Ecological effects of *Festuca costata* on the Drakensberg grasslands

Kabemba Mwambilwa

217080808

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University of KwaZulu-Natal
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UNIVERSITY OF
KWAZULU-NATAL

Declaration

I, Kabemba Mwambilwa, declare that:

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This research report does not contain any data, graphics, and other information from other persons, unless duly acknowledged.

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Kabemba Mwambilwa (217080808)

As the candidate's supervisor/co-supervisor, I certify that the above declaration is true to the best of my knowledge and have approved this dissertation for submission.

Signed: …………………………………...

Supervisor: Dr. Zivanai Tsvuura

Signed: …………………………

Co-supervisor: Professor: Kevin Kirkman

Abstract

Fire and herbivory are important in determining the vegetation structure in savannas and grasslands. In addition, anthropogenic activities have significantly contributed to alterations in the relative abundance and distribution of plant species in many grasslands through increased nitrogen deposition and elevated concentration of carbon dioxide in the atmosphere. Using a field experiment, the study explored the effect of neighbouring plants, defoliation, and fire on the ecological performance of a major C3 grass, *Festuca costata,* whose range is expanding in Afro-temperate grasslands of the Drakensberg Mountains in South Africa.

The experiment had three factors: fire at two levels (burned, unburned), defoliation by clipping 50mm above-ground surface, at four levels (no defoliation, defoliation of focal plant, defoliation of neighbouring plant within a 300 mm radius, and defoliation of both the focal and the nearest neighbouring grass within a 300 mm radius from the focal plant). The third factor was plant neighbourhood types at three levels (the focal plant growing alone, focal plant growing with other *F. costata* plants, focal plant growing with any other grass species) for a total of 24 treatment combinations with five replicates. Using a pot experiment under garden conditions, the study evaluated the influence of soil nutrient amendment with 140 KgHa^{-1} limestone ammonium nitrate in the performance of *F. costata.* The variables of interest in both experiments were; above-ground biomass production, tuft circumference, number of tillers and specific leaf area of the focal plant. Generalised Linear Models in SPSS were used to analyse the data from both experiments.

The results showed that burning had a significant negative effect on above-ground biomass production, number of tillers and tuft circumference of the focal plant (P < 0.001), with the unburned grassland showing greater mean values for all parameters than the burned grassland. Defoliation had significant negative effects on above-ground biomass production, number of tillers, tuft circumference while it showed strong positive influence on specific leaf area of the focal plant. Neighbourhood types were significantly negative for above-ground biomass production, number of tillers and tuft size of the focal plants (P< 0.001 in all cases).

Nutrient addition reduced the number of tillers of *F. costata* and tuft size and showed no significant effects on above-ground biomass production and specific leaf area. Defoliation significantly increased SLA, above-ground biomass production, number of tillers and tuft

circumference were not affected.. Plant neighbourhood types showed significant negative influences on tuft circumference. Defoliation accounted for the most variations in reduced tuft size, above-ground biomass and number of tillers, however, it resulted in increased specific leaf area.

These results suggest that defoliation by herbivores and use of fire may be complementary tools for managing high altitude grasslands under climate change. The findings of both the field and pot experiment suggest that *F. costata* may not be tolerant to selective herbivory. In addition, the study shows that the increase in nitrogen availability due to anthropogenic activity may have a negative influence on the performance of *F. costata*.

Key words: Climate change, Drakensberg, Annual fire-breaks, Herbivory, Focal plant, soil nutrients.

Preface

The work contained in this thesis was carried out at two sites with different climatic conditions (i.e. Highmoor Nature Reserve on the Drakensberg Mountains and Tainton Arboretum at the University of KwaZulu-Natal, Pietermaritzburg campus) under the supervision of Dr. Zivanai Tsvuura and Professor Kevin Kirkman.

Due to similarities in the experimental design and variables of interest, repetition was inevitable in some cases since the two experiments are presented as separate chapters. This thesis presents original work by the author which has not been submitted for examination purposes at another university. Note that tables and figures are presented as part of the main text.

Dedication

To my dear wife Nancy Malita Zulu and Children Charity, Paul and Monde I have the courage and strength to face each day because of you. To my profoundly loved elder sister and best friend Mbaita Mwambilwa.

Acknowledgements

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Chapter 1

Introduction

1.1 Background

Plant responses to competition, herbivory and fire differ with respect to biotic and abiotic conditions of their environment (Wisz et al., 2013; Bar-Massada et al., 2014). Several studies have outlined the interactions between plants and their environment (Alfaro et al., 2014; Klenderud et al., 2015; Kleynhans et al., 2016; Ward et al., 2017). Notable among the interactions which cause above-ground disturbance in plants are competition (Jesson et al., 2000; Gioria and Osborne, 2014), fire (Flannigan et al., 1998), herbivory (Riggs et al., 2015), climate change (McPherson and Weltzin, 2000) as well as disease outbreaks (Voelker et al., 2008). However, their direct influence may result in changes in plant structure reduction in plant height and reduction in biomass production due to reduced growth rate leading to poor reproductive performance (Lounda et al., 1990). This study, explored the competitive effects of neighbours on the ecological performance of a major grass whose range is expanding in Afro-temperate grasslands of the Drakensberg Mountains were explored. Disturbance can also indirectly affect plant communities by inducing changes in the plant structure (Moron and Crone, 2006; Sotomayor and Lortie, 2015), influencing photosynthesis and metabolic rates (Zhang et al., 2008) and interfering with reproductive capacity and chemical composition (Moron and Crone, 2006; McKechnie and Sargent, 2013; Pellegrine and Bellusci, 2014).

Competition alters plant community structures due to its influence on resource availability (McKechnie and Sargent, 2013). It may result in reduced plant nutrient uptake causing reduced growth and fertility rates (Schädler et al., 2007). A reduction in nutrient uptake lowers a plant's feeding value to herbivores (Schädler et al., 2007). Therefore, selective grazing by herbivores can reduce the competitive ability of preferred plants over their neighbours (van der Wal et al., 2000). However, the net effect of the various forms of disturbance on competitiveness of plants may also be a function of the nature of the competing plant species, environmental conditions as well as the type and level of disturbance (Newingham and Callaway, 2006). Some plants respond to competition by releasing into the soil toxic metabolites that interfere with other plants (Inderjit et al., 2006). This is a common characteristic among most invasive plant species

and can have a strong negative effect on seeding, germination, survival, growth, and reproductive performance of competitors (Callaway and Aschehoug, 2000; Inderjit and Callaway, 2003).

Invasive plant species are a threat to the biological diversity of ecosystems due to allotropic substances produced in their roots (Mack et al., 2001). Savannahs and grasslands are threatened by woody plant invasion, a phenomenon called bush encroachment (Bond, 2008). Scientists have over time attempted to explore the effectiveness of various management disturbance strategies to invasive plants species. Herbivory, fire and competition are the most common forms of stressors to which plants are subjected in terrestrial ecosystems (Boege, 2001; Schädler et al., 2007). These stressors are pivotal in determining the structure and function of the invaded plant community (Doyle et al., 2007).

South Africa's grassland biome covers approximately a third of the country's total landmass (Fig. 1.1) and plays a very significant economic and ecological function (O'Connor et al., 2004; Mucina and Rutherford, 2006). The past few decades have been associated with major alterations to native land cover for agricultural and commercial use as well impacts of climatic factors such as drought (Foley, 2005; Riitters, 2012). The magnitude of these changes is projected to continue increasing for long into the future. Efforts aimed at addressing these changes to the native land cover have paid attention to conversion of land to agricultural causes and urban development (Richards, 1996). This has overlooked other equally important causes such as climate change as there is sufficient evidence to support the conclusion that native vegetation distribution has a direct relationship with climatic variables and therefore, shifts in the pattern of climate may affect them (Aber, 2001; Carmel, 2011).
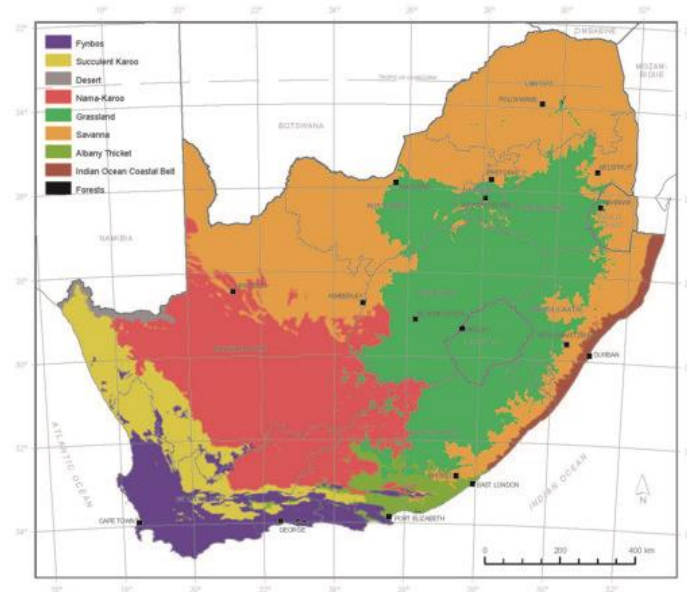
Figure 1.1   The map showing various vegetation biomes of South Africa. The green
area represents the grassland biome as described by Mucina and Rutherford,
2006

Climate change impacts related to warming and increased CO_2 concentration in the atmosphere
are predicted to result in a net increase in the relative dominance of C_3 over C_4 plants (Bond,
2008). Due to warmer environmental conditions, there is likely to be an increase in plant
species that thrive under warmer conditions (Sykes 2009).

1.1.1   Effect of fire on plants

Plant dynamics in each ecosystem can be influenced by the kind and frequency of disturbance
such as fire (Turner et al., 2003; Miller et al., 2011). There has been considerable research on
the effects of fire on grassland dynamics and functioning in southern Africa. However, little is
known about the ecological effects of annual burning on the structure and function of impacted
communities (O'Connor et al., 2004). Fire results in the loss of soil nitrogen and carbon due to
volatilisation (Bond, 2001). Fire can indirectly affect plant growth through its influence on the
chemical and physical characteristics of the soil, such as pH, electrical conductivity, available
nitrogen and carbon (O'Connor et al., 2004).

Huston (2014) reported sensitivity traits of some plant species to fire. Therefore, gaining
knowledge of plant traits is essential in understanding how plants evolve, as well as being

essential in providing insights into the species dynamics and responses to disturbances including herbivory and fire (Paula et al., 2009). The use of fire as a management strategy in grasslands can lead to a reduction in plant species diversity by eliminating sensitive species. (Valkó et al., 2014), or can result in increase in plant diversity by opening space for species with less competitive abilities as well as elimination of sensitive invasive species (Brooks et al., 2004). Some invasive plant species such as *Bromus madritensis* are known to respond favourably to disturbance by fire (Alba et al., 2015). Plant species diversity is positively correlated with the disturbance regime a biome receives. There is a positive correlation between disturbance and species diversity in plant communities (Gerstner et al., 2017; Guitet et al., 2018). In addition to fire disturbance, selective herbivory is a major determinant that influences species diversity and composition in grasslands as it reduces the competitive ability of preferred species relative to the unpalatable ones (Stein et al., 2010; Zhu et al., 2012; Liu et al., 2015; Korell et al., 2017).

A higher fire frequency results in savannas to have an increase in the herbaceous component with the inverse favouring the proliferation of the woody component (Booysen and Tainton, 1984). Continued exposure to high fire frequency results in accumulation of lower fuel load in a grassland (McGranahan et al., 2016). This reduces flame height and fire intensity, and consequently, this can lead to a reduction in mortalities for large trees (Jerman et al., 2004).

Fires have played a key role in determining the plant composition and functioning of African grasslands (Kirkman et al., 2013). However, most savanna plants have evolved strategies to tolerate the adverse effects of heat from fire exposure and defoliation by herbivores (Odhiambo, 2015; Long et al., 2017; Archibald et al., 2018). Owing to their higher competitive ability, fast growing plant species are better able to withstand continued and frequent exposure to fire in most tropical grasslands (Marshall et al., 2012; Ponge, 2013). Late dry season fires have been reported to positively impact grass productivity in the savanna as re-sprouting occurs at the onset of the subsequent rain season, however, they have also been reported to result in reduction in woody species composition (Bond and Midgley, 2012). The change in timing and frequency of fire can lead to changes in plant response; this has potential to result in shifts in species composition. Most studies, however, seem to focus on changes in species composition with respect to grass-shrub interactions while neglecting the changes that occur within the grasslands (Buhrmann et al., 2016; Guido et al., 2017).

Little et al., (2015) reported that different grass species exhibit different responses to fire disturbance. This is largely because primordial protection provided to tillers prior to germination. Species that exhibit delayed tiller formation following onset of the rain tend to accumulate less fuel and hence a reduction in fire intensity (Little et al., 2015). Consequently, such species are less likely to suffer much mortality due to fire. Species such as *Themeda triandra* tend to thrive in fire prone grasslands while *Panicum maximum* may be eliminated by frequent fires (Ripley et al., 2015).

