial for the growth of flowers and fruits, the delayed onset of rainfall in the first year of this study may have caused lower soil moisture levels, coupled with higher temperatures, increased exposure to solar radiation, and availability of soil nutrients in the recently burned site. These conditions may have caused the late-flowering C4 *T. triandra* species to experience earlier phenological processes under the annual winter plots (Munson & Long, 2017; Sherry et al., 2011). Reduced evaporation leading to increased soil water infiltration could lengthen the duration of plant phenological processes (Everson & Tainton, 1984), and could have resulted in the longer period of flowering observed under the triennial winter burn plots.

It has been shown that disturbances reduce the degree at which species compete for limiting soil resources, and as it may or not increase light availability, this may lead to an associated reduction of how available the other limiting soil resources are. This can affect productivity due to the alteration of these soil resources (soil nitrogen and water) (Fynn et al., 2004)**.** Burning in winter periods leads to more reduced soil nitrogen than burning in spring which suggests that how much the time of fire affects plant productivity depends on its effect on soil resources. This may influence how the species compete for the limiting resources, whereby the species that are weaker in competing are extirpated (Fynn et al., 2005).

A combined effect of double summer mowing and winter fire was reported to result in a high dominance of grasses like *T. triandra* and *Heteropogon contortus* in the mesic grassland, while when combined with a winter mow gives an almost the same results as in a triennial burn effect on species composition (Everson & Tainton, 1984), For example, short-grass species was reported to dominate annual winter burn, biennial winter burn and summer mowing plots, but a switch in dominance by taller grasses were found under the triennial winter burn, annual winter mow and unburned/unmowed plots, the short grasses were replaced by taller grasses under triennial winter burning, annual winter mowing and no defoliation because of the higher nitrogen and litter accumulation present in the soil (Fynn et al., 2005; Kirkman et al., 2014b). This shows that the characteristics (accumulated litter and higher soil resources) common to triennial winter burning and annual winter mowing could be the driving forces behind the same resultant effects observed**.** This supports our study where the same pattern of response of lengthened duration of flowering was observed under triennial winter burning and annual winter mowing (combination of double summer mowing and a single winter mow). The delayed timing and lengthened duration of the budding and flowering of the study species under the annual winter mowing plots could also be that the presence of accumulated litter reduces the evaporative loss of moisture from the surface of the soil making soil water and nitrogen readily available for growth, which could have resulted in a prolonged phenological events (Henn & Damschen, 2022).

Annual winter defoliation burning plots shortened the duration of flowering as was found under the annual winter burn, which follows the same trend of response for plant phenology under different fire frequencies. Studies have shown that fire removes litter which creates space for a quick regrowth of plants (Henn & Damschen, 2022). Fire completely removes litter and increases light intensity which causes desiccation of the soil surface (Fynn et al., 2004). The earlier timing and shortened duration of budding and flowering under annual winter burning could be due to the reduced soil moisture and nitrogen under these plots causing a reduced competition for reproduction and growth. The number of tillers per tuft for *Heteropogon contortus* was greater in the annual winter burning and lower in the annual winter mowing. This agrees with the study that dense shading at the base of fire-tolerant grasses often tends to reduce tiller numbers making the grasses less productive and less competitive (Everson et al., 2021) and another study at Ukulinga Research Farm showed that winter burning results in dominance of *Heteropogon contortus* (Fynn et al., 2005). Our results suggest that different defoliation time, type and frequencies leading to alterations in light intensity and canopy cover are mechanisms so important in the regulation of tiller initiation in perennial grass communities.

The response of these perennial grasses to defoliation (mowing or burning) is dependent on the level of plant growth stage and the season of defoliation which determines if the grass phenological events would be altered causing either early or delayed timing and shortened or lengthened duration of budding and flowering of the grass species (Tainton & Booysen, 1963). Mowing can stimulate flowering through removal of vegetation (Pyke, 2017). It is expected that summer mowing occurred when grasses were actively growing which makes the grasses vulnerable to defoliation at the point of growth when their tillers are elevated. Summer mowing would remove the buds of the reproductive tillers formed, and thus reduce flowering during the period of defoliation. Summer mowing would not completely remove all the buds but leave out some for continued growth. This confirms why summer mowing resulted in more buds per tiller of *Themeda triandra* and *Heteropogon contortus* and more tillers per tuft of *H. contortus* than winter defoliation. Research has shown that the effect of defoliation on grass phenology and growth depends on the plant height and size, and season, frequency and intensity of fire (Pyke, 2017). This could be why summer mowing quickened the timing and shortened the duration of budding and flowering than the winter defoliation plots in our study. This shows that the defoliation time (summer/winter) effect on grass phenology in our study depended on the season of defoliation which determined the height and age of the plant studied resulting in the observed responses.

In our study, warming increased soil temperature by about 1.5 - 2 °C as found in other studies (Ghebrehiwot et al., 2012; Mvelase, 2021a; te Beest et al., 2021). Warming delayed the time of budding and flowering by 1 and 2 days and increased their duration slightly, making its impact seem fairly insignificant compared to the influence of rainfall onset and quantity. We noticed a considerable contrast in the onset and duration of budding and flowering between the two study years, driven by differences in onset and quantity of rainfall. This suggests that a warmer climate is not a significant factor in driving grassland phenology. Although elevated temperature can accelerate photosynthesis, growth, and reproduction in plants (Gray & Brady, 2016) A study conducted in the alpine area of Sweden (Molau, 2000) found that higher temperatures resulted in an early occurrence of all plant phenophases, particularly for flowering, over five years. Several studies have shown that certain species experience early flowering as a result of experimental warming (Marchin et al., 2015; Woznicki et al., 2019).

These findings suggest that different stages of plant development may not all react the same way to climate change. This is because various components of plant phenophases change at different rates under global warming (Yang et al., 2020). However, plant phenological responses may be more pronounced in drier years when warming is combined with drought. However, other research has found that warmer temperatures do not affect the duration of flowering in subalpine plants, dwarf shrubs, and grass species (Huang et al., 2020; Jentsch et al., 2009; Liu et al., 2021; Sedlacek et al., 2015). It has been observed that not all species respond to warmer temperatures by advancing their phenological events. There is a lot of variation in how coexisting species respond to global warming (Donnelly et al., 2012; Gričar et al., 2022; Jarrad et al., 2008).

In our study, we observed that the number of buds per vegetative or flowering tiller and the total number of tillers per vegetative or flowering tiller was altered due to the time, type and frequency of defoliation. This suggests that the removal of biomass caused by these disturbances did affect the resources allocated to the tiller and bud bank common to the species studied. However, the type and season of defoliation had more effect, for example, mowing had more influence than fire, and summer defoliation had more effect than winter defoliation. So, where it was suggested that tussock grass tiller buds are more resilient to climatic perturbations than bud banks on rhizomes (Dalgleish et al., 2012), and that the belowground bud banks in perennial grass-dominated ecosystems act as a buffer to efficiently withstand short-term environmental stress (Russell et al., 2015) could be dependent on the season and type of stress. This is in line with our study showcasing that the alterations in the number of buds per tiller and number of tillers per vegetative and flowering tufts of the grass species detected under the single effect of the multi-term experimental warming and its combination with the long-term fire and mowing regimes were dependent on the type, time and frequency of defoliation and the plant height and age as at the time of occurrence which influenced how the species responded.

4.5 Conclusion

The results of this study indicate that the type, time, and frequency of defoliation and its interaction with the effect of climate change have a notable influence on the budding and flowering periods of the species studied, ultimately impacting the length of their reproductive cycle and altering the ratio of vegetative to flowering reproductive status. Additionally, warmer temperatures had a marginally significant effect on budding and flowering times and also impacted the duration of reproduction. Furthermore, the timing of rainfall during growing seasons in different years affected the budding and flowering times as well as the reproductive duration of the species, the number of buds per vegetative and flowering tiller were influenced, as did the total number of tillers per tuft compared to the control.

Changes in how plant phenology responds to variations in precipitation from year to year can either strengthen or weaken an ecosystem's ability to resist climate change. The timing of rainfall is a crucial factor in determining when plants undergo their phenological processes. This can be seen in how the ratio of vegetative to flowering status was higher in the ambient plots than the warmed plots. The annual winter mow, annual winter burn, summer and winter defoliation altered the phenology and the number of buds per tiller and tillers per tuft of all study species with different responses as a result of the season and type of defoliation. These changes could lead to mismatches between plants and animals, such as variations in seed production, which could impact the seed bank, early pollinators, and floral herbivores. As a result, ecosystem structure and function could be altered.

These findings show that plant species are sensitive and can alter their phenology to track changes in the timing of the annual climate of the study area. The response of timing and duration of budding and flowering of these studied grass species to the short-term effects of climate change (warming) and long-term management regimes (mowing) was sensitive and does preclude more pronounced shifts in the phenological events leading to changes in the density of buds per tiller per tuft and their relative allocation to either vegetative or sexual reproduction.

4.6 References

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Chapter 5: The interactive effect of climate change (drought and warming) and management factors (defoliation by fire and/or mowing) on species composition, soil seed bank and seed rain in a mesic grassland

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Abstract

Fire, grazing, and recurrent drought are some of the more common disturbances that impact many grasslands. Two ongoing experiments were used to investigate the impacts of these disturbances on grassland community dynamics. In the Drought-Net experiment, the combined effect of rainfall variation (drought (50%), ambient (100%), and wet (150%)) and temperature (warmed and ambient) manipulation on the species composition, soil seed bank, and seed rain of a mesic grassland was evaluated. In the second experiment, the combined effect of burning (annual, biennial, triennial, and unburned), defoliation frequency (three mows (summer mow with winter mow), two mows (summer mow with winter burn) and unmowed) and temperature (warmed and ambient) manipulation on the species composition, soil seed bank, and seed rain of a mesic grassland was conducted on the Ukulinga Grassland Fire Experiment (UGFE). Plant community composition was examined to determine sensitivity to climate and management. On the Drought-Net experiment, the main and interacting effects of warming and the various rainfall regimes did not impact the soil seed bank and seed rain ($p > 0.05$). On the UGFE, the main effect of warming and its interactions with the burning and mowing treatments had no significant effect on soil seed bank and seed rain ($p > 0.05$). The seed rain composition was only affected by mowing frequency, while the main effects of fire and mowing frequencies affected the soil seed bank ($p < 0.05$). The responses of the seedlings that germinated from the seed bank and seed rain were shown to be species-specific towards the management factors. But the lack of effect of drought and warming shows that mesic grasslands are resistant to

fluctuations in moisture and temperature regimes in the short term, and it may be that more prolonged drought and warming or a greater increase in temperature and reduction in rainfall would affect the species composition.

Keywords: **Drought-Net; Warming chamber; Seed bank; Seed rain; Fire; Mowing; Ukulinga Grassland Fire Experiment.**

5.1 Introduction

Grassland ecosystems are among the most anthropogenically impacted ecosystems (Vieira et al., 2015), and various ecological services and functions are negatively affected as a consequence (Kremen, 2005; Lavorel, 2013b). For developing conservation or restoration policies and practices, it is crucial to understand how vegetation can regenerate after being disturbed. The soil seed bank can be considered the memory that gives information on previous vegetation composition and environmental conditions before disturbance (Jakobsson et al., 2006). It also reflects the ability of the vegetation to regenerate after it has undergone significant disturbance (Li et al., 2017; Zermeño-Hemández et al., 2015).

A self-reinforcing feedback cycle is created when disturbances have an undesirable impact on the soil seed bank size and composition, negatively affecting future vegetation structure and composition. This cycle speeds up the degradation of grasslands (Gonzalez & Ghermandi, 2021). Soil seed banks lower the likelihood of local species extinction following disturbances and aid in vegetation recovery in degraded areas (Bakker & Berendse, 1999; Nolan et al., 2021; Zhan et al., 2007).

Soil seed banks help preserve the genetic and trait diversity of the local plant community and contribute to the re-establishment and maintenance of the genetic and trait diversity within the local population (Medeiros-Sarmento et al., 2021; Vandvik et al., 2016). The seed bank helps maintain a functionally diverse pool of propagules ready to germinate in response to variations in weather and environmental conditions like soil moisture, day length, and shading (del Cacho & Lloret, 2012). The soil seed banks species composition may differ from the standing aboveground plant communities due to variation in seed longevity (Lamb et al., 2022; Plue et al., 2021). This means some species may produce many seeds and potentially dominate the seed bank, while others produce few seeds and may have a reduced presence in the seed bank (Lamont & Enright, 2000). This can be unrelated to their dominance above ground (Olsen et al., 2016).

Recruitment may arise from the seed bank, whose distribution in space may differ from that of the seed rain (Dalling & John, 2008), because the seed bank includes species from previous vegetation composition in the seed rain and because the conditions that affect the germination, longevity and viability of seeds in the seed bank may differ from place to place. Spatial relations are even more complex when several species co-occur and when the activities of seed predators, herbivores, or physical disturbances have localized effects (Fenner, 1995).

Understanding the ecology and dynamics of habitat degradation requires knowledge of the seed rain (Gioria & Pyšek, 2015; Jakovac et al., 2021). The contribution of seeds of different species to the soil seed bank and plant community is determined by the aspects of seed rain, such as quantity and size of seeds (Jara-Guerrero et al., 2020; Price & Joyner, 1997; Salazar et al., 2011). Seed rain allows the spread and invasion of weeds in degraded sites, it alters the composition of the soil seed bank and in the regeneration processes of the sward, seed rain plays a decisive role (Török et al., 2018b).

Seed rain is the total quantity of seeds released from the mother plant per unit area within a set period (Arruda et al., 2018). Seed rain plays a key role in plants' phenological events, representing a demographic link between the seed and adult phases (Conquet et al., 2023; Saatkamp et al., 2019). Seed rain contributes to the regenerative potential of the plant community and, consequently, the resilience of the vegetation (Chabrerie & Alard, 2005; Falk et al., 2022). It plays a pivotal role in restoration ecology and biological invasion by allowing seeds to arrive at suitable uncolonized sites (Arruda et al., 2018). In mesic grasslands, vegetation regeneration is mainly limited by seeds, which corroborates the importance of vegetative reproduction under normal conditions for these perennial systems (Salazar et al., 2011).

The link between the initial species assemblages, the quantity of propagules produced, and the ability to accumulate in the soil seed reserves all influence the availability of seeds in disturbed sites (Snyman, 2013). When annuals predominate in the soil seed bank due to increased disturbance, a high resemblance between the soil seed bank and the vegetation is observed (Tedder et al., 2012). Disturbance and stress patterns shape plants' regeneration strategies (Chang et al., 2001). The quantity of seeds a plant produces and releases as seed rain is significantly influenced by disturbances such as grazing and burning (Snyman, 2005; Snyman, 2013). These disturbances such as burning and herbivory, are widely used in reducing the effects of competition among standing vegetation (Snyman, 2013).

Long-term heavy grazing leads to rangeland degradation, resulting in reduced seed bank species richness and seedling recruitment in degraded sites (Ma et al., 2010; Tessema et al., 2016). Plants in nutrient-rich environments experience more significant nitrogen losses through defoliation than species from nutrient-poor habitats (Bobbink et al., 2010; Kammer et al., 2022). Mesic and semi-arid grasslands are largely nitrogen-limited, while arid grasslands are limited by soil moisture (Blair et al., 2014b; Bobbink et al., 1998; Carboni et al., 2015; Kirkman et al., 2014b; Ren et al., 2017; Venter et al., 2020). Unsurprisingly, species in habitats with unlimited resources recover from defoliation more quickly than those in habitats with scarce resources (Bazzaz, 1996; Illius & O'Connor, 1999). For instance, depending on the intensity, grazing can significantly increase light availability. It may increase or decrease the amount of soil N available, influencing plant community structure, species richness, and composition through various mechanisms (Augustine & McNaughton, 1998; Sun et al., 2017). The open spaces created due to moderate to heavy grazing are suitable for the colonization of seeds, which are distributed heterogeneously (Sehrt et al., 2020).

Long-term heavy grazing is the most important factor contributing to degradation in South African rangelands (Snyman, 2013). Plants are prevented from seeding in some communal grazing areas due to continuous heavy grazing (Snyman, 2013). Under high grazing intensity, the biocrusts and grass cover that protect the soil are reduced. This causes edaphic modifications that lower the concentration and infiltration of nutrients, increase soil erosion, and accelerate vegetation cover loss (Hu et al., 2019). The soil seed bank may partially be reduced due to these losses (An et al., 2022).

Fire is a commonly used management tool for modifying the plant community by reducing undesirable grass cover and the shrub layer (Duquette et al., 2022; Leder et al., 2017). The propagules and nutrients concentrated beneath the shrub canopy are redistributed by wind after a fire occurs and homogenize vegetation distribution (Leder et al., 2015). Open spaces are established after fire, releasing nutrients and allowing plants to colonize and grow (Fox et al., 2022).

Availability of soil moisture and spatial distribution of the soil seed bank are the main environmental factors that limit the recruitment of long-lived grass species in degraded grasslands (Snyman, 2004; van Langevelde et al., 2016). Thus, seed rain and the soil seed bank are vital in colonizing available niches (Kiss et al., 2021). As a result, management factors that would maintain and stimulate the growth of long-lived grass species from seed rain and soil seed banks will help in sward re-establishment (Arán et al., 2017; Liu et al., 2022).

Drought can cause a rapid change in the plant community composition and the ecosystem functioning (Hoover et al., 2014; Williams & de Vries, 2020). It can also reduce the prevalence of dominant perennial grass species and increase cover of less dominant perennial and annual forbs (Munson et al., 2022). The soil seed bank composition reflects the plant community, and variations in climate conditions could affect the abundance of seeds in the seed banks of these plant communities (Laforgia et al., 2018; Marone & Pol, 2021). However, in perennial-dominated grassland ecosystems, the response of plant communities to extreme events is seldom quantified (Cleland et al., 2013), particularly in African grasslands.

Fire, grazing, and recurrent drought are some of the more common disturbances that impact many grasslands (Joyce et al., 2016; Oesterheld et al., 1999). These complex disturbance factors partly control how seeds persist and get into the soil seed bank, with grassland plant communities showing a wide range of seed longevity (Fenner, 1995; Loydi & Collins, 2021). Fire, grazing, and drought can also significantly reduce the quantity and modify the composition of seed production and seed rain.

The study of seed banks is extensive, while there are few studies on seed rain (Esmailzadeh et al., 2011; Leishman et al., 2000; Mahé et al., 2021). Rarely have studies combined and compared the species composition of the aboveground community and seedlings that germinated from the soil seed bank and seed rain under the effects of climate change and management. It is against this backdrop that this study sought to examine the effect of climate change (drought and warming) and management factors (fire and mowing) on sward species composition, soil seed bank, and seed rain of mesic grasslands on both the Drought-Net experiment and the Ukulinga Grassland Fire Experiment (UGFE) at the University of KwaZulu-Natal, South Africa. The objectives of the study were to determine the following: (1) if there was a correlation between the species composition of the sward, and the seed banks and seed rain under the impacts of climate change and management factors, and (2) the impact of warming under different rainfall regimes, different fire conditions, and mowing treatments on the species composition, richness, diversity, and evenness of the seed bank, and seed rain.

5.2 Methods

5.2.1 Study area

The experiment was conducted at the Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa (30°24′ S, 29°24′ E), a region with summer rainfall that receives an average of 838 mm of precipitation annually (Ward et al., 2020a). The average monthly minimum temperature is 8.8 °C in July during the mild winters, and the average monthly maximum temperature is 26.4 °C in February during the hot summers (Ward et al., 2020a).

These climatic variables result in a growing season that spans from October to April. The vegetation belongs to the grassland biome and a more recent classification place it in the KwaZulu-Natal Hinterland Thornveld where *Vachellia sieberiana* is dominant alongside *Hyparrhenia hirta*, *Themeda triandra* and other herbaceous plants (Mucina & Rutherford, 2006b). In the absence of fire, the dominant grass species is *Aristida junciformis*, while *Themeda triandra*, *Tristachya leucothrix* and *Heteropogon contortus*, with sparse woody cover, are common with regular burning (Morris & Fynn, 2001b). A C4 photosynthetic pathway is used by all grass species at this site (Ward et al., 2020a).

5.2.2 Experimental design

The Drought-Net experimental plots were established at the beginning of October 2019, where treatment application was initiated using a split-plot randomized block design down the slope gradient of the site. A weather station was established towards the end of January 2020, collecting temperature, precipitation, wind direction, solar irradiance, relative humidity, wind speed, and saturated water vapour pressure data. The site was mowed at the end of each growing season to remove moribund biomass and prevent woody encroachment. The plot size was 5.5m by 3.5m divided into six 1m^2 subplots, separated by ½ m wide corridors. Each plot was trenched around the edges to a depth of 0.5 m and lined with thick plastic to isolate each plot hydrologically. The experimental site consisted of three blocks, and in each of these blocks were three levels of precipitation: drought (50%), ambient rainfall (100%), and wet (150%). The warming treatment was applied at a subplot level with warmed and ambient subplots. Warming was applied using hexagonal open-topped warming chambers constructed from 2mm thick clear polycarbonate sheeting (Mu et al., 2017b; Wu et al., 2011c).

Rainout shelters were established following the Drought-Net protocol to control the incoming precipitation in the experimental plots (https://droughtnet.weebly.com/). Transparent corrugated roofing sheets were mounted on wooden frames to reduce 50% of the incoming precipitation. The intercepted rainfall from the drought plots was collected in gutters along the edge of the rainout shelters and piped onto the addition (wet) plot to increase precipitation by 50%.

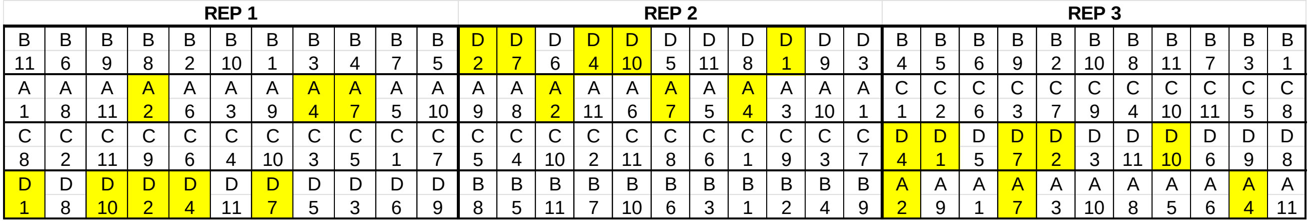
Figure 5.1: Drought-Net experimental plot at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

The Ukulinga Grassland Fire Experiment (UGFE), which was started in 1950, used a split-plot, full-factorial design with randomized blocks (three replicates). Within each block, four whole-plot treatments, and 11 subplot treatments, separated by 4 m pathways were applied. As a result, each whole-plot treatment in each block was made up of a row of 11 subplots (13.7 x 18.3 m in size) in three replicates, to which subplot treatments were distributed at random. The selected sub-plots were sampled in the whole plots of A (burned with no mowing defoliation) and D (burned with mowing in December and February). The subplots sampled in this study were annual (A2), biennial (A4), and triennial winter burning (A7). It also included the no burn but mowed twice (D1), the annual winter burn mowed twice (D2), the biennial winter burn mowed twice (D4), the triennial winter burn mowed twice (D7), and the winter mow as a substitute for burning and mowed in December and February (D10) (Table 5.1, and Fig. 5.2) (Fynn et al., 2004).

Table 5.1: The treatment plan of the UGFE showing the treatment codes (TC) against their description and time of application with further explanation in the second table below

TC	Time executed			Treatment groups		
	August	December	February	Burning frequency	Defoliation time/type	Defoliation frequency
A2	Annual burn			Annual burn	Winter fire	6 times per 6 year cycle
A4	Biennial burn			Biennial burn	Winter fire	3 times per 6 year cycle
A7	Triennial burn			Triennial burn	Winter fire	2 times per 6 year cycle
D1		Mowing	Mowing	Unburned	Summer mow	12 times per 6 year cycle
D2	Annual burn	Mowing	Mowing	Annual burn	Summer mow & winter fire	18 times per 6 year cycle
D4	Biennial burn	Mowing	Mowing	Biennial burn	Summer mow & winter fire	15 times per 6 year cycle
D7	Triennial burn	Mowing	Mowing	Triennial burn	Summer mow & winter fire	14 times per 6 year cycle
D10	Annual winter mow	Mowing	Mowing	Unburned	Summer mow & winter mow	18 times per 6 year cycle

Whole-plot	
A	**No mowing**
B	**One cut early in season (December)**
C	**One cut end of February**
D	**Two cuts, one at B (December) and one at C (February)**
Sub-plot	
1	**Control**
2	**Annual burn in the first week of August**
3	**Annual burn after the first 12.5 mm of spring rain**
4	**Biennial burn in the first week of August**
5	**Biennial burn after the first 12.5 mm of spring rain**
6	**Biennial burn in autumn**
7	**Triennial burn in the first week of August**
8	**Triennial burn after the first 12.5 mm spring rain**
9	**Triennial burn in autumn**
10	**Annual mowing in the first week of August**
11	**Annual mowing after the first 12.5 mm spring rain**



REP 1											REP 2											REP 3										
B 11	B 6	B 9	B 8	B 2	B 10	B 1	B 3	B 4	B 7	B 5	D 2	D 7	D 6	D 4	D 10	D 5	D 11	D 8	D 1	D 9	D 3	B 4	B 5	B 6	B 9	B 2	B 10	B 8	B 11	B 7	B 3	B 1
A 1	A 8	A 11	A 2	A 6	A 3	A 9	A 4	A 7	A 5	A 10	A 9	A 8	A 2	A 11	A 6	A 7	A 5	A 4	A 3	A 10	A 1	C 1	C 2	C 6	C 3	C 7	C 9	C 4	C 10	C 11	C 5	C 8
C 8	C 2	C 11	C 9	C 6	C 4	C 10	C 3	C 5	C 1	C 7	C 5	C 4	C 10	C 2	C 11	C 8	C 6	C 1	C 9	C 3	C 7	D 4	D 1	D 5	D 7	D 2	D 3	D 11	D 10	D 6	D 9	D 8
D 1	D 8	D 10	D 2	D 4	D 11	D 7	D 5	D 3	D 6	D 9	B 8	B 5	B 11	B 7	B 10	B 6	B 3	B 1	B 2	B 4	B 9	A 2	A 9	A 1	A 7	A 3	A 10	A 8	A 5	A 6	A 4	A 11

Figure 5.2: The plot plan of the UGFE at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The plots used for this study are highlighted.

5.2.3 Data collection

5.2.3.1 Plant community composition

To record species annual peak abundance, plant species composition surveys were conducted in January and March 2020. Using a modified Daubenmire method (Daubenmire, 1959), the percentage aerial cover (to the nearest 1%) of each species rooted inside each 1m x

1m subplot was estimated. The relative maximum cover values (between the early and late season sampling) of each species in the warmed and ambient subplots were used to determine the species cover. The species richness, which is the simplest indicator of species diversity was defined as the number of plant species (Keylock, 2005a) in a subplot. For plant diversity, the Shannon-Wiener Diversity Index, which is a function of the relative frequency of the plant species, and Pielou's Evenness, which shows the similarity in the relative abundance of different species in the site, were used (Keylock, 2005a; Mendes et al., 2008a).

5.2.4 Seed bank and seed rain

For soil seed banks, topsoil samples were collected in mid-winter (mid-August 2020) on 9 plots from the Drought-Net experiment and 24 plots from the UGFE. Samples were collected in both the ambient and warmed subplots, yielding a total of 18 and 48 samples for the two sites. In each subplot, three subsamples were collected systematically at three of the four corners of the 1m x 1m Drought-Net subplots and the 2m x 2m UGFE subplots respectively and combined as one composite site sample. Each subsample was taken from the top 10 cm of the topsoil layer and covered a 10 cm x 10 cm sampling area. In early September 2020 these samples were germinated in a greenhouse with unlimited water supply. Representative samples of each species were transplanted for identification after maturation. As soon as germination halted after twelve weeks, seedlings were counted and removed from the trays.

Seed traps made from 10 cm x 10 cm Astroturf carpet squares, based on the methods of (Sullivan et al., 2016), were deployed to catch seeds that dispersed into the plots. The seed traps were placed in early-December 2019 when seeds were maturing and dispersing, and the first collection, during which the seeds were dusted into brown paper bags, took place in early-January 2020. The seed traps were then replaced immediately with new carpet squares. The late season collection, which was scheduled to be collected towards the end of the growing season around late March, was carried out in mid-winter (mid-August 2020), due to COVID-19 pandemic restrictions. Three carpet squares per subplot were placed in the corners of the % cover quadrats, where species composition data was collected, of 1m x 1m on the drought net subplots and 2m x 2m subplots on the UGFE. The seed carpets were placed at the corners of a quadrat within the treatment plots, and the quadrat was at least 1 m away from the edge of the plot. This would prevent the influence of neighbouring plots. Two samples of each ambient and warmed subplot were taken for each plot, resulting in 18 and 48 samples for the two sites.

