

1 **THE RELATIVE TOLERANCE OF MESIC**
2 **GRASSLAND SPECIES TO**
3 **DEFOLIATION AND COMPETITION**

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8 By

9
10 **Naledi Zola Zama**

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PREFACE

The experimental work described in this thesis was performed in the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg South Africa. The study commenced on January 2015 and ran up until May 2018 under the supervision of Dr Michelle Tedder and co-supervised by Mr Craig Morris and Dr Ntuthuko Mkhize.

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

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We confirm that the above information is correct,

Dr Michelle Tedder
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Co-supervisor

DECLARATION 1: PLAGIARISM

I, **Naledi Zola Zama** declare that:

- (i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;
- (ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;
- (iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;
- (iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a) their words have been re-written but the general information attributed to them has been referenced;
 - b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;
- (v) where I have used material for which publications followed, I have indicated in detail my role in the work;
- (vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;
- (vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References sections.

Signed: Naledi Zola Zama

Date: 17 August 2018

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2 **DECLARATION 2: CONFERENCE/WORKSHOP PROCEEDINGS**
3

4 The * indicates primary presenter and corresponding author for all presentations.
5

- 6 **1.** Zama N *, Tedder M, Morris C, Mkhize N 2016. An assessment of the defoliation
7 tolerance of Increaser and Decreaser mesic grassland species. In: 51st Annual
8 Congress of the Grassland Society of Southern Africa, 3-8 July, George, South
9 Africa.
- 10
- 11 **2.** Zama N *, Tedder M, Morris C, Mkhize N 2016. An assessment of the defoliation
12 tolerance of Increaser and Decreaser mesic grassland species. In: College of
13 Agriculture, Engineering and Science Post-grad Research Day, November,
14 Durban, South Africa.
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17 explain the relative defoliation tolerance of mesic grassland species? In: School of
18 Life Sciences Annual Post Graduate Research Day, 23 May, Durban, South Africa.
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- 20 **4.** Zama N *, Tedder M, Morris C, Mkhize N. 2017. Competition and defoliation
21 tolerance of *Themeda triandra* and *Eragrostis curvula*. In: 52nd Annual Congress
22 of the Grassland Society of Southern Africa, 23-28 July, Hoedspruit, South Africa.

ABSTRACT

1
2 Effective grazing management is dependent on understanding grass species
3 responses to herbivory. These responses to herbivory can be broadly grouped into
4 categories, namely decreaser (plants that decline in abundance) and increasers
5 (plants that increase in abundance). Tolerance is defined as the capacity of a plant to
6 withstand herbivory, while suffering little loss in growth or its ability to reproduce and
7 it can be equated to the ability of the plant to compensate. The relevance of this
8 strategy to rangeland management has become increasingly apparent and has
9 allowed researchers to investigate more questions and test long-standing ideas within
10 the Grassland Science discipline. Therefore, the general aim of this research was to
11 determine how Increaser and Decreaser grass species common in mesic grasslands
12 tolerate defoliation and competition. Two experiments were conducted as controlled
13 pot trial experiments under shade cloth at the NM Tainton Arboretum. Simulated
14 herbivory in the form of clipping was used for both experiments. Categorising species
15 into four grazing response groups (Increaser I, II,III and Decreaser) has led to
16 generalisations made across and between species in terms of responses to herbivory.
17 To determine if these generalisations are appropriate, the growth response of two
18 Decreaser (*Themeda triandra* and *Tristachya leucothrix*) and two Increaser (*Eragrostis*
19 *curvula* and *Eragrostis plana*) grass species was investigated. Results indicate that
20 defoliation tolerance is not necessarily explained by response groups and differences
21 can be observed between species, within response groups. Grouping species into
22 response groups may be an over simplification. This implies that species identity may
23 be more important in understanding species composition changes within natural
24 communities than originally thought. Plant traits, such as shoot biomass, roots
25 biomass , tuft height and root to shoot biomass ratios also responded differently across
26 species highlighting the importance of further research on specific species as
27 generalisations may not be entirely useful. To provide more insight into this, the
28 response of *T. triandra* to defoliation and competition with *E. curvula* was investigated.
29 Results show that veld dominated by *T. triandra* and few *E. curvula* tufts should be
30 leniently grazed every other year with rest applied following a growing season, to allow
31 *T. triandra* tufts to regrow. A non-selective grazing system should be adopted by veld
32 managers during the growing season to lower the competitive pressure exerted on *T.*
33 *triandra* tufts by other species and to enhance growth. These results need to be
34 considered as a basis to understand how *T. triandra* swards respond on a small scale
35 and further investigations are necessary to validate impact on natural communities.

1 Overall, defoliation tolerance is species specific and depends on the combined effects
2 of defoliation and competition as these affect the cumulative and morphological
3 responses of important mesic grassland species.