A reduction in the frequency of fire favours an increase in woody species in the understorey. In contrast, species richness in grasslands is maximised by frequent fire as that tends to minimise the competitive effect of woody plants (Bowman et al., 2017). Establishment of woody plants is inhibited by sufficient fuel loads and frequent fires through mortality of seedlings and saplings of fire-sensitive species (Lunt et al., 2011; Brewer, 2015). With a higher fire frequency, woody species find it difficult to emerge and escape (Heinl et al., 2008; Balch et al., 2013), and this may explain the absence of large trees in fire-prone areas. Additionally, increasing the fire frequency in the savannas may lead to a marked reduction of species that are less fire tolerant (Jerman et al., 2004).

While mature trees may not suffer much damage from exposure to frequent fires, injury due to herbivory by large ruminants such as elephants may expose the injured part of the tree to fire (Shaw et al., 2002). Herbivore-induced scars may grow with repeated exposure to successive fires and eventually the tree is weakened and dies (Bowman et al., 2014). The combined effects of herbivory and frequent fire may inhibit smaller trees from developing into mature plants (Bowman et al., 2017). While fire plays a key role in influencing species composition in grassland, the differential tolerance of individual plant species to fire and their ability to recover post exposure is critical (Spasojevic et al., 2010). A clear understanding of individual plant species and conditions present in each biome are important in helping to understand the effects of fire on a given plant community (Tilman and Lehman, 2001; Cornelissen et al., 2017). Thus, the present study sought to evaluate the performance of *F. costata* subjected to recurrent fires at annual intervals.

Other factors that may affect the effect influence of fire include intensity, season of fire, soil heating, severity, which is a function of the available fuel load, and interval between successive fires (McGranahan et al., 2018). All the above causes, differ significantly within and between

fires. Fire intensity and severity are also determined by seasonality, site characteristics such as fuel load and the consequences of its impact are largely dependent on the specific plant species under consideration (Keeley 2009; Miller et al., 2012). The moisture content of the fuel affects the severity of the fire and this is strongly influenced by the season (Jolly et al., 2015; Parks et al., 2016).

While use of fire is cost-effective strategies in rangeland management compare other methods such as chemical control, inappropriate application can have negative ecological and economic consequences (Dube et al., 2013; Valkó et al., 2014). Depending on the intensity and timing of the fire, it can burn off all plant material, i.e. both moribund and recent growth thereby reducing the productivity of rangelands for livestock production (Little et al., 2015). In addition, if not properly managed fire can lead to economic losses by destroying property such as fencing poles and houses (Nyongesa and Vacik, 2018). Fire can also lead to soil nutrient losses and change in vegetation structure by encouraging the proliferation of woody plant species (Gandiwa, 2010; Ficken and Wright 2017)

1.1.2   Effect of climate on plant species diversity and composition

Understanding of the relationship between plant species composition and diversity with climate change is important (Zeng et al., 2016). Doxford and Freckleton (2011) reported differences in vegetation spatial response to broad-scale changes in climatic variables. Prevailing environmental temperatures during the growing season affects the rate at which different plants grow. Species competitive abilities are also determined by the difference in growth rates (Kirschbaum, 2004). The primary limiting factor for plant growth in each biome is water availability. As a result of reduced precipitation in certain areas due to climate change, the availability of soil water will continue to have a strong effect on plant communities at both local and landscape scales (Adel et al., 2014). Effects of reduced precipitation, which include among others reduction in size of water bodies such as lakes and rivers, forest diebacks, wetland degradation and grassland desertification have been extensively reported (Yin et al., 2012).

The inherent ability of any natural ecosystem to cope with stresses to biological systems depends on the ecological vulnerability to climatic changes (Schroter et al., 2005). In its report, the IPCC (2001) anticipated major effects of climate change to be the loss in species diversity.

The amount of precipitation a given biome receives directly influences its composition, function and structure (Allen et al., 2001). Reduced precipitation can influence physiological processes such as photosynthesis, cause plant mortality, predispose plants to pests and disease attacks as well as influence frequency and intensity of fire disturbance. The net effect of these changes can be a shift in plant community functional types with a potential to endanger the survival of some plant populations thereby affecting productivity of an ecosystem (Chapin, 2003).

Changes in precipitation and temperature have been shown to affect plant performance due to their influence on the capacity of a given soil type to retain moisture as well as its effect on physiological processes such as photosynthesis (Li et al., 2016; Tardieu, 2013). Increase in surface and atmospheric temperature results in elevated evaporation and transpiration rates resulting in drier soils (Khan et al., 2009). This tends to have a negative influence on plant performance leading to reduced land cover and exposing the bare soil to erosion (Morison and Lawlor, 1999; Sharrat et al., 2013). Naturally, plants have been known to have three response mechanisms to climate change; developing tolerance to the changing environment, migration to a more suitable environment, or face total mortality all together (Theurillat and Guisan, 2001). Variations in climate are common in many ecosystems with semi-arid and arid regions being more vulnerable to reduction in precipitation (Singh et al., 2014). This results in increased biodiversity loss, shifts in both atmospheric and terrestrial carbon balance as well as increased vegetation loss (Xu et al., 2016).

Anthropogenic activities, through high industrialisation and deforestation, have resulted in an increase in the emission of greenhouse gases, more especially CO_2 (Christensen et al., 2007; Kahn et al, 2007) and consequently affects functioning of terrestrial ecosystems (Runion et al., 2006;). Plant responses to disturbance are largely a function of resource availability in a given environment (Wisz et al., 2012; Wu et al., 2016; Costa et al., 2017). Elevation in the mean atmospheric temperature due to high CO_2 concentration is predicted to negatively influence the performance and productivity of C_4 grasses (Morgan et al., 2001; Santos, 2014). Generally, there is a difference in the chemical composition of C_3 and C_4 grass types and as a result, they exhibit different responses to changes in climatic conditions (Barbehenn et al., 2004, von Fischer et al. 2008). The C_3 species produce a three-carbon compound and have a shorter and lower optimum temperature range of $20 - 25^0C$ while C_4 species primarily produce a four-

carbon compound and have a wider environmental temperature range 30 - 45^{0}C (Ehleringer and Pearcy, 1983; Tardieu, 2013) and therefore, elevated CO_2 concentration in the atmosphere is likely to favour the establishment of C_3 species.

The anticipated increase in atmospheric carbon dioxide concentration will lead to an increase in the spread of undesirable C3 grass species which are known to thrive under elevated CO_2 conditions (Adjorlolo et al., 2012). The composition of plant (grasses) species on a large spatial scale is largely determined by climatic factors such as precipitation and temperature, therefore, the level of moisture held by the soil determines the occurrence and distribution of plants (Winslow et al., 2003). For example, Xu et al. (2006) found a strong positive correlation between available moisture and plant productivity with respect to above-ground biomass production in grasslands.

1.2   The Drakensberg Ecosystem

The grassland biome is important because it supports the both population and agricultural activities in southern Africa (Meter et al., 2002; O'Conner and Kuyler, 2005; Kirkman, 2006) and is estimated at about 360 600 km^2 (Carbutt et al., 2011). Mucina and Rutherford (2006) and encompasses and estimated 72 distinct plant species in the grassland biome which comprises of the Drakensberg Grassland, Mesic Highveld Grassland, Sub-escarpment Grassland and the Dry Highveld Grassland. The classification above is based on the minimum and maximum precipitation as well as temperature (climate) and the degree of disturbance by burning and herbivory (Carbutt et al., 2011). The Drakensberg grassland biome has recently been experiencing transformation because of increase in human activity as well as climate change (Adjorolo et al., 2012). The Highmoor Nature Reserve area on the Maloti-Park of the Drakensberg Mountains is characterised by grasslands dominated by *Themeda triandra, Aristida junciformis* and *Alleteropsis semialata* which are warm-season C_4 species (McGranahan et al., 2016). The site rests on the transition between sub-montane and montane grassland resulting in a mixture of warm-season species such as *T. triandra* and cold-season species such as *F. costata* occurring in large patches (Bussmann, 2006; O'Connor et al., 2004; McGranahan et al., 2018). Legally, approximately 5-10% of the Drakensberg grasslands is burned annually (Fig. 1.2) as a management strategy (O'Connor et al., 2004).

1.2.1 Research Problem

The Drakensberg Mountains of Southern Africa are characterised by a tropical montane climate favourable for the occurrence of grasslands comprising of both C_3 and C_4 photosynthetic pathways (Adjorlolo et al., 2012). Concerns have been raised in the past that C_3 grasslands dominated by *F. costata* are expanding and encroaching onto C_4 dominated grasslands. Other C_3 woody species have been reported to have an increase both in relative abundance and extent, a phenomenon called bush encroachment (O'connor et al., 2009), not only in the Drakensberg, but in many savannah ecosystems as well (Russell and Ward, 2014). The rise in dominance of woody plants and other C_3 grasses may negatively impact the use of fire as a management tool in most grassland and influence their dynamics and functioning in multiple ways. For instance, a reduction in fire frequencies may lower the productivity of grassland with respect to herbivore production due to increased bush encroachment, which directly impacts fire regimes in grasslands. However, there has been no research conducted to evaluate the effects of fire on the establishment of *F. costata* on these montane grasslands of the Drakensberg Mountains.

1.3 Objectives of the Study

This study aimed to determine the ecological conditions for the establishment and occurrence of *F. costata*. The study investigated the effect of annual burning on the performance of *F. costata*, a common C_3 specie. The specific objectives were;

   i. To evaluate the influence of annual burning fire breaks on *F. costata*.

   ii. To evaluate the influence of nitrogen addition and defoliation on the competitive interactions between *F. costata* and dominant C_4 grasses, and

1.4 Research Questions

   i. How does burning of annual fire-breaks affect the performance of *F. costata*?

   ii. How does *F. costata* respond to competition?

   iii. How does herbivory affect the performance of *F. costata?*

1.5 Scope of the study

This study explored the ecological effects of *F. costata* on montane grasslands in the Drakensberg. It used a combination of a greenhouse and field experiments to measure competitive interactions among C_3 and C_4 grasses.

Figure 1.2   A *Festuca costata* dominated grassland at Highmoor Nature Reserve in the Drakensberg. The greener grass in the background is part of a periodically-burnt fire-break. The foreground is outside the fire-break and not burnt. Notice the taller tufts of *F. costata*. The photograph was taken on 28th August, 2017 which is mid-winter.

1.6 Species description

Festuca costata is a C_3 evergreen perennial tussock-forming species native to the Afromontane conditions of the Drakensberg Mountains in southern Africa (Adjorlolo et al., 2012; McGranahan et al., 2016). Its altitudinal distribution ranges between 1830 to 2800 m.a.s.l. It is

normally found in mixed stands with other C_4 species including *T. triandra, Aristida monticola, Andropogon appendiculatus Alleteropsis similata and A. junciformis (*O'Connor et al., 200)

1.7 Outline of the thesis

Chapter 1 provides a general background on the effect of burning, defoliation and competition on the ecological effects of *F. costata* on dynamics of montane grasslands. Additionally, research objectives, description of the study area, and the scope of the study are outlined.

Chapter 2 explored the effect of fire on C_3-C_4 grass interactions in a montane ecosystem. The study evaluates the performance of *F. costata* under inter-specific as well as intra-specific interactions using a full factorial experiment under montane conditions in the Maloti-Park of the Drakensberg Mountains.

In Chapter 3, explored the effect of soil nutrient amendment on the competitive interactions between an evergreen C_3 grass, *F. costata* and two common C_4 grasses, *T. triandra,* and *A. junciformis.* Plants were also subjected to defoliation treatments in a fully factorial greenhouse pot experiment.

The thesis is concluded in Chapter4, which presented a discussion of the main findings of study, the relevance of the results, makes recommendations for future studies, and highlights the limitations of the study. Findings are discussed in terms of the effects of annual burning of fire-breaks, addition of a nitrogenous fertiliser, defoliation and neighbour competition on the functional traits of *F. costata.* The chapters in this thesis are prepared for presentation in different journals hence the difference in formatting. However, due to similarities in the experimental approach certain repetitions are unavoidable.

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Chapter 2

Influence of burning and defoliation on *Festuca costata* in the Drakensberg

Abstract

Fire is used to manage grasslands and savannas. The ability of a plant to recover from fire may be influenced by the frequency, seasonality and fuel load. This study sought to investigate the ecological influences of an evergreen C_3 grass, *Festuca costata,* on a high-altitude grassland in the Drakensberg Mountains of South Africa. Using a factorial experiment, we examined the effect of annual burning of fire-breaks (burned versus unburned sites), defoliation (cut vs uncut treatments) and competition from neighbours (above-ground parts of neighbours present vs removed) on the performance of *F. costata* over a five-month period (December 2017 to April 2018. Defoliation treatments were carried out at six-week intervals. Generalised linear models in SPSS were used to analyse the effects of treatments on above-ground biomass, number of tillers, specific leaf area and tuft size of *F. costata*. Automatic regression models were used to rank the treatments' contribution to the findings. The effect of annual burning was highly significant for above-ground biomass production, number of tillers and tuft circumference of the focal plant ($P < 0.001$), the unburned grassland showing greater mean values than the burned grassland. Defoliation had significant negative effects on above-ground biomass production, number of tillers, tuft circumference and specific leaf area of *F. costata*. Neighbourhood types were significantly negative for above-ground biomass production ($P < 0.001$), number of tillers ($P < 0.001$) and tuft size ($P = 0.001$) of the *F. costata*. While burning of annual fire-breaks had a negative effect on the performance of *F. costata*, the findings showed that the plant was more sensitive to defoliation than fire and neighbourhood types. Knowledge of the relationship between *F. costata* and its neighbours, herbivory and fire ecology will help in understanding dynamics of the Drakensberg grasslands in a changing climate.