There was a tag on each carpet square as it is easy to lose them when they become covered in litter. The seeds from the traps were germinated in the greenhouse.

5.2.5 Statistical Analysis

For the Drought-Net experiment and UGFE, the multivariate correlation between the soil seed bank and seed rain, soil seed bank and aboveground vegetation, and seed rain and aboveground vegetation was determined using a Mantel test with a Bray-Curtis distance measure. The relative abundance of all species within the soil seed bank, and seed rain were examined using a canonical correspondence analysis (CCA) to determine if rainfall variation and warming differentially affected them. The same analysis was done to determine the effect of warming under different fire and mowing treatments for all species within the soil seed bank, and seed rain. The R package "vegan" was used for both the mantle test and CCA and these analyses were conducted in R Studio version 4.2.3 (R Core Team, 2022).

To determine the overall main and interactive effects of warming under different fire and mowing frequencies, on the seedlings that germinated from the soil seed bank and seed rain, a permutational multivariate analysis of variance method (PERMANOVA) outlined in Anderson, (2001) and a Bray-Curtis dissimilarity matrix were used (Clarke & Warwick, 2001). The R package "vegan" contains the "adonis2" function, which was used to achieve this (Oksanen et al., 2019). Type III sums of squares were employed to examine the significance of the factors after the distance matrix had been permuted 999 times. To determine if there were significant effects of warming under different fire, and mowing treatments, on species composition, a one-way analysis of similarity (ANOSIM), which compares the similarity of communities among treatment groups using permutation procedures, was used. Additionally, using the "pairwise.adonis" function in R, a post hoc pairwise comparison of the results was carried out using a false discovery rate (FDR) correction and 100,000 permutations in order to further identify individual differences within each treatment group (Martinez, 2017). Where the model showed interactive significance, a Tukey's HSD pairwise post hoc test was used for multiple comparisons. The species that contributed the most to the differences in composition between treatments were then identified using a post hoc analysis, similarity percentages routine (SIMPER). These analyses were conducted for subsets of the data containing grasses only, forbs only and full species composition. The data set was structured and analysed in such a way to address each research questions. We reduced the interaction to address the questions we were interested in. Hence, only the rain*warm, defo*warm and burn*warm interactions were included.

Analyses of community structure were conducted using generalized linear models (GLM), as both grass, forb and full species richness, diversity, and evenness data did not meet the assumptions of an analysis of variance (ANOVA) even after transformations. The individual and interactive effects of warming under different fire, and mowing treatments, as well as rainfall variation and warming on grass and forb richness, Shannon-Weiner diversity and Pielou's evenness were assessed with GLM. Poisson distribution was used for richness, and a Gaussian distribution for diversity and evenness as the error distribution. No transformations were required for grass and forb richness, diversity, and evenness. The species indices were calculated using the package "vegan" in R Studio version 4.2.3.

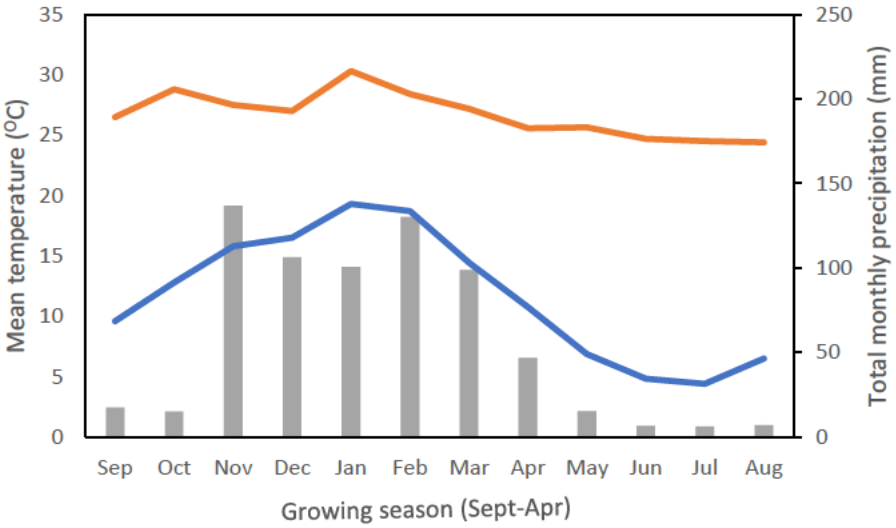
The GLM was achieved with the R package "lme4" (Bates et al., 2014) and "lmerTest" (Kuznetsova et al., 2017) and plotting with package "ggplot2", all conducted in R Studio version 4.2.3 (R Core Team, 2022).

5.3 Results

5.3.1 Climate

This has been corrected throughout the thesis with ‘’The description of the figures (5.3 A & 5.3 B) can be found under the results section of chapter three of this thesis’’.

A)



B)

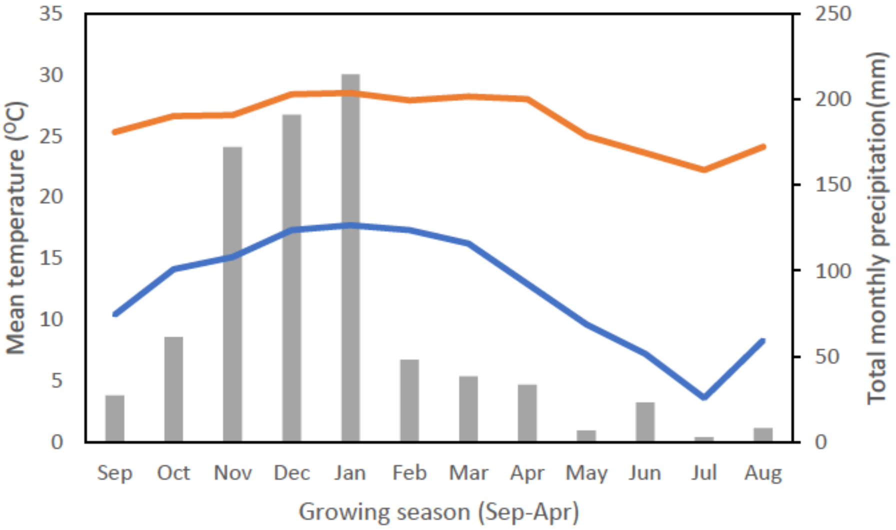


Figure 5.3: Growing season rainfall and temperature at Ukulinga Research Farm, KwaZulu-Natal, South Africa for the (A) 2019/2020 and (B) 2020/2021 growing seasons. Shown are mean monthly precipitation as bars and annual maximum temperature (orange), and minimum temperature (blue) as lines.

5.3.2 Similarity between seed bank, seed rain, aboveground vegetation under rainfall variation and warming

On the Drought-Net experiment, the Mantel test showed a correlation in the composition of the seedlings that germinated from the soil seed bank and seed rain (standardised Mantel statistic r = 0.258, p = 0.036, n = 999 permutations) and no significant correlation between aboveground species composition and seed bank (standardised Mantel statistic r = -0.206, p = 0.928, n = 999 permutations) and between aboveground vegetation and seed rain (standardised Mantel statistic r = -0.111, p = 0.749, n = 999 permutations).

A total of 275 seedlings of 19 species germinated from the soil seed bank and 205 seedlings of 12 species germinated from the seed rain respectively during the investigation period. Eight perennial and one annual grass and 10 forb species germinated from the soil seed bank while three perennial grasses and nine forb species germinated from the seed rain. The two dominant grasses in the seed bank were *Cymbopogon caesius* and *Hyparrhenia hirta*, while in the seed rain, *Eragrostis curvula* and *H. hirta* were dominant. *Conyza floribunda* was the dominant forb species in both the seed bank and seed rain. A total of 45 species were observed in the aboveground vegetation, of which 13 were perennial grasses and 32 were forbs with *T. leucothrix* and *T. triandra* dominating amongst grasses and *Cephalaria pungens, Crotalaria macrocarpa,* and *Dyschoriste burchelli* dominating amongst the forbs.

Three grasses, *E. curvula*, *H. hirta* and *Heteropogon contortus* and 5 forb species *C. floribunda*, *Ruellia cordata*, *Oxalis corniculata*, *Tagetes minuta,* and *Crabbea hirsute,* were common to both the seed bank and seed rain. Seven grass and one forb species were common to the seed bank and aboveground vegetation, namely *E. curvula, H. hirta, C. caesius*, *H. contortus, Eragrostis capensis, Brachiaria serrata*, *T. leucothrix*, and *Spermacoce natalensis*, while three grass and one forb species namely *E. curvula, H. hirta, H. contortus* and *Hibiscus aethiopicus* were common to the seed rain and aboveground vegetation.

5.3.3 Soil seed bank and seed rain species composition responses to rainfall variation and warming

The PERMANOVA analysis revealed no significant differences in the soil seed bank and seed rain species composition (Table 5.2). Under the interactive effect of rainfall variation and warming, the soil seed bank and seed rain species composition also did not differ significantly (Table 5.2).

Table 5.2: PERMANOVA results for the main and interactive effects of warming and rainfall variations on the species composition for all species in the soil seed bank (SSB) and seed rain (SRN) at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Showing the degrees of freedom (df), R^2-values and p-values. Significant effects ($p < 0.05$) are shown in bold

		SSB		SRN	
	df	R^2-value	p-value	R^2-value	p-value
RAIN (R)	2	0.046	0.618	0.041	0.594
WARM (W)	1	0.071	0.272	0.088	0.562
R*W	2	0.069	0.306	0.082	0.193

5.3.4 Soil seed bank and seed rain species richness and diversity responses to rainfall variation and warming

There were no significant main effects of rainfall variation and warming on grass and forb richness, diversity and evenness for the soil seed bank and seed rain (Table 5.3). The interaction between rainfall variability and warming also showed no significant effect on grass or forb richness, diversity, and evenness (Table 5.3).

Table 5.3: Generalised linear model (GLM) on the effect of rainfall variation and warming and their interaction on grass richness, forb richness, grass diversity, forb diversity, grass evenness, and forb evenness for (a) soil seed bank and (b) seed rain at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Showing the degrees of freedom (df), F-value and p-values. Significant effects ($p < 0.05$) are shown in bold

a)

		grass richness		forb richness		grass diversity		forb diversity		grass evenness		forb evenness	
	df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
RAIN (R)	2	-1.506	0.132	0.569	0.570	-1.951	0.080	1.430	0.183	-1.348	0.208	0.566	0.584
WARM (W)	1	-1.579	0.114	0.716	0.474	-1.682	0.124	0.365	0.723	-1.072	0.309	0.840	0.420
R*W	2	1.561	0.119	-0.884	0.377	1.543	0.154	-1.338	0.210	1.065	0.312	-1.236	0.245

b)

		grass richness		forb richness		grass diversity		forb diversity		grass evenness		forb evenness	
	df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
RAIN (R)	2	-0.448	0.654	-0.448	0.654	0.566	0.584	-1.348	0.208	0.152	0.882	0.053	0.959
WARM (W)	1	-0.490	0.624	-0.490	0.624	0.840	0.420	-1.072	0.309	0.071	0.945	0.036	0.972
R*W	2	0.680	0.496	0.680	0.496	-1.236	0.245	1.065	0.312	0.075	0.942	-0.160	0.876

5.3.5 Similarity between the soil seed bank, seed rain and aboveground vegetation under the effects of warming, fire and mowing

The UGFE Mantel test showed a correlation in the composition of the seedlings that germinated from the soil seed bank and seed rain, (standardised Mantel statistic r = 0.081, p = 0.041, n = 999 permutations). No correlation existed between aboveground species composition and seed bank (standardised Mantel statistic r = 0.073, p = 0.066, n = 999 permutations) or between seed rain and aboveground vegetation (standardised Mantel statistic r = -0.039, p = 0.763, n = 999 permutations).

A total of 368 seedlings comprising 27 species germinated from the soil seed bank and 269 seedlings comprising 25 species germinated from the seed rain, respectively. Twelve grass species, of which 11 were perennial and one was annual, and 15 forb species germinated from the soil seed bank while eight perennial grass species and 17 forb species germinated from the seed rain. The two dominant grasses in the seed bank were *H. hirta*, and *C. caesius,* while in the seed rain these were, *H. hirta* and *Digitaria longiflora. Conyza floribunda* and *O. corniculata* dominated the seed bank and seed rain as the forb species. A total of 60 species were observed in the aboveground vegetation. Nineteen were grasses, one was annual, 18 were perennial, and 41 were forbs. *Tristachya leucothrix* and *T. triandra* were dominant amongst the grasses and *Becium obovatum,* and *T. atriplicifolia* showed the highest dominance amongst the forbs.

Seven grasses, *H. hirta, E. curvula, Sporobolus africanus, Paspalum scrobiculatum, D. longiflora, T. leucothrix,* and *C. caesius* and three forb species *C. floribunda, O. corniculata,* and *Anthospermum hispidulum,* were common to both the seed bank and seed rain. Eight grass and two forb species were found in both the soil seed bank and aboveground vegetation, namely *E. curvula, E. capensis, E. racemosa, H. hirta, C. caesius, D. longiflora, T. triandra, T. leucothrix, Helichrysum nudifolium,* and *C. hirsute,* while six grass, *T. leucothrix, E. curvula, A. junciformis, H. hirta, D. longiflora, C. caesius* and six forb species, *Agathisanthemum chlorophyllum, C. hirsute, H. nudifolium, Pentanisia angustifolium, Spermacoce natalensis,* and *Hibiscus aethiopicus* were common between the seed rain and aboveground vegetation. This shows that grass species remained unchanged in dominance in the species composition aboveground while dominance in the soil seed bank and seed rain was shared between grass and forb species.

5.3.6 Soil seed bank and seed rain species composition responses to warming, fire, and mowing

For seedlings that germinated from the soil seed bank, burning and mowing frequency significantly influenced the species composition (p = 0.024 & 0.003), mowing frequency altered seedlings that germinated from seed rain (p = 0.050) while there was no effect of warming (Table 5.4). The fire frequency x warming and mowing frequency x warming interactions were not significant for the species composition in seed bank and seed rain (Table 5.4).

Table 5.4: PERMANOVA results for the main and interactive effects of warming under different conditions of fire and, mowing treatments and the pairwise comparisons for the main effect of fire frequency on all species in the soil seed bank and main effect of mowing frequency on the species composition for all species in the soil seed bank (SSB) and seed rain (SRN) at UGFE for the year 2019/2020. Showing the degrees of freedom (df), R^2-value and p-values. Significant effects ($p < 0.05$) are shown in bold

		SSB		SRN	
	Df	R^2-value	p-value	R^2-value	p-value
BURN(B)	3	0.102	**0.024**	0.079	0.142
MOWING(M)	2	0.098	**0.003**	0.064	**0.050**
WARM(W)	1	0.021	0.383	0.033	0.086
B*M	6	0.049	0.231	0.039	0.429
B*W	3	0.029	0.983	0.064	0.376
M*W	2	0.028	0.786	0.024	0.909

Pairwise comparison	SSB	SRN	Pairwise comparison	All species
	p-value	p-value		p-values
Two vs. Three	**0.035**	0.055	Unburned vs. Annual	**0.001**
Two vs. Unmowed	**0.035**	0.699	Unburned vs. Biennial	**0.001**
Three vs. Unmowed	**0.023**	**0.034**	Unburned vs. Triennial	0.159
			Annual vs. Biennial	0.156
			Annual vs. Triennial	0.159
			Biennial vs. Triennial	0.209

The pairwise comparisons for the main effect of fire frequency on all species in the soil seed bank for 2019/2020 showed that the species composition in the unburned plots differed from that of the annual and biennial plots. In the soil seed bank species composition, some species were identified by similarity percentage (SIMPER) analysis to have contributed the most to the differences in percentages between the fire treatments (Table 5.6).

Table 5.6: SIMPER results for the most influential species contributing to differences in all species in the soil seed bank between the four levels of fire frequency, unburned vs annual, unburned vs biennial, unburned vs triennial, annual vs biennial, annual vs triennial and biennial vs triennial on the UGFE. Species are listed in order of their contribution to the average Bray-Curtis dissimilarity between treatments, with a cut-off when the cumulative percent contribution reaches >50%

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in annual burn
Oxalis corniculata	16.45	17.46	0.17	1.5
Hyparrhenia hirta	15.05	15.97	1.5	0
Conyza floribunda	10.5	11.15	1	0.42
Digitaria longiflora	9.82	10.42	1.08	0

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in biennial burn
Hyparrhenia hirta	13.77	14.45	1.5	0.42
Cymbopogon caesius	10.17	10.67	0	1.33
Digitaria longiflora	8.99	9.45	1.08	0
Conyza floribunda	8.33	8.74	1	0
Oxalis corniculata	7.39	7.76	0.17	0.58
Anthospermum hispidulum	5.79	6.08	0.5	0.17

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in triennial burn
Hyparrhenia hirta	13.07	14.79	1.5	0.92
Oxalis corniculata	9.65	10.91	0.17	1.17
Conyza floribunda	8.14	9.21	1	0.58
Digitaria longiflora	7.81	8.83	1.08	0
Eragrostis curvula	7.24	8.19	0.42	0.83
Tristachya leucothrix	6.47	7.32	0	0.75

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in biennial burn
Oxalis corniculata	19.46	22.49	1.5	0.58
Cymbopogon caesius	13.2	15.25	0	1.33
Tristachya leucothrix	6.99	8.09	0.58	0.25
Commelina erecta	6.13	7.08	0	0.75
Conyza floribunda	5.15	5.95	0.42	0

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in triennial burn
Oxalis corniculata	17.37	20.49	1.5	1.17
Tristachya leucothrix	11.22	13.23	0.58	0.75
Eragrostis curvula	8.48	10	0.25	0.83
Hyparrhenia hirta	8.09	9.54	0	0.92
Conyza floribunda	7.39	8.72	0.42	0.58

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in biennial burn	Ave. abundance in triennial burn
Oxalis corniculata	12.83	14.15	0.58	1.17
Cymbopogon caesius	12.8	14.12	1.33	0.42
Hyparrhenia hirta	8.82	9.73	0.42	0.92
Tristachya leucothrix	8.82	9.73	0.25	0.75
Eragrostis curvula	6.29	6.94	0	0.83
Commelina erecta	4.94	5.45	0.75	0

There was a significant difference between the different burning frequencies. The unburned plots separate out from the other burned plots, in the soil seed bank. (Fig. 5.4).

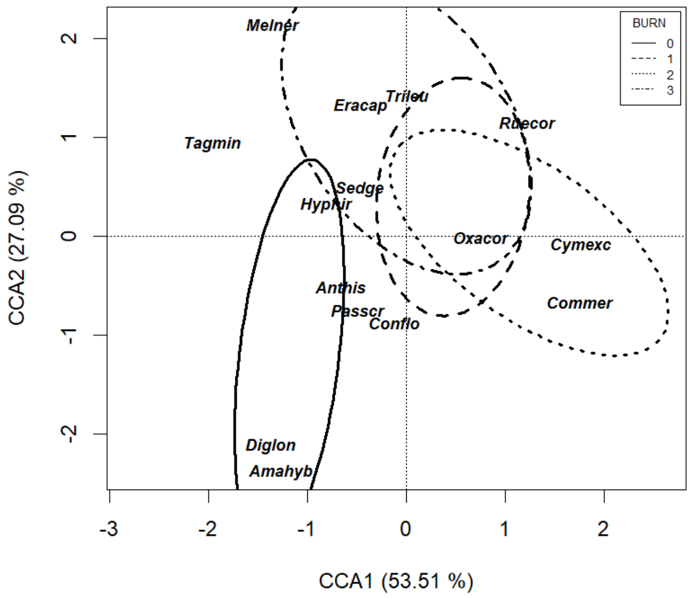


Figure 5.4: A CCA of seedlings that germinated from soil seed bank in 2019/2020 at the UGFE. Axes one and two account for 53.51% and 27.09% of the total variability in the environmental data set. The plots shown here are separated into the four burning frequency treatments (0 = unburned, 1 = annual burn, 2 = biennial burn 3 = triennial burn). Full species names are listed in the appendix.

The pairwise comparisons for the main effect of mowing frequency on all species in the soil seed bank for 2019/2020 showed that the species composition differed significantly under mowing. While for seed rain three mows plots differed from unmowed plots, two mows plots were not different from both plots.

Table 5.7: SIMPER results for the most influential species contributing to differences in all species in the soil seed bank and seed rain between the three levels of mowing frequency on the UGFE, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Species are listed according to their contribution to the average Bray-Curtis dissimilarity between treatments, with a cut-off when the cumulative percent contribution reaches >50%

	Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in two mows**	**Ave. abundance in three mows**
Soil seed bank	*Hyparrhenia hirta*	17.39	19.27	0.71	1.83
	Conyza floribunda	9.71	10.76	0.33	1
	Oxalis corniculata	9.14	10.13	0.79	0
	Digitaria longiflora	7.79	8.64	0.33	0.83
	Melinis nerviglumis	7.59	8.42	0.25	0.67
	Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in two mows**	**Ave. abundance in unmowed**
	Oxalis corniculata	14.95	16.81	0.79	1.22
	Cymbopogon caesius	10.52	11.83	0	1.17
	Tristachya leucothrix	7.14	8.03	0.63	0.22
	Hyparrhenia hirta	6.93	7.79	0.71	0.33
	Conyza floribunda	6.55	7.37	0.33	0.56
	Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in three mows**	**Ave. abundance in unmowed**
	Hyparrhenia hirta	17.27	18.36	1.83	0.33
	Oxalis corniculata	12.91	13.73	0	1.22
	Conyza floribunda	10.86	11.55	1	0.56
	Cymbopogon caesius	10.14	10.78	0	1.17
	Melinis nerviglumis	6.6	7.02	0.67	0

	Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in two mows**	**Ave. abundance in three mows**
Seed rain	*Hyparrhenia hirta*	22.59	26.72	0.79	2.33
	Oxalis corniculata	11.62	13.75	1.17	0.33
	Digitaria longiflora	11.39	13.48	0.42	1
	Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in two mows**	**Ave. abundance in unmowed**
	Oxalis corniculata	15.63	18.04	1.17	0.78
	Hyparrhenia hirta	12.67	14.62	0.79	0.67
	Conyza floribunda	12.64	14.58	0.63	0.78
	Digitaria longiflora	5.31	6.13	0.42	0.11
	Aristida junciformis	5.09	5.87	0	0.39
	Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in three mows**	**Ave. abundance in unmowed**
	Hyparrhenia hirta	25.19	28.09	2.33	0.67
	Digitaria longiflora	10.49	11.7	1	0.11
	Oxalis corniculata	10	11.15	0.33	0.78
	Spermacoce natalensis	9.71	10.83	0.83	0.11
	Conyza floribunda	8.63	9.62	0	0.78

Under the mowing frequency treatment in the seed bank, there was separation of unmowed, two mows, and three mows per year along the first CCA axis in order of decreasing mowing frequency. In the seed rain, three mows was separate from unmowed and two mows (Fig. 5.4).

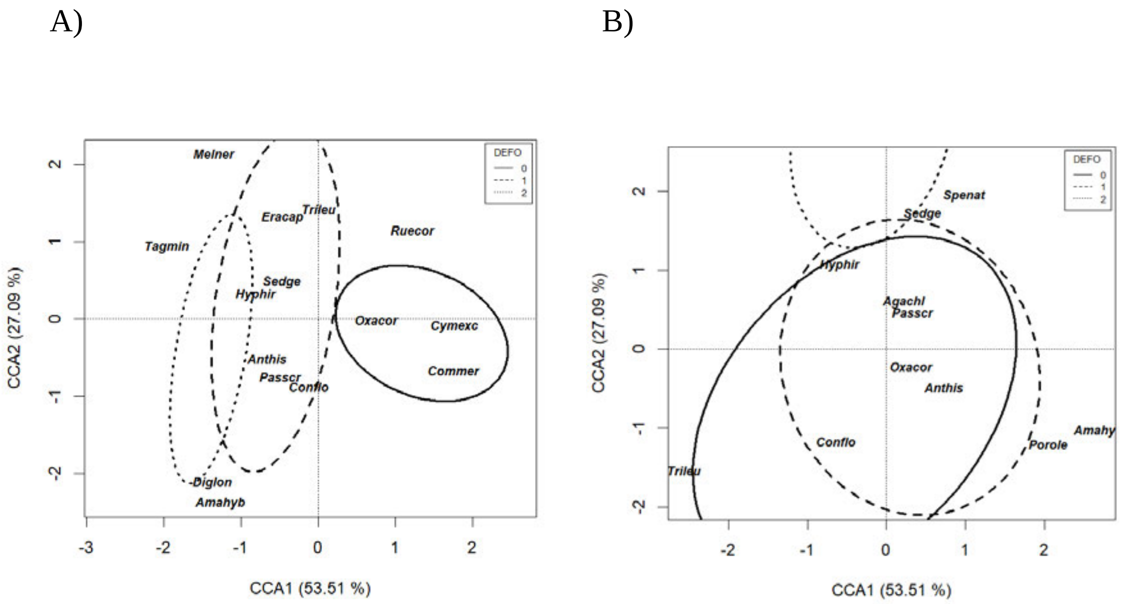


Figure 5.5: A CCA of species community composition of the A) soil seed bank, and B) seed rain in 2019/2020 at the UGFE. Axes one and two account for 53.51% and 27.09%, and 53.51% and 27.09% respectively of the total variability in the environmental data set. The plots shown here are separated into the three mowing frequency treatments (0 = unmowed, 1 = two mows, 2 = three mows). Full species names are listed in the appendix.

5.3.7 Soil seed bank, and seed rain species richness and diversity responses to warming, fire, and mowing

Species richness, evenness and diversity of the soil seed bank and seed rain were not affected under the main and interactive effects of warming under different burning and mowing frequencies between the functional groups of grasses and forbs (Table 5.8).

Table 5.8: The results of generalised linear model (GLM) of the main and interactive effects of warming under different conditions of fire and, mowing treatments on grass richness, forb richness, grass diversity, forb diversity, grass evenness, and forb evenness for (a) soil seed bank and (b) seed rain at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Showing the degrees of freedom (df), F-value and p-values. Significant effects (p < 0.05) are shown in bold

a)		grass richness		forb richness		grass diversity		forb diversity		grass evenness		forb evenness	
	df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
FIRE(F)	3	0.070	0.944	0.692	0.489	-0.594	0.557	1.347	0.187	-0.600	0.552	1.443	0.159
MOWING(M)	2	0.486	0.627	0.433	0.665	0.098	0.922	0.926	0.361	-0.080	0.937	0.947	0.337
WARM(W)	1	-0.101	0.921	0.627	0.531	-0.565	0.567	0.919	0.365	-0.612	0.545	0.968	0.340
BLOCK(B)	2	0.010	0.992	0.362	0.717	-0.341	0.735	0.624	0.537	-0.369	0.714	0.674	0.505
F*W	3	0.194	0.846	-0.727	0.467	0.839	0.408	-1.320	0.196	0.911	0.369	-1.417	0.166
M*W	2	-0.112	0.911	-0.568	0.570	0.046	0.963	-1.033	0.309	0.201	0.842	-1.095	0.282

b)		grass richness		forb richness		grass diversity		forb diversity		grass evenness		forb evenness	
	df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
FIRE(F)	3	0.257	0.797	-0.209	0.834	0.740	0.465	-0.880	0.385	0.740	0.465	-1.133	0.266
MOWING(M)	2	0.385	0.700	-0.933	0.351	0.568	0.574	-0.854	0.399	0.568	0.574	-1.154	0.257
WARM(W)	1	0.373	0.709	-0.335	0.738	0.506	0.616	-0.779	0.442	0.506	0.616	-1.169	0.251
BLOCK(B)	2	0.111	0.912	-0.207	0.836	1.203	0.238	-0.883	0.384	1.203	0.238	-1.264	0.215
F*W	3	-0.313	0.754	0.513	0.608	-0.585	0.563	1.161	0.254	-0.585	0.563	1.484	0.148
M*W	2	-0.418	0.676	0.921	0.357	-0.449	0.656	0.832	0.412	-0.449	0.656	1.132	0.266

5.4 Discussion

In comparison to forests, grasslands typically have a higher resemblance of species composition between the soil seed bank and the aboveground community, and as a result, the seed bank can help in maintaining and restoring the aboveground vegetation following disturbance (Hopfensperger, 2007; Loydi et al., 2012). The degree of resemblance in the sward and seed bank composition between grasslands varies greatly, with higher similarity generally observed in grasslands that are heavily disturbed, in areas with unstable growing environments (Kaul & Wilsey, 2021), in communities that are dominated by annuals (White et al., 2012) and areas that are overgrazed resulting in low seed production (Tedder et al., 2012). This study revealed no correlation between the aboveground vegetation and the seed bank as this grassland is neither heavily disturbed nor overgrazed and the growing conditions are fairly stable. This result is in line with previous studies where no correlation was found between aboveground community and seed banks in Burkina Faso and Botswana (Sanou et al., 2018; Tedder et al., 2012). There was no similarity between the species composition of the seed rain and aboveground vegetation under warming, rainfall variation and fire and mowing treatments, because less than half of the species present in the aboveground vegetation were found in the seed rain. There was a correlation between the species that germinated from the soil seed bank and seed rain at the Drought-Net experiment and UGFE. In line with this study, a high similarity between seed bank and seed rain in a perennial grassland in Sweden was observed (Jakobsson et al., 2006).