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9

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11 ***THEMEDA TRIANDRA* WHEN COMPETING WITH *ERAGROSTIS CURVULA***

12

13 CHAPTER FIVE: **SYNTHESIS AND RECOMMENDATIONS FOR FURTHER**
14 **RESEARCH**

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Dedicated to my Mother,

Lungisile Zama

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CHAPTER 1

INTRODUCTION

RATIONALE AND JUSTIFICATION FOR THE RESEARCH

An ongoing debate in plant-herbivore ecology, is how herbivores affect plant fitness (Jermy 1984; Belsky 1986a; Bernays and Graham 1988). A widely accepted resolution to this debate is that herbivory is generally detrimental and very rarely beneficial to plant fitness (Belsky 1986a; Paige 1992; Belsky et al. 1993). The ability of grasses to respond to grazing through defenses enables them to survive constant defoliation (Linder et al. 2018) and this resistance to grazing is measured by two components: (1) tolerance, and (2) avoidance (Rosenthal and Kotanen 1994; Briske 1996). Traits that assist plants in deterring herbivores (avoidance mechanisms) have been identified for numerous South African grasses (Heady 1964; O'Reagain 1993), but knowledge on grazing tolerance is lacking (Del-Val and Crawley 2004) especially in terms of the different grazing response groups (Morris 2016). Although research indicating Increaser species to be more tolerant of herbivory than Decreasers exists (Del-Val and Crawley 2004), similar studies have not been performed on the common mesic grassland species of South Africa (Morris 2016). It is also not clear whether tolerance or avoidance is the mechanism by which increaser species increase under grazing. This supports the need to investigate the grazing tolerance of common South African mesic grassland species, as this will assist in better management strategies. In addition, it is important to investigate traits influencing grazing tolerance including root and shoot biomass (Chapin and Slack 1979; Marquis 1996, Oesterheld and McNaughton 1991). This understanding of how plant traits respond to defoliation may assist in creating predictors for certain levels of tolerance. Herbivory and competition are important factors that affect plant growth (Painter and Belsky 1993) and South African grasslands are experiencing degradation due to increasing heavy grazing

1 (Neke and Du Plessis 2004; O'Connor et al. 2011). Studies reveal that the effects of
2 selective grazing can change species composition within grasslands (Milchunas et al.
3 1988; Owen-Smith 1999) by promoting a community of highly unpalatable species
4 (Little et al. 2015). Findings of this research will assist in determining the mechanisms
5 controlling the replacement of important foraging species such as *Themeda triandra*
6 Forssk. by less palatable species such as *Eragrostis curvula* (Schrad.) Nees.

7 **OUTLINE OF DISSERTATION STRUCTURE**

8 Herbivory tolerance is an important mechanism that induces species composition
9 changes within grasslands, therefore studying this mechanism is crucial, as it will
10 assist rangeland managers to better anticipate change. It is especially important in
11 instances whereby abundance of late successional species is reduced or these
12 species are at a risk of becoming locally extinct. This study has two experimental
13 chapters examining the defoliation tolerance of mesic grassland species and
14 assessing how selective frequent defoliation and competition can affect species
15 fitness. The final chapter focuses on recommendations and future research
16 possibilities. The specific aims, research questions and hypotheses are for the
17 experimental chapters are described below.

18 **AIMS, OBJECTIVES, RESEARCH QUESTIONS AND HYPOTHESES**

19 **Chapter 3: The defoliation tolerance of Increaser and Decreaser mesic grassland** 20 **species**

21 The aim of this experiment was to determine how four Increaser and Decreaser grass
22 species common in mesic grasslands respond to different frequencies and intensities
23 of defoliation.

24 .

1 **Objectives:**

- 2 1. To determine the difference in defoliation tolerance, in terms of aboveground
3 phytomass production, of Decreaser and Increaser species.
- 4 2. To determine the difference in defoliation tolerance between individual species,
5 regardless of grazing response group.
- 6 3. To understand the morphological responses (cumulative growth, tuft structure
7 and resource allocation) of those species differing in grazing tolerance to
8 various levels of defoliation frequency and intensity.

9 **Research questions and hypotheses:**

- 10 1. Objectives 1 and 2 address the question, how does defoliation tolerance differ
11 in Decreaser and Increaser mesic grasses relative to undefoliated plants? It
12 was hypothesized that differences in defoliation tolerance would be greater
13 between Decreasers and Increasers than between species within each group.
- 14 2. Objective 3 addresses the question, how does defoliation frequency, intensity,
15 and their interaction affect the;
- 16 a) Cumulative growth (above- and belowground) of mesic grasses? It
17 was hypothesized that frequent and severe defoliation would reduce
18 cumulative growth of grazing-tolerant grasses less than that of
19 grazing-sensitive grasses.
- 20 b) Tuft structure of mesic grasses? It was hypothesized that frequent
21 and severe defoliation will reduce tuft height and tillering in grazing-
22 sensitive grasses.
- 23 c) Resource allocation? It was hypothesised that frequent and severe
24 defoliation would decrease resource allocation to root growth,

1 resulting in a reduced root: shoot biomass ratio in grazing-sensitive
2 grasses.

3 Chapter 4: **The effect of frequent selective and non-selective defoliation of**
4 ***Themeda triandra* in competition with *Eragrostis curvula***

5 The aim of this experiment was to determine the response of *Themeda triandra* to
6 defoliation and interspecific competition with *Eragrostis curvula*.