Key words: Biodiversity**,** climate change, herbivory, veld condition.

2.1   Introduction

Fire is an important tool in the maintenance of biodiversity in mesic grasslands (O'Conner et al., 2004; Bond et al., 2005, Lechmere-Oertel, 2014) and is therefore important in maintaining ecosystem health.   Most grassland plants can recover from exposure to fire due to their regenerative capacity through both sexual and asexual reproduction (Morgan, 1999; Scasta et al., 2014). The ability of a plant to recover from fire is influenced by the frequency, seasonality and fuel load of the fire (Burkle et al., 2015; Viana-Soto et al., 2017), which may be influenced by the climate, herbivory, and time since the last fire. Here, investigation on the effects of burning annual fire-breaks on the performance of an Afro-temperate grass whose range has been reported to be expanding in the recent past (Adjorlolo et al., 2012).

Fire regimes characterised by short intervals have the potential to negatively affect the regeneration ability of plants because of depletion of their storage reserves and modification of their vegetative cover (Anderson et al., 2005; Eugenio and Lloret, 2004). More frequent fires may be associated with spatial changes in vegetation structure (Albert et al., 2008). A combination of fire, competition and herbivory influences mesic grasslands with potential to result in undesirable changes in the structure, particularly with regards to species composition, productivity and plant vigour (Heisler et al., 2004). Fires may also play an indirect facilitation role on enhancing competition among plants by opening spaces and allowing new plants to emerge and gain dominance. Fire also hinders certain plant species from completing their life cycle and stores enough reserves to support post disturbance regrowth (Lloret et al., 2003; Albert et al., 2008). A key aspect in understanding the behaviour of fire in grassland is knowledge of the growth characteristics of the plants (Little et al., 2015). An increase in the proportion of moribund material due to senescence correspondingly increases the ability of grasslands to support fires (Cheney and Sullivan, 2008). The curing level of grass is described as the proportion of flammable dead material in grasslands and is positively correlated to the fire behaviour (Anderson et al., 2011). The degree of curing is an important indicator of the susceptibility of grasslands to fire (Kidnie et al., 2016).

Many factors affect fire behaviour in grasslands and these include the prevailing winds, slope and relative humidity (Trollope et al., 2002). The direction of fire relative to wind direction tends to affect the vegetation differently (Booysen and Tainton, 2012). Fires which burn in the

direction of the wind, called headburns, will tend to have a more adverse effect on the tree species while that which burns against the wind direction (i.e. backburns), tend to be more intense at ground level and will likely have a more profound effect on the grass species and inhibit new growth (Trollope et al., 2002). Critical factors in the use of fire as a management tool in grasslands include frequency and intensity, and the final decision on its use must consider the available fuel load and veld conditions (Dube, 2013).

Moribund material creates mulch which inhibits photo-penetration in grasslands, which may lead to mortality of certain grass species. Removal of moribund material by fire will help stimulate tiller formation in most grass species (Little et al., 2015), which results in higher productivity and utilisation by herbivores. Use of fire to manage grasslands must always try to ensure that it does not promote an increase in undesired consequences such as invasion by tolerant unpalatable species (Valkó et al., 2013).

Fire also indirectly affects vegetation through its effect on the soil. For example, fire affects water holding capacity of soil, organic matter contained in a soil, and soil texture (DeBano, 2000; Certin, 2005; Mataix-Solera et al., 2011). Negative effects of fire on soil organic matter may result in a reduction in the cation exchange capacity (Moody et al., 2017). Generally, there is a temporal increase in nutrient cations from the ash. However, nitrogen tends to show a decreasing trend due to its high volatility because of exposure to high temperature (Downing et al., 2017).

In South Africa, burning of annual fire breaks on the Drakensberg is guided by the protected areas Act number 57 of 2004 and covers between 5-10% of the total grassland and should occur before mid-winter (O'Connor et al., 2004). The use of fire is an important management strategy in most grassland in Southern Africa and given the landmass they occupy, there is need to pay closer attention to its specific effects on the vegetation composition and diversity (O'Connor et al., 2004). Prescribed fires can be used to promote the establishment of favourable grass species thereby increasing the livestock productivity in grasslands through improved palatability and grazing value (McGranahan et al., 2016; Wu et al., 2017).

The tropical-montane climatic conditions on the Drakensberg Mountains create a favourable environment for the occurrence of both C_3 and C_4 plant species, particularly grasses (Adjorlolo

et al., 2012). The Drakensberg grasslands are characterised by *Themeda triandra* which is a highly palatable grass, *Aristida junciformis* a less palatable increaser species and *Alleteropsis semialata* which are warm-season C_4 grass species.

Many areas of the Drakensberg occur on the transition between sub-montane and montane grassland resulting in a mixture of warm-season species such as *T. triandra* and cold-season C_3 species such as *Festuca costata* occurring in large patches (McGranahan et al., 2016; Bentley and O'Connor, 2018). In addition these areas occur on state protected and private land, both of which use fire as a management tool.

However, little has been done to understand the effects of burning annual fire breaks on the performance of the dominant plant species, especially *F. costata*. This species is evergreen, and its abundance may impact fire regimes. This study, therefore, sought to determine the response of *F. costata* to annual burning of fire-breaks and defoliation while growing under varying levels of competition with C_4 grasses that dominate the landscape. It was hypothesised that a combination of burning, defoliation and above-ground competition will increase the performance of *F. costata*. The variables of interest in the study were above-ground biomass (ABG) production, number of tillers, tuft size as tuft circumference (TC), and specific leaf area (SLA).

2.2 Materials and Methods

2.2.1 Study site

The study was conducted on an Afromontane grassland at Highmoor Nature Reserve, a high-altitude site (1850 meters above sea level) in the central region of the Maloti-Drakensberg Park (20° 32′ S, 29° 62′ E). Highmoor is characterised by a mean annual precipitation of 1400mm occurring largely during the summer months (October to April) with mean annual maximum temperature of 21°C in January and mean minimum temperature of -1°C in July, with frost as a common occurrence.

The Southern Africa soil and terrain database classifies Highmoor soils as Euritric Regosols, which is a "rest group" of soils that does not directly belong to any specific soil group as a general classification of land formation, hence, result from erosion on the mountains (FAO,

2001; ISRIC, 2008). Highmoor is characterised by grasslands dominated by *T. triandra, A. junciformis* and *A. semialata* which are warm-season C_4 species, and cold-season, C_3 species such as *Festuca costata* occurring in large patches (Grieve and Downs, 2015).

2.3 Data collection

2.3.1 Experimental design

The experiment had three factors: fire at two levels (burned, unburned), and defoliation at four levels (no defoliation, defoliation of focal plant, defoliation of neighbouring plant within a 300mm radius, and defoliation of both the focal and the nearest neighbouring grass within a 300mm radius from the focal plant). The third independent factor was competition, at three levels (focal plant growing alone, focal plant growing with other *F. costata* plants, focal plant growing with any other grass species), giving a total of 24 treatment combinations. Each treatment was replicated five times giving a total of 120 focal tufts spaced at least 2m from each other in a fully randomised design. The first defoliation and measurement of the above-ground biomass, number of tillers, tuft circumference and specific leaf area for the focal plants were undertaken between 14th December 2017 and 19th April 2018. The exercise was repeated three times at 6-week intervals.

2.3.1.1 Above-ground biomass

Measurements of above-ground biomass were taken from both the focal and neighbouring plants through clipping at 50mm aboveground. Samples were obtained by cutting at 50mm above the soil surface. The cut material was shaken to remove soil particles, then bagged into sample bags that were carefully labelled and transported to the University of KwaZulu-Natal in Pietermaritzburg, where samples were oven-dried (60°C, 48 h) before weighing.

2.3.1.2 Number of tillers

The total number of tillers on focal tufts was measured three times during the experiment from December 2017 to April 2018 at six weeks intervals. The counts were made on predefined sampling tufts, three per treatment combination and were used consistently throughout the experiment. The tufts were marked with polyvinyl chloride (PVC) rings 76.2mm in diameter, which were fixed with wire clips into the soil. Individual tillers in the ring were counted every

six weeks (Fig. 2.1). Both live and dead tillers within the ring were counted and the dead ones removed after each count. Tillers were classified as dead when they showed evidence of drying or missing or show advanced signs of senescence. This procedure allowed for all tillers to be counted and new ones recorded, and the data was used to calculate the effects of treatments on tiller numbers per focal tuft.

2.3.1.3   Tuft circumference

The circumference of tufts of all focal plants was measured at the start and end of the experiment. The measurements were taken by tying a string firmly around the tuft, the points of intersection were marked, and the string was then stretched on a measuring ruler to obtain the actual reading (Lardner et al., 2003). This procedure was carried out twice between December 2017 and April 2018

2.3.1.4   Specific leaf area

The sampling procedure for specific leaf area (SLA) followed a modified method recommended by Cornilessen et al. (2003). Two leaves were sampled per tuft for each recording and the respective SLAs were obtained by dividing the area of individually-sampled leaves by their oven-dry mass (60°C, 48 hr) weighed to 0.01g and expressed in mm^2g^{-1}. Fully expanded and physiologically active leaves were collected for this purpose. Four tufts were selected per treatment. Whole tillers with leaves attached were removed from the sample tufts, wrapped in moist newsprint paper and sealed in a plastic to avoid loss of moisture and stored in a cooler bag containing ice until processing in the laboratory within one hour after collection. Specific leaf area was measured using a LI-3000C (Li-Cor, Lincoln, NE, USA) leaf area meter.

2.4   Data Analysis

The effect of the treatments on the dependent variables (i.e. above-ground biomass, number of tillers, specific leaf area, and tuft circumference) were compared using Generalised Linear Models, poison distribution with identity link. The independent variables were burning, defoliation and plant neighbourhood types. Automatic linear regression models were used to rank the treatments' contribution to the observed means. Examination of residuals revealed that the data did not meet the assumptions of ANOVA and therefore, Generalised Linear Models

and regression analyses were conducted using IBM SPSS v. 25. Where factors with multiple levels showed significant results (e.g. defoliation and plant neighbourhood types), I used Least Significant Difference (LSD) *post hoc* test at 0.05 to separate means among treatments.

2.5 Results

2.5.1 Above-ground biomass production

Above-ground biomass production of the focal plants in the unburned grassland was greater than that of the burned grassland (i.e. 63.0 ± 3.3g and 23.2 ± 3.3g per tuft of the focal plant, respectively). The defoliation effects differed significantly (Table 2.1) with defoliation of the neighbouring plant showing a higher mean (82.3 ± 5.7g) followed by the control (54.2 ± 5.7g), defoliation of focal plant (19.3 ± 3.3g) and defoliation of both the focal and neighbouring plants showing the least values (16.55 ± 3.2g) for above-ground biomass of the focal plant. The effects of neighbourhood types showed significant differences (Table 2.1) with *F. costata* surrounded by other *F. costata* plants showing a higher mean (63.3 ± 4.0g), *F. costata* surrounded by other grasses (39.1 ± 4.0g) and *F. costata* growing alone (26.8 ± 4.0g).

1   Table 2.1   Effects of annual burning, defoliation and plant neighbourhood types on above-ground biomass (g) production, number of
2   tillers, tuft circumference (mm) and specific leaf area (mm^2g^{-1}) of the focal plant.

Source	Above-ground biomass (g)			Number of tillers		Tuft circumference (mm)		Specific leaf area (mm^2g^{-1})	
	Wald's χ^2	df	P	Wald's χ^2	P	Wald's χ^2	P	Wald's χ^2	P
Burning (B)	74.019	1	**<0.001**	1.660	0.198	25.983	**<0.001**	0.232	0.630
Defoliation (D)	131.387	3	**<0.001**	114.368	**<0.001**	27.652	**<0.001**	23.490	**<0.001**
Neighbourhood types (N)	43.082	2	**<0.001**	54.745	**<0.001**	13.260	**0.001**	.595	0.743
B * D	23.788	3	**<0.001**	44.550	**<0.001**	4.125	0.248	35.031	**<0.001**
B * N	15.295	2	**<0.001**	5.907	0.052	5.909	0.052	4.889	0.087
D * N	43.660	6	**<0.001**	48.657	**<0.001**	22.600	**0.001**	4.391	0.624
B * D * N	20.338	6	**0.002**	48.645	**<0.001**	19.272	**0.004**	10.370	0.110