Under the Drought-Net experiment and UGFE, the ratio of perennial grass species in the soil seed bank compared to the seed rain was 8:3 and 11:8, respectively, and annual grass species was 1:0 and 1:0, respectively. The ratio of perennial grass species in the aboveground vegetation compared to the soil seed bank was 13:8 and 18:11, respectively, and annual grass species was 0:1 and 1:1, respectively. However, between the aboveground vegetation and the seed rain, the ratio of perennial grass species was 13:3 and 18:8, respectively, and annual species was 0:0 and 1:0, respectively. For the Drought-Net experiment and UGFE, the ratio of forb species between aboveground vegetation and soil seed bank was 32:10 and 41:15, respectively, and for seed rain was 32:9 and 41:17, respectively. The huge disparity in the ratio of forb species between the aboveground vegetation and seed bank and seed rain could be the driving reason for the lack of overall similarity observed in this study and also reflects the diversity of mesic grasslands. Both annual and perennial forb species are in great abundance in the seed banks of many grasslands that are dominated by perennial plants, with only a smaller fraction of the seed bank being occupied by perennial grasses (Mndela et al., 2022). This is explained in part by the fact that the small-seeded annual forb species typically generate their seeds in large quantities, resulting in their high relative abundance in the seed bank (Val et al., 2020).

An increased abundance of grass and forb seedlings in the soil seed bank suggests that the soil seed bank may play a significant role in regeneration. However, a decreased abundance of grass and forb emergents indicates that the soil seed bank is transient and is consequently less beneficial for restoration efforts (Ghebrehiwot et al., 2012). Species richness is measured as the total number of species, and in our study, we recorded 27 as the highest in the soil seed bank. This shows that in our study, the species richness is low compared to past research carried out in the mesic grasslands of South Africa (Ghebrehiwot et al., 2012), where a total of 37 species in the soil seed bank was recorded. It was confirmed in their study that the soil seed bank of mesic grasslands of South Africa has a variety of plant species, which makes it a valuable resource for rehabilitation (Carbutt & Kirkman, 2022; O'Connor, 1991). The contrasting results could be due to the treatment type applied and the experiment duration.

These results agree with the study, that in grasslands that experience limited disturbance, the aboveground community is more influenced by vegetative growth than by the species composition of the soil seed bank (Scott & Morgan, 2012). Perennial grasses dominate the community in this study, resulting from efficient vegetative reproduction. Due to the poor seed longevity of the large-seeded perennial species abundant in mesic grasslands, they do not generally develop persistent seed banks even when seed predators are absent (Snyman, 2005). A reduced number of perennial grasses are expected to be recorded in the soil seed bank and seed rain. It shows that most grass species or individuals are not reproducing annually and that the overrepresentation of these perennial grass species in the soil seed bank and seed rain may be because of extensive production of their small seed and good dispersal ability (Poschlod et al., 2013).

One of the most dominant species in the aboveground vegetation of the Drought-Net experiment and UGFE, *T. leucothrix*, (25.13% and 14.2%, respectively), represents only 2.86% of the germinable soil seed bank with none in the seed rain of the Drought-Net experiment, while under the UGFE, it comprised 7.1% of the soil seed bank and 3.15% of the seed rain. Therefore, it is likely that this species invests most of its reproductive resources in vegetative spreading. Given that these perennial grasses are well under-represented in the soil seed bank, their role in re-establishing the plant community may be insignificant (Scott & Morgan, 2012). These results confirm previous conclusion that in mesic tall grassland, there is not always a good representation of the dominant perennial grasses in the soil seed bank (Ghebrehiwot et al., 2012). The decisive factor for lack of similarity between species composition of seed bank and sward and seed rain and sward in grasslands is the existence of perennials, not necessarily their high density (Dreber et al., 2011). *Tristachya leucothrix* was represented in lower quantities in the seed rain than it was in the seed bank. This showed how the seed bank was a little closer to the sward in terms of species composition in our grassland.

Rainfall variation and warming did not affect the composition of the seed bank and seed rain. This opposes the theory that grassland vegetation is recognized to be susceptible to increased temperature and changes in precipitation in relation to changing environmental conditions (S. R. White et al., 2012). Consistently, past findings have revealed that both the soil seed bank and the standing vegetation can be insusceptible to warmer temperatures (An et al., 2020; Luo et al., 2017). Incongruently, a study examining the effects of severe drought on the seed bank of calcareous grassland on a long-term scale conducted in the Buxton Climate Change Impacts Laboratory at Derbyshire, UK, found that drought significantly altered the species composition of the seed bank and aboveground community (Basto et al., 2018).

The seed bank, which is regarded as a decisive factor in determining the resistance and resilience of systems, buffers plant community responses to changes in rainfall regimes (Parra et al., 2021). According to a previous study neither the vegetation nor the seed bank responded to the precipitation addition, which corresponds with our study (Basto et al., 2018). Under the rainfall variation and warming treatments, the ratio of forb to grass species found in the seed bank was 10:9 and seed rain was 9:3 while in the aboveground vegetation was 32:13. The annual forb species (*C. floribunda*) predominated the seed bank and seed rain in this mesic grassland, whilst perennial grasses predominated the aboveground community (*T. leucothrix* and *T. triandra*). Despite this, the cover of forbs was high in the aboveground community, seed bank and seed rain. Forbs are deep-rooted plants and are more resistant to drought-related variations in soil moisture than shallow-rooted grasses (Tumber-Dávila et al., 2022). These characteristics of forbs could be responsible for the insusceptibility of the aboveground species composition to rainfall variation and warming effects. In our experiment, forbs constitute the largest proportion of vascular plant species and contribute the greatest proportion to the biodiversity of all growth forms (Briggs & Knapp, 2001).

Similarly, to the non-effect response from rainfall variation and warming, unlike mature plants, many seeds can tolerate a far greater range of climate change, particularly to the extremes of drought and temperature (Loydi & Collins, 2021). Seeds can undergo long periods of suspended growth and development (a state of diapause) which accords them the opportunity to be able to withstand longer periods of harsh environmental conditions (Blath et al., 2021). The general trend is that for perennial rangelands, soil seed banks play an important role as a buffer and reservoir, but it is highly improbable that degraded rangelands can be restored only from these seed banks (Snyman, 2013).

Fire frequency had a significant main effect on the species composition of the soil seed bank. The most influential species between the annual and biennial, annual and triennial and biennial and triennial burn plots was *Oxalis corniculata*, where its abundance increased in the annual and triennial burn as compared to the biennial burn plots. This is followed by a grass species *Cymbopogon caesius* between the annual and biennial and biennial and triennial burn plots, with high abundance in the biennial burn plots as compared to both the annual and triennial burn plots. It was changed to *Tristachya leucothrix* between annual and triennial burn plots with increased abundance in the triennial burn plots. This shows a change in the dominance of grasses and how stable forbs were.

It indicates that not all species will respond the same way to the same fire frequency because of the variations in the life histories of these plants, such as, the early stage of the species' growth, microhabitat requirements and their sensitivity to fire (Navarra et al., 2011). The grass species *T. leucothrix* increased in abundance with an intermediate level of fire frequency. Evaporation due to decreased litter and canopy cover in burned areas leads to drier soils which combined with the reduced rainfall that was received over the study's one-year duration, could have led to the observed changes in sward composition. The dominance and presence of perennial grass species in the sward with their large seeds mostly found just a few millimeters below the surface of the soil makes them susceptible to fire and less abundant in the soil seed bank, and other species in the soil seed bank with smaller seeds can emerge from deep layers of soil where heat impacts will be minimal (Diamond et al., 2012; Kellerman, 2006). The response of grasses and forbs to the effect of summer mowing under different burning frequency was not the same as seen between the seed bank, and seed rain.

The soil seed bank was dominated by annual forb species (*O. corniculata*) and a perennial grass species (*C. caesius*). The seed rain was also dominated by the same annual forb species (*O. corniculata*) and a perennial grass species (*H. hirta*) between the two mows and unmowed plots showing how forbs remained unchanged and grasses varied in their dominance. Both the forb and grass species varied in their responses as mowing frequency decreased between the seed bank and seed rain. The abundance of the two most influential species in the soil seed bank increased with decreasing mowing frequency and for the seed rain their abundances decreased. The pattern of response to the influence of summer mowing under different burning frequencies between the forbs and grasses of the seed bank and seed rain was different.

The influence of summer defoliation with differing winter defoliation on the species composition of the soil seed bank and seed rain was significant. A perennial grass species (*H. hirta*) contributed the most to the differences in the germinable seedlings of the soil seed bank and seed rain between two and three mows and three mows and unmowed plots, with increased abundance in the three mows plots as compared to the two mows and unmowed plots. This shows that the abundance of grass species in both the soil seed bank and seed rain increased with increased mowing frequency. The results of this study also show that the dominance of *H. hirta* could be because of the high rate of defoliation by mowing which promote seedling emergence and survival of *H. hirta*. The opened spaces as a result of mowing allows seedlings to emerge and survive for some plants species, due to an increased light availability and reduced intra-specific competition from near adult plants (Chejara et al., 2012). *H. hirta* seedlings has been found in a two-year field experiment in Australia to have high abundance under mowing as compared to unmowed areas (Chejara et al., 2012).

The second most significant contributor to the soil seed bank species composition between the two mows and three mows plots was a forb species *C. floribunda* which had high abundance in the three mows plots, and between the three mows and unmowed was *O. corniculata* which was high in abundance in the unmowed plots. It indicates that the abundance of forb species was species-specific in its response to mowing frequency in the soil seed bank. In the seed rain, species that contributed the most to the differences between the two mows and three mows plots and between three mows and unmowed was *O. corniculata* which had a lower abundance in the three mows as compared to both the two mows and unmowed plots. This shows that in seed rain there was no variation in forb species dominance and its abundance increased with decreased mowing frequency. It shows that grass dominance remained stable with varied dominance in forbs in the soil seed bank, and seed rain had both stable dominance of grasses and forbs under the influence of summer mowing with differing winter defoliation but with varied dominance in forbs. Overall, the pattern of the response of grasses and forbs in the soil seed bank and seed rain under the influence of summer mowing with differing winter defoliation was not the same.

Delayed responses of seed bank composition to disturbances have been found in other experiments, with reduced impact of warming and rainfall variation on a short-term basis (Spence et al., 2016) or under the effect of defoliation by mowing and grazing (Prevey, 2014). The results of this study are in line with other research works, proposing that the rate of change of seed bank composition is strongly dependent on the intensity and duration of disturbance (mowing and fire) (Fidelis et al., 2012; MacDougall et al., 2013; MacDougall & Turkington, 2005; Török et al., 2021).

Species diversity, richness, and evenness of the seed rain and soil seed bank did not vary over time under the main and interactive effects of burning frequency, mowing frequency and warming treatments between the functional groups of grasses and forbs. This is not consistent with past study that the reduced species richness in the seed rain and seed bank can be ascribed to the influence of burning (Snyman, 2013).

5.5 Conclusion

The changes in the composition of the seed bank and seed rain can be explained in relation to the two functional groups. Grasses were found to have reacted differently under the influence of burning frequency in the soil seed bank. The abundance of grass and forb species in the seed bank and seed rain responded the same under each mowing treatment. This implies that grasses are species-specific concerning their response mechanisms under burning frequency in the soil seed bank. These results also indicate that responses of the seed bank and seed rain are independent of vegetation changes, suggesting that altered precipitation regimes and increased temperature do not influence seed production or persistence (or both). This shows that mesic grasslands are resilient to climate change in the short term, and it may be that more prolonged drought and warming or a greater increase in temperature and reduction in rainfall would affect the species composition of the seed bank and seed rain later on as it progresses.

Overall, in the results of this study, it is interesting to speculate that forbs were better represented in both the seed bank and seed rain than grasses. The increased abundance of the weedy pioneer annual forb species *Conyza floribunda* and *Oxalis corniculata* might be linked to their persistent seed bank and the apparent resistance of the species composition to climate change. The findings of this study confirm that seedling recruitment only has a minimal impact on regeneration in mesic grasslands. The mesic grasslands' seed banks and seed rain have limited capacity for recruitment. It is doubtful that soil seed reserves will accumulate over time because the perennial grass species did not create a persistent seed bank throughout the research year. The main conclusion of the study is that the seed bank and seed rain will only have a minor role in restoring the degraded areas and will not restore the level of diversity currently present in our mesic grasslands.

5.6 References

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Appendix 5: Name of species in abbreviation (SA) are written in full for the species composition in (A) soil seed bank (SSB) and (C) seed rain (SRN)

SA	SSB	SRN
Cymcae	*Cymbopogon caesius (Cymbopogon excavates)*	
Diglog	*Digitaria longiflora*	
Eracur	*Eragrostis curvula*	
Eracap	*Eragrostis capensis*	
Hyphir	*Hyparrhenia hirta*	
Melner	*Melinis nerviglumis*	
Passcr	*Paspalum scrobiculatum*	*Paspalum scrobiculatum*
Trileu	*Tristachya leucothrix*	*Tristachya leucothrix*
Agachl		*Agathisanthemum chlorophyllum*
Amahyb	*Amaranthus hybridus*	*Amaranthus hybridus*
Anthis	*Anthospermum hispidulum*	*Anthospermum hispidulum*
Conflo	*Conyza floribunda*	*Conyza floribunda*
Oxacor	*Oxalis corniculata*	*Oxalis corniculata*
Porole		*Portulaca oleracea*
Ruecor	*Ruellia cordata*	
Spenat		*Spermacoce natalensis*
Tagmin	*Tagetes minuta*	

Chapter 6: Effects of warming and different rainfall regimes on plant community composition and biomass in a mesic grassland

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Abstract

Temperature increases due to changing climatic conditions are projected to enhance variations in rainfall patterns, considerably impacting grassland composition and ecosystem function. The combined effect of different rainfall regimes (drought (50%), ambient rainfall (100%), and wet (150%)) and temperature manipulation (warmed and ambient) on the species composition and biomass of a mesic grassland was evaluated at Ukulinga Research Farm (URF), University of KwaZulu-Natal, Pietermaritzburg, South Africa. The warming treatment was applied using open-topped warming chambers, and the rainfall treatment was applied using rainout shelters to intercept 50% of the ambient rainfall. The intercepted rainfall was piped onto the neighbouring plot to increase rainfall by 50%. This resulted in six treatment combinations which were replicated three times and arranged in a split-plot randomized block design. Species composition data were collected in two sampling events (January and March) during the growing season for two years 2019/2020 and 2020/2021, while aboveground biomass was collected in April 2021. Plant community composition was examined to determine sensitivity to experimental warming and drought and whether shifts in plant community composition resulted in changes in productivity. In 2019/2020, the main effect of rainfall variation and their interaction with warming had an impact on the grass species composition ($p = 0.008$, and 0.006, respectively), with just the main effect of warming being seen in the following year (2020/2021). No effect on the forb composition was seen in either year. While there was no evidence of an interaction impact, the main effects of rainfall and warming on biomass production were significant ($p = 0.0003$ and 0.0046, respectively). In conclusion, this study demonstrated how quickly drought reduced the grass community composition, resulting in productivity changes within two years of treatment application.

Keywords: Drought-Net; Warming chamber; Richness; Diversity; Ukulinga Research Farm.

6.1 Introduction

Climate change affects global temperature and precipitation patterns (Korell et al., 2020). Future climatic changes have been predicted by several studies (Himes et al., 2020; J. Li et al., 2020), and these changes are projected to affect the composition of the vegetation and system functions significantly (Komatsu et al., 2019; Kreyling et al., 2008; Lavorel & Garnier, 2002). Warming speeds up the drying of the land surface, potentially resulting in the early occurrence of drought (Sheffield et al., 2012). Drought effects on the functioning of ecosystems depend on the species present, their abundance, phenological stage, and interaction with other factors like temperature (Dreesen et al., 2012; Hoeppner & Dukes, 2012). Temperature affects plant metabolic rates, life cycle events, distribution range and productivity (Bykova et al., 2012; Dewan et al., 2020).

Ecosystem productivity change is partially driven by species diversity (Schuldt et al., 2019; Smith et al., 2009; Zuo et al., 2020). While maintaining the stability of species richness, vegetation composition may be modified by species reordering, the loss of stability in species dominance, or asynchrony (Berauer et al., 2019; Muraina et al., 2021; Zhang et al., 2019). Alterations in the structure of the plant community are typically anticipated to play a significant role in determining how ecosystems respond to extreme events such as drought and warming (Thakur et al., 2022). Climate change, in the long-term, significantly impacts the vegetation composition and structure which can lead to reduced productivity (Wayne et al., 2014). Factors that influence how changing environmental conditions will impact vegetation composition and structure include community types, geographical distribution, species and the number of plant functional types (Alzarhani et al., 2019; Newbold et al., 2020). Projecting the consequences of environmental change on systems and recognizing positive feedback between the plant community and climate depends on how plant communities respond to warming (Shi et al., 2015). It has been established that elevated temperature increases community aboveground net primary production (Baldwin et al., 2014; Kardol et al., 2010); shifts species composition and phenology (Jentsch et al., 2009; Jiang et al., 2021); and causes shifts in plant functional diversity or ecosystem functioning (Gillison, 2018; Hu et al., 2021). In addition, the interactive effect of increased temperature and other global climatic factors may significantly modify plant biomass production, community composition, and diversity

(Reyer et al., 2013). Recently, the increasing extent of global environmental change is modifying functions of the ecosystem, leading to loss of biodiversity (Bjorkman et al., 2020), alterations in community composition (Ernakovich et al., 2014b; García et al., 2018), and reductions in ecosystem resilience (Grimm et al., 2013a; Oliver, Heard, et al., 2015).

Extreme droughts have profound and lagged impacts on the functioning and structure of an ecosystem (Smith, 2011b; Wilcox et al., 2020). Ecosystems must either exhibit strong resistance while drought occurs or increase resilience (i.e., ability to recover quickly) after its occurrence. Changing climatic conditions are expected to cause global rainfall and warming alterations and are projected to influence individual organisms, community composition, and ecosystem processes within grasslands (Weltzin et al., 2003). Mesic grasslands extend over an area of 40% of the earth's terrestrial surface, supplying numerous essential services and functions (Bardgett et al., 2021; Egoh et al., 2011; Gibson, 2009). As a result of anthropogenically modified disturbance regimes, with changes in resource availability and variability of inter-annual climate, there is a possibility of global modifications in the grassland ecosystem's structure and composition (Kirkman et al., 2014a). Experimental studies on responses of productivity to extreme drought are inconsistent, with some indicating that primary production was not resistant to extreme droughts in arid systems (Golodets et al., 2013; Nanzad et al., 2021), semi-arid systems (Hoover et al., 2022; Xu et al., 2021), and mesic systems (Deng et al., 2017; Felton et al., 2020a; Stuart-Haëntjens et al., 2018), while other studies revealed that the response of the primary productivity to such extremes remained stable in semi-arid systems (Meng et al., 2021; Zhang et al., 2019) and mesic systems (Chelli et al., 2016b; Hoeppner & Dukes, 2012). The reasons for these observed differences may depend on the time of occurrence of such extreme events, the type of species, and site differences (Zhang et al., 2019).

However, there is a dearth of information on the effect of climate warming using experimental manipulation of temperature and precipitation on species composition and biomass production in the mesic grasslands of South Africa. Against this backdrop, this study sought to conduct a multi-year manipulative experiment of combined precipitation and temperature manipulation on the mesic grassland plant community composition and biomass production. Species composition responses and biomass production were examined under single and combined warming and rainfall regime treatments. It was hypothesized that species composition would be sensitive to the main and interactive effects of warming and drought, leading to productivity shifts relative to unmanipulated control treatments. The objective of this study was to assess how warming, rainfall variation and their interactions affect the species composition and biomass production in the mesic grasslands of South Africa.

6.2 Materials and methods

6.2.1 Study area

The experiment was conducted at the Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa (30 ° 24′ S, 29 ° 24′ E), a region with summer rainfall that receives an average of 838 mm of precipitation annually (Ward et al., 2020c). There is an average minimum temperature of 8.8 °C in July, during the mild winters, and an average maximum temperature of 26.4 °C in February, during the hot summers (Ward et al., 2020c). These climatic variables work together, forming a growing season from September to April. The vegetation is grassland, and more recent classifications place it in the KwaZulu-Natal Hinterland Thornveld (Mucina & Rutherford, 2006c), where *Vachellia sieberiana* is dominant alongside *Hyparrhenia hirta*, *Themeda triandra* and other herbaceous plants. *Themeda triandra*, *Tristachya leucothrix,* and *Heteropogon contortus* underlying a sparse woody canopy are common under regular burning, while *Aristida junciformis* is dominant in the absence of fire (Morris & Fynn, 2001a). All native grass species follow the C4 photosynthetic pathway (Ward et al., 2020c).

6.2.2 Experimental Design

The experimental plots are part of the Drought-net Research Coordination Network (https://droughtnet.weebly.com/) and were established at the beginning of October 2019, where treatment application was initiated using a split-plot randomized block design across the slight slope gradient of the site. A weather station was established and started functioning towards the end of January 2020, collecting solar irradiance, temperature, wind direction, precipitation, relative humidity, wind speed, and saturated water vapour pressure data. The site was mowed at the end of each growing season to remove moribund biomass and prevent woody encroachment. The plot size was 5.5 m by 3.5 m, divided into six subplots of 1 m each buffered by ½ m wide corridors. Moreover, each plot was trenched around the edges to a depth of 0.5 m and lined with thick plastic to isolate each plot hydrologically. The experimental site consisted of three blocks, and in each of these blocks were three plots with different levels of precipitation: drought (50%), ambient rainfall (100%), and wet (150%). The warming treatment was applied at a subplot level with warmed and ambient subplots. Warming was applied using hexagonal open-topped warming chambers constructed from 2 mm thick clear polycarbonate sheeting (Mu et al., 2017a; Wu et al., 2011a).

Rainout shelters were established following the Drought-Net protocol to limit the incoming precipitation (https://droughtnet.weebly.com/). Transparent corrugated plastic roofing sheets were mounted on wooden frames to reduce 50% of the incoming precipitation. The intercepted rainfall from the drought plots was collected in gutters along the edge of the rainout shelters and piped onto the neighbouring (wet) plots to increase precipitation by 50%.

Figure 6.1: Drought-net experimental plot at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa.

6.2.3 Aboveground biomass sampling

6.2.3.1 Double sampling technique

The double sampling technique was used to non-destructively determine vegetation biomass through a combination of visual estimation and clipping (Pechanec & Pickford, 1937). The double sampling method describes the relationship between clipped (y) and estimated (x) biomass values. Aboveground biomass was estimated visually using one observer to reduce any possible bias. The yields of plants in all the quadrats were based on a scale of 1-10 where 1 represented the least biomass and 10 the most. In addition, 10 quadrats (0.5 m by 0.5 m) across the range of biomass present were collected from areas adjacent to the treatment plots to avoid destructive sampling during the experiment. Biomass in each quadrat was then clipped, oven-dried for 48 hours at 60 °C, and weighed. These data were used to develop a linear regression, $y = ax + b$, which was then used to calibrate the data to estimate the aboveground productivity in kg/ha (Barnes et al., 1982a; Kirkman, 1999; Reich et al., 1993). The double sampling yield estimation technique is the most suitable method for quickly estimating the yield of each quadrat while simultaneously assigning ranks to each species in the quadrat using the dry-weight-rank technique. This method was used in combination with the dry-weight-rank method for estimating total biomass yield. Aboveground biomass data collection and sampling were carried out towards the end of the growing season in April 2021.

6.2.3.2 Dry-weight-rank method

The dry-weight-rank approach is a straightforward technique that employs ranks to measure the dominant species biomass contributed in a particular site ('t Mannetje & Haydock, 1963). Following a ranking of the area, the three dominant species within the quadrat were identified and grouped in accordance with how much biomass they contributed. All other species in the quadrat were ignored, with the highest contributing species being ranked 1, the second highest being ranked 2, and the lowest being ranked 3. The composition percentage was calculated from the ranks using a series of multipliers, with rank 1 equaling 70.2, rank 2 equaling 21.1, and rank 3 equaling 8.7. This was done by assessing the impact of the dominant species on the total biomass ('t Mannetje & Haydock, 1963). When a quadrat only contained one species, it was awarded ranks 1, 2, and 3 (cumulative ranking). Similarly, depending on the biomass contributed by the two species in a quadrat, one species could be ranked 1 and 2, 1 and 3, or 2 and 3, with a shared rank given to the other species.

6.2.4 Plant community composition

Plant species composition surveys were conducted in January and March 2020 and 2021 to record species' annual peak abundance. Using a modified method described in Daubenmire, (1959), the percentage of aerial cover (to the nearest 1%) of each species rooted inside each 1 m by 1 m subplot was estimated. The species abundance was calculated using the relative maximum cover between the early and late season sampling values of each species in the warmed and ambient treatments. The number of plant species in a plot was defined as species richness, the simplest indicator of species diversity (Keylock, 2005b). The Shannon-Weiner Diversity Index, which is a function of the relative abundance of the varying plant species, and Pielou's Evenness, which depicts the similarity in the relative abundance of different plant species, were employed to measure plant diversity (Keylock, 2005b; Mendes et al., 2008b).

6.2.5 Statistical analysis

A non-metric multidimensional scaling (NMDS) ordination was created using a Bray-Curtis distance measure to show how the species composition altered among treatments. These analyses were conducted using R Studio version 4.2.3 (R Core Team, 2023) and the meta-MDS function from the vegan package. Data were transformed prior to ordination using a Wisconsin double standardization and square root transformation. The maximum cover value between early and late-season samples for each species was used and converted to relative cover to capture the maximum abundance of each species and prevent discrepancies caused by seasonal sampling. An appropriate dimensionality was chosen for the NMDS analysis, and an iteration with the lowest stress level was chosen after 30 iterations of NMDS ordination with random starts were run. The NMDS has been configured in such a way that the principal axes account for the most variance. The sites were then placed as points to the NMDS plot and assigned to different treatment groups.

Permutational multivariate analysis of variance method (PERMANOVA) (Anderson, 2001) and a Bray-Curtis dissimilarity matrix were used to assess the overall main and interaction impacts of rainfall variance and warming on species composition (Clarke & Warwick, 2001). The R package "vegan" contains the "adonis2" function, which was used to achieve this. The significance of the factors was examined using Type III sums of squares after the distance matrix had undergone 999 permutations. A one-way analysis of similarity (ANOSIM), which evaluates the similarity of communities among treatment groups using permutation procedures, was performed to ascertain whether there were significant effects of rainfall variation, warming, and their interactions on species composition. Additionally, using the "pairwise.adonis" function in R, a post hoc pairwise comparison of the results was carried out using a false discovery rate (FDR) correction and 100,000 permutations to identify further individual differences within each treatment group (Martinez, 2017). Where the model showed interactive significance, a Tukey's HSD pairwise post hoc test was used for multiple comparisons. The species most responsible for the compositional variations between treatments were subsequently determined using the post hoc analysis, SIMPER (Similarity Percentages Routine) run in PAST version 4.