7 **Objectives:**

- 8 1. The first objective was to determine the defoliation tolerance, in terms of the
9 aboveground phytomass production, of *T. triandra* when growing with clipped
10 and unclipped *E. curvula*.
- 11 2. The second objective was to determine how *T. triandra* responds to different
12 levels of competition from *E. curvula* (clipped and unclipped).
- 13 3. The third objective was to understand the morphological responses (tillering
14 and tuft height) of *T. triandra* to various levels of defoliation and competition.

15 **Research question and hypothesis:**

- 16 1. Objective 1 addresses the question, is *T. triandra* tolerant to defoliation when
17 interacting with defoliated and undefoliated tufts of another species? It was
18 hypothesized that tolerance to defoliation would be reduced by the presence of
19 another species.
- 20 2. Objective 2 addresses the question, what is the effect of defoliation of *T.*
21 *triandra* on the interactions between *T. triandra* and *E. curvula*? It was
22 hypothesized that defoliation would cause *T. triandra* to experience greater
23 competitive suppression.

1 3. Objective 3 addresses the question, how do defoliation and competition affect
2 the morphological structure (tillering and tuft height) of *T. triandra*? It was
3 hypothesized that defoliation and competition would reduce tillering rate and
4 tuft height of *T. triandra*.

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CHAPTER 2

LITERATURE REVIEW

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

In Southern Africa, grasslands are defined by their ability to prevent or limit vegetation change, beyond the expected climax. The eastern parts of South Africa are referred to as the Wet Fire Climax grasslands, known as Fire Dependent Ecosystems (FDEs) (Bond et al. 2003). Within FDEs, succession is limited by fire (Bond et al. 2003). In contrast is the western part of South Africa, referred to as the climatic climax grasslands (Tainton 1984), also known as Climate Dependent Ecosystems (CDEs) (Tainton 1984). These CDEs are arid environments whereby succession is limited by rainfall (Bond et al. 2003).

The effect of fire and moderate grazing may reduce the abundance of the species present within grasslands but this change is not permanent (O'Connor 1985). In contrast to this is the conclusion that heavy grazing may result in a grassland becoming so modified that it cannot return into its natural state (Tainton 1972). The debate surrounding the effect of grazing within South African grasslands is an ongoing discussion, which requires further investigations to provide supporting empirical evidence.

Humid fire climax grasslands of South Africa

Humid grasslands occupy a large proportion of the eastern parts of the country (Acocks 1975). These areas are cool and receive a high summer rainfall of at least 600 mm (Tainton 1999a). Due to this high rainfall volume, soil leaching takes place resulting in infertile soils (Tainton 1999a). There are two broad grassland types in

1 eastern South Africa, those which occur in areas that could potentially be savanna and
2 those in areas of potential forest (Tainton 1999a).

3 ***Fire climax grassland of potential savanna and potential forest***

4 ***Distribution***

5 Fire climax grasslands of potential forest are found in areas of low elevation whereby
6 there are bush clumps growing along few trees and in high elevations and they are
7 composed of short grasses (Tainton 1999a). Fire climax grasslands of potential
8 savanna occur in areas that receive less rainfall and are dominated by taller grasses
9 than potential forest grasslands (Tainton 1999a). In summary, grasslands that occur
10 in areas of potential forest are those that grow under good conditions and grasslands
11 that occur in areas of potential savanna grow in areas where conditions for growth are
12 less suited to woody species.

13 ***Vegetation structure and composition***

14 The common species found in grasslands of potential forest occurring at low elevation
15 include; *Themeda triandra* Forssk. *Tristachya leucothrix* Trin. ex Nees, *Cymbopogon*
16 *validus* (Stapf) Burt Davy and *Heteropogon contortus* (L.) P. Beauv. ex Roem. &
17 Schult. amongst others (Tainton 1999a). With increasing degradation, grass species
18 in the coastal regions have been replaced by the less desirable and a low quality
19 *Aristida junciformis* Trin. & Rupr. (Tainton 1999a). Further south, species replacement
20 has generally been with temperate species and pioneer subtropical grasses, such as
21 *Eragrostis plana* Nees (Tainton 1999a). In the northern regions, good palatable
22 species, such as *Themeda triandra* Forssk. are lost from the veld and forbs may
23 increase in abundance (Tainton 1999a).

1 In areas of high elevation, these grasslands are composed of short grasses and the
2 main species making up this cover are *Themeda triandra*, *Tristachya leucothrix*,
3 *Eragrostis racemosa* (Thunb.) Steud. and *Alloteropsis semialata* (R.Bt.) Hitchc. among
4 other grass species growing alongside a few forbs that may increase in cover under
5 bad management (Tainton 1999a). Mismanagement may include heavy grazing or
6 selective grazing which results in less palatable grasses increasing in density and
7 reducing the grazing value of the grassland. An example of such is the dominance of
8 *Aristida junciformis* (Ngongoni) in veld, making it completely unusable to the animals
9 (Tainton 1999a). If heavy grazing continuous, species such as *E. plana* may also
10 begin to dominate grasslands (Tainton 1999a).