3

The interaction between burning and defoliation was significant. A combination of no burning and defoliation of the neighbouring plants resulted in the largest overall above-ground biomass of the focal plant while annual burning and defoliation of both the focal and neighbouring plants showed the least overall mean above-ground biomass per focal tuft (Fig. 2.3a).
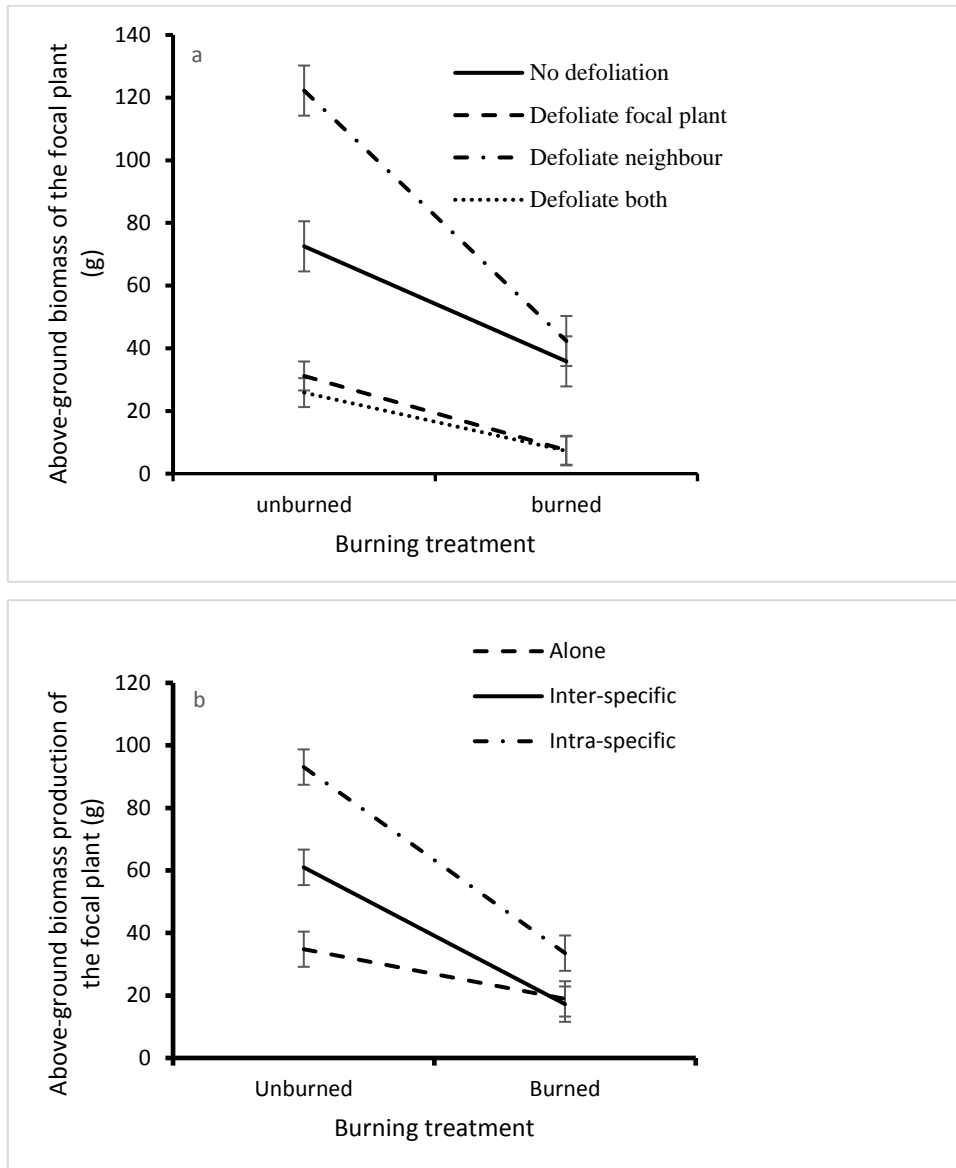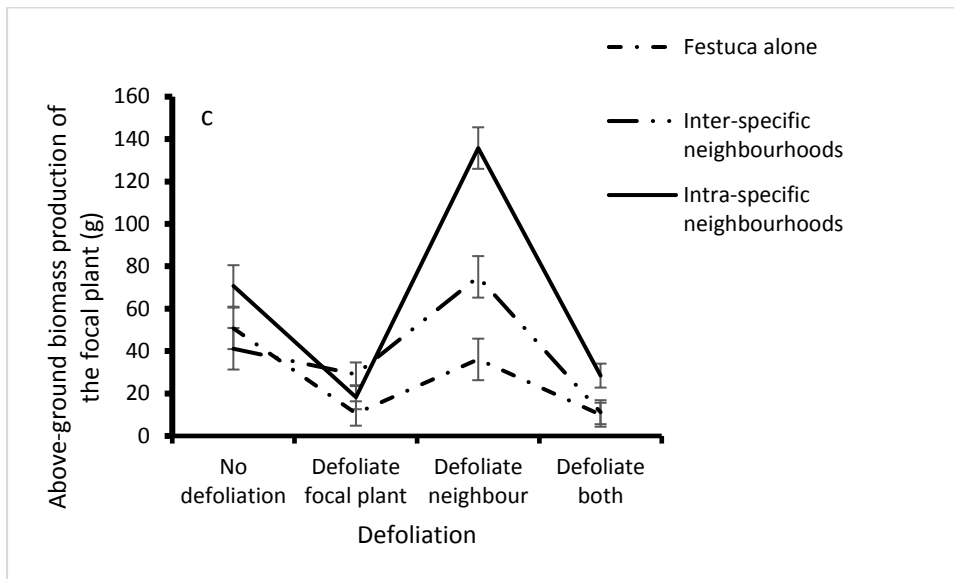
Figure 2.1   Mean (± SE) effects of (a) interactions between burning treatment and defoliation on above-ground biomass production of the focal plant, (b) interactions between burning treatment and plant neighbourhood types on above-ground biomass production of the focal plant and (c) interactions between defoliation and plant neighbourhood types on above-ground biomass (g) production of the focal plant.

The interactions between burning and plant neighbourhood types were significant (Table 2.1), The focal plant tufts in the unburned grassland showed the highest above-ground biomass means while the tufts in the burned grasslands had a reduced above-ground biomass production (Fig. 2.3b). The focal plants occurring with between intra-specific neighbourhoods at unburned sites had higher above-ground biomass than those occurring in inter-specific neighbourhoods at burned (i.e. 93.06 ± 5.66 versus 17.22 ± 5.66g).

The interactions between defoliation and plant neighbourhood types were significant (Table 2.1), with the interactions between defoliation of the neighbouring plants and *F. costata* growing with inter-specific neighbourhood types showing (Fig. 2.3c) the largest overall mean aboveground biomass and the combination of defoliation of both the focal and neighbouring plants with competition showing the least overall mean biomass. The combination of defoliation of the neighbouring plants with intra-specific neighbourhoods resulted in high biomass of the focal plants (135.8 ± 9.8g) while the combination of defoliation of both the focal

and neighbouring plants with *F. costata* growing without above-ground competition resulted in the least mean biomass (10.0 ± 5.7g).

A combination of burning, defoliation and neighbourhood type treatments significantly affected above-ground biomass of the focal plant (Table 2.1). No burning and defoliation of the neighbouring plants with intra-specific neighbourhoods showed strong positive effects on the above-ground biomass production of the focal plants. The burning, defoliation of both the focal and neighbouring plant with inter-specific neighbourhoods showed negative effects (i.e. 207.70 ± 13.85 versus 4.59 ± 8.00).

Defoliation was the major contributors to the variation in above-ground biomass production for the focal plant while neighbourhood types had the least effect (i.e. 64% versus 9%). There was a weak correlation ($r = 0.41$, $P < 0.001$) between the expected and observed variation in mean above-ground biomass production.

2.5.2   Number of tillers

Defoliation of the focal plant had strong negative effects on number of tillers while defoliation of the neighbouring plants resulted in increased tiller abundance of the focal plant (Fig. 2.4a). The effects of plant neighbourhood types were significant (Table 2.1). Inter specific neighbourhoods showed positive effects on tiller production while removal of all neighbouring plants resulted in reduced number of tillers for the focal plant (Fig. 2.4b). No defoliation did not significantly affect the focal plant, defoliation of the neighbouring plants resulted in significant increase in the tiller numbers and defoliation of both the focal and neighbouring plants resulted in significant reduction in tiller numbers of the focal plant.
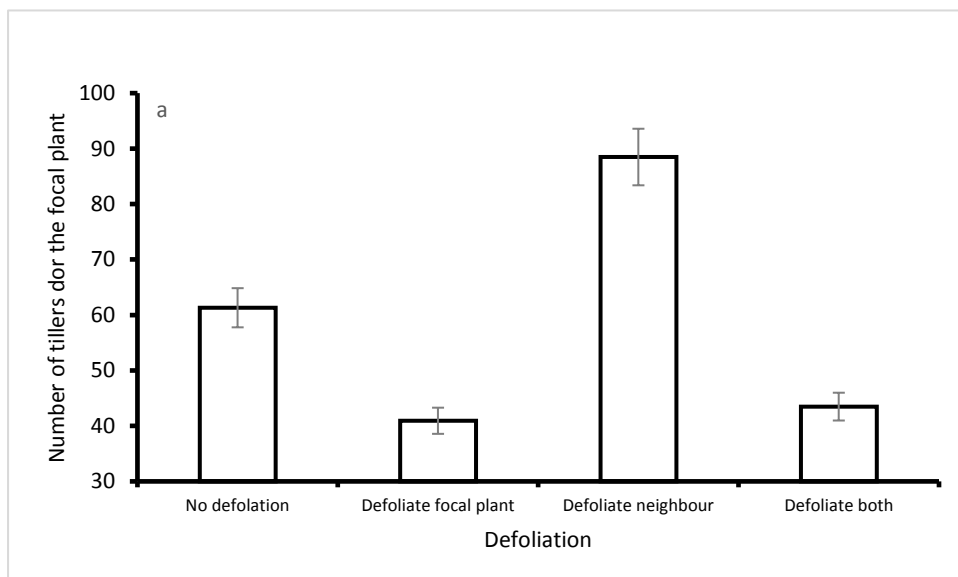
Figure 2.2   Mean (± SE) effects of (a) defoliation and (b) neighbourhood types on number of tillers of the focal plant.

The interactions between burning and defoliation were significant with the unburned grassland having a higher overall mean tiller production than the burned sites (Table 2.1, Fig. 2.5a). The combination of no defoliation and defoliation of both the focal and neighbouring plants on the unburned grassland showed a higher mean number of tillers while a combination of defoliation of the focal plant and defoliation of both the focal and neighbouring plants in the burned grassland resulted in least mean number of tillers of the focal plant.
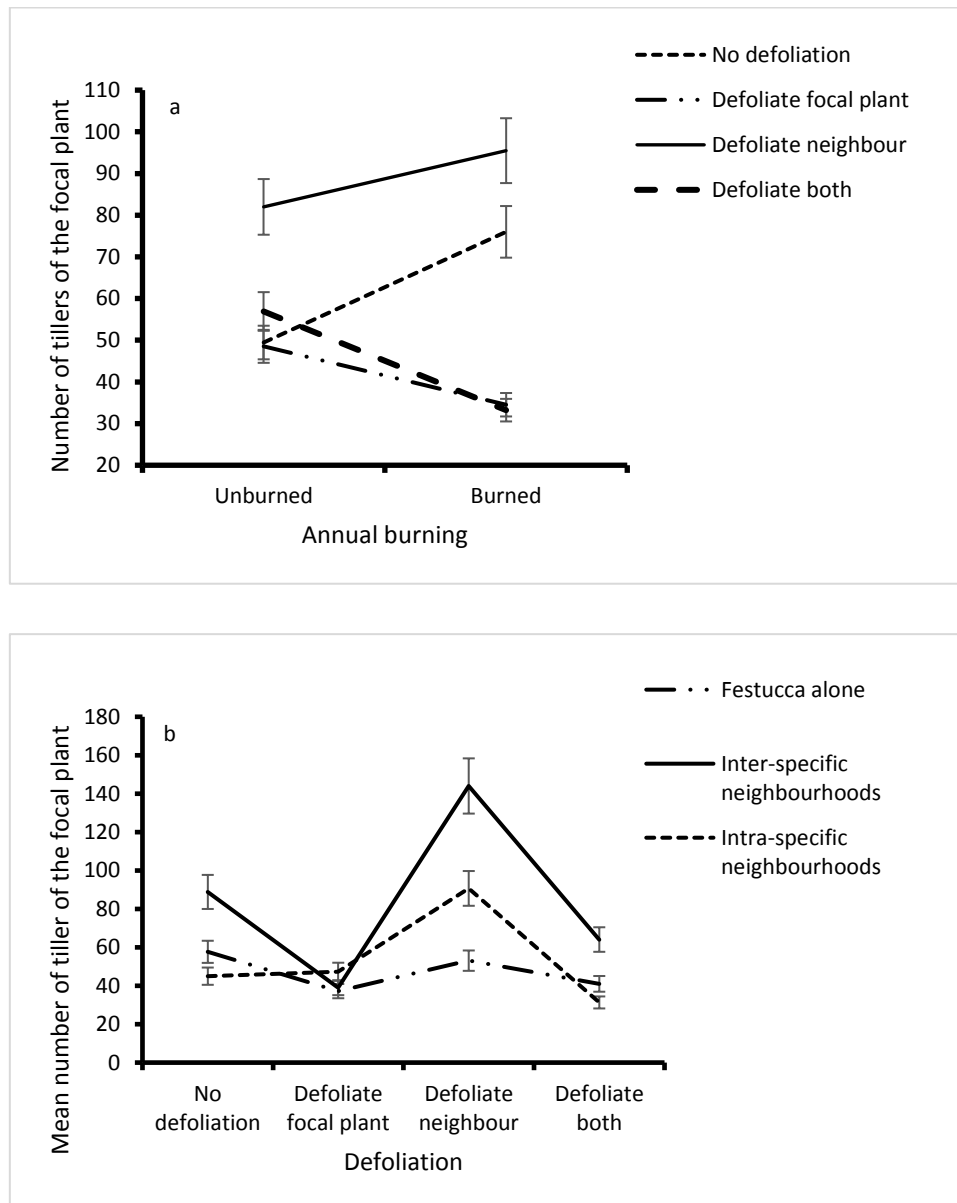
Figure 2.3   Mean (± SE) effects of combinations of (a) annual burning and defoliation and (b) the interactions between defoliation and plant neighbourhood types on the number of tillers of the focal plants.