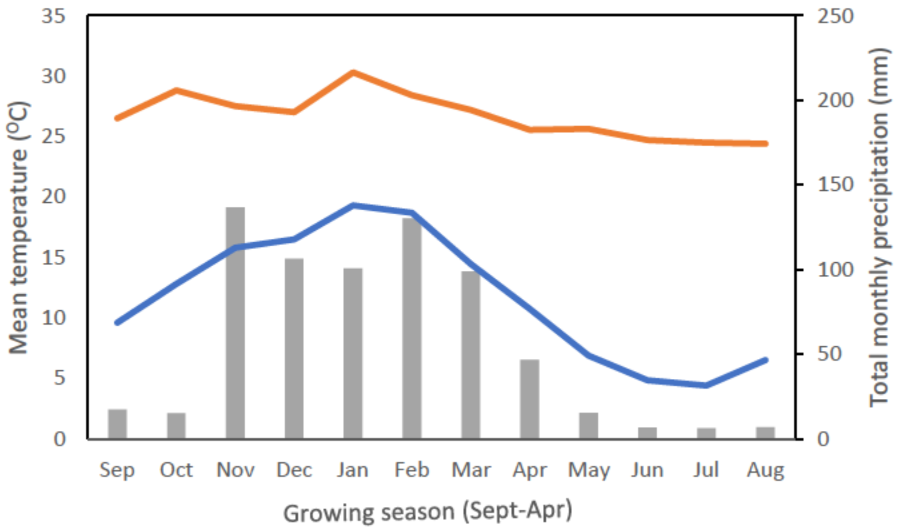
Split-plot analyses of variance were used to examine community structure. This was because the data on biomass, and the richness, diversity, and evenness of grasses and forbs met the requirements for analysis of variance (ANOVA). Split-plot analysis of variance was used to assess how precipitation variability and warming manipulation and their interactions affected biomass production, species richness, diversity, and evenness. Although, the species richness data is in the form of a count data which would be fit for a Poisson distribution. Poisson distribution is often used when data is skewed. it was stated that Poisson distribution can be used when data is not normal, is highly skewed and has outliers (Green, 2021). Our data was not skewed, because the data fitted a normal distribution. This made our analysis appropriate. Data distribution was checked prior to analysis and was found to meet the assumptions of ANOVA. Thus, the analysis used was appropriate. The warming treatment was regarded as a subfactor, and the rainfall variation treatment was the main factor. The normality of the data was assessed using the Shapiro-Wilk test. For each test, a significance level of 0.05 was used. When treatment effects or interactions were significant, means were separated using posteriori least-squares means tests with Bonferroni corrections for multiple comparisons. In the model, rain, warm and rain*warm interactions were set as the fixed factors, and block as the random factor. We reduced the interactions to address the questions we were interested in, in order to observe how grassland composition and productivity respond to warming under different rainfall regimes. For this reason, we have included only the rain*warm interactions.

6.3 Results

6.3.1 Climate

The description of the figures (6.2 A & 6.2 B) can be found under the results section of chapter 3539 three of this thesis.

A)



B)

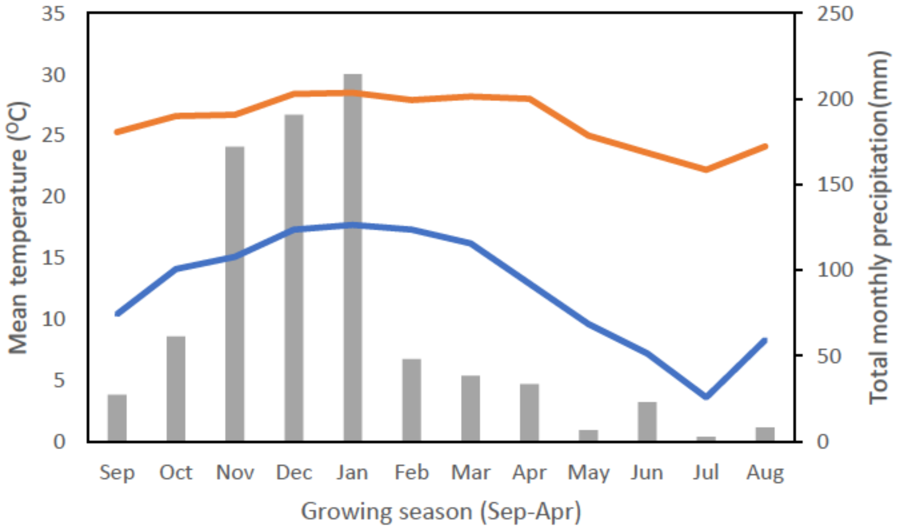


Figure 6.2: Growing season rainfall and temperature at Ukulinga Research Farm, KwaZulu-Natal, South Africa for the (A) 2019/2020 and (B) 2020/2021 growing seasons. Shown are total monthly precipitation as bars and annual maximum temperature (orange), and minimum temperature (blue) as lines.

6.3.2 Species composition responses to rainfall variation and warming

In 2019/2020, a total of 45 species were observed, of which 13 were perennial grasses and 32 were forbs, with *Tristachya leucothrix* and *Themeda triandra* dominating amongst grasses. *Cephalaria pungens, Crotalaria microcarpa,* and *Dyschoriste burchelli* showed the highest dominance amongst the forbs. In 2020/2021 there was a total of 42 species, with 12 perennial grasses and 30 forbs. *Tristachya leucothrix* and *Themeda triandra* were the dominant grasses, and *Cephalaria pungens* and *Thunbergia atriplicifolia* were the dominant forbs.

Table 6.1: PERMANOVA results for the main and interactive effects of rainfall variation and warming on the species composition for all species, grass sp and forb sp for the years (A) 2019/2020 and (B) 2020/2021, with the stress values and goodness of fit (GOF) values (C). The stress values depict the difference in the distance among treatments in the ordination space as compared to the distance among treatments in the actual study sites. Stress values <0.2 are considered good fit to run the NMDS for the data. The GOF helps to define if a data follows a normal distribution with values <0.1 termed as a better fit on the Drought-Net experiment.

A)

		All sp		Grass sp		Forb sp	
	df	R^2-value	p-value	R^2-value	p-value	R^2-value	p-value
RAIN(R)	2	0.146	0.080	0.247	**0.008**	0.094	0.766
WARM(W)	1	0.072	0.166	0.102	0.060	0.054	0.562
R*W	2	0.146	0.093	0.208	**0.006**	0.098	0.732

B)

		All sp		Grass sp		Forb sp	
	df	R^2-value	p-value	R^2-value	p-value	R^2-value	p-value
RAIN(R)	2	0.117	0.429	0.066	0.873	0.163	0.052
WARM(W)	1	0.136	**0.004**	0.153	**0.041**	0.094	0.057
R*W	2	0.064	0.972	0.026	0.996	0.098	0.606

C

	2020	2021
Stress value for all species	0.112	0.131
GOF for all species	<=0.047	<=0.046
Stress value for grass species	0.084	0.083
GOF for grass species	<=0.027	<=0.029
Stress value for forb species	0.099	0.134
GOF for forbs species	<=0.0299	<=0.045

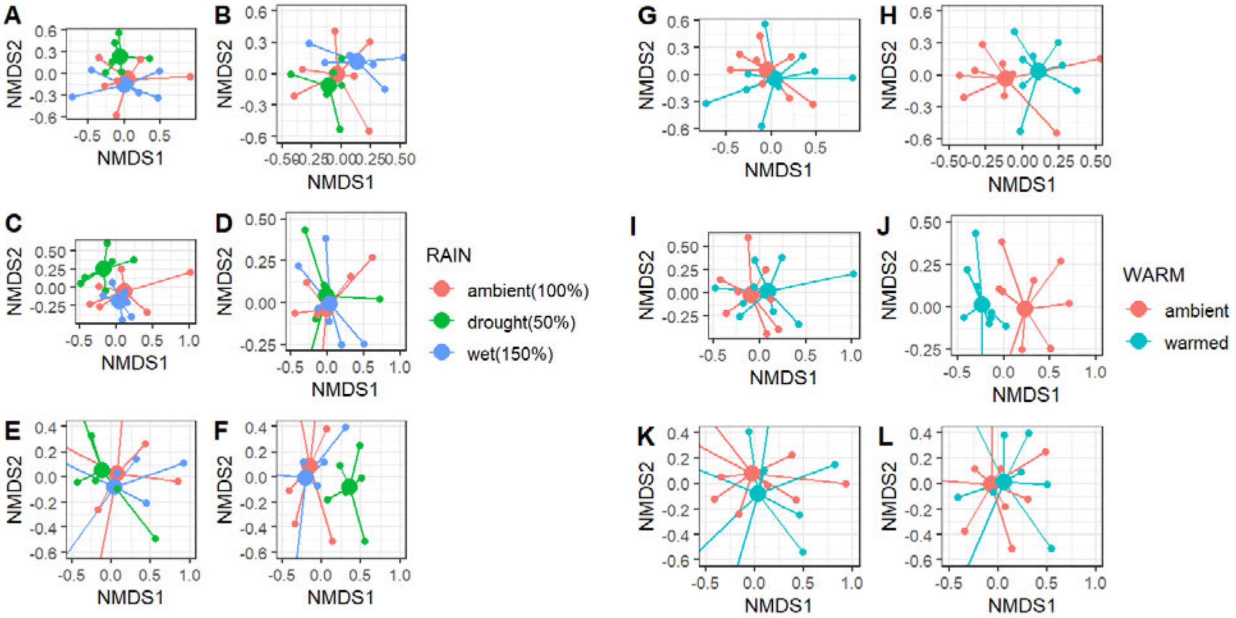


Figure 6.3: Two dimensional non-metric multidimensional scaling (NMDS) ordination of the main effect of rainfall variation (A-F) and warming (G-L) on overall (A+B+G+H), grass (C+D+I+J) and forb (E+F+K+L) species composition for 2019/2020 (1st & 3rd columns) and 2020/2021 (2nd & 4th columns) on Drought-Net experiment. Figure 6.3 "C", "H" & "J" are significant while others are not. Ordination is based on species abundance data. The colours show centroids for the different frequencies under the rainfall variation and warming treatments. The lines connect plot points to their centroids.

In 2019/2020, rainfall variation, and its interaction with warming significantly affected grass species composition but there was no observed main effect of warming ($R^2 = 0.247$, $p = 0.008$, $R^2 = 0.208$, $p = 0.006$, & $R^2 = 0.102$, $p = 0.060$, respectively) (Table 6.1 A). The ordination showed grass composition in drought plots was less variable than ambient and wet.

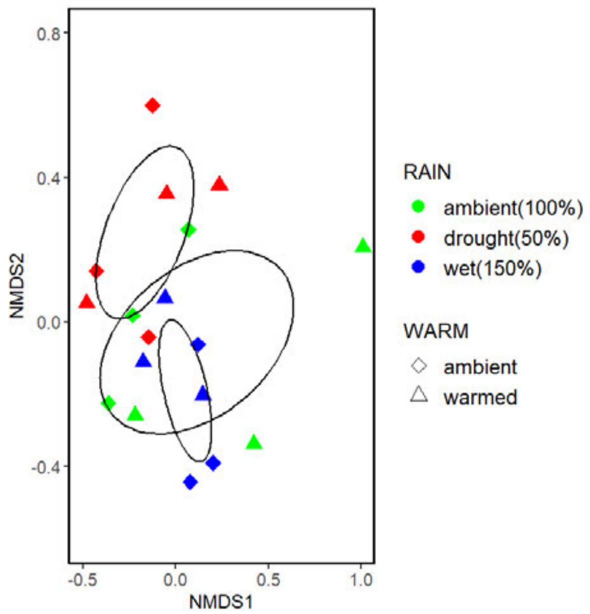


Figure 6.4: Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the interactive effect of rainfall variation and warming on grass species composition for 2019/2020 on Drought-Net experiment at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Ordination is based on grass species cover-abundance data. There were two subplots under the warming treatments. The ellipses connect the plots points to the three levels of rainfall variation.

The Tukey pairwise comparison for the main effect of rainfall variation on grass species for 2019/2020 showed drought was significantly different to wet and ambient rainfall, and for the interaction effect between rainfall variation and warming, the plots experiencing both warming and drought had significantly different grass species composition to all the other plots.

Table 6.2: SIMPER results for the most influential species contributing to divergence in grass community composition between the A) ambient (100% rainfall) and drought (50%) and B) wet (150% rainfall) and drought for the year 2019/2020 on the Drought-Net trials, at UGFE. Species are listed in order of their contribution to the average Bray-Curtis dissimilarity between treatments. Species that increases are identical in bold and those that decreased in abundance with drought are in light font.

A)

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in 100% rainfall	Ave. abundance in 50% rainfall
Tristachya leucothrix	25.52	42.69	50.5	26.5
Cymbopogon caesius	6.745	11.29	9.5	2.33
Themeda triandra	**6.267**	**10.49**	**10.2**	**11.3**
Heteropogon contortus	4.412	7.382	4.17	0.833

B)

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in 150% rainfall	Ave. abundance in 50% rainfall
Tristachya leucothrix	16.85	26.83	30.5	26.5
Cymbopogon caesius	14.59	23.23	20.3	2.33
Brachiaria serrata	13.43	21.38	18	0
Themeda triandra	8.247	13.13	17.8	11.3

Tristachya leucothrix was the most influential species contributing to the divergence between the ambient and drought plots (Table 6.2 A) and wet and drought plots (Table 6.2 B) for the year 2019/2020. Grasses (*Tristachya leucothrix, Cymbopogon caesius, Themeda triandra and Heteropogon contortus*) accounted for > 50% of the difference in community composition between the ambient and drought plots. A similar pattern occurred between the wet and drought plots (Table 6.2 A & B). The dominant grass (*T. leucothrix*) and all other grasses had lower abundances in the drought plots as compared to the ambient plots except *T. triandra* which increased by about 1% in abundance in the drought plots.

In 2020/2021, warming significantly affected overall species (grasses and forbs) ($R^2 = 0.136$, p = 0.004, Table 6.1 B & Fig. 6.3 B) and grass species composition with no effect on the forb composition ($R^2 = 0.153$, p = 0.041, Table 6.1 B, & Fig. 6.3 B). ANOSIM showed that overall species composition between the ambient temperature and warmed plots differed significantly (R statistic = 0.261, p = 0.002) with a significant difference also observed in the grass species composition between ambient temperature and warmed plots (R statistic = 0.219, p = 0.003).

Table 6.3: SIMPER results for the most influential species contributing to divergence in A) overall species and B) grass community composition between the ambient temperature (tmp) and warmed treatments for the year 2020/2021 on the Drought-Net trials, at Ukulinga Research Farm, University of KwaZulu Natal, Pietermaritzburg, South Africa. Species are listed in order of their contribution to the average Bray-Curtis dissimilarity between treatments. Species that increased are indicated in bold and those that decreased in abundance with warmed treatment are in light font

A)

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in ambient temp plots	Ave. abundance in warmed plots
Cymbopogon caesius	3.415	6.432	22.1	14.4
Indigofera hilaris	3.249	6.119	15	6.13
Setaria sphacelate	3.116	5.87	17.1	0.625
Heteropogon contortus	2.945	5.547	15.7	1.25
Tristachya leucothrix	**2.908**	**5.477**	**73.6**	**73.8**
Brachiaria serrata	2.885	5.435	8.57	7.25
Cephalaria pungens	2.815	5.302	20	8.75
Themeda triandra	2.607	4.911	22.9	21
Thunbergia atriplicifolia	2.392	4.506	11.4	10.4
Dyschoriste burchelli	2.367	4.459	15	5.5

B)

Species	**Ave. dissimilarity**	**Contribution (%)**	**Ave. abundance in ambient tmp plots**	**Ave. abundance in warmed plots**
Cymbopogon caesius	3.415	6.432	27.2	17.8
Setaria sphacelate	3.249	6.119	18.9	0.556
Heteropogon contortus	3.116	5.87	16.7	1.11
Tristachya leucothrix	**2.945**	**5.547**	**71.1**	**72.2**
Themeda triandra	2.908	5.477	25	20.9

Cymbopogon caesius was the most influential species contributing to the divergence in the overall species (Table 6.3 A) and grass community composition (Table 6.3 B) between the ambient temperature and warmed treatments for 2020/2021. Five species (*Cymbopogon caesius, Indigofera hilaris, Setaria sphacelate, Heteropogon contortus*, and *Tristachya leucothrix*) accounted for about 30% of the difference in community composition between ambient temperature and warmed treatments in the second year of the study as seen in the SIMPER results (Table 6.3 A & B). The dominant grass (*C. caesius*) and all other grasses had lower abundances in the warmed plots except *Tristachya leucothrix* which increased by 0.2 to 1% in the overall and grass species abundance in the warmed plots.

6.3.3 Species richness and diversity responses to rainfall variation and warming.

On the Drought-Net plots, species richness varied greatly between the functional groups of grasses and forbs. The values for forb richness ranged from 1 to 14, whereas those for grass richness ranged from 1 to 8.

Table 6.4: The main effects of rainfall variation and warming and their interactions on grass richness, forb richness, grass diversity, forb diversity, grass evenness and forb evenness for the years (A) 2019/2020 and (B) 2020/2021 on the Drought-Net trials, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa using a split-plot analysis of variance (ANOVA). Showing the degrees of freedom (df), F-value and p-values. Significant effects ($p < 0.05$) are shown in bold

A)

		Grass richness		Forb richness		Grass diversity		Forb diversity		Grass evenness		Forb evenness	
	df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
RAIN(R)	2	0.911	0.471	0.289	0.763	0.223	0.808	0.293	0.760	0.426	0.679	0.131	0.880
WARM(W)	1	1.633	0.248	2.919	0.138	0.448	0.528	1.588	0.254	2.878	0.140	0.782	0.410
R*W	2	0.833	0.479	1.949	0.222	2.184	0.193	0.525	0.616	4.984	0.053	0.010	0.989

B)

		Grass richness		Forb richness		Grass diversity		Forb diversity		Grass evenness		Forb evenness	
	Df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
RAIN(R)	2	1.300	0.367	4.164	0.105	2.789	0.174	3.121	0.152	0.333	0.734	4.889	0.084
WARM(W)	1	7.759	**0.032**	0.012	0.917	14.392	**0.009**	0.003	0.956	5.025	0.066	0.649	0.451
R*W	2	0.103	0.903	3.611	0.093	0.535	0.611	2.541	0.158	0.781	0.499	0.287	0.759

In 2020/2021 there was a strong main effect of warming with reduced grass richness, and diversity in the warmed plots (Fig. 6.5).

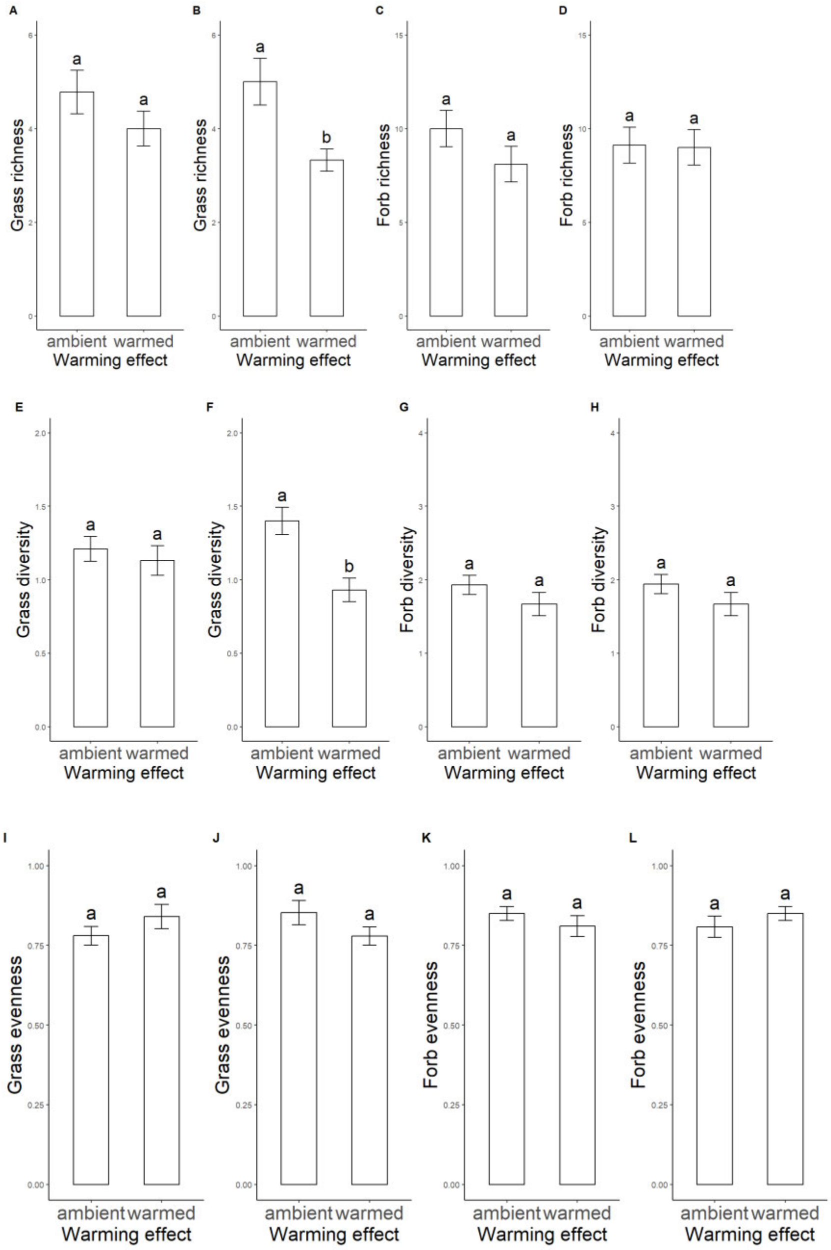


Figure 6.5: Main effects of warming on grass (A - B) and forb (C - D) richness (first rows), grass (E - F) and forb (G - H) diversity (second rows) and grass (I - J) and forb (K - L) evenness (last rows) for the year 2019/2020 (First and third columns) and 2020/2021 (Second and fourth columns) respectively on Drought-Net experiment. Letters in common and "NS" indicate non-significance ($p > 0.05$).

Rainfall variation had no significant main effect on grass richness, diversity and evenness for both years. Over the two years, there were no significant main and interactive effects of rainfall variation and warming on forb richness, diversity and evenness (Table 6.4 A & B). The interaction between rainfall variability and warming showed no significant effect over time on either grass richness or diversity (Table 6.4 A & B).

6.3.4 Aboveground biomass (ANPP) (Kg/ha)

Rainfall variation significantly affected biomass production ($p = 0.0003$) (Table 6.5). The drought treatment significantly reduced biomass production (4156.8 kg/ha ± 344.01), compared to the ambient and wet treatments (6167.5 kg/ha ± 294.42, & 5363.2 kg/ha ± 294.12, respectively) (Fig. 6.7 A). Warming reduced biomass production ($p = 0.0046$) (Table 6.5) with ambient plots having greater biomass (5720.7 kg/ha ± 357.04) than warmed plots (4737.7 kg/ha ± 322.33) (Fig. 6.7 B).

Table 6.5: The main effects of rainfall variation and warming, and their interaction on aboveground biomass in 2020/2021 on the Drought-Net experiment, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa using a split plot analysis of variance (ANOVA). Showing the degrees of freedom (df), sum of squares (Sum-sq), mean square (Mean-sq), f-value and p-values. Significant effects ($p < 0.05$) are shown in bold

	df	Sum-sq	Mean-sq	F-value	p-value
RAIN(R)	2	12290608	6145304	17.1	**0.0003**
WARM(W)	1	4348432	4348432	12.2	**0.0046**
R*W	2	71875	35937	0.1	0.9056
RESIDUALS	12	4312494	359375		

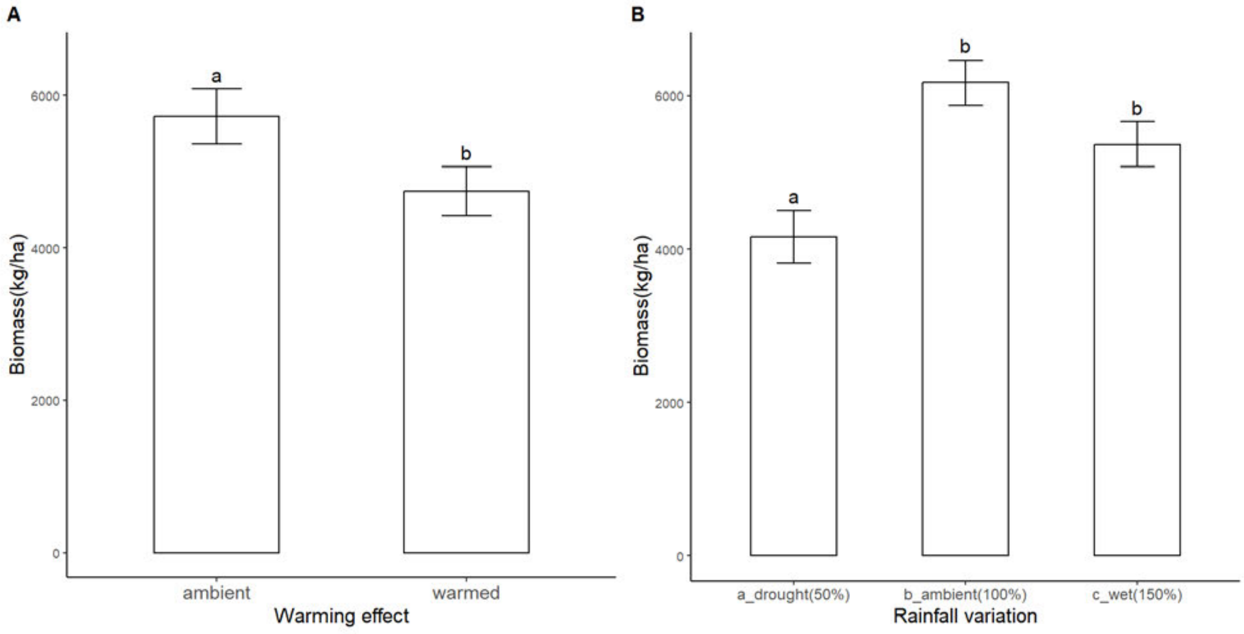


Figure 6.6: **Mean aboveground biomass (±SE) under the main effects of rainfall variation (A) and warming effect (B) on the Drought-Net experiment, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Letters in common indicate non-significance ($p > 0.05$).**

There was no discernible interaction between warming and rainfall regimes on the aboveground biomass ($p = 0.9056$) (Table 6.5).

6.4 Discussion

This study examined the impact of warming and rainfall variability on species composition, richness, diversity, and aboveground biomass. Individual analyses of the species composition of grasses and forbs revealed differences in how the two functional groups respond to shifting rainfall patterns and warming. The grass species composition changed in 2019/2020 due to below-average rainfall, which increased the severity of the drought treatment. The species which contributed the most to the differences in the composition between ambient and reduced rainfall and between increased and reduced rainfall was *Tristachya leucothrix* with its average abundance reduced by between 16 and 50% in the drought plots. *Tristachya leucothrix* occurs mostly in areas with high rainfall, increasing in abundance in optimal and under-utilised conditions, and are low in abundance in intermediate and over utilised conditions (Steenekamp & Bosch, 1995).

In contrast, *T. triandra* increased its average abundance by approximately 10% under drought conditions. This follows past studies that *T. triandra* is a keystone species that is an indicator species in South African mesic grasslands (Snyman et al., 2013). This grass species is adapted to stable environmental conditions and changes in its abundance have previously been associated with a difference in the grazing regimes, species cover, richness and ecosystem function, leading to a decline in veld condition (Ghebrehiwot et al., 2012). The increase in abundance under drought conditions shows that the species is resistant to short-term rainfall fluctuation. *Tristachya leucothrix*, alongside *Cymbopogon caesius, T. triandra,* and *Heteropogon contortus* contributed about 72% to differences in the composition between ambient and reduced rainfall, while between increased and reduced rainfall, *Tristachya leucothrix, Cymbopogon caesius* and *Brachiaria serrata* contributed about 71.4%.

There was no effect of rainfall variation on forb species. This shows how sensitive grasses are to changes in rainfall as compared to forbs. However, in 2020/2021, neither the species composition of grasses nor forbs demonstrated any response to rainfall variation. The ambient weather conditions in 2019/2020 were much warmer and drier than in 2020/2021, which may have contributed to the enhanced influence of rainfall variability on the response of grass species that year. The differing responses of different functional groups observed in 2019/2020 could be because of the shallow root systems in many grasses, making them susceptible to drought-related variations in soil moisture (Fay et al., 2003; Morecroft et al., 2004). The various growth forms and adaptation strategies of plants, including the leaf and root structure, bud positioning, and different timing of phenological events, are likely causes of this variation in how other plant functional groups respond to altered precipitation patterns (Grant et al., 2017c). The observed changes in the species' responses to rainfall variation cannot be defined by their inherent features but by moisture availability in the study area (Titshall et al., 2000).

Despite being very responsive to drought conditions, warming only slightly increased the average abundance of *T. leucothrix* (by 1 to 2%) compared to the ambient plots in the overall grass species composition. The species which contributed the most to the differences in the composition between ambient and warmed plots was *Cymbopogon caesius* with its average abundance reduced by 7 to 10% in the warmed plots. While forbs were unaffected, the warming treatment significantly affected the species composition of grasses in both years. This study found only one interactive effect between rainfall and warming, which affected grass species composition. This finding is consistent with another study where it was found that plants only experience evident stress when both warming and drought are present simultaneously and that this effect may be a result of both high-temperature stress and decreased water availability (De Boeck et al., 2016). Temperature increases are predicted to cause heat stress and stunt growth, and shallow-rooted species experience adverse effects from warming because of water stress (Dorji et al., 2013). In an alpine steppe, investigations revealed that warming enhanced the abundance of deep-rooted plants, such as forbs (Dorji et al., 2014).