11 The grass species found in potential savanna areas grow taller but are of similar
12 species composition to potential forest areas, with *Hyparrhenia hirta* (R. Brown)
13 Hitchcock occurring more abundantly (Tainton 1999a). Grass cover is less stable and
14 mismanagement could result in invasion by species such as *Sporobolus africanus*
15 (Poir.) Robyns & Tounay, *Eragrostis plana* and *Eragrostis curvula* (Tainton 1999a).

16 **Seasonal growth, primary productivity and usefulness for agriculture**

17 Grass growth in potential forest grasslands is limited to the period from October to
18 March because of the dry, cold winters (Tainton 1999a). Rapid grass growth takes
19 place in spring and by the end of December approximately 80% of the season's growth
20 has occurred (Tainton 1999a). The highly leached soils limit production, thus 3 to 3.5
21 tons of forage production per hectare per annum can be expected (Tainton 1999a).
22 Growth in potential savanna grassland occurs between September and April (Tainton
23 1999a). Summer growth may be limited by drought in this area (Tainton 1999a).
24 Leaching can range from moderate to high, depending on the rainfall and soil type,
25 affecting soil fertility (Tainton 1999a). The favorable moisture levels of these

1 grasslands make them suitable for development and thus they are likely to be
2 converted into cultivated pastures. The moisture level makes these grasslands
3 particularly suitable for high productivity when fertilizer is applied (Tainton 1999a).

4 **MESIC GRASSLANDS OF SOUTHERN AFRICA**

5 The three floristic regions discussed here are those considered to be mesic and
6 receive more than 600 mm of rain per annum.

7 ***Central inland plateau***

8 This region comprises of the *T. triandra* – *E. curvula* grassland and is composed of the
9 following grass species, *Themeda triandra*, *Eragrostis curvula* and *Setaria sphacelata*
10 (Schumacher) Moss, among others, growing alongside other growth forms including
11 the forbs *Helichrysum rugulosum* Lessing and *Hermannia depressa* N.E Brown
12 (Tainton 1999a). The soils in this region are red and yellow in colour and often
13 ploughed when grasslands have been converted for crop production. These
14 grasslands receive annual rainfall between 600 – 700 mm (Bezuidenhout and
15 Bredenkamp 1991). The central inland plateau also comprises of the *Panicum*
16 *coloratum* Linnaeus – *E. curvula* grassland and the main grass species found there
17 are *T. triandra*, *E. curvula* and *E. plana*, among many others with other plant species,
18 such as *Pentzia globose* Lessing and *Felicia filifolia* (Vent.) Burt Davy frequently
19 occurring. The annual rainfall is 600 mm with a dry, clayey soil type (O'Connor and
20 Bredenkamp 2004).

21 ***Eastern mountains and escarpment***

22 The grassland types of the eastern mountains and escarpment have a higher rainfall
23 than those found in the central inland plateau. Found in the lower slopes of the
24 Drakensberg is the *Rhus dentata* Thunb. – *Leucosidea sericia* Eckl. & Zeyh shrubland

1 which is composed of mainly *Poa annua* L., *Hyparrhenia hirta* and *Trachypogon*
2 *spicatus* (L.f) Kuntze with an annual rainfall of >900 mm (Eckhardt et al. 1993). In the
3 same floristic region is the *Monocymbium ceresiiforme* (Nees) Stapf – *Tristachya*
4 *leucothrix* grassland that receives an annual rainfall of >1000 mm (Du Preez 1991).
5 The Eastern Transvaal Escarpment is dominated by *Loudetia simplex* (Nees) C.E.
6 Hubb.– *Diheteropogon filifolius* (Nees) Clayton grasslands which receive an annual
7 rainfall of between 1100 and 1500 mm. In this area, the common grass species are
8 *Ctenium concinnum* Nees and *Alloteropsis semialata*, with other plants such as
9 *Eriosema angustifolium* Burtt Davy and *Helichrysum platypterum* DC. (Deall et al.
10 1989). In the Alpine Drakensberg plateau is the *Merxmuellera* Drakensberg – *Festuca*
11 *caprina* Nees grassland which comprises of *Festuca caprina* and *Eragrostis caesia*
12 Stapf among grass species (Morris 1994).

13 ***Eastern lowlands***

14 The eastern lowlands include the grasslands of the eastern Drakensberg, in KwaZulu-
15 Natal and the Eastern Cape. The rainfall in this area is approximately 850 mm and the
16 dominant grasses include *Hyparrhenia hirta* and *Sporobolus pyramidalis* P. Beauv.
17 and the non-grasses include *Acacia sieberiana* DC., *Walafriida densiflora* (Rolfe) Rolfe
18 and *Rhus rehmanniana* (Engl.) (Smit et al.1992).