The interaction between defoliation and plant neighbourhoods was highly significant for the number of tillers of the focal plant (Table 2.1). The interaction between inter-specific and intra-specific neighbourhood types and defoliation of the focal plants were highly significantfor tillers numbers. The interaction between intra-specific neighbourhoods with *F. costata* growing alone under defoliation of both the focal and neighbouring plant significantly reduced the number of tillers of the focal plants (Fig. 2.5b).

The interactions between annual burning, defoliation and neighbourhood types were highly significant in influencing number of tillers (Table 2.1). Annual burning, defoliation of the neighbouring plants and inter-specific neighbourhoods showed higher positive effects on number of tillers while defoliation of both the focal and neighbouring plants in the burned grasslands showed the most negative effect (148.67 ± 20.98 versus 24.56 ± 3.47).

2.5.3 Tuft circumference

Annual burning of fire-breaks resulted in a significant reduction in mean tuft circumference of the focal plants (275 ± 10mm versus 213 ± 7mm). Defoliation of the focal plant negatively affected tuft circumference, defoliation of the neighbouring plants significantly affected the tuft circumference of the focal plant (Fig. 2.6a). The effects of growing with neighbours were significant for tuft circumference of the focal plant (Table 2.1) with *F. costata* surrounded by other grasses showing larger tuft circumferences. *F. costata* growing alone showed the least expansion on focal plant tuft circumferences (Fig. 2.6b)
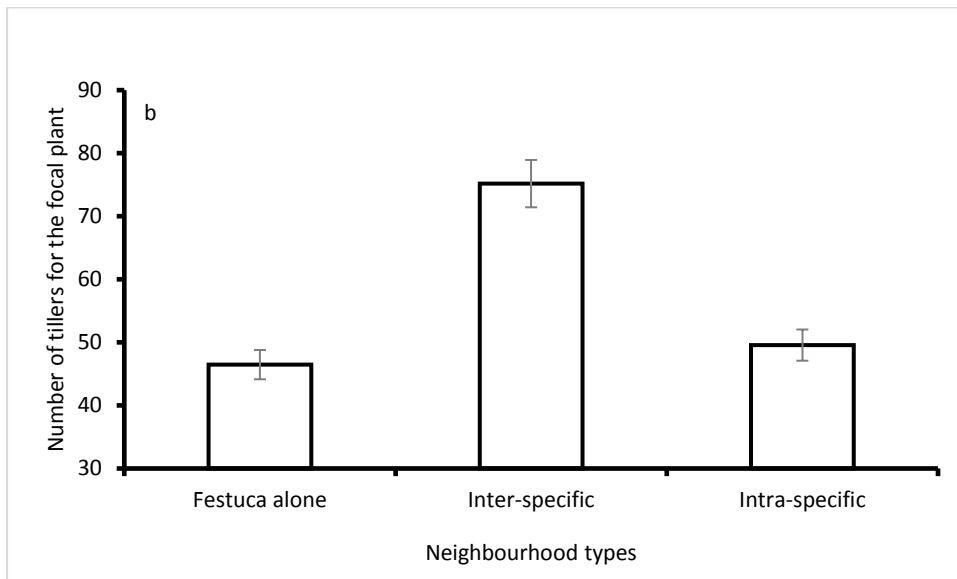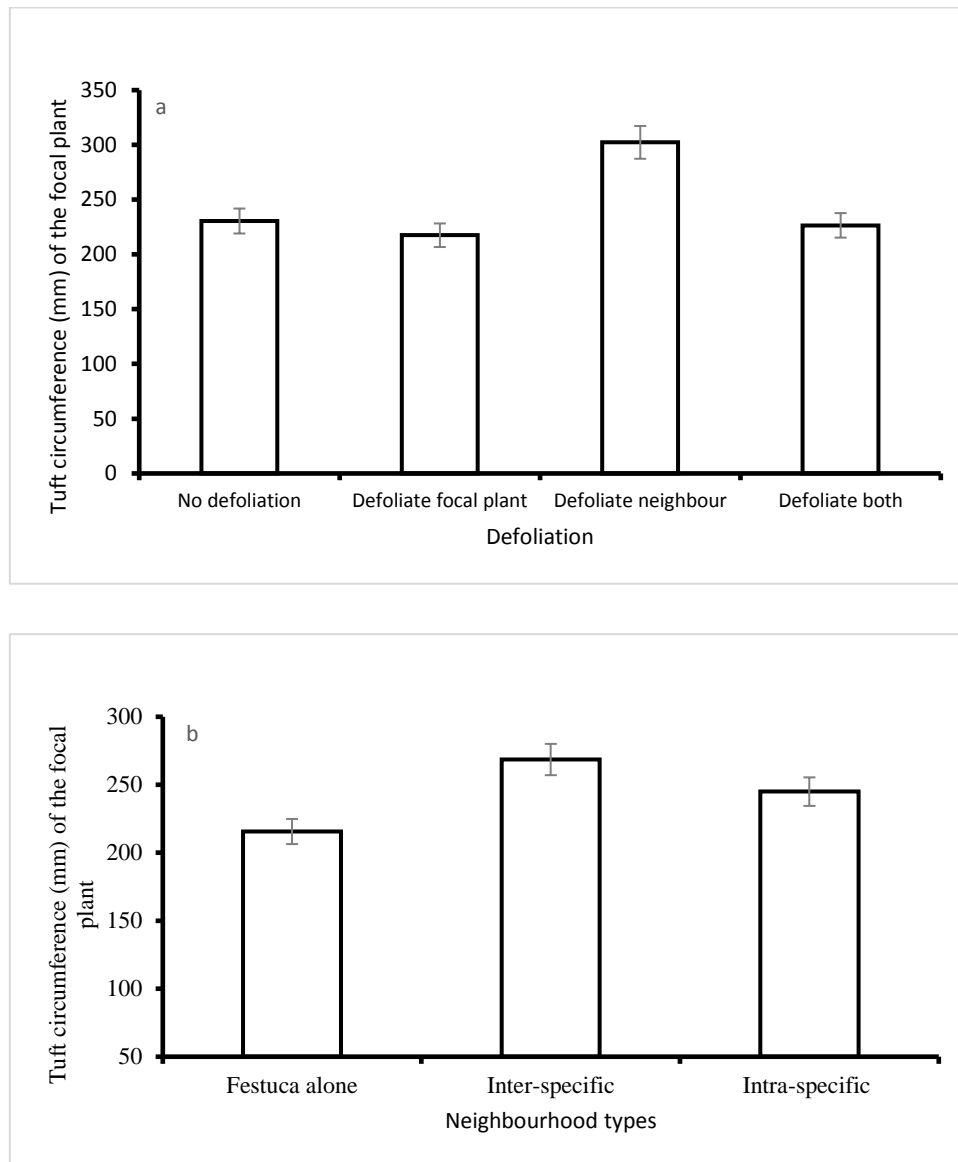
Figure 2.4   Mean (± SE) effects of (a) defoliation and (b) neighbourhood types on tuft circumference (mm) of the focal plant.

The interactions between defoliation and neighbourhood types were significant (Table 2.1). The interactions between inter and intra-specific neighbourhood types had larger means for tuft circumference for the focal plant. The interaction between intra-specific neighbourhood types and *F. costata* growing alone (neighbouring plants within a radius of 300mm removed) with defoliation of both the focal and neighbouring plants had the least means (Fig. 2.7).
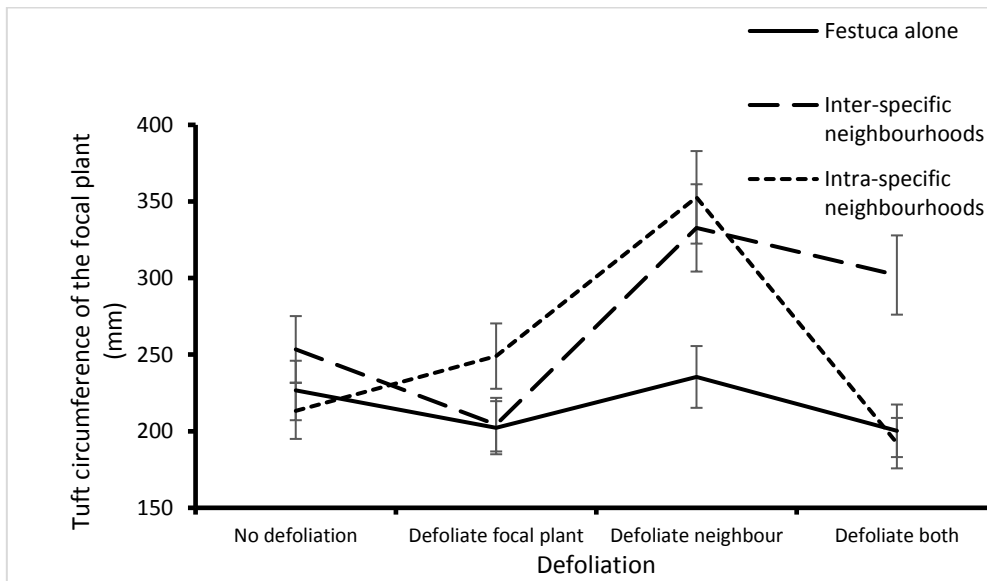
Figure 2.5   Interaction plot for defoliation and neighbourhood types on the tuftcircumference of the focal plants.

The interactions between annual burning, defoliation and competition were also significant (Table 2.1) with the interactions between no burning, defoliation and competition showing the highest mean tuft circumference for the focal plants (284.28 ± 34.43 mm) while the interactions between burning of annual fire-breaks, defoliation and competition had the least means mean tuft circumference (Fig. 2.7). The combination of treatments i.e. burning, defoliation of the neighbouring plant and intra-specific neighbourhoods resulted in highest effects on mean tuft circumference means while annual burning, defoliation of the focal plant and inter-specific neighbourhoods had the least effect (Fig. 2.7).

2.5.4 Specific leaf area (SLA)

Specific leaf area was strongly influenced by defoliation (Table 2.1, Fig. 2.8). The interaction between burning and defoliation was significant (Table 2.1). Defoliation of the neighbouring plant and defoliation of both the focal and neighbouring plants with no burning resulted in significant increase in SLA. The defoliation of the neighbouring plants and no defoliation with annual burning resulted in significant reduction in the SLA of the focal plants (Fig. 2.9).
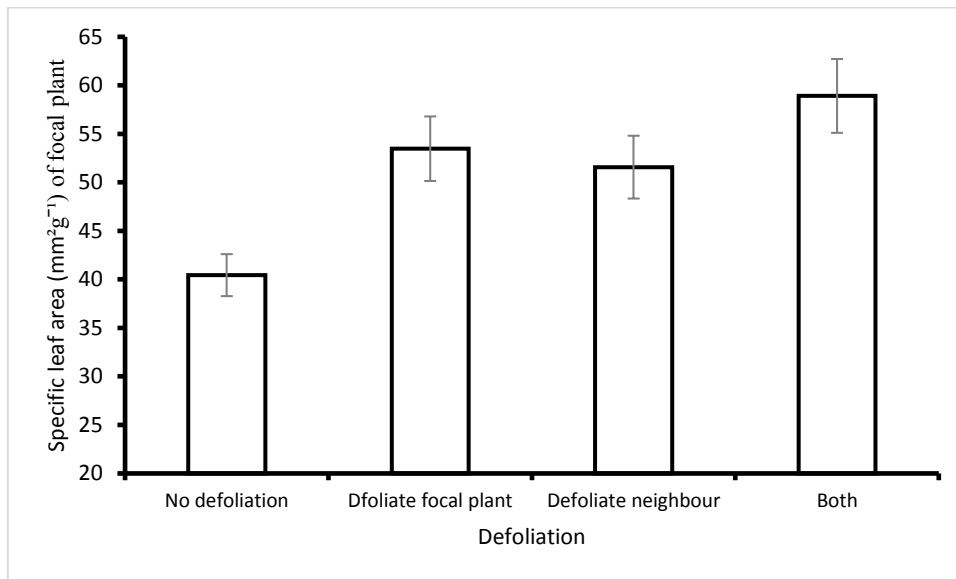
Figure 2.6   Mean (±SE) effects of defolaition on the specific leaf area of the focal
plant
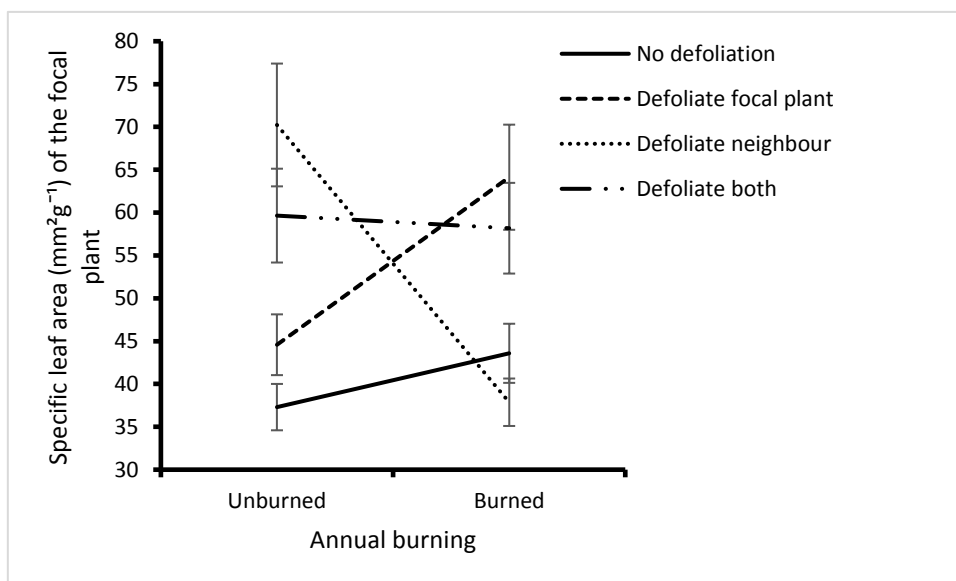
Figure 2.7   Interaction plot for annual burning and defoliation treatments of the
specific leaf area of the focal plant