The grass and forb species richness were unaffected by rainfall variance in either year. Warming decreased grass richness in 2020/2021 but had no effect on forb richness during the two-year period. Experimental warming often decreased species richness in old-field community plots, especially during drought (Hoeppner & Dukes, 2012). Over the two years, the variation in rainfall had no significant impact on the species diversity and evenness of grass and forbs. This supports the finding that there were no enduring variations in species evenness between precipitation treatments (Hoeppner & Dukes, 2012). Warming had no significant effect on grass and forb species diversity and evenness in 2019/2020. Grass richness and diversity were drastically reduced in 2020/2021, while grass and forb evenness and forb richness and diversity were unaffected by warming.

Where rainfall varied, drought decreased aboveground biomass by between 1000 and 2000 kg/ha. Shortening of the growth season or delayed germination, which results in decreased plant recruitment rates, can also contribute to this (Fay et al., 2003; Walck et al., 2011b). The reduced abundance of the grass functional group under the drought treatment resulted in a significant decrease of ANPP levels, whereas forbs showed no discernible effect. In this study, warming also had a negative impact on aboveground biomass. Studies on how plants in dryland ecosystems react to warming (Musil et al., 2005) have demonstrated that a temperature increase may push the ambient conditions higher than is ideal for photosynthesis and increase evaporative stress. This scenario predicts a loss in aboveground biomass, richness, and diversity due to rising temperatures. In grasslands, high plant species richness improves the temporal stability of the aboveground annual plant production (Roscher et al., 2011; Venail et al., 2015).

Since species richness is expected to influence the vegetation's capacity to withstand and recover from perturbations like droughts, the decline in aboveground biomass in our study may be explained by the reduced grass species richness observed (Van Ruijven & Berendse, 2010). The temporal stability of the aboveground ANPP is improved by higher plant species richness (Gross, Börger, Soriano-Morales, et al., 2013; Lehman & Tilman, 2000). Enhanced inter-annual variability in the production of aboveground biomass and increased susceptibility to droughts could result from a reduction in species richness in grassland ecosystems brought on by global warming (Hoeppner & Dukes, 2012). The current investigation confirmed that decreased soil moisture limits the productivity of aboveground vegetation. In contrast, warming effects could be advantageous when enough water is present. For instance, warming in temperate grasslands of Canada during a year with an advanced timing of snowmelt greatly enhanced aboveground biomass (Winkler, Lubetkin, et al., 2019). Under increased soil moisture, night warming slightly increased ANPP in the Chihuahuan Desert grassland (Collins et al., 2017). The benefits of global warming frequently manifest in moist areas, like the tundra and alpine systems (Walck et al., 2011b). Climate warming either benefits or does not impact biomass if soil moisture is available (Nielsen & Ball, 2015). By contrast, climate warming can limit how plants grow and survive when there is a water shortage. For example, warming significantly reduced aboveground biomass in hot and dry summers of an upland grassland in French Massif Central Region (Cantarel et al., 2013). Drought-induced by warming, rather than warming itself, reduced plant growth in an arid grassland, China (Liu et al., 2021). In an alpine grassland of the Tibetan Plateau, a shortage of soil moisture caused by warming greatly decreased the plant community's ANPP (Fu et al., 2013) and warming-induced drought has been shown to lower plant biomass production in a dry alpine meadow of the Tibetan Plateau (Ganjurjav et al., 2021). These findings demonstrate how warming's indirect effect on ANPP, specifically in vulnerable dry ecosystems, is caused by a decrease in soil moisture (Berdugo et al., 2019; Harrison, 2020). Increased temperatures with high moisture are believed to enhance plant performance, according to studies from temperate, boreal, and Arctic environments (Bjorkman et al., 2018; Oehri et al., 2022).

In a South African context and in contrast to this study, Mvelase, (2021) found that during summer growth, ANPP were significantly increased under warming in comparison to ambient plots in Drakensberg grasslands. The Drakensberg region has an average annual rainfall of 1380 mm, while our study location only receives 838 mm, making it much drier. This disparity in annual rainfall may explain why different results were obtained. The impacts of warming on vegetation may vary depending on the duration of warming, ambient rainfall, and type of system. The decrease in aboveground productivity in our study was caused by limiting photosynthetic capacity and the plant community's stability in dry years when both increased temperature and drought conditions frequently co-exist (Liu et al., 2021).

6.5 Conclusion

In general, the results of this study show that, in the short term, both the main and interactive effects of drought and warming had a significant impact on the grass species composition. This effect was particularly noticeable in the first year of the experiment, demonstrating how quickly grasses responded. As observed in our study, certain grasses produced less biomass than under ambient conditions, leading to shifts in aerial cover composition. Both warming and rainfall treatments affected the composition of grass species, which reduced the abundance of *T. leucothrix* and other grass species under reduced rainfall compared to ambient and increased rainfall. There was a slight increase in *T. triandra* cover under drought and *T. leucothrix* cover under increased temperature. These two grasses are perennial and palatable, indicating no reduction in ecosystem services, especially the grazing value, but there may be a limit in the grazing capacity. As a result, there may be a considerable reduction in production by the plant community, increasing the inter-annual variations of community dynamics and presenting a significant decline in the biomass of grasses with shallow roots. This results in reduced community stability and increased biomass of forbs, which means that forbs in our mesic grasslands appeared more resistant to short-term climate change, indicating no direct loss of ecosystem services.

The results support the hypothesis that plant community composition is sensitive to both the main and interactive effects of warming and drought, resulting in changes in species composition, which resulted in reduced productivity relative to unmanipulated control plots. Hence, further study is strongly advised to encourage a better understanding of species' response to drought and warming in mesic grasslands to develop effective management strategies that mitigate future climate change occurrences.

6.6 References

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Chapter 7: Effects of climatic (warming) and management factors (defoliation by fire and/or mowing) on plant community composition and biomass in a mesic grassland

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Abstract

Increasing temperatures, attributed mainly to increased greenhouse gas emissions, are a leading cause of climate change. There is evidence that changing climatic conditions significantly affect terrestrial ecosystem structure and function. In this study, the combined effect of burning (annual, biennial, triennial, and unburned), defoliation frequency (three mows (summer mow with winter mow), two mows (summer mow with winter burn) and unmowed) and temperature (warmed and ambient) manipulation on the aboveground species composition and biomass in a mesic grassland was investigated at the Ukulinga Grassland Fire Experiment, University of KwaZulu-Natal, Pietermaritzburg, KwaZulu-Natal. The warming treatment was applied using open-topped warming chambers. Species composition data were collected in two sampling events (January and March) during the growing season for two years 2019/2020 and 2020/2021, while aboveground biomass was measured in April 2021. Plant community composition was examined to determine sensitivity to the impact of long-term burning and mowing frequency under ambient and warmed conditions and whether shifts in plant community composition resulted in changes in productivity using generalized linear models. The results showed that there was a main effect of warming, burning and mowing regimes on the species composition, and aboveground biomass ($P < 0.05$). This resulted in a shift in plant community composition which led to reduced biomass under regular burning and increased temperature with increased biomass in the ambient and mowed sites.

Keywords: **Warming chamber; Richness; Diversity; Productivity; Ukulinga Grassland Fire Experiment; Ukulinga Research Farm.**

7.1 Introduction

Increasing temperatures, attributed mainly to increased greenhouse gas emissions, are a leading cause of climate change (Kumar et al., 2018). Signs of climate change are the enhanced inter-annual variability of precipitation and temperature (Mulder et al., 2017; Thornton et al., 2014b). Due to interactions between environmental variation, species richness, and ecosystem services, this climatic variability also significantly affects services and the functioning of the ecosystem (Oliver, Marshall, et al., 2015; Seddon et al., 2016). For instance, climatic variability affects species interactions and plant phenological events (Inouye, 2020; Yang & Rudolf, 2010), resulting in a change in ecological functioning including biodiversity, production, and diminishing ability of the terrestrial ecosystem to absorb carbon (Bakure et al., 2022; Hoffmann et al., 2016). Grasslands are generally described as disturbance-driven systems. This, combined with climatic variations may change grassland function in ways that are unexpected (MacDougall et al., 2013; Turner et al., 2020). However, not all grasslands would be affected by the same degree (Post & Knapp, 2020). Mesic grasslands are characterised by a complex disturbance regime where the interaction of these disturbances affects the diversity and composition of the plant community (Qin et al., 2020). As a result, human-induced disturbance regimes, with inter-annual variability of precipitation, temperature and resource availability, are anticipated to considerably impact plant community structure and composition (Harris et al., 2016; Kertész et al., 2017). The ability of natural grasslands to withstand disturbances is crucial for their preservation. Understanding how climate change and disturbances like fire and mowing interact in these grasslands is therefore essential for preserving the ecosystem function and global productivity patterns. The interactions between environmental variations and disturbance are crucial because they have the potential to boost (Berg et al., 2010; Tylianakis et al., 2008), reduce (Nolan et al., 2021), or alter (Bai et al., 2021) the response of plant ANPP to climatic variations. Mowing and fire may influence soil nutrients, moisture retention, litter levels, and productivity (Gates et al., 2017). Given the significant impact of changes in soil fertility and associated habitat productivity on ecosystem composition (Schütte et al., 2019), it is reasonable to expect that fire and mowing will alter species interactions. These disturbances may also have an impact on litter levels, which are an important factor in determining diversity and community composition (Freitag et al., 2021; Fynn et al., 2004; Tilman, 1993), most likely by having a negative impact on seedling recruitment and germination in many species (Fynn et al., 2005). Since arid systems produce very little litter, it is anticipated that the importance of litter will decrease as aridity increases. Extensive research has investigated how warming affects plant communities in grasslands since they make up a sizable fraction of the earth’s ecosystem (Saugier et al., 2001), and as a result, they have significant economic and ecological importance (Ganjurjav et al., 2018). Increased temperatures can increase plant community productivity (Hudson et al., 2009; Wu et al., 2021b) and can change interactions between species (van der Putten et al., 2016; Wang et al., 2019). Given that various species react differently to temperature changes, warming can affect the relative abundances of species, competition between species, and species coexistence (Gilman et al., 2010). Grassland ecosystem functions and services may be reduced as a result of warming-induced reductions of biodiversity, which is primarily controlled by community composition (Ganjurjav et al., 2018).

In temperate grasslands, climate change may cause productivity to rise due to temperatures already near optimum for plant growth and a longer growing season (Chen et al., 2021; Shaver et al., 2000). Alternatively, declines in soil water content brought on by greater evapotranspiration may reduce plant productivity if precipitation does not increase (Craine et al., 2012; Niklaus et al., 1998). Reduced soil moisture primarily restricts aboveground productivity by reducing stomatal conductance, and photosynthetic rates (Habermann et al., 2019). Therefore, water availability plays a crucial role in determining how plant communities will respond to future temperature increases and soil dryness.

Research on the impacts of fire and mowing on the plant community has been conducted extensively, especially in the mesic grasslands of KwaZulu-Natal (Fynn et al., 2004, 2005; Kirkman et al., 2014b; Morris & Fynn, 2001b; Uys et al., 2004; Ward et al., 2020a). This study contributes to the body of literature by investigating the impacts of warming on aboveground biomass, species composition, richness, diversity and evenness of grassland under various burning and mowing frequencies, at the Ukulinga Grassland Fire Experiment (UGFE) at the University of KwaZulu-Natal in the mesic grasslands of South Africa. The objectives of this study were to (i) assess how burning frequency altered plant community composition and productivity, (ii) examine how summer mowing under different burning frequency affect aboveground biomass and species composition, (iii) determine how summer defoliation with differing winter defoliation altered aboveground biomass, species composition, richness, diversity, and evenness of grasses and forbs under warmed and ambient conditions, in the mesic grasslands of South Africa.

7.2 Materials and methods

7.2.1 Study area

The experiment was conducted at the Ukulinga Research Farm of the University of KwaZulu-Natal in Pietermaritzburg, South Africa (30°24′ S, 29°24′ E), a region with summer rainfall that receives an average of 838 mm of precipitation annually (Ward et al., 2020a). The average monthly lowest temperature is 8.8°C and occurs in July, during the mild winters, and the average monthly maximum temperature is 26.4°C and occurs in February during the hot summers (Ward et al., 2020a). These climatic variables work together to form a growing season which spans from September to April. The vegetation belongs to the grassland biome and a more recent classifications place it in the KwaZulu-Natal Hinterland Thornveld (Mucina & Rutherford, 2006c). *Vachellia sieberiana* dominates the vegetation alongside *Hyparrhenia hirta*, *Themeda triandra*, and other herbaceous plants. The grass species dominant in the absence of fire is *Aristida junciformis*, while *Themeda triandra*, *Tristachya leucothrix* and *Heteropogon contortus* underlying a sparse woody canopy are common under regular burning (Morris & Fynn, 2001b). A C4 photosynthetic pathway is used by all grass species (Ward et al., 2020a).

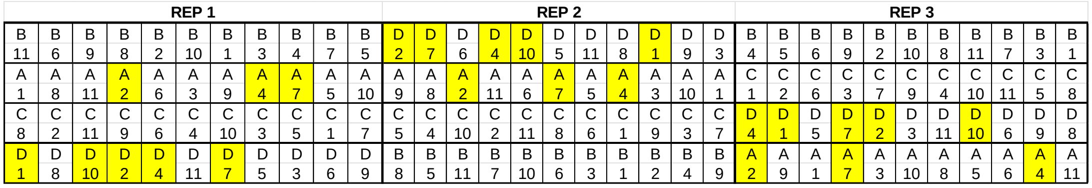
7.2.2 Experimental design

The Ukulinga Grassland Fire Experiment (UGFE), which was started in 1950, used a split-plot, full-factorial design with randomized blocks (three replicates). within each block, four whole-plot treatments, and 11 subplot treatments, separated by 4-m pathways were applied. As a result, each whole-plot treatment in each block was made up of a row of 11 subplots (13.7 x 18.3 m in size) in three replicates, to which subplot treatments were distributed at random. Selected sub-plots were sampled in the A (winter burn treatments with no summer mowing defoliation) and D (winter burn treatments with mowing in December and February) whole plots. The subplots sampled in this study are annual (A2), biennial (A4), and triennial winter burning (A7). It also included (D1 (no burn treatment, but mowed twice in summer), D2 (annual winter burn mowed twice in summer), D4 (biennial winter burn mowed twice in summer), D7 (triennial winter burn mowed twice in summer), and D10 (winter mow as a substitute for the winter burn and mowed twice in summer), (Table 7.1, and Fig. 7.1) (Fynn et al., 2004).

Table 7.1: The treatment plan of the UGFE showing the treatment codes (TC) against their description and time of application

TC	Time executed			Treatment groups		
	August	December	February	Burning frequency	Mowing frequency	Defoliation frequency
A2	Annual burn			Annual burn	Unmowed	6 times per 6 year cycle
A4	Biennial burn			Biennial burn	Unmowed	3 times per 6 year cycle
A7	Triennial burn			Triennial burn	Unmowed	2 times per 6 year cycle
D1		Mowing	Mowing	Unburned	Two mows	12 times per 6 year cycle
D2	Annual burn	Mowing	Mowing	Annual burn	Two mows	18 times per 6 year cycle
D4	Biennial burn	Mowing	Mowing	Biennial burn	Two mows	15 times per 6 year cycle
D7	Triennial burn	Mowing	Mowing	Triennial burn	Two mows	14 times per 6 year cycle
D10	Annual winter mow	Mowing	Mowing	Unburned	Three mows	18 times per 6 year cycle

Whole-plot	
A	**No mowing**
B	**One cut early in season (December)**
C	**One cut end of February**
D	**Two cuts, one at B (December) and one at C (February)**
Sub-plot	
1	**Control**
2	**Annual burn in the first week of August**
3	**Annual burn after the first 12.5 mm of spring rain**
4	**Biennial burn in the first week of August**
5	**Biennial burn after the first 12.5 mm of spring rain**
6	**Biennial burn in autumn**
7	**Triennial burn in the first week of August**
8	**Triennial burn after the first 12.5 mm spring rain**
9	**Triennial burn in autumn**
10	**Annual mowing in the first week of August**
11	**Annual mowing after the first 12.5 mm spring rain**



REP 1											REP 2											REP 3										
B 11	B 6	B 9	B 8	B 2	B 10	B 1	B 3	B 4	B 7	B 5	D 2	D 7	D 6	D 4	D 10	D 5	D 11	D 8	D 1	D 9	D 3	B 4	B 5	B 6	B 9	B 2	B 10	B 8	B 11	B 7	B 3	B 1
A 1	A 8	A 11	A 2	A 6	A 3	A 9	A 4	A 7	A 5	A 10	A 9	A 8	A 2	A 11	A 6	A 7	A 5	A 4	A 3	A 10	A 1	C 1	C 2	C 6	C 3	C 7	C 9	C 4	C 10	C 11	C 5	C 8
C 8	C 2	C 11	C 9	C 6	C 4	C 10	C 3	C 5	C 1	C 7	C 5	C 4	C 10	C 2	C 11	C 8	C 6	C 1	C 9	C 3	C 7	D 4	D 1	D 5	D 7	D 2	D 3	D 11	D 10	D 6	D 9	D 8
D 1	D 8	D 10	D 2	D 4	D 11	D 7	D 5	D 3	D 6	D 9	B 8	B 5	B 11	B 7	B 10	B 6	B 3	B 1	B 2	B 4	B 9	A 2	A 9	A 1	A 7	A 3	A 10	A 8	A 5	A 6	A 4	A 11

Figure 7.1: The plot plan of the UGFE at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The plots used for this study are highlighted.

7.2.3 Aboveground biomass sampling

7.2.3.1 Double sampling technique

The double sampling technique was used to determine vegetation biomass by a combination of estimation and clipping (Pechanec & Pickford, 1937). The double sampling method describes the relationship between clipped (y) and estimated (x) biomass values. Aboveground biomass was estimated visually using one observer to remove from estimated weights any possible bias. The yields of plants in all the quadrats were based on a scale of 1-10 where 1 represented the least biomass and 10 the most. In addition, 10 quadrats (0.5 m by 0.5 m) across the range of biomass present were collected from areas outside the treatment plots in order to avoid destructive sampling during the experiment. Biomass in each quadrat was then clipped, oven-dried for 48 hours at 60 °C and weighed. The double sampling yield estimation technique seems to be the most suitable method for quickly estimating the yield of each quadrat, while simultaneously assigning ranks to each species in the quadrat using the dry-weight-rank technique. The dry-weight estimate is entered on the data processing spreadsheet for each quadrat to the right of the data for the dry-weight-rank analysis. The spreadsheet is set up to use the linear regression formula $y = a+bx$, and at the top of the spreadsheet, the a and b coefficients of the regression equation are inserted. Linear regression is used to calibrate the data in order to estimate the aboveground productivity, in kg/ha (Barnes et al., 1982b; Kirkman, 1999; Reich et al., 1993). This method was used in combination with the dry-weight-rank method for estimating total biomass yield. Aboveground biomass data collection and sampling was carried out towards the end of the growing season in April 2021.

7.2.3.2. Dry-weight-rank method

’t Mannetje & Haydock, (1963) developed the dry weight rank approach, a straightforward technique that employs ranks to measure the dominant species biomass contributed in a particular site. Following a ranking of the area, the three dominant species within the quadrat were identified and grouped in accordance with how much biomass they contributed. All other species in the quadrat were ignored, with the highest contributing species being ranked 1, the second highest being ranked 2, and the lowest being ranked 3. The composition percentage was calculated from the ranks using a series of multipliers, with rank 1 equalling 70.2, rank 2 equalling 21.1, and rank 3 equalling 8.7. This is done by assessing the impact of the dominant species on the total biomass (’t Mannetje & Haydock, 1963b). When a quadrat only contained one species, it was awarded ranks 1, 2, and 3 (cumulative ranking). Similar to this, depending on the biomass contributed by the two species in a quadrat, one species could be ranked 1 and 2, 1 and 3, or 2 and 3, with a shared rank given to the other species.

7.2.4 Plant community composition

To record species annual peak abundance, plant species composition surveys were conducted in January and March 2020. According to the modified method described in Daubenmire, (1959), the percentage of aerial cover (to the nearest 1%) of each species rooted inside each 1m x 1m subplot was estimated. The relative maximum cover values (between the early and late season sampling) of each species in the warmed and ambient subplots was used to determine the species abundance. The species richness, which is the simplest indicator of species diversity was defined as the number of plant species (Keylock, 2005b) in a subplot. For plant diversity, the Shannon-Weiner Diversity Index, which is a function of the relative frequency of the plant species, and Pielou's Evenness, which shows the similarity in the relative abundance of different species in the site, were used (Keylock, 2005b; Mendes et al., 2008b).

7.2.5 Statistical analysis

A non-metric multidimensional scaling (NMDS) ordination was created using a Bray-Curtis distance measure to show how the species composition altered among treatments. These analyses were conducted using R Studio version 4.2.3. (R Core Team, 2023) and the meta-MDS function from the vegan package (Oksanen et al., 2019). Using a Wisconsin double standardization and square root transformation, data were transformed prior to ordination. The maximum cover value between early and late-season samples for each species was used and converted to relative cover in order to prevent discrepancies caused by seasonal sampling. An appropriate dimensionality was chosen for the NMDS analysis, and an iteration with the lowest stress level was chosen after 30 iterations of NMDS ordination with random starts were run. The sites were then placed as points on the NMDS plot and assigned to different treatment groups.

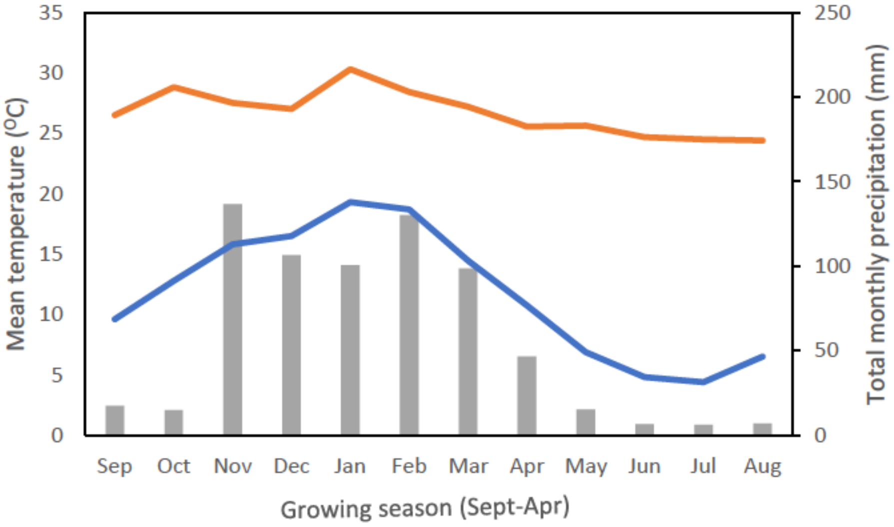
Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) and a Bray-Curtis dissimilarity matrix were used to assess the overall main and interaction impacts of long-term burning and mowing frequencies under the ambient and warmed conditions on species composition (Clarke & Warwick, 2001). The R package "vegan" contains the "adonis2" function, which was used to achieve this (Oksanen et al., 2019). The significance of the factors was examined using Type III sums of squares after the distance matrix had undergone 999 permutations. A one-way analysis of similarity (ANOSIM), which evaluates the similarity of communities among treatment groups using permutation procedures, was performed to ascertain whether there were significant effects of fire and mowing frequencies under the ambient and warmed conditions on species composition. Additionally, using the "pairwise.adonis" function in R, a post hoc pairwise comparison of the results was carried out using a false discovery rate (FDR) correction and 100,000 permutations in order to further identify individual differences within each treatment group (Martinez, 2017). Where the model showed interactive significance, a Tukey’s HSD pairwise post hoc test was used for multiple comparisons. The species that were most responsible for the compositional variations between treatments were subsequently determined using the post hoc analysis, SIMPER which was run in PAST version 4. A type III Analysis of Variance was used to examine community structure. This was due to the unbalanced design of the data. The species richness data is in the form of a count data which would be fit for a Poisson distribution. Poisson distribution is often used when data is skewed. it was stated that Poisson distribution can be used when data is not normal, its highly skewed and has outliers (Green, 2021). Our data was not skewed, thus, we used of the Gaussian method because the data fitted a normal distribution. This made our analysis appropriate. Data distribution was checked prior to analysis and was found to meet the requirements of a Gaussian distribution. The model residuals were checked for normality and variance homogeneity assumptions, where p-values > 0 .05 indicate no violation of homogeneity and normality assumptions. Type III ANOVA was used to assess how long-term burning and mowing frequency under warmed and ambient conditions affected biomass production, species richness, diversity and evenness. When treatment effects or interactions were significant, means were separated using posteriori least-ssquares means test with Bonferroni corrections for multiple comparisons. The dataset was structured and analysed in such a way as to address each research question. We reduced the interactions to address the questions we were interested in, in order to observe how grassland species composition and biomass respond to warming under different burning and mowing regimes. For this reason, we have included only the fire*warm and mowing*warm interactions. Plotting was done with ggplot2. A type III ANOVA was performed using the package lme4 and lmerTest (Kuznetsova et al., 2017) in R version 4.2.3 (R Development Core Team, 2023).

7.3 Results

7.3.1 Microclimate conditions

The description of the figures (7.2 A & 7.2 B) can be found under the results section of chapter 3539 three of this thesis.

A)



B)

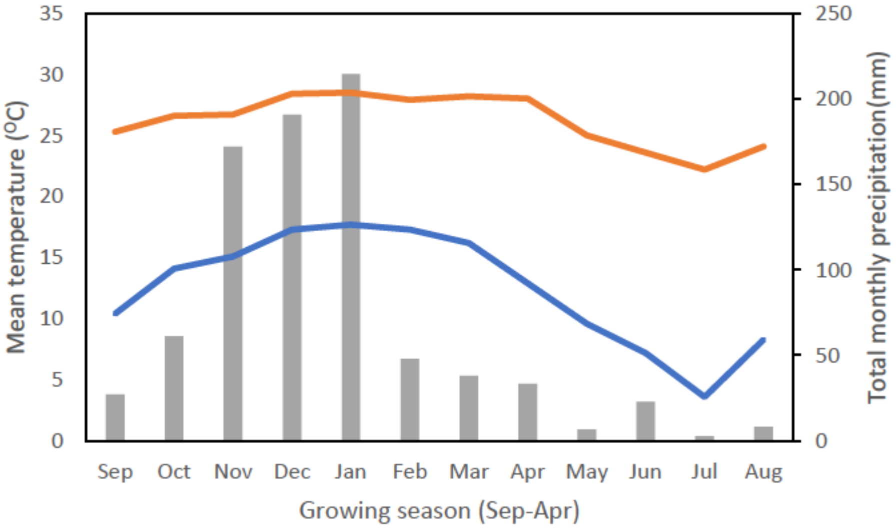


Figure 7.2: Growing season rainfall and temperature at Ukulinga Research Farm, KwaZulu-Natal, South Africa for the (A) 2019/2020 and (B) 2020/2021 growing seasons. Shown are mean monthly precipitation as bars and annual maximum temperature (orange), and minimum temperature (blue) as lines.

7.3.2 Species composition responses to warming under different fire and mowing treatments

In 2019/2020, 60 species were observed in the aboveground vegetation. Nineteen were grasses; one was annual (*Melinis repens*), eighteen were perennial, and 41 were forbs. *Tristachya leucothrix* and *Themeda triandra* were dominant amongst the grasses, and *Becium obovatum* and *Thunbergia atriplicifolia* showed the highest dominance amongst the forbs. Thirteen perennial grasses and 43 forbs were recorded in 2020/2021, giving a total of 56 species. *Tristachya leucothrix* and *Brachiaria serrata* dominated the grass species, and *Afroaster hispida* and *Acalypha angustata* dominated the forb species.