19 ***Species composition and fertilization in mesic grasslands***

20 In a long-term experiment in a mesic grassland, fertilization resulted in changes in
21 species composition (Fynn and O'Connor 2005). Nitrogen fertilization did not reduce
22 the abundance of *Eragrostis curvula*, *Eragrostis plana* and *Panicum maximum* (Jacq.),
23 instead sites fertilized by nitrogen only were dominated by *Eragrostis curvula* and sites
24 fertilized by nitrogen and phosphorus were dominated by *Panicum maximum* (Fynn

1 and O'Connor 2005). Short grass species including *Themeda triandra* declined in
2 abundance when nitrogen levels were increased and the opposite effect was observed
3 for tall grass species (Fynn and O'Connor 2005). The type of nitrogen was also
4 important as it influenced the abundance of some species (Fynn and O'Connor 2005).
5 For example, in sites fertilized by ammonium sulphate rather than ammonium nitrate,
6 certain species including *Tristachya leucothrix* and *Eragrostis curvula* were more
7 abundant and the opposite effect was observed for *Cymbopogon caesius* (Nees) Stapf
8 (Fynn and O'Connor 2005).

9 **EFFECTS OF RAINFALL AND GRAZING**

10 Vegetation response to grazing has been interpreted as uni-directional according to
11 the Clementsian concept of succession (Clement 1936). However, possible alternate
12 states of community change have also been suggested (Westoby et al. 1989). Long
13 term studies on the *H. hirta* tall grasslands of KwaZulu-Natal found that the response
14 to grazing supported the alternate states model described by Westoby et al. (1989)
15 and their findings support the Decreaser – Increaser classification of species response
16 to grazing (Foran et al. 1978).

17 In mesic grasslands, there is low variation in rainfall and these grasslands are less
18 susceptible to changes in species community structure in response to grazing
19 pressure (Du Toit and Aucamp 1985). The heavily grazed sourveld communal
20 grasslands of the Transkei have maintained a general dominance of *T. triandra* with
21 *Aristida junciformis* dominating in certain parts (McKenzie 1982). In contrast, *T.*
22 *triandra* and *Eragrostis lehmanniana* Nees decreased in abundance and *A. congesta*
23 Roem. & Schult. and *Tragus koelerioides* Ascherson increased as a result of heavy
24 grazing during summer in sweetveld semi-arid grasslands (O'Connor and
25 Bredenkamp 2004).

1 Studies have revealed that Decreaser – Increaser responses of grass species to
2 grazing severity are reliant on climate and topo-edaphic conditions (Truter 1988;
3 Bosch 1989; Strobach 1989). In this instance, *T. triandra* reacted as an Increaser in
4 areas of higher rainfall but a Decreaser in areas that receive less rainfall (Bosch 1989).

5 Heavy grazing pressure may also have a negative effect on seed production as
6 inflorescences are consumed by the herbivores thus restricting culm growth (O'Connor
7 1991; O'Connor and Pickett 1992). Grass species that are considered sensitive to
8 disturbances are vulnerable to local extinction in areas that may experience
9 inconsistent rainfall and continuous heavy grazing (Owen-Smith and Danckwerts
10 2004). The local extinction of such species allows for species replacement by less
11 palatable annual grasses that produce small seeds or that may reproduce vegetatively
12 through stolons (Owen-Smith and Danckwerts 2004). The effects of grazing are also
13 influenced by the type of animal feeding in an area. For example, sheep are
14 considered destructive grazers as they concentrate their feeding in smaller areas and
15 can select particular plant parts thus making their grazing impact greater than cattle at
16 a similar stocking rate (Tainton 1972; Danckwerts 1989).

17 There are certain anti-herbivore defenses that grasses have developed to withstand,
18 tolerate or avoid grazing. Some increaser grasses, such as *Cynodon dactylon* (L.)
19 Pers. have a prostrate growth habit and use stolons to regrow (Tainton 1981;
20 Danckwerts 1989). Others, such as *Eragrostis plana* produce tough culms with fibrous
21 leaves (O'Reagain 1993) which may reduce its acceptability to grazers. Besides
22 physical defences, there are also grass species that produce secondary chemical
23 compounds to deter grazers. These include aromatic grasses in the genera
24 *Bothriochloa* and *Cymbopogon* which tend to be avoided by cattle (Danckwerts 1989).
25 The presence of tannins in certain grasses may also affect their acceptability (Ellis

1 1990; Du Toit et al. 1991; Chesselet et al. 1992). An example condensed tannins in
2 *Eragrostis chloromelas* Steud. may deter grasshopper feeders (Dini and Owen-Smith
3 1995).

4 **SPECIES COMPOSITION SHIFTS**

5 Ecologists assume that plant species distribution, abundance, composition and
6 biomass are a result of the climate and soil conditions (Bond and Keeley 2005). When
7 environmental conditions change, the vegetation will also change and this could lead
8 to vegetation degradation (Malan and Niekirk 2005) which is also known as
9 retrogression (Bothma 1989). Veld improvement, also known as progressive
10 succession can also occur if veld is managed correctly (Bothma 1989). Retrogression
11 involving grass species change may then affect the carrying capacity of the veld
12 (Malan and Van Niekirk 2005). It is important to know the indicator species within a
13 certain system as this allows change to be detected and management changes to be
14 made (Malan and Van Niekirk 2005). Certain species, such as *Eragrostis*
15 *lehmanniana* and *Aristida* species, tend to invade veld that has been mismanaged
16 (Van Oudtshoorn 1999). Continued mismanagement will result in the veld becoming
17 dominated by less desirable and less palatable species, making it less suitable for
18 grazing (Malan and Van Niekirk 2005). In communal areas, grassland retrogression
19 is common, especially during periods of drought (Malan and Van Niekirk 2005). In
20 addition is the frequent lack of guidance and interaction from researchers to communal
21 farmers. Common in tribal areas, is soil erosion caused by heavy grazing and
22 unplanned grazing systems. Continuous heavy grazing on the same veld makes the
23 soil more susceptible to erosion and this affects all soil types in South Africa (Malan
24 and Van Niekirk 2005).