2.6   Discussion

2.6.1   Above-ground biomass production

The ability of plant to produce biomass is determined by species type, management factors (i.e. burning, herbivory, nutrient addition) and environmental factors (i.e. temperature, precipitation, soil fertility) they are subjected to. In this study, *F. costata* was subjected to three disturbance regimes namely annual burning, defoliation and competition. The results of our study show that annual burning of fire-breaks had a negative effect on the ability of *F. costata* to accumulate above-ground biomass. The unburned grassland had significantly more above-ground biomass than the burned grassland. These results are consistent with findings of other studies Johnson (2001), Eugenio and Lloret (2004), Govender et al. (2006), Le Roux and Morris (2010), Wu et al., (2013) that reported reductions in productivity in grasslands frequently subject to annual burning. Species such as *T. triandra* have been reported to thrive in fire-prone environments (Synman et al., 2013). However, the results of this study suggest that the ability of *F. costata* to accumulate above-ground biomass was reduced in annually burned sites by 63%, which suggests that the species may be sensitive to repeated exposure to fire disturbance.

Different forms of defoliation occur in grasslands and plant responses are largely dependent on level and frequency of defoliation. Defoliation agents such as large herbivores, insects and human beings all exert different levels of herbivory on species of their choice. The findings of this study strongly suggest a very poor response to repeated defoliations by *F. costata*. The control and plants whose neighbouring plants were defoliated showed higher above-ground biomass production. Defoliation of the focal plant and both the focal and their neighbouring plants reduced biomass production by 64.4% and 69.5% relative to the control. Defoliation of the neighbouring plant resulted in increases in above-ground biomass production by 52%. The loss in above-ground biomass productivity is consistent with the results recorded by Morris and Tainton (1993). However, the findings in this study conflict with the results of Loeser et al. (2004) who recorded a positive effect of defoliation on net primary productivity in grasses. The combined effects of annual burning, defoliation and competition were significant with the unburned grassland having higher productivity in terms of above-ground biomass compared to the annually burnt fire-breaks.

Findings of this study suggest that competition has a positive influence on the performance of *F. costata*. Intra-specific competition seemed to result in greater accumulation of above-ground biomass followed by inter-specific competition. These results are contrary to studies (e.g. del-Val and Crawley, 2004; Skálová et al., 2013; Hortal et al., 2017) that reported negative influences from both inter-specific and intra-specific competition on above-ground biomass production.

2.6.2 Number of tillers

The ability of plants to initiate tiller formation is an important indicator of species productivity (Assuero and Tognetti, 2010). The results from this study suggest that annual burning did not influence tiller formation. Defoliation, however, had negative influences on the ability of *F. costata* to produce new tillers. Defoliated tufts showed a significantly lower number of tillers compared to undefoliated control plants. Removal of neighbouring plants resulted in increased tiller formation by the focal tuft of up to 44%. Contrary to these findings, Zhang and Romo (1995) reported an increase in tiller formation for *Agropyron dasystachyum* when subjected to defoliation at 6 weeks intervals, Anderson and Frank (2003) also reported a positive effect of defoliation on total active number of tillers. Results in this study are in agreement with Morris and Tainton (1993), who reported a reduction in tiller abundance for *A. junciformis* when subjected to repeated defoliation. The combined effects of annual burning, defoliation and competition significantly affected the focal plants with the unburned grasslands having a higher mean tiller number per tuft.

2.6.3 Tuft circumference

Annual burning of fire-breaks had a highly significant effect on the target plant's tuft circumference. Burnt grassland recorded lower individual tuft circumferences. Defoliation of the focal plant as well as that of the focal and neighbouring plants resulted in lower mean tuft circumferences of the focal tufts relative to the control, of 5.6% and 1.7%, respectively. Competition from neighbouring plants also negatively affected tuft circumference of the focal plants with inter-specific competition accounting for the largest variation in tuft size. A combination of no burning, defoliation and competition generally showed higher mean values for tuft circumference of the focal plant.

2.6.4 Specific leaf area

Specific leaf area is important for both physiological and ecological functions in plants. Above-ground productivity in grasses is directly related to specific leaf area (Lui et al., 2017). Changes in leaf characteristics significantly affect plant performance, such as growth and productivity (Wright et al., 2004; He et al., 2006). The results of this study show that defoliation of the focal plant resulted in increased SLA, which is consistent with Zheng et al. (2010), who recorded an increase in SLA in *Carex appendiculata* and *Stipa grandis* following grazing. However, they also recorded a decrease in SLA for *Stipa baicalensis*. The conflicting results clearly indicate that plant responses to various forms of disturbance vary with respect to species.

2.7 Conclusion

The effects of burning, defoliation and neighbourhood types were studied on *F. costata*. This comprised determining how fire, defoliation and neighbour presence affected above-ground biomass production, number of tillers, tuft circumference and specific leaf area of the focal plant. While the study showed a negative effect of annual burning on the functional traits of the focal plant, the findings suggest that *F. costata* is may be sensitive to selective herbivory. It is therefore, logical to conclude that a combination of selective herbivory, as the species is not palatable and not voluntarily consumed by herbivores, and annual burning may have severe debilitating consequences on the performance of *F. costata*. The response of the focal plant to disturbance by fire may have landscape implications on the Drakensberg grasslands whose possible negative consequences may be compounded by climate change. Knowledge of the relationship between *F. costata* and its neighbours, herbivory and fire ecology will help in understanding dynamics of the Drakensberg grasslands in a changing climate. Therefore, a grassland management strategy purposefully targeting the defoliation of *F. costata* may help in halting its reported increase on the Drakensberg.

2.8 Acknowledgements

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Chapter 3

Influence of nitrogen addition, defoliation and neighbouring plants on a high-altitude C_3 grass, *Festuca costata*

Abstract

Understanding the effect of global climate change on plant species and communities is critical in gaining knowledge of the mechanisms by which plants cope with environmental complexities. In Afro-temperate grasslands of southern Africa, increasing abundance of evergreen C_3 grasses may displace C_4 grasses and impact fire regimes. Using a pot experiment in a green house, we evaluated the effect of the addition of limestone ammonium nitrate fertiliser on the performance of a C_3 grass, *Festuca costata,* when subjected to defoliation treatments (i.e. no defoliation, defoliation of *F. costata*, defoliation of a neighbouring plant and defoliation of both *F. costata* and a neighbouring plant). The *F. costata* plants were grown in different neighbourhood types (*F. costata* growing alone, growing with *Themeda triandra,* or with *Aristida junciformis).* At six-week intervals over a 5-month period, the number of tillers on *F. costata* were counted and concurrently measured above-ground biomass production, tuft circumference, and specific leaf area (SLA). The effect of the treatments on these dependent variables were compared using generalised linear models. Nutrient addition showed a significant negative effect on the number of tillers of *F. costata* and tuft size but showed no significant effects on above-ground biomass production and SLA. Defoliation significantly reduced above-ground biomass production, number of tillers and tuft circumference while SLA increased. Plant neighbourhood types showed significant negative influences on tuft circumference. Defoliation accounted for the most variations in reduced tuft size, above-ground biomass and number of tillers, however, it resulted in increased SLA. Consequently, a management strategy using selective herbivory may alter the relative dominance on common C_3 species in the high altitude range of the Drakensberg grasslands.

Key Words: Climate change, anthropogenic activities, elevated CO_2 .

3.1 Introduction

Anthropogenic activities have significantly contributed to changes in the abundance and distribution of plant species in many terrestrial ecosystems (Mariotte et al., 2014; Borer et al., 2014). For example, at least 60% of the grassland biome in South Africa is completely transformed, with a further 23% currently under agricultural use and only 2% protected (O'Connor and Kuyler, 2009). Elevated atmospheric concentration of greenhouse gases (CO_2 and nitrogen) with the accompanying change in climate are likely to result in changes in grassland productivity (Polley et al., 2014). In addition, the increase in global temperatures due to climate change has been reported to cause shifts in the relative dominance of C_3 grasses against C_4 grasses (Adjorlolo et al., 2012). The dominance of C_3 species has been reported to alter fire regimes, which have been used as a management tool for maintaining the diversity and health of grasslands (McGranahan et al., 2016). These changes could affect yields, nutrients and species composition as well as growth characteristics of plants in grasslands (Pallet et al., 2016; van Oijen et al., 2018). However, there is a dearth of knowledge on the interactions between global climate change, resource availability and productivity under different management regimes particularly in grasslands (Craven et al., 2016).

Shifts in resource availability could negatively affect biodiversity in grasslands. For example, an increase in nitrogen supply may result in a reduction in legume availability and consequently reduce the N fixation rate in grasslands (Hartwig, 1998; Suding et al., 2005). While nitrogen availability does not have a direct effect on physiological processes such as photosynthesis, it is often the most limiting nutrient for plant growth in many terrestrial ecosystems (Craine and Dybzinski, 2013), such as grasslands in South Africa (Craine et al., 2008). An increase in nitrogen deposition in the atmosphere is projected to result in alterations in the species composition in the grasslands (Zhou et al., 2002; Pallet et al., 2016; You et al., 2017). The maintenance or change in species diversity and composition in a grassland because of invasive species can also be explained by their differences in competitive abilities under global climatic change (MacDougall, 2004; Callaway, 2007; Valledares et al., 2015).

Predicted changes in environmental conditions due to global climate change are likely to favour the establishment of new grass species in non-native areas to the competitive exclusion of native species (Seabloom et al., 2003). In less productive plant communities, above-ground

competition is of less importance compared to belowground competition (Casper and Jakson, 1997; Schenk, 2006). The inherent characteristics of plants in grasslands determine the extent to which they suffer exclusion because of competition from invasive species (Breitschwerdt et al., 2018). Fast growing species are less likely to suffer from competitive exclusion compared to the slow growing species as they can effectively compete for resources such as soil nutrients, light and water (Grime, 1977; Craine, 2005; Funk, 2013).

Herbivory has been shown to have strong negative influences on the survival, growth and fecundity of various plant species (Parmesan, 2001; Moron and Crone, 2006). Studies using different animals have shown that herbivory negatively affects above-ground biomass production in some grassland species (e.g. *Trifolium ripens* and *T. pratense*) as well as cause changes in species composition (Hulme, 1996). Other studies, however, have shown that controlled herbivory tends to increase plant heterogeneity in grassland (van Klink et al., 2015) Environmental conditions such as available soil moisture and nutrients also play an important role in determining plant responses to herbivory (Ncube et al., 2012; Ahanger et al., 2017). Plants have evolved, through their biochemical and physical features, to cope with defoliation pressure by minimising the probability of being defoliated or through rapid replacement of lost material (Dolch and Tcharntke, 2000).

Soil nutrients play a major role in limiting plant growth in a habitat (Shrivastava, 2014). The competitive ability of plants may influence species composition and diversity in the ecosystem (Grime, 1973). However, Tilman (1981) stated that resource availability is more important in determining species composition and diversity in a biome than their competitive abilities. Plant responses to nitrogen application varies by both species and the environment (Walker et al., 2001; Tatarko and Knops, 2018).

Human population growth coupled with rapid industrial development are posing a major conservation challenge on southern African grassland biomes (Lehmann and Parr, 2016; Osborne et al., 2018). The grassland biome has important ecosystem functions such as water and nutrient cycling, carbon sequestration, soil stabilisation and pasture for both domestic and wild animals (Reyers et al., 2005). With close to 30% of the total grassland biome transformed due to anthropogenic activities, it is the second most threatened biome in South Africa after the Fynbos (Fairbanks et al., 2000; Neke and Du Plessis, 2004). The grassland biome of Southern

Africa, estimated to be second in size to the savanna, comprises slightly under 30% of the total land mass and is endemic to about 2520 angiosperms (Carbutt and Edwards, 2005; Mucina and Rutherford, 2006).

This study sought to evaluate the effects of defoliation and plant neighbourhood types on *F. costata* grown under soil nitrogen amendments. It was predicted that;

i. Nutrient addition increases above-ground biomass production of *F. costata* grasses because they occur in nutrient-limited ecosystems

ii. *F. costata* plants growing with neighbours attain smaller sizes (i.e. above-ground biomass production, tuft circumference, number of tillers) due to competition than plants growing without neighbours

iii. Defoliation of *F. costata* will result in increased above-ground biomass production because of compensatory growth.