Table 7.2: PERMANOVA results for the main and interactive effects of fire frequency, defoliation frequency and warming on the species composition for all species, grass sp and forb sp for the years (A) 2019/2020 and (B) 2020/2021, with the stress values and goodness of fit (GOF) values (C). The stress values depict the difference in the distance among treatments in the ordination space as compared to the distance among treatments in the actual study sites. Stress values <0.2 are considered good fit to run the NMDS for the data. The GOF helps to define if a data follows a normal distribution with values <0.1 termed as a better fit on the Drought-Net experiment on the UGFE. Showing the degrees of freedom (df), R^2-value, p-values. Significant effects ($p < 0.05$) are shown in bold

A)

		All sp		Grass sp		Forb sp	
	df	R^2-value	p-value	R^2-value	p-value	R^2-value	p-value
FIRE(F)	3	0.109	**0.002**	0.118	**0.008**	0.062	0.336
MOWING(M)	2	0.155	**0.001**	0.131	**0.003**	0.166	**0.001**
WARM(W)	1	0.016	0.558	0.013	0.669	0.024	0.214
F*M	6	0.057	0.067	0.068	0.054	0.047	0.165
F*W	3	0.033	0.975	0.036	0.885	0.043	0.906
M*W	2	0.015	0.997	0.007	0.999	0.023	0.963

B)

		All sp		Grass sp		Forb sp	
	df	R^2-value	p-value	R^2-value	p-value	R^2-value	p-value
FIRE(F)	3	0.118	**0.007**	0.143	**0.005**	0.069	0.162
MOWING(M)	2	0.130	**0.001**	0.128	**0.001**	0.153	**0.001**
WARM(W)	1	0.043	**0.024**	0.022	0.311	0.051	**0.009**
F*M	6	0.053	0.106	0.047	0.258	0.054	0.095
F*W	3	0.028	0.992	0.024	0.963	0.040	0.843
M*W	2	0.024	0.855	0.022	0.820	0.018	0.973

C	2020	2021
Stress value for all species	0.144	0.128
GOF for all species	<=0.028	<=0.027
Stress value for grass species	0.123	0.104
GOF for grass species	<=0.026	<=0.024
Stress value for forbs species	0.174	0.141
GOF for forbs species	<=0.035	<=0.027

While warming showed no significant effect in 2019/2020, fire frequency and mowing frequency significantly affected species composition for all species (R^2 = 0.016, 0.109, 0.155, p = 0.558, 0.002, 0.001, respectively), and for grasses (R^2 = 0.013, 0.118, 0.131, p = 0.669, 0.008, 0.003, respectively) and forbs independently (R^2 = 0.024, 0.062, 0.166, p = 0.214, 0.336, 0.001, respectively) in 2019/2020 (Table 7.2 A).

In the aboveground species composition for the years 2019/2020 and 2020/2021, some species in the overall and grass composition were identified by similarity percentage (SIMPER) analysis to have contributed the most to the percentage difference between the fire treatments (Appedix A, Table 7.3 A & B), mowing treatments (Appendix B, Table 7.4 A, B & C), and warming treatment (Appendix C, Table 7.5 A & B).

In the overall species composition, *Tristachya leucothrix* was the most influential species contributing to the divergence between the unburned and annual burn and the unburned and biennial burn plots over 2019/2020 and 2020/2021, respectively. *Tristachya leucothrix* contributed the most to the percentage difference between the unburned and triennial burn plots for 2019/2020, while a forb species *Afroaster hispida* was the most influential and contributed the most to the divergence between these plots in 2020/2021. The greatest contributor to the difference between annual and biennial burn plots was *Tristachya leucothrix* in 2019/2020 but changed to *Diheteropogon amplectens* in 2020/2021. *Alloteropsis semialata* was the most influential species between annual and triennial burn plots in 2019/2020 and was changed to *Afroaster hispida* in 2020/2021. There was no change in the species (*Tristachya leucothrix)* that contributed the most to the percentage difference between the biennial and triennial burn plots for both years (Appendix A, Table 7.3 A).

Tristachya leucothrix contributed the most to the difference in the grass community composition between the unburned and annual, unburned and biennial, and unburned and triennial burn plots over the two years of study. A similar pattern occurred between the biennial and triennial burn plots (Appendix A, Table 7.3 B). In 2019/2020, *Tristachya leucothrix* contributed the most to the difference in grass community composition between the annual and biennial burn plots for 2019/2020, while *Diheteropogon amplectens* contributed the most in 2020/2021. *Alloteropsis semialata* was the most influential species between annual and triennial burn plots in 2019/2020 and was changed to *Tristachya leucothrix* in 2020/2021.

Tristachya leucothrix was the most influential species, contributing to the divergence between the two mows and three mows plots over the two years in the overall species. In 2019/2020, *Tristachya leucothrix* still contributed the most to the percentage difference between the two mows and unmowed and three mows and unmowed plots, and this changed to *Afroaster hispida* in 2020/2021

(Appendix B, Table 7.4 A). *Tristachya leucothrix* contributed the most to the percentage difference in the grass community composition between two mows and three mows, two mows and unmowed, and three mows and unmowed for 2019/2020 and 2020/2021 (Appendix B, Table 7.4 B). In 2019/2020, the forb species that contributed the most to the percentage difference between the two mows and three mows was *Anthospermum streyi*, while *Thunbergia atriplicifolia* for two mows and unmowed and three mows and unmowed. *Afroaster hispida* contributed most to the percentage difference between two mows and three mows, two mows and unmowed, and three mows and unmowed for 2020/2021 (Appendix B, Table 7.4 C). *Tristachya leucothrix* contributed the most to the percentage difference in the overall species composition and *afroaster hispida* in the forb community composition between the ambient and warmed plots for 2020/2021 (Appendix C, Table 7.5 A & B).

The results for the pairwise comparison (PERMANOVA) for the main effect of fire frequency on overall and grass species composition for 2019/2020 and 2020/2021 showed that unburned plots were significantly different to annual, biennial and triennial plots. Annual burn plots were significantly different from triennial burn plots while no difference was observed between the plots of annual and biennial burn and biennial and triennial burn. In 2019/2020, grass species composition differed only between the unburned and annual burn plots and annual and triennial burn plots. There were no significant differences between the unburned and biennial burn plots, unburned and triennial burn plots, annual and biennial burn plots and biennial and triennial burn plots. The NMDS graphs showed that treatments are less similar to one another in terms of species composition in the year with higher rainfall, with the centroids further apart (Fig. 7.3 A).

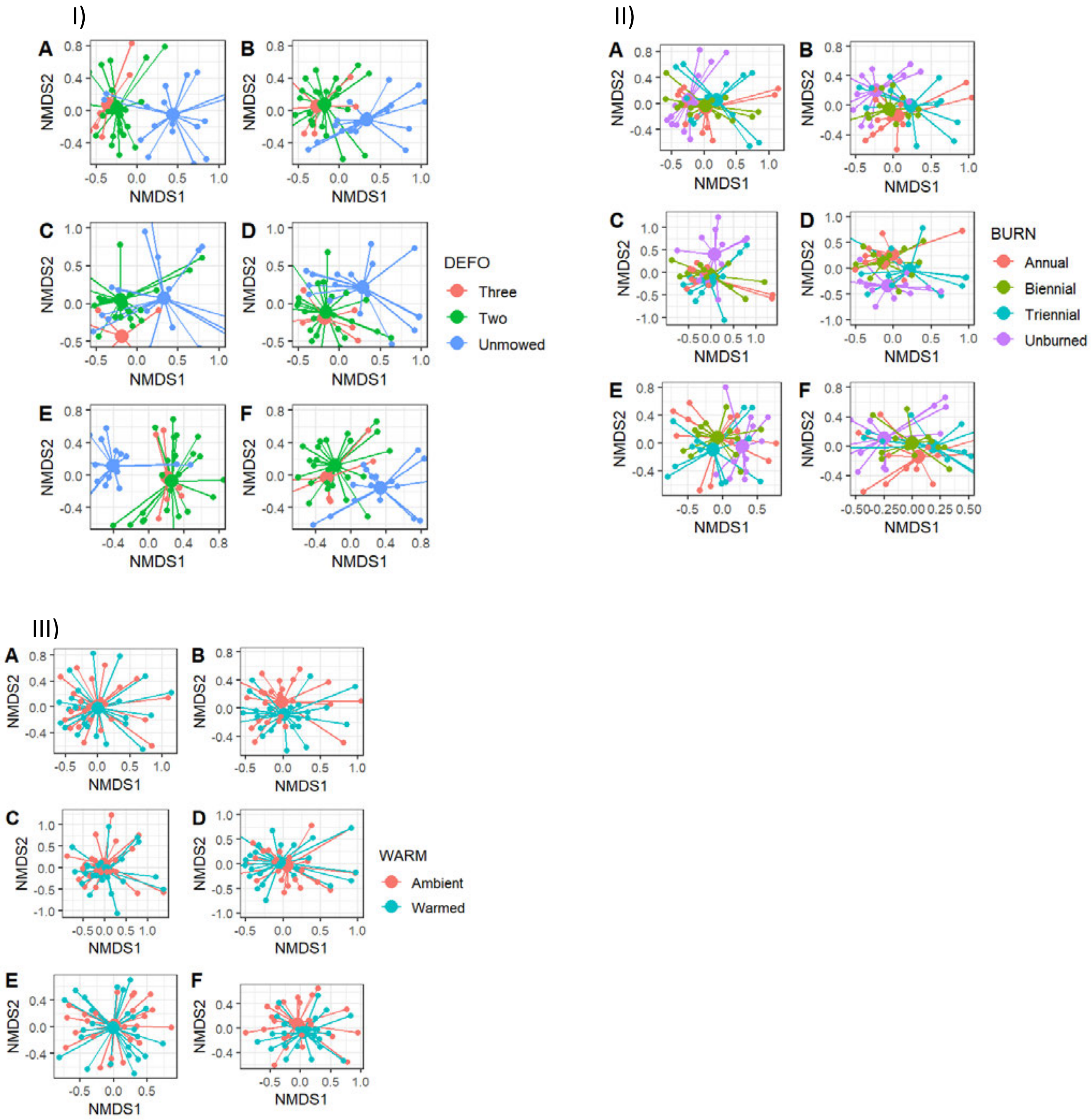


Figure 7.3: Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the main effect of mowing frequency (I), burning frequency (II), and warming effect (III), on overall (A – B), grass (C – D) and forb (E - F) species composition for 2019/2020 (First columns) and 2020/2021 (Second columns) at UGFE. Ordination is based on species abundance data. The colors show centroids for the different frequencies under each treatments, and the lines connect plot points to their centroids. Under plots II (E & F are not significant) and III (A, C, D &E are not significant).

The results for the pairwise comparison (PERMANOVA) for the main effect of mowing frequency on overall, grass and forb species composition for 2019/2020 and 2020/2021. The overall, grass and forb species in the unmowed plots were significantly different from the two and three mows plots over two years, but in 2020/2021, grass species composition in unmowed plots differed from the two mows plots only where no difference occurred between the two mows and three mows plots and the three mows and unmowed plots. The NMDS graphs showed for the main effect of mowing frequency, where the unmowed is very different from the mowed plots, with the overall, grass and forb species composition becoming less variable with higher mowing frequency (Fig. 7.3 B).

The results for the pairwise comparison (PERMANOVA) for the main effect of warming on overall, grass and forb species composition for 2019/2020 and 2020/2021. The overall and forb species in the ambient plots were significantly different from the warmed plots, while grass species composition did not differ between the plots. The NMDS graphs showed the overall and forb species composition becoming less variable in the warmed plots (Fig. 7.3 C).

7.3.3 Species richness, diversity and evenness responses to fire, mowing and warming

Across the treatments, forb species richness varied, from 1 to 19, whereas grass richness ranged from 1 to 9. Grass species richness was affected by the main effect of mowing frequency, and forb richness by burning frequency (Table 7.6).

Table 7.6: The effect of fire frequency, defoliation frequency and warming, and their interaction on grass richness, forbs richness, grass diversity, forbs diversity, grass evenness, and forbs evenness for the years (A) 2020 and (B) 2021 on UGFE at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa using split plot type III analysis of variance. Showing the degrees of freedom (df), F-value and p-values. Significant effects ($p < 0.05$) are shown in bold

A)

		Grass richness		Forb richness		Grass diversity		Forb diversity		Grass evenness		Forb evenness	
	Df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
FIRE(F)	3	0.115	0.951	3.862	**0.019**	0.645	0.592	2.095	0.122	1.696	0.188	0.073	0.974
MOWING(M)	2	8.634	**0.001**	1.334	0.279	4.388	**0.021**	0.854	0.436	1.090	0.348	1.004	0.378
WARM(W)	1	1.252	0.272	0.943	0.339	1.279	0.267	0.047	0.829	0.454	0.505	0.369	0.548
BLOCK	2	3.309	0.049	0.567	0.573	1.380	0.265	0.504	0.608	0.278	0.759	0.810	0.453
F*W	3	0.092	0.964	1.781	0.172	0.075	0.973	1.845	0.160	0.905	0.449	1.053	0.384
M*W	2	0.358	0.702	1.128	0.337	0.355	0.704	0.847	0.439	0.126	0.882	0.265	0.769

B)

		Grass richness		Forb richness		Grass diversity		Forb diversity		Grass evenness		Forb evenness	
	df	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
FIRE(F)	3	1.741	0.179	1.939	0.145	1.643	0.200	1.280	0.299	0.982	0.413	0.145	0.932
MOWING(M)	2	1.407	0.261	2.337	0.114	0.568	0.573	10.012	**<0.001**	3.966	**0.029**	13.779	**<0.001**
WARM(W)	1	0.001	0.979	13.382	**<0.001**	0.285	0.598	24.247	**<0.001**	1.618	0.213	11.557	**0.002**
BLOCK	2	0.704	0.502	1.311	0.283	1.966	0.157	2.922	0.067	0.644	0.532	0.822	0.448
F*W	3	0.419	0.741	0.623	0.606	0.184	0.907	0.764	0.523	0.255	0.857	0.796	0.506
M*W	2	0.603	0.554	0.041	0.960	0.485	0.620	0.509	0.606	0.341	0.714	1.583	0.221

In 2019/2020, forb richness was mainly altered by fire frequency (Fig. 7.4) while grass richness and diversity were affected by mowing frequency (Fig. 7.5). Grass and forb species evenness and forb diversity were not affected by the main effects of fire, mowing and warming, or their interactions (Table 7.6 A).

In 2020/2021, grass and forb evenness with forb diversity varied significantly under the main effect of mowing frequency where it increased with decreasing mowing frequency likewise, forb richness, diversity and evenness were significantly altered under the main effect of warming where it increased under the ambient temperature (Table 7.6 B & Fig. 7.6).

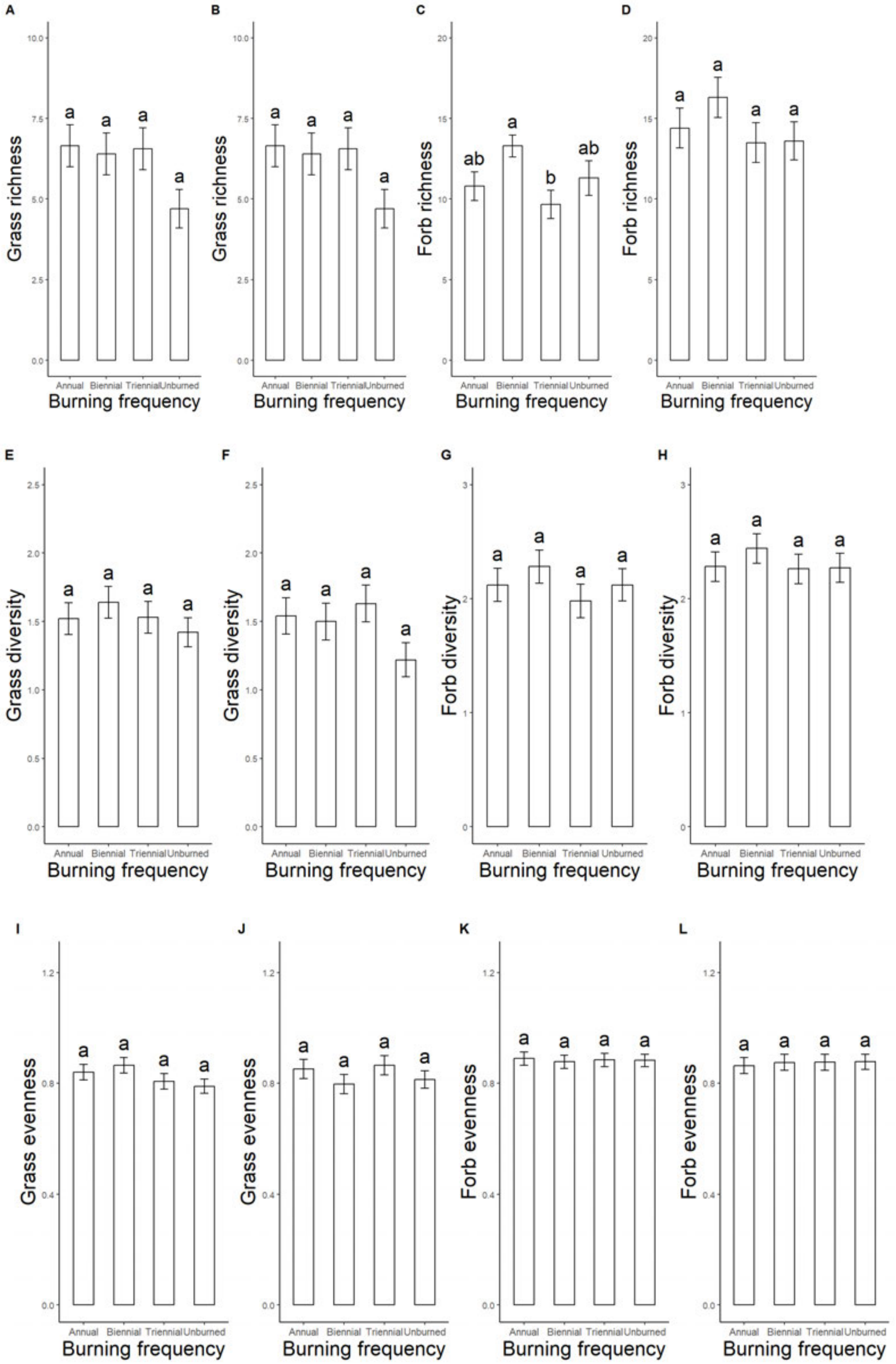


Figure 7.4: **Main effects of burning frequency on grass (A - B) and forb (C - D) richness (first row), grass (E - F) and forb (G - H) diversity (second row) and grass (I - J) and forb (K - L) evenness (last row) for the year 2019/2020 (First and third columns) and 2020/2021 (Second and fourth columns) respectively at UGFE. Letters in common indicate non-significance ($p > 0.05$).**

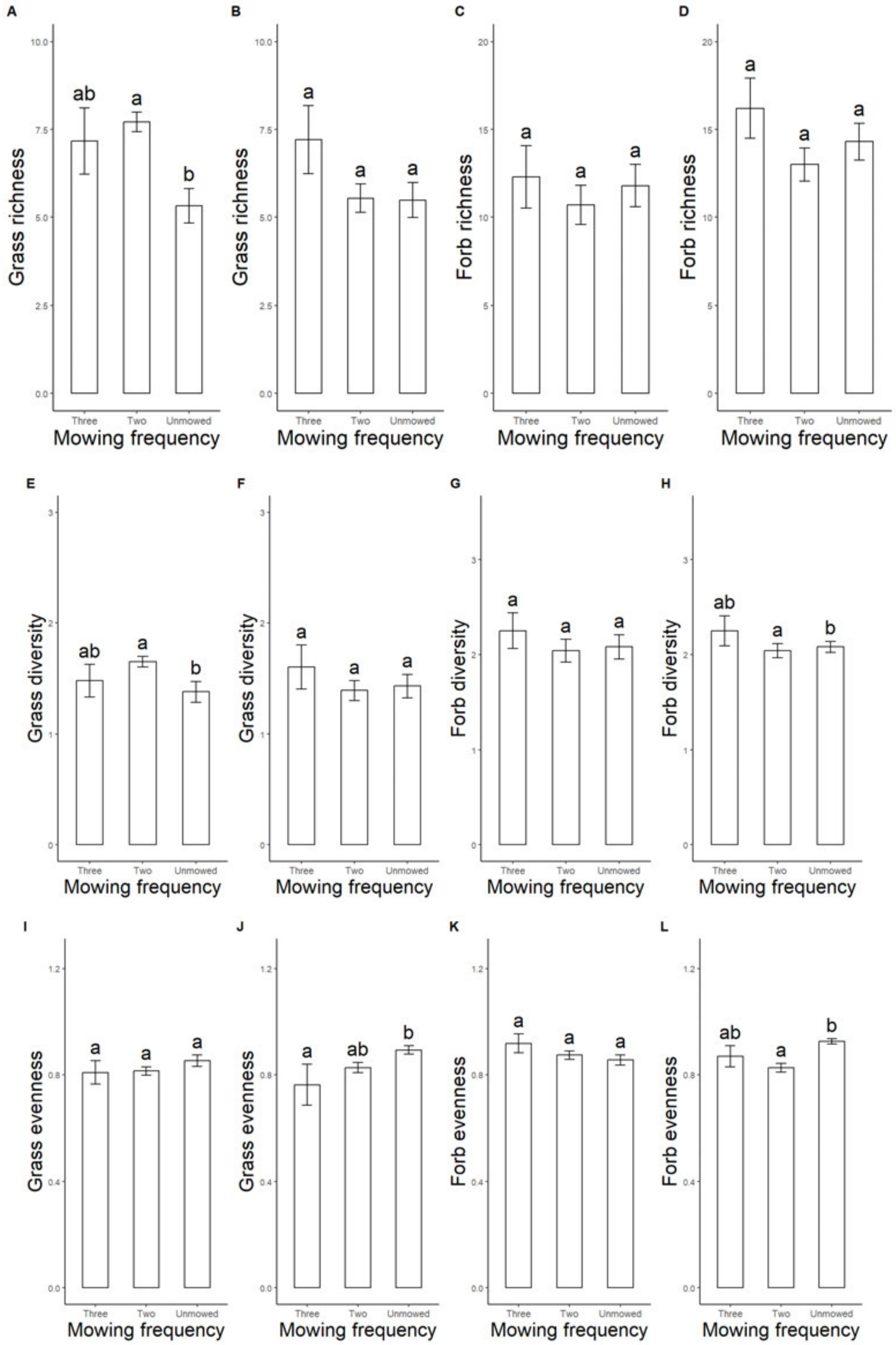


Figure 7.5: **Main effects of mowing frequency on grass (A - B) and forb (C - D) richness (first row), grass (E - F) and forb (G - H) diversity (second row) and grass (I - J) and forb (K - L) evenness (last row) for the year 2019/2020 (First and third columns) and 2020/2021 (Second and fourth columns) respectively at the UGFE. Letters in common indicate non-significance ($p > 0.05$).**

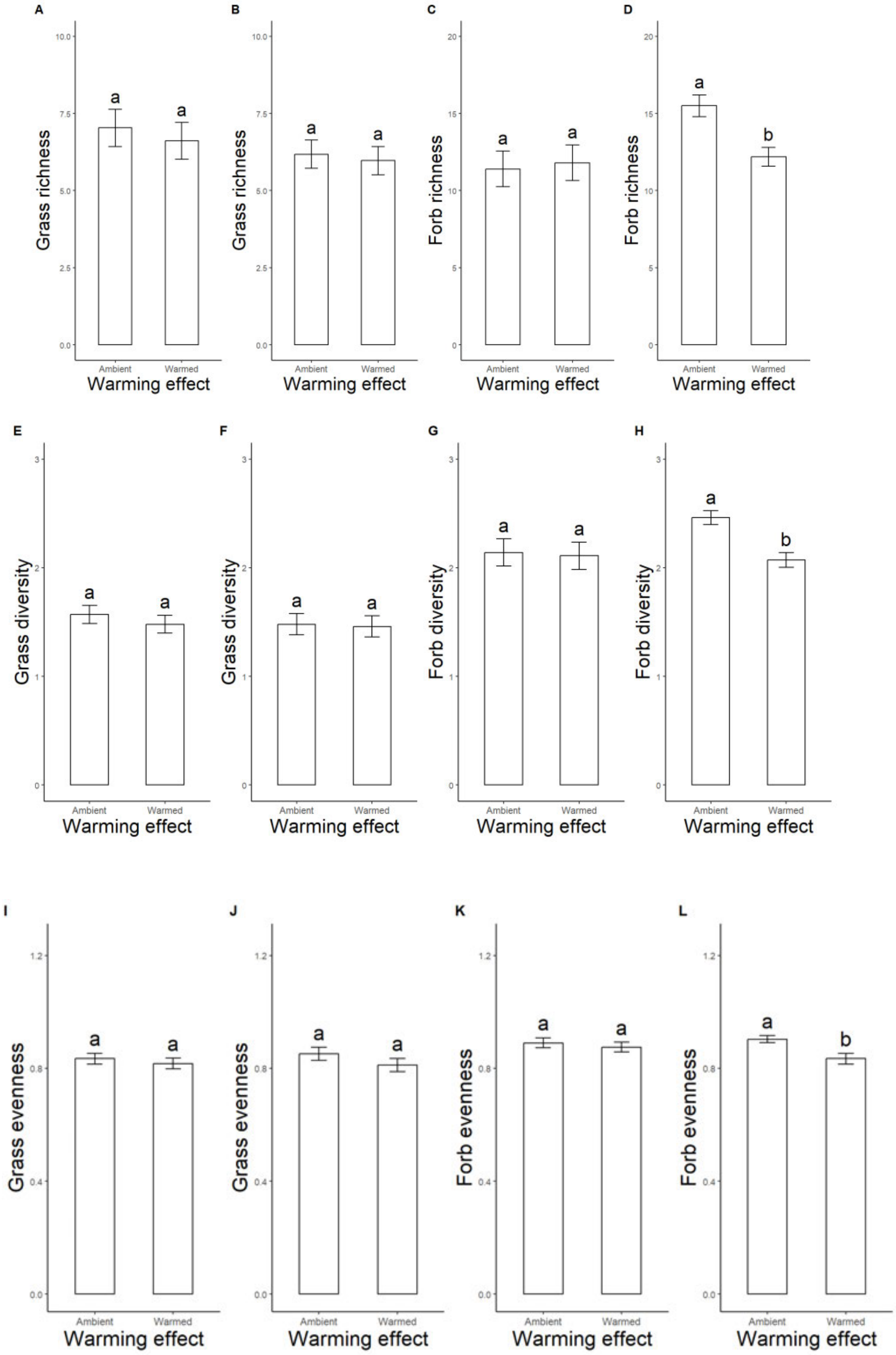


Figure 7.6: **Main effects of warming on grass (A - B) and forb (C - D) richness (first row), grass (E - F) and forb (G - H) diversity (second row) and grass (I - J) and forb (K - L) evenness (last row) for the year 2019/2020 (First and third columns) and 2020/2021 (Second and fourth columns) respectively at UGFE. Letters in common indicate non-significance ($p > 0.05$).**

The overall interaction effects of fire, and mowing frequency under ambient and warmed conditions were not significant for either group in both years 2019/2020 and 2020/2021 (Table 7.6 A & B).

7.3.4 Aboveground biomass (ANPP)

Aboveground biomass varied significantly between the different burning frequencies ($p < 0.001$, Table 7.7). Biomass was highest in the unburned treatment (4247.0 ± 227 kg/ha), followed by the triennial burn (3541.0 ± 150 kg/ha), with the least biomass recorded in the biennial and annual burns (3029.0 ± 190 kg/ha and 2635.0 ± 178 kg/ha, respectively) (Fig. 7.7 A). This shows that aboveground biomass decreased with increasing burning frequency.

Table 7.7: The main effects of fire frequency, defoliation frequency and warming, and their interactions on aboveground biomass for the year 2020/2021 on the UGFE, at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa using split plot type III analysis of variance. Showing the degrees of freedom (df), F-value and p-values. Significant effects ($p < 0.05$) are shown in bold

	Df	F-value	p-value
FIRE(F)	3	49.638	**<0.001**
MOWING(M)	2	9.759	**0.001**
WARM(W)	1	98.203	**<0.001**
BLOCK(B)	2	9.8403	**0.006**
F*M	6	0.397	0.676
F*W	3	0.359	0.783
M*W	2	0.093	0.912
F*M*W	6	0.077	0.926

Aboveground biomass was significantly altered between the different mowing frequencies ($p = 0.001$, Table 7.8), where both the two mows and three mows were the same and were different to the unmowed treatment (3831.0 ± 296 kg/ha, 3486.0 ± 202 kg/ha & 3044.0 ± 157 kg/ha respectively, Fig. 7.7 B).