1 ***Arid grasslands***

2 Climatic factors strongly affect plant establishment and growth in semi-arid grasslands
3 (Shmida and Wilson 1985). Variations in rainfall and temperature correlate to
4 aboveground primary production and botanical composition (Bai et al. 2007;
5 Auerswald et al. 2012). Few studies have linked changes in precipitation and
6 temperature to shifts in botanical composition (Ren et al. 2012). One study on the
7 temperate Mongolian steppe (semi-arid) demonstrated that grazing intensity had little
8 effect on species composition and diversity observed over a grazing period of six years
9 (Ren et al. 2012). The results obtained in this study do not support the claims of the
10 intermediate disturbance hypothesis assuming that moderate grazing should increase
11 species diversity and heavy grazing will shift species composition from previously
12 dominant towards opportunistic species (Connell 1978; Milchunas and Lauenroth
13 1993).

14 Precipitation can be used to account for the differences observed in the primary
15 productivity in semi-arid environments at a global level (Lauenroth 1979).
16 Precipitation-use efficiency (PUE) is a concept developed and used for semi-arid
17 environments (LeHouerou 1984 cited in Sala et al. 1988). The PUE is a ratio of
18 aboveground net primary productivity to precipitation that explains the relationship
19 between water cycle and ecosystem carbon (Jia et al. 2015). The PUE index
20 decreases with an increase in evapotranspiration and aridity (LeHourou 1984). Factors
21 explaining or affecting production may also depend on the spatial scale at hand
22 (O'Connor et al. 2001). For example, at individual sites the effects of fire may limit
23 productivity (Briggs and Knapp 1995) and species richness (Tilman and Downing
24 1994). In semi-arid grasslands, grazing pressure may alter the species composition
25 from perennials to annuals (O'Connor et al. 2001). A decline in basal cover is also
26 generally accompanied by changes in species composition (Wiegand et al. 2004). This

1 change in species composition will often further reduce basal cover and increase
2 runoff, further reducing soil nutrients and lowering the productivity within the grassland
3 community (Milchunas and Lauenroth 1993; O'Connor and Roux 1995; Snyman 1998;
4 O'Connor et al. 2001; O'Connor and Breidenkamp 2004).

5 ***Mesic grasslands***

6 The negative impacts of grazing in arid environments differ to those in mesic
7 grasslands (Hayes and Holl 2003). Results of studies conducted in mesic grasslands
8 suggest that maintaining the type, frequency and intensity of disturbance within
9 management regimes is necessary (Denslow 1980; Milchunas and Lauenroth 1993;
10 Knapp et al. 1999). In general, mesic grasslands are more productive than arid
11 grasslands (Hayes and Holl 2003). This accumulation of growth is drastically affected
12 by an increase in invasive grass species (Foin and Hektner 1986; Hobbs and Mooney
13 1986; Davis and Sherman 1992; Callaway and Davis 1993). For example, alien
14 species can reduce native species abundance by lowering establishment from the
15 seedling stage rather than affecting plants in their adult stage (Yurkanis et al. 2005;
16 Fukami et al. 2013). There are grass species that are declared as category 1 weeds
17 in South Africa such as *Arundo donax* L. , *Cortaderia jubata* Lemoine (ex Carriere)
18 Stapf. and *Nassella tenuissima* (Trin.) Barkworth. (Henderson 2001). Another example
19 is *Ammophila arenaria* (L.) Link that has invaded South African coastline, particularly
20 in the Western and Eastern Cape, replacing native species (Hertling and Lubke 2000).

21 **DECREASERS AND INCREASERS**

22 Ecological classification of grass species depends on their response to grazing and
23 terms such as “Decreasers”, “Increasers” and ‘Invaders” have been developed
24 (Dyksterhuis 1949). Species found in areas of little to no disturbance with stable/climax
25 environments are Decreasers and Increasers, whereas Invaders are common in

1 disturbed and unstable environments (Dyksterhuis 1949). Veld in an excellent
2 condition would have a greater cover of Decreaser species than Increaser species. As
3 the veld condition declines, driven by intensive grazing, the cover of the Increaser
4 species increases up until a certain point when its cover also decreases, further
5 resulting in bare ground (Dysterhuis 1949). The key point in this classification is that
6 Increaser species are better able to withstand the effects of heavy grazing better than
7 Decreaser species and this theory has been commonly used to explain species
8 replacement within grasslands.