This has relevance because it helps generate knowledge in trying to understand the effect of increased nitrogen deposition in the atmosphere because of global climate change on species composition and diversity in grasslands (Zavaleta et al., 2003; Stevens et al., 2004).

3.2   Materials and Methods

3.2.1   Study species

Festuca costata is a C_3 evergreen perennial tussock-forming species native to the Afromontane conditions of the high-altitude grasslands in southern Africa (Adjorlolo et al., 2012; McGranahan et al., 2016). Its altitudinal distribution ranges between 1830 to 2800 m.a.s.l. *Festuca costata* is normally found in mixed stands with C_4 grasses including *Themeda triandra, Aristida monticola, Andropogon appendiculatus, Alleteropsis similata* and *Aristida junciformis* (O'Connor et al., 2004). *Themeda triandra* and *Aristida junciformis* represent the extremes in terms of value for grazing and succession – a grassland dominated by *T. triandra* is considered to be in climax state while dominance of *A. junciformis* is an indication of disturbance and low quality grazing (Snyman et al., 2013; Mucina and Rutherford, 2006).

3.2.2 Experimental design

A full factorial pot experiment was conducted with three factors: nitrogen as limestone ammonium nitrate made up of 28% N and applied at 140kg ha^{-1} by element mass at two levels (no nitrogen, nitrogen applied) every six weeks from 14th December 2017 to 19th April 2018; defoliation (no defoliation, defoliation of focal plant, defoliation of a neighbouring grass, defoliation of both the focal and neighbouring plant) and plant neighbourhood types (focal plant growing alone, focal plant growing with *Themeda triandra*, focal plant growing with *Aristida junciformis*). The treatments were replicated five times for a total of 120 focal plants in a fully randomised design (i.e. 2 nitrogen levels × 4 defoliation levels × 3 neighbourhood levels × 5 replicates). Plants were grown in 98L drums (450 mm top diameter × 350 mm bottom diameter × 622 mm height) three-quarter filled with coarse river sand obtained from a commercial supplier (Fig. 3.1). Prior to commencement of the experiment, the soil was sterilised using methyl bromide for 48hrs to kill all unwanted seed. The *F. costata* plants were obtained from Highmoor Nature Reserve (20° 32' S, 29° 62' E), which lies in the central part of the uKhahlamba-Drakensberg Park, a World Heritage Site. *T. triandra* and *A. junciformis* were sourced from the University of KwaZulu-Natal (UKZN)'s agricultural campus in Pietermaritzburg (29° 37' S, 30° 24' E). All the plants were defoliated to 50 mm above-ground to ensure the all plants in the study were the same size and allowed to establish for four weeks before commencing treatments. The study was conducted during the rainy season; however, supplementary irrigation was carried out at 3-day intervals during periods of dry spell.

Figure 3.1 *Festuca costata* growing with *Aristida junciformis* in a pot experiment at the Tainton Arboretum, University of KwaZulu-Natal, Pietermaritzburg.

3.2.3   Above-ground biomass

Three defoliations were carried out as treatment combinations during the experiment. The samples were collected from the grasses that were cut at 50mm above the soil surface. The cut grass was put in brown paper bags and oven-dried (60°C, 48hr) before weighing and recording. All analysis of above-ground biomass used grass dry weight from the three defoliations.

3.2.4   Number of tillers

Number of tillers on focal tufts were counted at 6-week intervals during the period of the experiment. Counts were done on predefined sampling tufts, three per treatment combination and the same plants were used consistently throughout the experiment. I counted individual tillers and removed dead tufts after each count. Tillers were classified as dead when they showed evidence of drying or missing or showed advanced signs of senescence. This procedure allowed for all tillers to be counted and new ones to be recorded.

3.2.5 Specific leaf area

The sampling procedure for specific leaf area (SLA) followed a modified method recommended by Cornilessen et al. (2003). Two leaves were sampled per tuft for each recording. A composite SLA was obtained by dividing the area of individually-sampled leaves by their oven dry mass weighed to 0.01g and was expressed in mm^2g^{-1}. Fully expanded but physiologically active leaves were collected for this purpose. Four tufts were selected per treatment combination. Whole tillers with leaves attached were removed from the sample tufts, wrapped in moist newsprint paper and sealed in a plastic bag to avoid loss of moisture and stored in a cooler bag containing ice until processing in the laboratory within one hour. Leaf area was measured using a LI-3000C (Li-Cor, Lincoln, NE, USA). Specific leaf area values were derived from all leaves sampled per plant.

3.2.6 Tuft circumference

The circumference of tufts of all focal plants was measured at the start and end of the experiment. The measurements were taken by tying a string firmly around the tuft and then transposing it on to a measuring tape graduated in mm (Fig. 3.2). The points of intersection

were marked, and the string was then stretched on a measuring ruler to obtain the actual reading. Measurements of tuft circumference were carried out twice during the experiment.

Figure 3.2   Tuft circumference measurements on the focal plant, *F. costata*, in a greenhouse experiment at the Tainton Arboretum, University of KwaZulu-Natal, Pietermaritzburg.

3.3   Data analysis

The effect of the treatments (limestone ammonium nitrate, defoliation and neighbourhood types) on above-ground biomass, number of tillers, SLA and tuft circumference were compared using generalised linear models following a Poisson distribution with the identity link function. To account for missing values due to mortality and large variation in the number of tillers and specific leaf area, the data were log $(x + 1)$ transformed. Automatic Linear Regression models were used to rank the treatments' contribution to the observed means. Where factors with multiple levels showed significant results (e.g. defoliation and plant neighbourhood types), Bonferroni *post hoc* test was to separate means among treatments. All statistical analyses were conducted in IBM SPSS Statistics v. 25.

3.4   Results

3.4.1   Above-ground biomass production

Above-ground biomass production was similar between fertilised and unfertilised plants (i.e. 1.65 ± 0.13g versus 1.47 ± 0.13g per tuft of the focal plant). The effects of defoliation differed significantly (Table 3.1) with defoliation of the focal and defoliation of both the focal and neighbouring plants showing the least above-ground biomass production (0.43 ± 0.13 and 0.44 ± 0.13g per focal plant respectively) The control showed the highest mean above-ground biomass production of the focal plants relative to *F. costata* growing with either *T. triandra* and *A. junciformis* (3.15 ± 0.23g). Plant neighbourhood types differed significantly for above-ground biomass production of the focal plants (Table 3.1) with *F. costata* growing alone showing larger mean biomass production (2.07 ± 0.16g) than *F. costata* growing with *T. triandra* (1.35 ± 0.16g) and *F. costata* growing with *A. junciformis* (1.26 ± 0.16g).

Table 3.1   Effects of limestome ammonium nitrate, defoliation and plant neighbourhood types on above-ground biomass (g) production, number of tillers, tuft circumference (mm) and specific leaf area (mm^2g^{-1}) of the focal plant.

Source		Above-ground biomass (g)		Number of tillers		Tuft circumference (mm)		Specific leaf area (mm^2g^{-1})	
	df	Wald's χ^2	P	Wald's χ^2	P	Wald's χ^2	P	Wald's χ^2	P
Limestone ammonium nitrate (LAN)	1	2.74	**< 0.001**	12.33	**< 0.001**	5.558	**0.018**	3.31	0.07
Defoliation (D)	3	128.91	**< 0.001**	47.31	**< 0.001**	21.241	**< 0.001**	11.84	0.008
Neighbourhood types (PNT)	2	15.43	< 0.14	3.95	0.12	4.258	0.12	3.05	0.22
LAN * D	3	2.90	**0.01**	11.38	0.26	3.187	0.36	1.33	0.72
LAN * PNT	2	2.76	**0.001**	13.83	0.08	5.87	**0.05**	1.56	0.46
D * PNT	6	13.73	0.64	4.26	0.91	6.27	0.39	11.85	0.07
LAN * D * PNT	6	6.22	**< 0.001**	619.59	0.24	2.62	0.86	2.01	0.92

3

The interactions between defoliation and plant neighbourhood types were significant for above-ground biomass production of the focal plant (Table 3.1). *Festuca costata* growing alone and *F. costata* growing with *T. triandra* with defoliation of both the focal and neighbouring plant had significantly higher above-ground biomass production (Fig. 3.3).
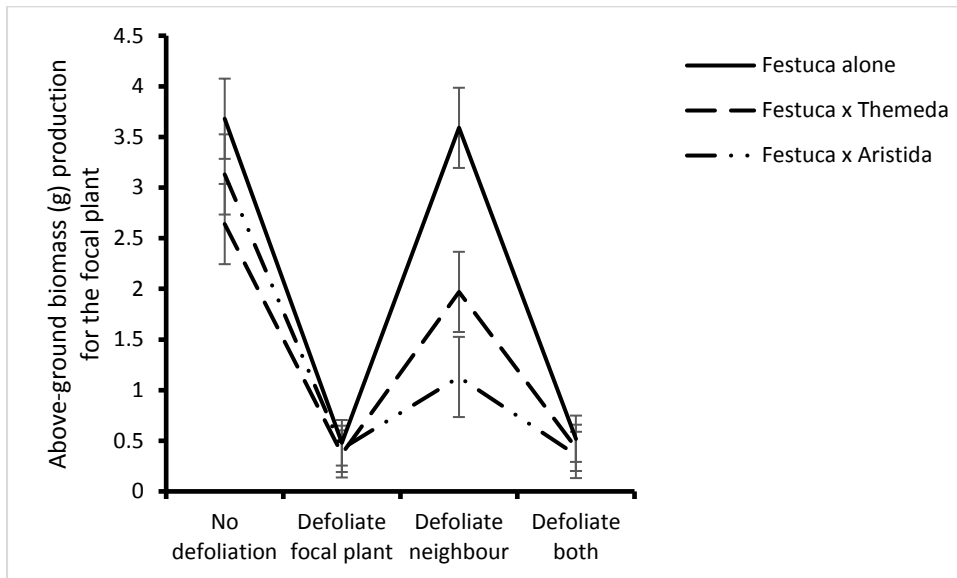
Figure 3.3   Mean (±SE) above-ground biomass (g) production of the focal plant for the interaction between defoliation and plant neighbourhood types.

3.4.2   Number of tillers

Application of limestone ammonium nitrate had no significant effects on the number of tillers formed per tuft of the focal plant (i.e. 4 ± 0.2 versus 3 ± 0.2). Defoliation also negatively affected the number of tillers of the focal plants (Fig. 3.4). Competition from surrounding plants did not significantly affect the tiller numbers for *F. costata* (Table 3.1).

Figure 3.4   Mean ($\pm$ SE) effects of defoliation on number of tillers of the focal plant.

3.4.3 Tuft circumference

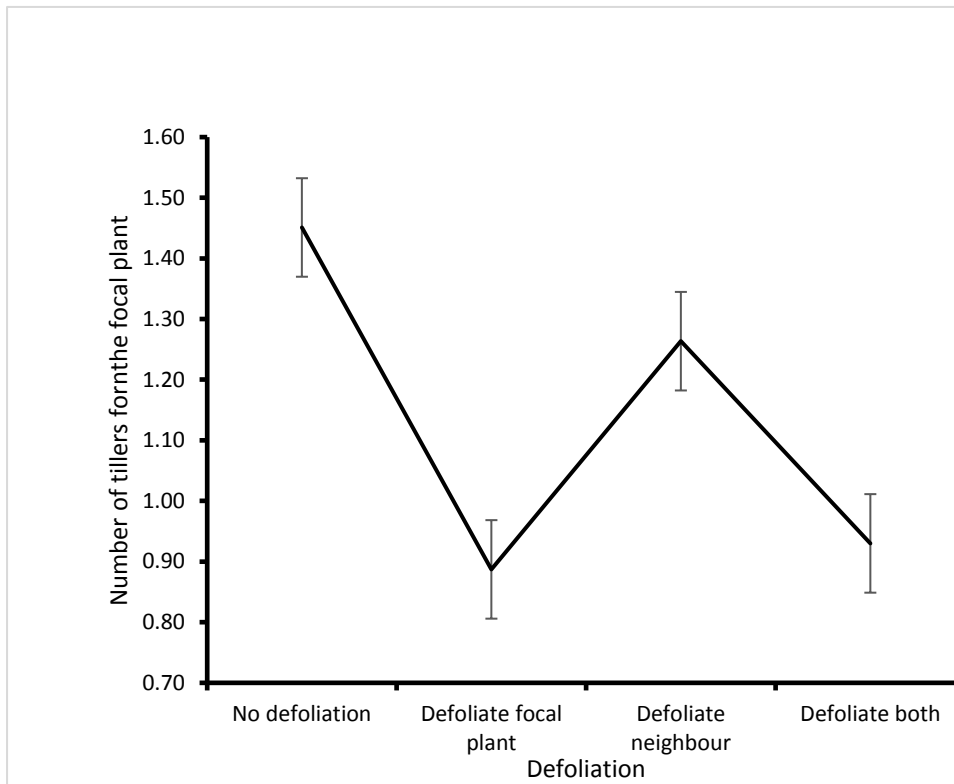The application of the fertilizer resulted in reduced tuft circumference of the focal plants (Table 3.1; Fig. 3.5). Defoliation also negatively affected the focal plants through reduced tuft circumference.