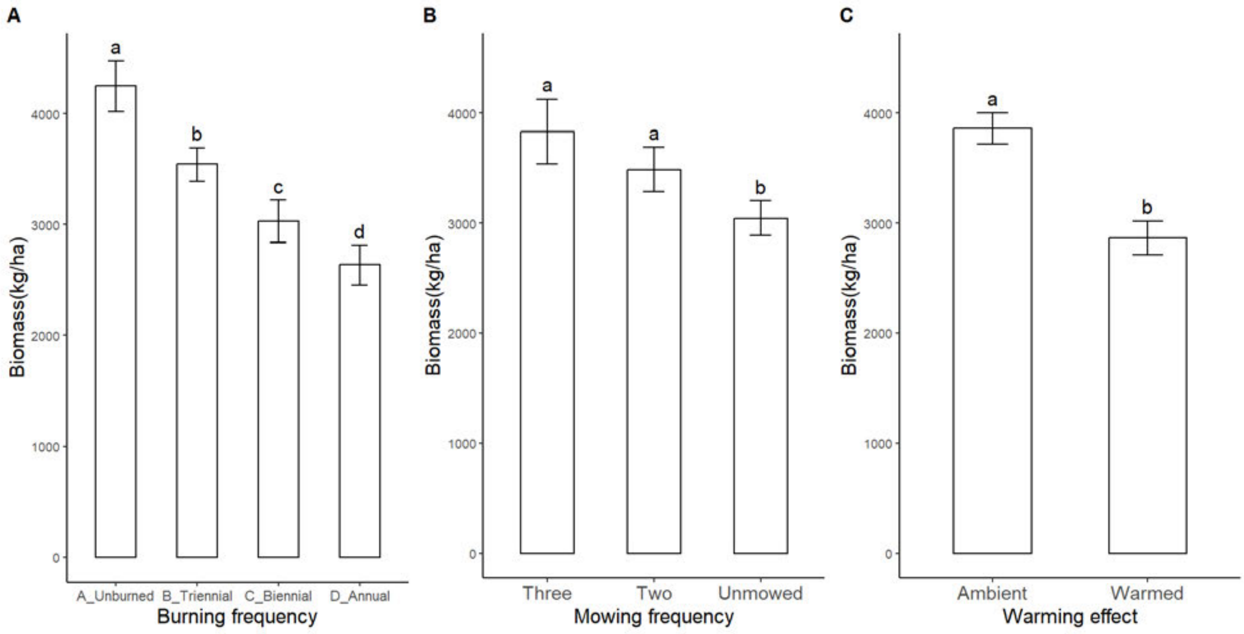


Figure 7.7: **Main effects of burning frequency (A), mowing frequency (B), and warming effect (C) on aboveground biomass for the year 2020/2021 at UGFE. Letters in common indicate non-significance ($p > 0.05$).**

Warming considerably impacted the aboveground biomass ($p < 0.001$, Table 7.8), with the ambient temperature plots having greater biomass (3861.0 ± 141 kg/ha) than warmed plots (2866.0 ± 155 kg/ha). (Fig. 7.7 C). There was no discernible interaction between fire, mowing and warming on the aboveground biomass.

7.4 Discussion

7.4.1 Temporal differences driven by interannual rainfall variability

In 2019/2020 60 species were recorded, with 19 grasses and 41 forbs, while in 2020/2021 56 species were recorded, with 13 grasses and 43 forbs, respectively. The grass species cover was altered from *Tristachya leucothrix* and *Themeda triandra* in 2020 to *Tristachya leucothrix* and *Brachiaria serrata* in 2021, and for forbs, *Becium obovatum*, and *Thunbergia atriplicifolia* to *Afroaster hispida* and *Acalypha angustata*. This shift in the cover of grass species could be a result of the fact that the year 2019/2020 was drier as compared to 2020/2021 which could have affected the production of *Themeda triandra* allowing for the emergence of a sub-dominant grass species *Brachiaria serrata*. South African mesic grasslands are driven by the total rainfall required for plant growth and development (A. Knapp et al., 2006) and it has been hypothesised that the traits of the dominant plant species have an impact on interactions between species and community structure patterns (Gross, Börger, Soriano-Morales, et al., 2013).

7.4.2 Influences of burning frequency on species composition, richness, diversity, evenness and biomass

In 2019/2020, *T. leucothrix* was dominant and contributed the most to the differences in the overall species composition between the annual and biennial burn plots with a greater abundance in the biennial burn plots. A decreased abundance of *T. triandra, Brachiaria serrata* and *Heteropogon contortus* was observed in the biennial burn plots as against the annual burn plots. The species *Alloteropsis semialata* dominated and contributed the most to the differences in the overall species composition between the annual and triennial burn plots resulting in a greater abundance in the triennial burn plots, followed by *T. triandra, T. leucothrix* and *B. serrata* which had lesser abundance in the triennial burn than the annual burn plots. Biennial burn and triennial burn plots had *T. leucothrix* as the most dominant and highest contributor to the differences in the overall species composition with more abundance in the biennial burn than the triennial burn plots.

In 2020/2021 the dominance shifted to *Diheteropogon amplectens* followed by T. leucothrix with a decreased cover of *D. amplectens* and an increased cover of *T. leucothrix* in the biennial burns as compared to the annual burn plots. A forb species, *Afroaster hispida* dominated, with the highest contribution to the differences in the species composition between annual and triennial burn plots. There was greater abundance of *A. hispida* in the annual burn than the triennial burn plots. The biennial and triennial burn plots still maintained the dominance of *T. leucothrix* with the highest contribution to the differences in the species composition and a reduced abundance in the triennial burn compared to the biennial burn plots. The change of dominance from the grass species *A. semialata* to a forb species *A. hispida* between the annual burn and triennial burn showed that burning frequency affected overall species composition with more evidence apparent in grasses than forbs. This implies that fire frequency influences the dominance of the grass species but an increased abundance of the dominant grass species (*T. leucothrix*) with decreased fire frequency was observed while *T. triandra* which was part of the species group that contributed >50% to the differences in the species composition between the levels of fire frequency increased in abundance with increased fire frequency.

The dominance of the short grass species *T. leucothrix,* in the frequently burned plots, could be due to its ability to tiller belowground making it insusceptible to fire and able to tolerate undecomposed litter could have resulted in the high abundance observed in the biennial burn (Uys et al., 2004). This contrasts with the other short grasses (like *T. triandra*) which are known for their aboveground tillering strategy making them sensitive to shading and litter accumulation resulting in the increased abundance of *T. triandra* as fire occur frequently in our study (Fynn et al., 2005). This implies that grasses responded differently to fire frequency based on the positioning of their tillers. Fire not only accelerates vegetation growth but also stimulates dormant seeds in the soil, alters species composition, and increases forage output (Tokozwayo et al., 2022). Forb species composition was not altered under the different burning treatments which implies that the responses of forbs to burning is different from that of grasses and that forbs have higher tolerance of fire.

Forb species richness was affected by fire frequency in 2019/2020, where the biennial burn was different from the triennial burn (9.7 ± 0.87) with the highest mean (13.3 ± 0.68). Annual burn (10.8 ± 0.89) did not differ significantly from either. This shows that forb species richness increased with moderate burning which is in support of the intermediate disturbance hypothesis (Collins et al., 1995). Grass richness and diversity and forb diversity were not affected by the burning frequency in both years. These findings suggest that the species richness and diversity in these mesic grasslands may be independent of fire frequency. This is supported by a number of other studies that found no discernible variation in species richness and diversity as a result of burning (Gates et al., 2017; Uys et al., 2004) and mowing (Randa & Yunger, 2001). In contrast, at the Konza Prairie Biological Station (KNZ) in North America and the Ukulinga Research Farm (URF) in South Africa, found that species richness increased in KNZ and decreased in URF with decreasing fire frequency (Kirkman et al., 2014b). The plausible reason for the difference in the response of species richness to fire frequency between the two studies could be traceable to the reduced mean annual precipitation of 790 mm as compared to the higher average annual precipitation of 838 mm in our study. Soil moisture and nutrient availability decreases under frequent fire (Collins & Calabrese, 2012). This shows that the high moisture level experienced in our study may have mitigated and given resistance to the direct effects of fire frequency on species richness.

The study showed that the long-term effect of fire frequency significantly affected the aboveground biomass across the plots. It was greatest in the unburned and triennially burned treatments with the least biomass recorded in the biennial and annual burns. Grasses are known to contribute the most to aboveground biomass in mesic systems, therefore, its reduction under the annual burn site may have caused a great decline in the biomass produced by these sites. The biomass from the previous season is removed during burning every year on the annual burn plots while the unburned and triennial plots have multiple seasons to build up biomass, which accounted for the highest biomass realised in these plots. Investigations of ANPP responses to various fire frequencies have revealed that ANPP increases most after a fire in a site that is burned infrequently and can be higher than ANPP observed in sites that are burned annually (Briggs & Knapp, 1995). Interspecific competition for resources is likely lower in burned than in unburned grassland because resource availability is released after fire, which causes plant density to be relatively lower in burned than in unburned sites (McCarron & Knapp, 2003). As a result, the diversity and richness of subdominant plants (grasses and forbs) are decreased due to increased competition by the dominant C4 grasses (Sasaki & Lauenroth, 2011). Consequently, annual burning may indirectly hinder the establishment or persistence of alien species by enhancing the dominance of C4 grasses (Smith & Knapp, 1999), which leads to decreased aboveground biomass as seen in our study. Similar findings also found that biomass decreased with increased burning frequency (Mvelase, 2021b; Oluwole et al., 2008).

7.4.3 The influence of summer mowing under different burning frequencies

In 2019/2020, the grass species which dominated and contributed the most to the differences in the grass species composition between the two mows (D2, D4, and D7) and the unmowed (A2, A4, and A7) was *Tristachya leucothrix* where the abundance of the grass species decreased as defoliation declined. *Tristachya leucothrix* dominated and contributed the most to the differences in the grass composition between the two mows and unmowed for the year 2020/2021 with a reduced abundance of *T. leucothrix* in the unmowed plot as compared to the two mows. These results showed that summer mowing under different burning frequencies had an impact on the grass species composition with changes resulting in a more increased cover of dominant grasses in the mowed than the unmowed plots, which means that the dominant grass cover decreased with reduced defoliation frequency. The dominant grass species *T. leucothrix*, remained the same on both plots. Overall, summer mowing under different fire frequencies maintained the dominance of grasses over the two years of study.

In 2019/2020, the forb species that had the highest dominance and contributed the most to the differences in the species composition between two mows and unmowed areas was *Thunbergia* *atriplicifolia*. This species showed an increase in abundance in the unmowed area. *Afroaster hispida* was the most dominant and highest contributor to the differences in the forb species between the two mows and unmowed in 2020/2021, with a decreased abundance in the unmowed plots. This indicates that the dominant forb species varied in their responses to summer mowing under different fire frequencies. Firstly, they are species-specific where *T. atriplicifolia* increasing with decreasing defoliation frequency and *A. hispida* decreasing concurrently. Secondly, the dominance changed from *T. atriplicifolia* to *A. hispida* in the following year which could be as a result of the impact of defoliation frequency. Overall, the responses of forbs to the influence of summer mowing under different burning frequencies are different from that of grasses whereby forbs are less well suited to increased defoliation frequency than grasses are.

The mowing frequency affected grass richness and diversity in 2019/2020 with two mows having a higher value of richness and diversity as compared to unmowed. Contrastingly, the study carried out at Konza Prairie, observed that mowing frequency showed no decrease in species diversity (Collins et al., 1998), and a non-significant effect of mowing frequency was shown on species richness (Ward et al., 2020a). In 2020/2021, Grass evenness, forb evenness and diversity were higher in the unmowed than the two mows. As mentioned in recent studies, the trade-off between the availability of nutrients and light is a significant factor influencing species diversity in grasslands (Harpole et al., 2016, 2017). An increase in ANPP caused by high nutrient availability reduces the amount of light that is available to individual plants (Avolio et al., 2014; Bobbink et al., 2010). This leads to greater biomass recorded in the two mows compared to the unmowed plots where a lesser biomass with a lower value of grass diversity was recorded. This implies that grass diversity in this mesic area increases with increased defoliation frequency and does not support the intermediate disturbance hypothesis. Defoliation by mowing is expected to remove aboveground biomass and may enhance relative growth rates or production of aboveground tissues, while this may reduce carbon allocation to roots (Zhang et al., 2021; Zhao et al., 2008).

Other studies have shown that, as a form of disturbance, summer mowing or clipping has been shown to maintain species richness and diversity in grasslands all over the world (Piqueray et al., 2019; Piseddu et al., 2021). The removal of aboveground biomass by burning results in the availability of light, which is in line with the study that light availability has been identified as a key factor in determining species diversity (Aavik et al., 2008; Fynn et al., 2004). In the prairies, for instance, annual burning reduces species diversity by favouring the dominance of C4 grass species, while this effect is negated by summer mowing (Copeland et al., 2002). In South Africa, dormant-period (winter) burning has been shown to result in dominance by the C4 grass *Themeda triandra*, while summer burning eliminates this species (Morris, 2021). Aboveground biomass was significantly altered between the different mowing frequencies, where two mows had higher biomass than the unmowed treatment. This confirms that mowing during the growing season results in compensatory growth which increases total biomass production (Gates et al., 2017; Wan et al., 2016; Zhao et al., 2008).

7.4.4 The influence of substituting a winter burn with a mow

The grass species in the year 2019/2020 that had the most dominance and contribution to the difference in species composition between two mows plots (mowed twice in summer with a winter burn) and three mows plots (mowed twice in summer with a winter mow), as well as the difference between two mows and unmowed plots and three mows and unmowed plots, was *Tristachya leucothrix.* The species was more abundant in the mowed plots with a winter mow as compared to the mowed plots with a winter burn, and least abundant in the unmowed plots. The forb species *Anthospermum streyi* dominated and contributed the most to the difference in the species composition between two and three mows plots with an increased abundance of forbs species on the mowed plots with a winter mow as compared to the winter burn plots. The two and three mows compared with unmowed had *Thunbergia atriplicifolia* as the most dominant and contributor to the differences in the species composition. Forb species were more abundant in the unmowed plots.

In 2020/2021, *T. leucothrix* had the highest dominance and contribution to the differences in the species composition between the two mows and three mows plots, two mows and unmowed and three mows and unmowed. The grass species were lower in abundance in the mowed plots with a winter mow as compared to the plots with the winter burn and lowest in the unmowed plots. *Afroaster hispida* dominated and contributed the most to the differences in the species composition between the two and three mows, and two and three mows compared with unmowed. Forb species were more abundant in the three mows plots as compared to the two mows plots, while a lower abundance was found in the unmowed compared to the two and three mows.

These changes in the response of *Tristachya leucothrix* to the effect of winter burn being substituted with a winter mow could be interlinked with rainfall variations. The grass species had a higher abundance and dominance in the winter mow plots than in the winter burn plots in 2019/2020 but the opposite was observed in the second year where Tristachya leucothrix was of higher abundance and dominance in the winter burn plots. The reason for the reduced abundance of *Tristachya leucothrix* under the two mows plot (summer mow with winter burn) in 2019/2020 in the lower rainfall year could be because of reduced soil moisture and nitrogen. Winter burning is said to result in reduced soil nitrogen than spring burning (R. Fynn et al., 2004), this leads to a competitive balance among species resulting in the removal and/or suppression of species that are weak in competing for soil moisture and nitrogen. This could be the same reason there were more abundance of *Tristachya leucothrix* in the winter burn plots in the higher rainfall year 2020/2021 as compared to the winter mow plots. The winter mow plots favored higher abundance of Tristachya leucothrix in the lower rainfall year than the higher rainfall year. Forb species responded the same across the years with higher abundance and dominance in the winter mow plots than the winter burn plots. The response of species composition to the effect of a winter burn substituted for a mow could be related with the availability of soil moisture and nitrogen in these mesic grasslands. This could be because of higher moisture availability realised in the second year, and as such wet conditions might have cushioned the effect of increased defoliation frequency (Gates et al., 2017).

7.4.5 Warming effects

Alterations in plant species composition occur when species differ in how they react to temperature, fire, and other environmental and management conditions (Deutsch et al., 2008). Climate warming can enhance vegetation productivity and change the species composition in many ecosystems since temperature regulates the rate of practically all biochemical processes (Noyce et al., 2019). Warming may have an immediate impact on plants by reducing their photosynthetic capacity during the growth season or may have an indirect impact by modifying many secondary biological processes (Körner & Basler, 2010).

Warming impacts became apparent in the second year of study. The plant species which dominated and contributed the most to the differences in species composition between warmed and ambient plots in 2020/2021 were *Tristachya leucothrix* and *Afroaster hispida* where both species abundances declined under warmed temperatures. The results indicate that warming had an impact on both grass and forb species. It might indicate that both grasses and forbs disappearing from the warmer sites are sensitive to soil moisture variability. A warmer climate may make this mesic grassland more susceptible to water stress (Schneider et al., 2014). The observed impact of warming on the species composition suggests either the possibility that the amount of ambient rainfall received in the plots is reduced indirectly by warming chambers or, it may be, that the moderate temperature increase of about 1.5 – 2 °C observed during the day increased evapotranspiration (Kumar et al., 2018). In most grasslands, it is crucial to understand that temperature variations, both seasonal and interannual, are common (Deutsch et al., 2008), and ours is no exception, it is still possible that the rise in temperature seen in our study may have been within the expected range of variation for this mesic system. Similar to our findings, other studies observed changes in species composition in a northern temperate grassland where there was an impact of warming on the composition of the plant community after it commenced, but no effects were seen by the second year when the study ended (Deutsch et al., 2008). Over the course of nine years of field observations, Ganjurjav et al., (2018) concluded that as the environment warmed, the proportion of grasses in plant composition decreased while the abundance of sedges increased.

In contrast to our findings, it was found that the warming effect on the plant community composition was not significant after 2 years of study in the Drakensburg Afromontane grasslands, South Africa (Mvelase, 2021b). The Drakensburg has significantly higher average annual rainfall than Ukulinga which is one of the reasons why the results differ. As a result, various factors influence species composition, richness, and diversity variation at different spatial and temporal scales and their response to warming.

In this study, the richness, diversity, and evenness of forbs were significantly impacted by warming. Similarly, it was shown that warming has a considerably detrimental impact on species richness when compared to the control (Leuzinger et al., 2011). In addition, warming reduced species diversity in an alpine meadow (Ma et al., 2017). The aboveground biomass under the warmed plot was lower than the ambient plot. A reduction in grassland aboveground biomass may be caused by warming-induced soil water deficits (Breshears et al., 2005), which concurrently reduce water availability and cause a decrease in plant photosynthetic rates (Wang et al., 2019).

7.5 Conclusion

Our findings shed light on the response of the mesic grassland plant community to multi-year warming as well as the long-term effects of fire and mowing. Although the vegetation showed only slight modifications in the composition of the plant species and aboveground biomass in response to warming, these modifications appeared in both years and were affected by fire and defoliation history. This finding shows that soil moisture availability may be the main factor influencing how the species in these mesic grasslands respond to the changing environment. Similar to this, we found that in our mesic grasslands, mowing enhanced productivity. We also observed that the plots with the lowest biomass were those that were warmed, unmowed, and regularly burned. This implies that disturbances such as fire and mowing could interact with climate change to affect ecosystem processes, particularly plant production, which might have an impact on the sustainability and ecosystem services of these mesic grasslands.

It was observed that fire frequency had no effect on forb species composition over the two years of study but affected grass species composition in the first year of study. *Themeda triandra*, a keystone species in our study area, was less abundant as fire frequency decreased, while *Tristachya leucothrix* increased. The reduced abundance of *T. triandra* as one of the dominant grasses, may have contributed to the reduced biomass in the warmed, unmowed, and regularly burned. Conversely, grasses were more abundant as defoliation increased while forbs were less abundant, which contributed to the increased biomass in the mowed plots. This demonstrates how the species composition and productivity of the mesic grasslands, which depends on soil moisture availability, respond differently, and are impacted independently by both fire and mowing.

7.6 References

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Appendix 7 A

Table 7.3: SIMPER results for the most influential species contributing to differences in A) all species and B) grass composition between the four levels of fire frequency for the years a) 2019/2020 and b) 2020/2021 on the UGFE, at Ukulinga Research Farm, University of KwaZulu Natal, Pietermaritzburg, South Africa. Species are listed in order of their contribution to the average Bray-Curtis dissimilarity between treatments, with a cut-off when the cumulative percent contribution reaches >50%.

Aa) Unburned vs. Annual Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in annual burn
Tristachya leucothrix	7.81	10.66	42.7	29.4
Themeda triandra	6.69	9.10	15.8	32.9
Brachiaria serrata	4.35	5.92	4.75	17.1
Eustachys paspaloides	3.86	5.25	4	18.3
Digitaria longifolia	3.22	4.39	7.92	10.4
Cymbopogon caesius	3.04	4.13	6.83	8.33
Aristida junciformis	2.91	3.95	12.3	5.25
Heteropogon contortus	2.79	3.79	4.58	11.6
Alloteropsis semialata	2.46	3.35	9.17	1.83
Becium obovatum	1.95	2.65	4.17	6.6

Ab) Unburned vs. Annual Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in annual burn
Tristachya leucothrix	4.64	7.14	54.4	45.6
Afroaster hispida	4.42	6.80	62.5	55
Diheteropogon amplectens	3.89	5.98	2.5	29
Cymbopogon caesius	3.33	5.13	8.83	23.7
Hyparrhenia hirta	2.89	4.45	3.33	23.1
Brachiaria serrata	2.50	3.85	21.8	6.25
Heteropogon contortus	2.30	3.55	4.17	18.6
Acalypha angustata	2.18	3.36	7.92	19.2
Becium obovatum	1.62	2.5	7.08	11.3
Commelina africana	1.62	2.49	7.92	11.9
Themeda triandra	1.58	2.43	9	14.8
Helichrysum miconiifolium	1.56	2.40	11.1	12.4
Hibiscus aethiopicus	1.49	2.30	8.92	9.75

Aa) Unburned vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in biennial burn
Tristachya leucothrix	8.34	11.45	42.7	35.1
Eustachys paspaloides	4.38	6.02	4	18.8
Themeda triandra	4.06	5.58	15.8	19.3
Aristida junciformis	3.43	4.71	12.3	8.75
Alloteropsis semialata	3.24	4.45	9.17	8.25
Thunbergia atriplicifolia	2.65	3.64	0.25	11
Brachiaria serrata	2.45	3.36	4.75	10.1
Becium obovatum	2.09	2.88	4.17	7.75
Cymbopogon caesius	2.01	2.76	6.83	3.42
Agathisanthemum chlorophyllum	1.93	2.64	2.83	7.92
Digitaria longifolia	1.85	2.53	7.92	1.92
Diheteropogon amplectens	1.78	2.45	1.92	7.33

Ab) Unburned vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in biennial burn
Tristachya leucothrix	4.09	6.99	54.4	64.6
Afroaster hispida	3.86	6.61	62.5	62.9
Brachiaria serrata	2.47	4.23	21.8	7.92
Cymbopogon caesius	2.28	3.91	8.83	18.3
Diheteropogon amplectens	2.27	3.9	2.5	20.1
Helichrysum miconiifolium	2.00	3.43	11.1	19.2
Themeda triandra	1.76	3.01	9	15.3

Commelina africana	1.73	2.96	7.92	14.2
Eriosema cordatum	1.61	2.76	6.58	12.9
Acalypha angustata	1.56	2.68	7.92	15.4
Aristida junciformis	1.49	2.56	8	6.25
Hyparrhenia hirta	1.48	2.54	3.33	10.8
Thunbergia atriplicifolia	1.40	2.40	5.83	11.3
Zornia capensis	1.35	2.32	7.33	9.42

Aa) Unburned vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in triennial burn
Tristachya leucothrix	8.89	11.69	42.7	20.3
Alloteropsis semialata	7.04	9.26	9.17	30.3
Aristida junciformis	4.62	6.07	12.3	19.5
Themeda triandra	4.47	5.87	15.8	14.4
Becium obovatum	2.80	3.68	4.17	11.6
Berkheya setifera	2.63	3.45	2.5	10.8
Eustachys paspaloides	2.51	3.29	4	9.67
Heteropogon contortus	2.47	3.24	4.58	8.92
Digitaria longifolia	1.96	2.57	7.92	0.25
Acalypha angustata	1.93	2.54	0.17	9.25

Ab) Unburned vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in triennial burn
Afroaster hispida	5.77	8.52	62.5	37.5
Tristachya leucothrix	5.53	8.17	54.4	35.6
Brachiaria serrata	3.97	5.86	21.8	35.4
Aristida junciformis	3.42	5.05	8	24.2
Commelina africana	2.42	3.57	7.92	19.6
Acalypha angustata	2.29	3.39	7.92	21.3
Cymbopogon caesius	1.91	2.82	8.83	14.6
Hyparrhenia hirta	1.8	2.66	3.33	12.5
Becium obovatum	1.79	2.64	7.08	12.9
Berkheya setifera	1.69	2.5	1.25	10.8
Helichrysum miconiifolium	1.63	2.4	11.1	7.92
Graderia scabra	1.61	2.38	6.92	15.4
Themeda triandra	1.51	2.23	9	9.67

Aa) Annual vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in biennial burn
Tristachya leucothrix	5.63	8.18	29.4	35.1
Themeda triandra	5.49	7.99	32.9	19.3
Brachiaria serrata	4.55	6.61	17.1	10.1
Eustachys paspaloides	4.04	5.86	18.3	18.8
Heteropogon contortus	2.74	3.99	11.6	4.92
Thunbergia atriplicifolia	2.63	3.83	4.58	11
Digitaria longifolia	2.36	3.43	10.4	1.92
Cymbopogon caesius	2.24	3.26	8.33	3.42
Agathisanthemum chlorophyllum	2.19	3.19	6.5	7.92
Aristida junciformis	2.16	3.14	5.25	8.75
Becium obovatum	2.10	3.05	6.67	7.75

b) Annual vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in biennial burn
Diheteropogon amplectens	3.79	6.49	29	20.1
Tristachya leucothrix	3.75	6.41	45.6	64.6
Afroaster hispida	3.27	5.6	55	62.9
Cymbopogon caesius	3.26	5.58	23.7	18.3
Hyparrhenia hirta	2.36	4.04	23.1	10.8
Heteropogon contortus	2.09	3.58	18.6	5.83
Helichrysum miconiifolium	1.79	3.07	12.4	19.2
Commelina africana	1.67	2.86	11.9	14.2
Themeda triandra	1.63	2.79	14.8	15.3
Acalypha angustata	1.56	2.67	19.2	15.4
Becium obovatum	1.46	2.49	11.3	8.33
Argyrolobium stipulaceum	1.45	2.48	9.17	6.5
Thunbergia atriplicifolia	1.44	2.46	10.1	11.3

Aa) Annual vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in triennial burn
Alloteropsis semialata	6.14	8.08	1.83	30.3
Themeda triandra	5.92	7.78	32.9	14.4
Tristachya leucothrix	5.86	7.71	29.4	20.3

Brachiaria serrata	4.16	5.48	17.1	6.17
Aristida junciformis	3.89	5.12	5.25	19.5
Eustachys paspaloides	3.69	4.86	18.3	9.67
Heteropogon contortus	3.46	4.56	11.6	8.92
Becium obovatum	2.69	3.54	6.67	11.6
Digitaria longifolia	2.22	2.91	10.4	0.25
Thunbergia atriplicifolia	2.18	2.87	4.58	8.92

b) Annual vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in triennial burn
Afroaster hispida	4.68	6.81	55	37.5
Tristachya leucothrix	4.53	6.59	45.6	35.6
Brachiaria serrata	3.93	5.72	6.25	35.4
Diheteropogon amplectens	3.65	5.31	29	11.3
Cymbopogon caesius	3.07	4.47	23.7	14.6
Aristida junciformis	2.74	3.99	0.83	24.2
Hyparrhenia hirta	2.62	3.82	23.1	12.5
Heteropogon contortus	2.18	3.18	18.6	4.17
Commelina africana	2.18	3.18	11.9	19.6
Acalypha angustata	2.02	2.94	19.2	21.3
Becium obovatum	1.75	2.55	11.3	12.9
Graderia scabra	1.64	2.38	1.92	15.4
Helichrysum miconiifolium	1.57	2.29	12.4	7.92
Themeda triandra	1.57	2.28	14.8	9.67

Aa) Biennial vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in biennial burn	Ave. abundance in triennial burn
Tristachya leucothrix	6.51	8.93	35.1	20.3
Alloteropsis semialata	6.35	8.72	8.25	30.3
Aristida junciformis	4.38	6.01	8.75	19.5
Eustachys paspaloides	4.17	5.72	18.8	9.67
Themeda triandra	3.72	5.11	19.3	14.4
Thunbergia atriplicifolia	3.04	4.18	11	8.92
Becium obovatum	2.75	3.77	7.75	11.6
Heteropogon contortus	2.39	3.29	4.92	8.92
Brachiaria serrata	2.26	3.1	10.1	6.17
Acalypha angustata	2.17	2.98	4.42	9.25

b) Biennial vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in biennial burn	Ave. abundance in triennial burn
Tristachya leucothrix	5.03	8.02	64.6	35.6
Afroaster hispida	4.83	7.69	62.9	37.5
Brachiaria serrata	3.85	6.14	7.92	35.4
Aristida junciformis	2.88	4.59	6.25	24.2
Diheteropogon amplectens	2.16	3.45	20.1	11.3
Cymbopogon caesius	2.13	3.39	18.3	14.6
Helichrysum miconiifolium	2.12	3.38	19.2	7.92
Commelina africana	2.09	3.33	14.2	19.6
Hyparrhenia hirta	1.76	2.81	10.8	12.5
Themeda triandra	1.74	2.77	15.3	9.67
Acalypha angustata	1.57	2.50	15.4	21.3
Becium obovatum	1.56	2.48	8.33	12.9