9 The grasslands of KwaZulu-Natal have a long history of veld deterioration and the
10 impacts are manifested through increased soil erosion and poor animal production
11 (Foran et al. 1978). A study was conducted to develop a method of testing the
12 condition of the veld under three bioclimatic conditions, namely the Highland Sourveld,
13 Moist tall Grassveld and Dry Tall Grassveld that are deemed important to the livestock
14 industry in KwaZulu-Natal. As observed by Foran et al. (1978), results indicated that
15 firstly; *T. triandra* was present in all of the bioclimatic groups but at varying
16 percentages, secondly; the responses of the most common species were not different
17 across the bioclimatic groups, thirdly; *Themeda triandra* was abundant under excellent
18 conditions and decreased when veld was under-utilized or over-utilized and fourthly;
19 other species also changed their abundance with a change in veld condition but this
20 change was particularly difficult to assess for species occurring at low abundance
21 (Foran et al. 1978). An interesting point observed by Foran et al. (1978) is that these
22 results supported the grazing responses of the Decreaser and Increaser groups as
23 described by Dyksterhuis (1949).

24 A later study categorised species occurring in the mountains of the Drakensberg into
25 the ecological groups of Decreasers and Increaser I species (Everson and Tainton

1 1988). The common Decreaser species in the region are *Themeda triandra* and
2 *Heteropogon contortus* (L.) Beauv. Ex Roemer & J.A Schultes and the common
3 Increaser I species are *Tristachya leucothrix* and *Alloteropsis semialata* (Everson et
4 al. 1988). According to knowledge of species response to grazing, Increasers are
5 assumed to tolerate frequent defoliation better than Decreasers (Dyksterhuis 1949;
6 Foran et al. 1978). Everson et al. (1988)observed that in Decreasers the nodes where
7 tillers are developed are situated above ground and in Increaser I species, these
8 nodes are normally below the surface of the soil providing protection from intense
9 defoliation (Everson et al. 1988). Another case whereby Increasers are more tolerant
10 than Decreasers is under shading. For example, Increasers were able to tolerate more
11 shading than Decreasers but when the light intensity was extremely low all species
12 were negatively affected, regardless of the response group (Everson et al. 1988).
13 Mesic and arid grasslands in southern Africa vary in their species composition, forage
14 quality, forage availability and response to grazing (Danckwerts et al. 1993). For
15 example, in mesic areas, species compositional change is predictable, as both heavy
16 grazing and insufficient grazing reduce carrying capacity, while in arid areas species
17 compositional change is event-driven (Danckwerts et al. 1993).

18 The generally accepted theory describing the process of compositional change in
19 southern African grasslands is that change is predictable and that it takes place over
20 a long period of time with retrogression possible as a response to herbivory
21 (Decreaser-Increaser approach) (Dyksterhuis 1958; Foran et al. 1978). This is largely
22 due to the fact that most of the research done in southern Africa is in mesic grasslands
23 where conditions for growth are predictable (Danckwerts et al. 1993) or in equilibrium
24 systems where rainfall is high therefore providing a sufficient supply of forage for
25 animals (Ellery et al. 1995, Van Oudtshoorn 2006).

1 ***The Increaser – Decreaser model***

2 The Increaser-Decreaser model is still largely used in mesic grasslands of southern
3 Africa (Tainton 1981). This model indicates that a decline in carrying capacity would
4 result from over-utilization or under-utilization (Danckwerts et al. 1993). The
5 predominant management principle applied in mesic grasslands has been that grazing
6 should be sufficient to prevent the increased abundance of unpalatable Increaser
7 species but less intense as to prevent the presence of species not adapted to high
8 grazing intensities (Danckwerts et al. 1993). Although this model has been extensively
9 used, there are criticisms associated with its use. This model assumes that grazing is
10 the single most important factor that plant species respond to, yet evidence exists
11 suggesting that certain species show a minor response to grazing gradients (Mentis
12 1982; O'Connor 1985). In addition to this, using this model and focusing on the effects
13 of grazing alone may over simplify species compositional changes in mesic grasslands
14 (Danckwerts et al. 1993). There are other factors, such as fire, which are extensively
15 used in the management of mesic grasslands in southern Africa (Trollope 1989). The
16 effects of fire as a management strategy may be greater than those of grazing, under
17 reasonable stocking rates (Danckwerts 1990). In summary, in mesic grasslands, the
18 philosophy of a predictable and gradual change applies and for arid grasslands an
19 event-driven approach is more applicable. However, it must be noted that in southern
20 Africa, many grasslands are transitional between the two models and this makes
21 research-driven management even more important.