Neighbourhood types showed no significant effects on tuft circumference (Table 3.1) although *F. costata* growing alone showed marginally higher tuft sizes than that growing with *T. triandra* or with *A. junciformis*. There was significant interaction between addition of limestone ammonium nitrate and plant neighbourhood on tuft circumference (Table 3.1). The combination of no addition of limestone ammonium nitrate and *F. costata* growing with *A. junciformis* showed the larger mean tuft circumference of the focal plant compared with the combination of addition of limestone ammonium nitrate and *F. costata* growing with *A. junciformis* (i.e. 51.1 ± 4.9 mm versus 29.6 ± 4.9 mm).
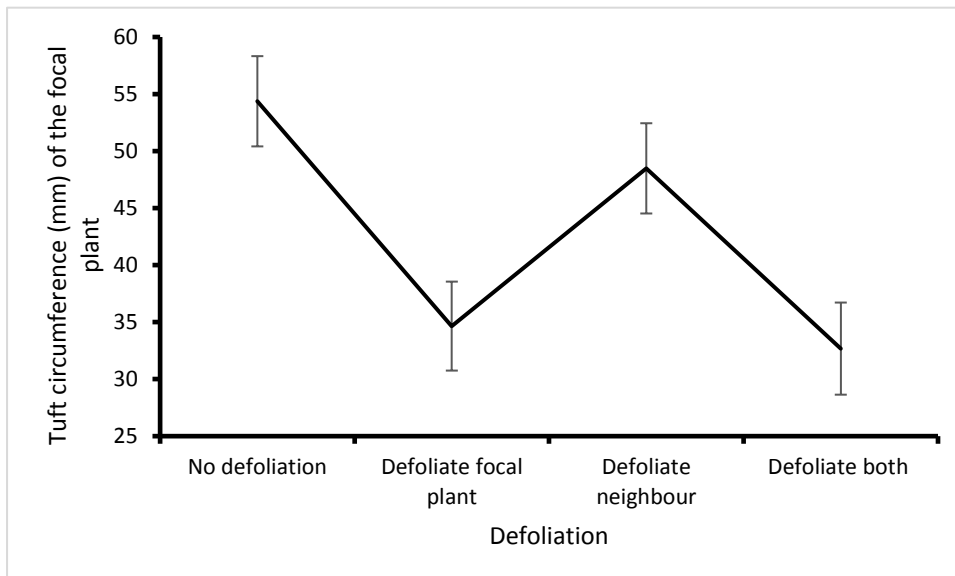
Figure 3.5   Mean (± SE) effects of defoliation on the tuft circumference of the *F. costata* plants.

3.4.4   Specific leaf area

The effects of soil nutrient amends with limestone ammonium nitrate were not significant for changes in specific leaf area measurements of the focal plant (Table 3.1). Defoliation of both the focal and neighbouring plants had significant effects on the SLA while defoliation of the neighbouring plants had no significant effects on the specific leaf area of the focal plants (Table 3.1, Fig. 3.6). The effects of competition from surrounding plants showed no significant differences on the specific leaf area (Table 3.1).

Figure 3.6   Mean ($\pm$ SE) effects of defoliation on the specific leaf area (mm^2g^{-1}) of the focal plants.

3.5   Discussion

Results of the study showed that soil nitrogen amendments (Table 3.1)   did not affect above-ground biomass and specific leaf area of *Festu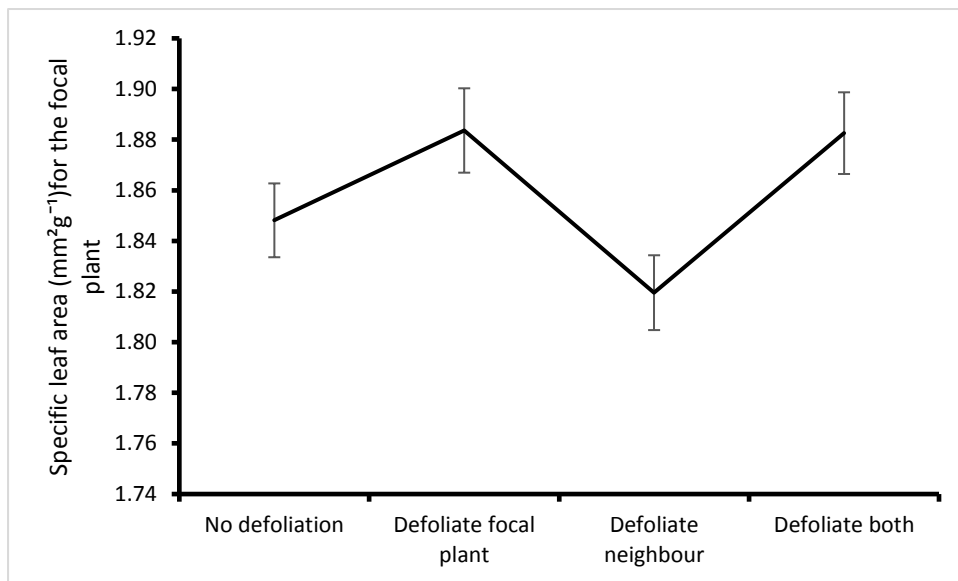ca costata* while it significantly reduced the number of tillers and the overall size of individual tufts. The unfertilised plants produced more above-ground biomass than fertilised plants. Some studies have reported negative influence of soil nutrient amendments with nitrogen application on native grasses based on short term studies (James et al., 2011). In their meta-analysis of the effect of soil nutrient amendments with N and P, Soons et al. (2017) concluded that soil nutrient amendment reduced plant diversity in grasslands as it tended to facilitate growth of vigorous species to the exclusion of their slow growing neighbours. Tsvuura and Kirkman (2013) and Ward et al. (2017), also reported increase in biomass of *Panicum maximum* in sites amended with both nitrogen and phosphorus fertilizers. This could be credited for the poor response of *F. costata* to addition of the limestone ammonium nitrate fertilizer. These findings seem to support the argument that competition is more important than nutrient availability in determining species composition and diversity in ecosystems (Grime 1973).

 Results of the current study however, conflict with the findings by Lee et al. (2017), who reported increased above-ground biomass production for *Mascanthus x giganteus* (believed to be a cross between *Mascanthus sinensis* and *Mascanthus sacchariflorus*) following soil nutrient amendment with nitrogen under greenhouse conditions. This study also did not consider changes in soil properties such as pH because of nitrogen addition and their influence on the performance of *F. costata*. It is possible that such shifts in soil pH could have confounding effects on the growth and development of *F. costata*. Such indirect effects of nitrogen addition on species diversity have been reported in long term nutrient amendment studies (e.g. Fynn and O'Connor 2005; Ward et al., 2017). The results further contrast with the findings by Batista et al. (2014), who recorded a positive influence of nitrogen fertilizer application on tiller formation and consequently the above-ground biomass production for *Brichiaria ruziziensis* under greenhouse conditions.

In the current study a finding of a reduction in above-ground biomass production as a result of defoliation is not in conformity with the findings of Stevens and Gowings (2014), who reported reductions in above-ground biomass production for *Anthoxanthum odoratum* L., *Plantago*

lanceolota L., and *Prunella vulgaris* L. in a pot experiment set up to determine the effect of interaction between nitrogen addition to the soil and simulated grazing (defoliation) under greenhouse conditions. The study by Stevens and Gowings (2014) furthermore, their study suggested that competition had a strong positive effect on above-ground biomass of their study plants which contrasts with the findings of this study where *F. costata* growing or *T. triandra* and *A. junciformis* showed a strong negative effect of competition in the study plant. Gillingham et al. (1998) reported an increase in shoot biomass of pastures in a grass/legume mixture following soil nutrient amendments with phosphorus and nitrogen fertiliser. However, Fiala et al. (2011) reported a reduction in above-ground biomass production for *Calamagrostis epigelos* following soil nutrient amendments with nitrogen under limited moisture conditions. This study however, did not assess the effects of nutrient amendments on the belowground biomass production of the focal plants, which could be substantial for many grassland plants besides grasses (see Bond 2016). In this study, there was an inverse relationship between soil nutrient amendments and above-ground biomass production of the focal plant.

Two most important attributes of defoliation that influence plant response are intensity (level of defoliation) and frequency (how often the defoliation is applied). Defoliation significantly altered all the functional traits of the focal plants under evaluation. These findings are in conformity with results reported by Bakker et al., (2006), Ngatia et al., (2015) that indicated a strong negative effect of defoliation on plant performance (). Other researchers also reported positive interactions between selective defoliation and plant performance for *Triglochin maritama* when subjected to different levels of competition and herbivory in a field experiment (Van Der Wal et al., 2000; Cook-Patton et al., 2014). The current results differ with the above findings principally because the plants in this study were transferred from their native environment into a pot experiment. This is because grasses show diverse responses to herbivory (Ferarro and Oesterheld, 2002). Two factors could be attributed to the observed increase of *F. costata* in the Drakensberg grasslands. Firstly, elevated CO_2 concentration in the atmosphere due to anthropogenic activities creates conditions favourable for C_3 plants whose physiological functions such as photosynthesis thrive with increase in available CO_2. Secondly the increase in deposition of atmospheric nitrogen due to climate change, too much available nitrogen is generally considered to be one of the leading causes of biodiversity change across many biomes. Further, *F. costata* maintains a high fuel moisture content during the dry

season when annual burning is instituted (McGranahan et al., 2016), therefore, it remains in active vegetative state allowing it to gain dominance against its neighbours which undergo dormancy after burning.

3.6 Conclusion

F. costata showed negative response to defoliation both under soil nutrient amendment with LAN and competition from surrounding plants. Consequently, a management strategy using selective herbivory may alter its relative dominance on common C_4 species in the Drakensberg grasslands. Competition from surrounding plants not affects the performance of *F. costata* while soil nutrient amendment with LAN had a negative influence on the performance of *F. costata*.

3.7 Acknowledgements

3.8   References

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Chapter 4

Discussion, Conclusion and Recommendations

This study was set up to investigate the effects of annual burning of fire-breaks, soil nutrient amendments with limestone ammonium nitrate, simulated herbivory by clipping up to 50mm above the soil surface and neighbourhood types on the performance of *Festuca costata,* a C_3 Afro-temperate grass. Understanding the relationship between environmental factors, anthropogenic activities, plant characteristics and ecosystem variables is a crucial step towards gaining knowledge about the biodiversity of ecosystems.

4.1   Discussion

Wild fires have a very significant contribution to ecosystem degradation in most rangelands (Canu et al., 2014). However, prescribed fires have been used as a management tool in the maintenance of grasslands (McGranahan et al., 2016). The present study showed that burning of annual fire-breaks in a montane grassland has a negative effect on the performance of a C_3 grass, *Festuca costata,* whose abundance and coverage in the Drakensberg is increasing.

This loss in productivity could be attributed to loss of essential nutrients due to volatilisation. The results underpin the importance of fire in management of grasslands which may have implications for grassland species composition and diversity (Chameni, 2012). The loss in productivity is consistent with findings by Koerner and Collins (2014) who reported a reduction in grassland productivity when subjected to both fire and herbivory. The results are also in conformity with findings by Wu et al. (2013) who observed a reduction in productivity of above-ground biomass production for burned grassland in comparison with unburned sites with similar species.

Grazing is reported to promote above-ground biomass production (Jeddi and Chaieb, 2010). The finding of this study seems to suggest that F. costata exhibit poor response to selective herbivory. Defoliation accounted for the most variation in influencing the reduction in above-ground biomass production of *Festuca costata.* The results of this study are in conformity with results by Morris and Tainton (2012), who reported a reduction in biomass production among common C_4 species such as *T. triandra* and *A. junciformis* when the grasses were subjected to

uncontrolled grazing. The negative effect of defoliation has the potential to shift dominance patterns in plant communities (Ayala et al., 2011; Little et al., 2015)

Soil nutrient amendment with limestone ammonium nitrate (LAN) in the pot experiment did not influence above-ground biomass of the focal plant in the short term. Specific leaf area was also not affected by the addition of LAN fertiliser to the soil. Studies have recommended taking consideration of the physiological state of the plants when evaluating the effects of various treatments (Junker et al., 2015; Jing et al., 2016).

Functional traits such as above-ground biomass production, specific leaf area and tiller numbers are important indicators of the performance of a given grass species (Hendrickson et al., 2000; Irving et al., 2015; Głąb et al., 2015). Neighbours of focal plants had significant effects on above-ground biomass, total number of tillers and tuft circumference. Interspecific competition accounted for much of the variation in the means of these parameters. These results are consistent with findings of other studies (del-Val and Crawley, 2004; Skálová et al., 2013) that report strong negative effects of inter and intra-specific competition on target plants, and the extent of these effects depended on the species being evaluated.

4.2   Conclusion

The use of fire by protected area management to create fire-breaks in montane grasslands of the Drakensberg negatively influences the performance of a *Festuca costata*. Defoliation also showed negative influences on the performance of the species, while the presence of interspecific neighbours had no negative effects on *F. costata*. The combined use of fire in fire-break sites and herbivory on *F. costata* may be important for controlling the spread of the species in montane grasslands.

4.3   Recommendations

The present study has shown that fire and defoliation play a major role in influencing the performance of *F. costata.* However, soil nutrient amendments did not seem to significantly influence the performance of the target species. In view of the foregoing it is recommend the following follow-up studies:

- A long-term study will help to determine the residual effects of soil nutrient amendment with limestone ammonium nitrate on the performance of *F. costata*.
- The effect of burning on root traits of *F. costata*
- The effect of defoliation on root traits (e.g. below ground biomass production) of *F. costata*.

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