Ba) Unburned vs. Annual Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in annual burn
Tristachya leucothrix	12.63	18.7	42.7	29.4
Themeda triandra	10.37	15.35	15.8	32.9
Brachiaria serrata	6.99	10.36	4.75	17.1
Eustachys paspaloides	6.20	9.18	4	18.3
Digitaria longifolia	5.24	7.75	7.92	10.4
Cymbopogon caesius	4.97	7.35	6.83	8.33

b) Unburned vs. Annual Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in annual burn
Tristachya leucothrix	11.9	18.97	54.4	45.6
Diheteropogon amplectens	9.11	14.52	2.5	29
Cymbopogon caesius	8.11	12.92	8.83	23.7
Hyparrhenia hirta	7.02	11.19	3.33	23.1
Brachiaria serrata	6.50	10.36	21.8	6.25
Heteropogon contortus	5.45	8.69	4.17	18.6
Themeda triandra	4.19	6.69	9	14.8

Ba) Unburned vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in biennial burn
Tristachya leucothrix	14.52	21.69	42.7	35.1
Eustachys paspaloides	7.21	10.78	4	18.8
Themeda triandra	6.78	10.12	15.8	19.3
Aristida junciformis	5.70	8.52	12.3	8.75
Alloteropsis semialata	5.34	7.97	9.17	8.25
Brachiaria serrata	4.42	6.61	4.75	10.1

b) Unburned vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in biennial burn
Tristachya leucothrix	11.17	20.67	54.4	64.6
Brachiaria serrata	6.70	12.41	21.8	7.92
Diheteropogon amplectens	6.34	11.77	2.5	20.1
Cymbopogon caesius	6.31	11.68	8.83	18.3
Themeda triandra	4.82	8.92	9	15.3

Ba) Unburned vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in triennial burn
Tristachya leucothrix	14.65	20.35	42.7	20.3
Alloteropsis semialata	11.71	16.27	9.17	30.3
Aristida junciformis	7.61	10.57	12.3	19.5
Themeda triandra	7.07	9.82	15.8	14.4
Heteropogon contortus	4.5	6.25	4.58	8.92

b) Unburned vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in unburned	Ave. abundance in triennial burn
Tristachya leucothrix	14.5	22.53	54.4	35.6
Brachiaria serrata	10.02	15.57	21.8	35.4
Aristida junciformis	8.20	12.75	8	24.2
Cymbopogon caesius	4.89	7.61	8.83	14.6
Hyparrhenia hirta	4.66	7.24	3.33	12.5
Themeda triandra	3.89	6.05	9	9.67

Ba) Annual vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in biennial burn
Tristachya leucothrix	9.81	15.6	29.4	35.1
Themeda triandra	9.21	14.66	32.9	19.3
Brachiaria serrata	7.89	12.56	17.1	10.1
Eustachys paspaloides	6.84	10.88	18.3	18.8
Heteropogon contortus	4.42	7.03	11.6	4.92

b) Annual vs. Biennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in biennial burn
Diheteropogon amplectens	9.19	17.15	29	20.1
Tristachya leucothrix	9.12	17.03	45.6	64.6
Cymbopogon caesius	8.09	15.1	23.7	18.3
Hyparrhenia hirta	5.69	10.62	23.1	10.8
Heteropogon contortus	4.99	9.31	18.6	5.83
Themeda triandra	4.17	7.79	14.8	15.3

Ba) Annual vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in triennial burn
Alloteropsis semialata	10.13	14.02	1.83	30.3
Tristachya leucothrix	9.85	13.63	29.4	20.3
Themeda triandra	9.52	13.17	32.9	14.4
Brachiaria serrata	6.79	9.39	17.1	6.17
Aristida junciformis	6.34	8.77	5.25	19.5

b) Annual vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in annual burn	Ave. abundance in triennial burn
Tristachya leucothrix	11.11	16.51	45.6	35.6
Brachiaria serrata	9.01	13.38	6.25	35.4
Diheteropogon amplectens	8.08	12	29	11.3
Cymbopogon caesius	7.11	10.56	23.7	14.6
Aristida junciformis	6.31	9.37	0.83	24.2
Hyparrhenia hirta	5.96	8.86	23.1	12.5
Heteropogon contortus	4.85	7.21	18.6	4.17
Themeda triandra	3.83	5.69	14.8	9.67

Ba) Biennial vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in biennial burn	Ave. abundance in triennial burn
Tristachya leucothrix	11.42	16.4	35.1	20.3
Alloteropsis semialata	11.31	16.25	8.25	30.3
Aristida junciformis	7.64	10.98	8.75	19.5

Eustachys paspaloides	7.09	10.2	18.8	9.67
Themeda triandra	6.48	9.31	19.3	14.4
Heteropogon contortus	4.51	6.48	4.92	8.92

b) Biennial vs. Triennial Burn

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in biennial burn	Ave. abundance in triennial burn
Tristachya leucothrix	13.01	20.91	64.6	35.6
Brachiaria serrata	9.26	14.87	7.92	35.4
Aristida junciformis	6.99	11.22	6.25	24.2
Diheteropogon amplectens	5.58	8.96	20.1	11.3
Cymbopogon caesius	5.47	8.79	18.3	14.6
Hyparrhenia hirta	4.44	7.13	10.8	12.5
Themeda triandra	4.42	7.10	15.3	9.67

Appendix 7 B

Table 7.4: SIMPER results for the most influential species contributing to differences in A) all species, B) grass and C) forb composition between the three levels of mowing frequency for the years a) 2019/2020 and b) 2020/2021 on the UGFE, at Ukulinga Research Farm, University of KwaZulu Natal, Pietermaritzburg, South Africa. Species are listed in order of their contribution to the average Bray-Curtis dissimilarity between treatments, with a cut-off when the cumulative percent contribution reaches >50%.

Aa) Two Mows vs. Three Mows

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in three mows
Tristachya leucothrix	8.93	13.15	35.2	45.3
Themeda triandra	6.07	8.93	26.9	21.8
Eustachys paspaloides	4.36	6.42	18.2	4.17
Aristida junciformis	3.01	4.43	12.3	1.5
Anthospermum streyi	2.68	3.94	2.71	9.67
Heteropogon contortus	2.48	3.65	8.13	5.83
Alloteropsis semialata	2.30	3.39	8.5	0.83
Digitaria longifolia	2.22	3.26	3.08	9.17
Cymbopogon caesius	2.15	3.16	1.67	7
Becium obovatum	2.08	3.06	0.96	7.5

b) Two Mows vs. Three Mows

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in three mows
Tristachya leucothrix	4.62	7.96	57.7	52.8
Afroaster hispida	3.87	6.66	60.8	65.8
Brachiaria serrata	2.19	3.78	15.1	17.5
Hyparrhenia hirta	2.16	3.71	15.5	6.67
Acalypha angustata	1.85	3.18	15	11.7
Cymbopogon caesius	1.76	3.02	9.71	7.67
Helichrysum miconiifolium	1.61	2.77	11.5	10.8
Commelina africana	1.61	2.77	4.58	11.7
Themeda triandra	1.46	2.51	11.5	12.2
Eragrostis capensis	1.45	2.49	8.04	12
Thunbergia atriplicifolia	1.43	2.46	4.63	11.7
Becium obovatum	1.41	2.43	4.71	8.67
Aristida junciformis	1.39	2.39	2.13	7.5
Ledebouria apertifolia	1.37	2.35	2.21	10
Eriosema cordatum	1.34	2.31	3.63	11.2

Aa) Two Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in unmowed
Tristachya leucothrix	6.53	8.39	35.2	22.9
Alloteropsis semialata	4.99	6.42	8.5	21.4
Themeda triandra	4.91	6.31	26.9	11.8
Brachiaria serrata	3.95	5.08	5.75	17.4

Aristida junciformis	3.85	4.95	12.3	13.6
Eustachys paspaloides	3.73	4.80	18.2	8.11
Thunbergia atriplicifolia	3.62	4.65	0.08	16.2
Becium obovatum	3.34	4.29	0.96	16.3
Heteropogon contortus	2.56	3.29	8.13	7.22
Acalypha angustata	2.27	2.92	0.08	10.4

b) Two Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in unmowed
Afroaster hispida	4.63	6.86	60.8	42.2
Tristachya leucothrix	4.61	6.83	57.7	38.9
Diheteropogon amplectens	3.66	5.42	7.04	30.8
Brachiaria serrata	3.23	4.79	15.1	21.7
Cymbopogon caesius	3.10	4.59	9.71	28.1
Commelina africana	2.69	3.99	4.58	25.7
Aristida junciformis	2.58	3.82	2.13	20.8
Hyparrhenia hirta	2.00	2.97	15.5	10.3
Becium obovatum	1.89	2.81	4.71	17.2
Helichrysum miconiifolium	1.80	2.67	11.5	14.7
Acalypha angustata	1.74	2.59	15	18.6
Aloe maculata	1.74	2.58	0.21	15.6
Vernonia natalensis	1.66	2.46	0.67	15
Themeda triandra	1.65	2.45	11.5	13.1

Aa) Three Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in three mows	Ave. abundance in unmowed
Tristachya leucothrix	8.29	10.35	45.3	22.9
Themeda triandra	4.79	5.98	21.8	11.8
Alloteropsis semialata	4.42	5.51	0.83	21.4
Brachiaria serrata	3.98	4.97	1	17.4
Thunbergia atriplicifolia	3.66	4.56	0.5	16.2
Becium obovatum	3.29	4.10	7.5	16.3
Aristida junciformis	2.89	3.61	1.5	13.6
Digitaria longifolia	2.87	3.58	9.17	6.5
Cymbopogon caesius	2.79	3.48	7	8.22
Anthospermum streyi	2.34	2.92	9.67	1.67
Acalypha angustata	2.32	2.89	0	10.4

b) Three Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in three mows	Ave. abundance in unmowed
Afroaster hispida	4.41	6.55	65.8	42.2
Tristachya leucothrix	4.32	6.41	52.8	38.9
Diheteropogon amplectens	3.19	4.74	5	30.8
Brachiaria serrata	3.14	4.66	17.5	21.7
Cymbopogon caesius	3.04	4.51	7.67	28.1
Aristida junciformis	2.68	3.97	7.5	20.8
Commelina africana	2.20	3.27	11.7	25.7
Becium obovatum	1.75	2.59	8.67	17.2
Helichrysum miconiifolium	1.65	2.44	10.8	14.7
Acalypha angustata	1.64	2.43	11.7	18.6
Aloe maculata	1.63	2.42	0	15.6
Vernonia natalensis	1.58	2.35	0	15
Eriosema cordatum	1.52	2.25	11.2	12.6
Themeda triandra	1.49	2.22	12.2	13.1

Ba) Two Mows vs. Three Mows

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in three mows
Tristachya leucothrix	14.2	22.4	35.2	45.3
Themeda triandra	9.21	14.53	26.9	21.8
Eustachys paspaloides	6.99	11.04	18.2	4.17
Aristida junciformis	4.63	7.305	12.3	1.5
Heteropogon contortus	3.85	6.07	8.13	5.83

b) Two Mows vs. Three Mows

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in three mows
Tristachya leucothrix	12.84	24.29	57.7	52.8
Brachiaria serrata	6.21	11.75	15.1	17.5
Hyparrhenia hirta	5.60	10.6	15.5	6.67
Cymbopogon caesius	4.62	8.74	9.71	7.67
Themeda triandra	4.04	7.64	11.5	12.2

Ba) Two Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in unmowed
Tristachya leucothrix	11.42	16.02	35.2	22.9
Themeda triandra	8.33	11.7	26.9	11.8
Alloteropsis semialata	8.32	11.69	8.5	21.4
Brachiaria serrata	6.52	9.15	5.75	17.4
Eustachys paspaloides	6.50	9.13	18.2	8.11
Aristida junciformis	6.48	9.09	12.3	13.6

b) Two Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in unmowed
Tristachya leucothrix	11.55	17.94	57.7	38.9
Diheteropogon amplectens	8.96	13.91	7.04	30.8
Brachiaria serrata	7.71	11.98	15.1	21.7
Cymbopogon caesius	7.66	11.89	9.71	28.1
Aristida junciformis	5.99	9.31	2.13	20.8
Hyparrhenia hirta	4.92	7.64	15.5	10.3
Themeda triandra	4.21	6.54	11.5	13.1

Ba) Three Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in three mows	Ave. abundance in unmowed
Tristachya leucothrix	15.12	19.89	45.3	22.9
Themeda triandra	8.34	10.97	21.8	11.8
Alloteropsis semialata	7.82	10.29	0.83	21.4
Brachiaria serrata	7.01	9.29	1	17.4
Cymbopogon caesius	5.34	7.02	7	8.22
Digitaria longifolia	5.30	6.98	9.17	6.5

b) Three Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in three mows	Ave. abundance in unmowed
Tristachya leucothrix	12.56	19.05	52.8	38.9
Diheteropogon amplectens	8.73	13.24	5	30.8
Brachiaria serrata	8.60	13.05	17.5	21.7
Cymbopogon caesius	8.38	12.72	7.67	28.1
Aristida junciformis	7.00	10.62	7.5	20.8
Themeda triandra	4.25	6.45	12.2	13.1

Ca) Two Mows vs Three Mows

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in three mows
Anthospermum streyi	6.67	8.67	2.71	9.67
Agathisanthemum chlorophyllum	5.06	6.58	6.46	3.5
Becium obovatum	4.92	6.40	0.96	7.5
Indigofera hilaris	4.19	5.45	2.46	7
Gerbera ambigua	3.78	4.91	4.25	3
Senecio coronatus	3.73	4.85	2.75	4.67
Hibiscus aethiopicus	3.28	4.26	3.13	5
Dyschoriste burchelli	3.25	4.22	5.54	2.5
Graderia scabra	3.01	3.91	2.25	4
Tephrosia multijuga	2.98	3.88	1.58	3.33

b) Two Mows vs Three Mows

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in three mows
Afroaster hispida	6.46	10.59	60.8	65.8
Acalypha angustata	3.03	4.96	15	11.7
Helichrysum miconiifolium	2.58	4.22	11.5	10.8
Commelina africana	2.49	4.09	4.58	11.7
Becium obovatum	2.26	3.71	4.71	8.67
Thunbergia atriplicifolia	2.23	3.65	4.63	11.7
Ledebouria apertifolia	2.19	3.60	2.21	10

Hibiscus aethiopicus	2.11	3.45	7	10
Graderia scabra	2.06	3.38	8.67	8
Eriosema cordatum	2.04	3.35	3.63	11.2
Dyschoriste burchelli	1.99	3.26	7.75	7
Senecio coronatus	1.91	3.13	1.92	9.17

Ca) Two Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in unmowed
Thunbergia atriplicifolia	8.72	9.99	0.08	16.2
Becium obovatum	8.19	9.38	0.96	16.3
Acalypha angustata	5.25	6.01	0.08	10.4
Chamaecrista plumosa	4.52	5.18	0	8
Agathisanthemum chlorophyllum	4.39	5.03	6.46	4.33
Berkheya setifera	3.58	4.09	1.25	7.22
Dyschoriste burchelli	3.39	3.88	5.54	5.78
Vigna vexillate	3.18	3.64	2.29	4.44
Pentanisia angustifolia	2.86	3.28	2.46	4

b) Two Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in two mows	Ave. abundance in unmowed
Afroaster hispida	8.03	11.56	60.8	42.2
Commelina africana	4.69	6.75	4.58	25.7
Becium obovatum	3.23	4.64	4.71	17.2
Helichrysum miconiifolium	3.01	4.33	11.5	14.7
Acalypha angustata	2.97	4.27	15	18.6
Aloe maculate	2.86	4.11	0.21	15.6
Vernonia natalensis	2.81	4.05	0.67	15
Zornia capensis	2.38	3.42	5.79	11.9
Thunbergia atriplicifolia	2.33	3.35	4.63	11.9
Eriosema cordatum	2.31	3.33	3.63	12.6
Crabbea hirsute	2.17	3.12	0.42	11.7

Ca) Three Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in three mows	Ave. abundance in unmowed
Thunbergia atriplicifolia	8.19	9.55	0.5	16.2
Becium obovatum	7.60	8.86	7.5	16.3
Acalypha angustata	4.98	5.81	0	10.4
Anthospermum streyi	4.7	5.48	9.67	1.67
Chamaecrista plumosa	4.27	4.98	0	8
Agathisanthemum chlorophyllum	3.09	3.59	3.5	4.33
Indigofera hilaris	3.03	3.53	7	0.67
Berkheya setifera	2.98	3.47	0	7.22
Dyschoriste burchelli	2.73	3.19	2.5	5.78
Hibiscus aethiopicus	2.50	2.92	5	2.56

b) Three Mows vs. Unmowed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in three mows	Ave. abundance in unmowed
Afroaster hispida	7.15	10.44	65.8	42.2
Commelina africana	3.55	5.18	11.7	25.7
Becium obovatum	2.76	4.02	8.67	17.2
Acalypha angustata	2.53	3.69	11.7	18.6
Helichrysum miconiifolium	2.51	3.67	10.8	14.7
Aloe maculata	2.49	3.64	0	15.6
Vernonia natalensis	2.48	3.63	0	15
Eriosema cordatum	2.34	3.42	11.2	12.6
Zornia capensis	2.12	3.09	8.83	11.9
Thunbergia atriplicifolia	2.08	3.03	11.7	11.9
Dyschoriste burchelli	2.04	2.98	7	11.7
Rhynchosia minima	1.92	2.81	8.33	7.5
Graderia scabra	1.91	2.79	8	11.1

Appendix 7 C

Table 7.5: SIMPER results for the most influential species contributing to differences in A) all species and B) forb species composition between the two levels of warming treatment for the year 2020/2021 on the UGFE, at Ukulinga Research Farm, University of KwaZulu Natal, Pietermaritzburg, South Africa. Species are listed in order of their contribution to the average Bray-Curtis dissimilarity between treatments, with a cut-off when the cumulative percent contribution reaches >50%

A) Ambient vs. Warmed

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in ambient	Ave. abundance in warmed
Tristachya leucothrix	4.42	6.95	54.1	46
Afroaster hispida	4.35	6.83	57.9	51
Diheteropogon amplectens	2.86	4.49	10.2	21.3
Brachiaria serrata	2.85	4.48	18.2	17.5
Cymbopogon caesius	2.68	4.22	16.7	16
Hyparrhenia hirta	2.03	3.19	12	12.9
Acalypha angustata	2.02	3.17	9.58	22.3
Commelina africana	2.00	3.15	9.29	17.5
Aristida junciformis	1.98	3.12	9.42	10.2
Helichrysum miconiifolium	1.88	2.96	7.33	18
Themeda triandra	1.67	2.62	9.92	14.5
Becium obovatum	1.65	2.59	6.58	13.2
Heteropogon contortus	1.44	2.26	8.46	7.92

B) **Ambient vs. Warmed**

Species	Ave. dissimilarity	Contribution (%)	Ave. abundance in ambient	Ave. abundance in warmed
Afroaster hispida	7.39	11.2	57.9	51
Acalypha angustata	3.41	5.18	9.58	22.3
Commelina africana	3.36	5.1	9.29	17.5
Helichrysum miconiifolium	3.13	4.75	7.33	18
Becium obovatum	2.75	4.18	6.58	13.2
Zornia capensis	2.21	3.36	6.17	10.8
Thunbergia atriplicifolia	2.16	3.28	6.71	9.79
Eriosema cordatum	2.13	3.23	4.92	11
Graderia scabra	2.09	3.17	8.29	10.7
Dyschoriste burchelli	2.08	3.15	5.67	12.6
Rhynchosia minima	1.87	2.83	2.92	8.38
Argyrolobium stipulaceum	1.81	2.74	4.17	7.58

Chapter 8: General Conclusion

This research assessed the effects of climate change (rainfall variation and warming) and management factors (defoliation and fire) on biomass, species composition, grass phenology, and grass regenerative responses from bud banks, seed banks, and seed rain in the mesic grasslands of South Africa.

Findings from the first objective (Chapter 3) demonstrate that drought delayed both budding and flowering onset in the short term, reducing reproductive duration. In mesic grassland, reproductive duration is associated with yearly growing season rainfall variations (La Pierre et al., 2011). The onset of flowering in a grass community is closely linked with changes in the allocation and subsequent reductions in nutrient and water uptake which delay grass species greening up (Cleland et al., 2006). Even as this occurred, the response of these grasses to drought was species-specific (van der Weide et al., 2014). This conforms with the findings of the fourth objective (Chapter 6), where drought increased the abundance of *Themeda triandra* and reduced that of the other grasses, such as *Tristachya leucothrix*. The abundance of *T. triandra* can be attributed to their prominent tufts, which makes them tolerant to drought and enhances their capacity to compete for limited resources (Everson et al., 2021). Warming significantly lengthened the reproductive duration and advanced onset of budding in *Tristachya leucothrix*, indicating that grass phenology's response to the warming and drought effect was species-specific (Arfin Khan et al., 2018; Cleland et al., 2006; Jentsch & Beierkuhnlein, 2008). *Tristachya leucothrix* was more abundant under warming than other species. The difference in the responses of *T. triandra* and *T. leucothrix* to drought and warming could be based on the stability of the belowground bud banks (van der Weide et al., 2014). Under the first objective of our study (Chapter 3), the total number of buds per tiller and number of tillers per tuft were not sensitive to the short-term drought and warming effect (Qian et al., 2022a; van der Weide et al., 2014). This indicates a mechanism for the resistance and abundance of the two grasses *(T. triandra and T. leucothrix)* under drought and warming conditions. The contrasting response of grass phenology to drought and warming aids species coexistence in these mesic systems (Cleland et al., 2006). The observed shifts in phenological response can disrupt ecosystem processes (Cleland et al., 2006) leading to reduced community stability and increased biomass of forbs, indicating that forbs in our mesic grasslands appeared more resistant to short-term climate change, with no direct loss of ecosystem services.

The results support the hypothesis that grass phenology and plant community composition were sensitive to short-term climate change, resulting in changes in species composition and reduced productivity. Hence, further study is strongly advised to encourage a better understanding of species' response to drought and warming in mesic grasslands to develop effective management strategies that mitigate future climate change occurrences.

Under objective 2 (Chapter 4), the study species *T. leucothrix*, *T. triandra, and H. contortus* budded and flowered earlier under the summer defoliation and annual winter burning (AWB). In contrast, tufts under winter defoliation and annual winter mowing (AWM) budded later. The duration of budding and flowering was shortened under summer defoliation and AWB and extended under winter defoliation and AWM. Under objective 5 (Chapter 7), both winter defoliation and AWB reduced abundance of *T. leucothrix* compared to summer defoliation and AWM in 2019/2020, while in 2020/2021, *T. leucothrix* was more abundant under AWB and summer defoliation than AWM. The response of forbs was species-specific, with a greater abundance of forbs under AWM and no winter defoliation than AWB. The change in grass species response per year indicates that the response of these species to long-term defoliation is likely determined by species composition and the availability of soil moisture (Everson et al., 2021; Ott et al., 2019a), and that *T. leucothrix* becomes more abundant with greater soil moisture. The duration of flowering for *T. triandra* was reduced by annual burning and prolonged by triennial burning. The resultant effect of winter defoliation type (AWB & AWM), summer defoliation (by mowing), and fire frequency could be based on the interspecific variations between grass phenological events and the frequency of removing litter accumulation which are important in determining the species community of mesic grasslands likewise the type, time and frequency of defoliation (Kahlert et al., 2005). For instance, in objective 5, grasses *Themeda triandra* and *Tristachya leucothrix* were both fire tolerant due to their high abundance under annual winter burning. However, under frequent burning, the abundance of *T. triandra* are increased while *T. leucothrix* is reduced likely due to the positioning of their tillers allowing them to tolerate litter accumulation (Fynn et al., 2005; Kitchen et al., 2009b; Uys et al., 2004).

These results indicate that reduced biomass production under the different defoliation frequencies could be partly linked to the observed responses from both the grass phenology and bud banks. Mesic grasslands strongly rely on vegetative recruitment from bud banks for the persistence of the plant community (Ott & Hartnett, 2012b). This indicates why tufts in a vegetative state had a greater number of buds per tiller and number of tillers per tuft than flowering tufts. Greater abundance of *T. leucothrix* and higher number of tillers per tuft was observed under AWB, but annual winter mowing (AWM) still produced the greatest biomass compared to the no winter defoliation and annual winter burning (AWB) (objective 5). This could partly be because forbs were not a focus of the study and they may contribute to these responses. Differences in rooting depth may also be important as forbs have deep root systems which makes them better competitors for water and nutrients than grasses (Kitchen et al., 2009b). In general, the results showed that the type, time, and frequency of disturbance caused a difference in phenology and composition of belowground bud banks, which partly influenced species composition and productivity through the effect of the disturbance on soil moisture and light (Ghebrehiwot et al., 2009; Ott et al., 2019a). The opposing conclusions between Chapters 3 and 4 can be likened to the insurance hypothesis whereby the variation of species' responses to changes in the environmental condition of an ecosystem can insure it against reduction in its functioning.

The effect of disturbance and climate change (warming) reduced the number of buds per tiller and the number of tillers per tuft of the grass species (Ott, 2014). This is confirmed by how warming reduced the abundance of *Tristachya leucothrix* in our study, delaying the time of budding and flowering and increasing their duration slightly (Cleland et al., 2006). Research showed that as a result of experimental warming, the number of buds and tillers per tuft was reduced (Ott, 2014). This correlates with our study where warming treatments had a lower number of buds per tiller and number of tillers per tuft than under ambient temperatures. It shows that grass and forb composition, phenology, and bud banks are sensitive to soil moisture variability in mesic grasslands. The reduced abundance of *T. leucothrix*, as one of the dominant grasses, may have contributed to the reduced biomass under warming, annual winter burning, and no winter defoliation.

The overall combined effect of short-term climate change (drought and warming) and management factors (fire and defoliation) on sward species composition of soil seed bank, and seed rain under objective 3 (Chapter 5) shows that the response was species-specific (Everson et al., 2021). The abundance of grass and forb species in the seed bank and seed rain responded similarly under summer defoliation and annual winter mowing (Ghebrehiwot et al., 2012; H.

Snyman, 2013), while grasses are species-specific concerning their response mechanisms under burning frequency in the soil seed bank (Snyman, 2015). The annual forb species (*Conyza floribunda*) predominated the seed bank and seed rain in this mesic grassland, whilst perennial grasses predominated the aboveground community (*T. leucothrix* and *T. triandra*).

Rainfall variation and warming did not affect the composition of the seed bank and seed rain. These results also indicate that responses of the seed bank and seed rain are independent of vegetation changes, suggesting that altered precipitation regimes and increased temperature do not influence seed production or persistence (or both). It is interesting to note that forbs were better represented in both the seed bank and seed rain than grasses. The increased abundance of the weedy pioneer annual forb species *Conyza floribunda* and *Oxalis corniculata* might be linked to their persistent seed bank and the apparent resistance of the species composition to climate change. The findings of this study confirm that seedling recruitment only has a minimal impact on regeneration in mesic grasslands. The mesic grasslands' seed banks and seed rain have limited capacity for recruitment. It is doubtful that soil seed reserves will accumulate over time because the perennial grass species did not create a persistent seed bank throughout the research period.

The main conclusion of this study is that under different defoliation frequencies, types and timing, the species-specific seasonal patterns of species composition, phenological development and bud bank production were strongly influenced by the resultant effect of these disturbances on the availability of soil moisture and light intensity. This resulted in a reduced productivity of the grass community in our mesic grassland. The interspecific variations in the phenological pattern of grass species and their composition influenced the competitive relationships amongst these species which was an important mechanism in driving changes in community structure. This further demonstrates that the features of the dominant species can govern community system responses to seasonally altered disturbance regimes in mesic grasslands. Over the short term, warming and the associated reduction in soil moisture have the potential to strongly affect the sustainability of the mesic system.

Rainfall variations and warming both influenced the grass phenological events and species composition, but their contrasting responses were based on annual rainfall onset which has important implications for adopting disturbance regimes under future climate change and for developing policy frameworks for grassland management. The lack of effects of drought and warming on the belowground bud bank may suggest that bud production is closely associated with the rate at which tillers and tufts are produced. This is clear given the high abundance of *Themeda triandra* and *Tristachya leucothrix* under both drought and warming. With the effects of warming and drought on the species community and biomass, our study suggests that the mesic system was stabilized by the persistence of buds and tillers through seasonally determined disturbance regimes. Within the community structure, the shifts in the aboveground production were largely driven by bud banks rather than by seed banks and seed rain. The resistance of the dominant species to the experimental warming and rainfall variations may help explain these findings.

The combined effects of short-term climate change and defoliation timing and frequency (mowing and fire) on the species composition, phenology and bud banks in this mesic system is a panacea to improving and predicting impacts of future climate change on community structure. More studies are recommended to conduct long-term experimental warming and rainfall variations combined with long-term management practices, to compare the relative impact of these factors and understand better their responses for effective management of this mesic system.

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