22 ***Veld condition assessment in KwaZulu-Natal in mesic grasslands***

23

24 Hardy and Hurt (1999) describe the different methods that can be used to assess the
25 condition of veld in KwaZulu-Natal, whereby a veld condition score (VCS) is calculated
26 for each site of the farm and the “health” of the vegetation is determined. One such

1 approach used to assess veld is the Benchmark method (BM) where the species at a
2 particular site are recorded and placed into grazing response groups (Hardy and Hurt
3 1999). These groups are Decreaser, Increaser I, Increaser II and Increaser II species
4 (Hardy and Hurt 1999, Tainton 1999b). The abundances of the species in each group
5 and their grazing values are then used to produce a VCS (Hardy and Hurt 1999). This
6 method is considered simple and allows for appropriate interpretations of the veld
7 condition (Hardy and Hurt 1999). A second approach is the Ecological index method
8 (EIM), originally proposed by Vorster (1982) for assessing the veld condition in the
9 Karoo biome. The EIM is used to compare the current condition of the veld using
10 species abundances and weightings to compare them to a benchmark site (Vorster
11 1982). The EIM divides and categorizes species into response groups with a weighting
12 allocated to each category (Hurt and Bosch 1991). The EIM was later modified for use
13 in determining veld health in fire-climax grassland (Heard et al. 1986). In contrast, the
14 Degradation gradient method (DGM) was proposed by Mentis (1983) to be used in
15 climatic-climax grasslands. The DGM uses an approach of quantifying vegetation
16 condition along an ordination axis using multivariate procedures (Hurt and Bosch
17 1991). Finally, is the Weighted Key Species method (WKSM) developed to overcome
18 the pitfalls of the BM and EIM as it only uses the important key species that are known
19 to respond to grazing in a particular site (Hardy and Hurt 1999). The WKSM uses
20 weighting from key species abundances to monitor changes in species composition
21 (Hurt and Bosch 1991). Essentially, veld condition assessments are a useful in
22 determining the state of the vegetation and monitoring change. The decision of which
23 method to use may depend on expertise, available resources and type of grassland.
24 Although Hurt and Bosch (1991) indicate that most of the methods used in southern
25 Africa are not suitable and that the DGM and WKSM may indeed be the better options
26 as they are capable of monitoring changes in range condition.

1 **VEGETATION DYNAMICS IN GRASSLANDS**

2 Grassland vegetation is thought to have co-evolved with grazing animals and this has
3 resulted in grasslands having some level of grazing tolerance (Milchunas et al. 1988).
4 Milchunas et al. (1988), raised a key question - why do plant species within
5 communities' respond differently to herbivore grazing pressure? The answer to this
6 question has not been adequately determined from models of community structure
7 that already exist (Milchunas et al. 1988). Models that do not fully explain how
8 grassland communities respond to grazing by herbivores include the intermediate-
9 disturbance hypothesis (Connell 1978) and Huston hypothesis (Huston 1979). The
10 intermediate-disturbance hypothesis (IDH) suggests that species richness is highest
11 at intermediate levels of disturbance (Connell 1978). The Huston hypothesis (Huston
12 1979) states that diversity is maintained at a high level if disturbance frequency is
13 higher than the rate of competitive exclusion. However, the Huston model also groups
14 together different types of disturbances on a single axis and this is a problem because
15 grazing may or may not be a disturbance within a grassland depending on its
16 evolutionary history. The IDH, however has also received criticism as many of the
17 experimental and observational studies using it have ignored the effects of productivity
18 (Mackey and Currie 2001). In addition, the predictions of IDH are only achievable with
19 certain assumptions (Huston 2014). Such assumptions include the fact that the IDH
20 was designed for environments that are species rich (Huston 2014), such as
21 rainforests. Furthermore, criticisms of IDH have been attributed to its simplicity and
22 lack of ability to account for the spatial and intensity aspects associated with
23 disturbance (Fox 2013). Different to the IDH, is the Intermediate Productivity
24 Hypothesis (IPH) (Humped back model) which has been supported by a number of
25 studies (Grime 1977; Silvertown 1980; Moore and Keddy 1989; Virtanen et al. 2012).
26 These studies incorporate productivity by clipping and weighing of plant material at the

1 end of the growing season (see Al-Mafti et al. 1977). However others have criticised
2 both models (IDH and IPH) for their inability to explain long term species diversity
3 (Chesson and Huntly 1993; Shea et al. 2004).

4 Non-equilibrium systems are those found in dry areas receiving variable annual rainfall
5 (Ellis and Swift 1988, Ellery et al. 1995). This variation in weather conditions will
6 decrease forage quality and availability (Fernandez-Gimenez and Allen-Diaz 1999).
7 An example of a non-equilibrium system is the Turkana district located in the arid
8 northwest of Kenya (Ellis and Swift 1988). This environment experiences major
9 perturbations including drought that may last for a period of a year or more (Ellis and
10 Swift 1988). It was shown that in Turkana and possibly other arid areas, equilibrium
11 conditions are not present (Ellis and Swift 1988). These equilibrium conditions include
12 the assumptions that plant growing conditions are constant over time (Ellis and Swift
13 1988) and that herbivores can control vegetation biomass (Noy-Meir 1975;
14 McNaughton 1979). Non-equilibrium models allow for an alternative to the succession
15 model theory for understanding the changes observed in arid rangelands (Ellis and
16 Swift 1988). According to Milton and Hoffman (1994), the succession model does not
17 explain how unpalatable perennials can replace palatable perennials. Westoby et al
18 (1989) indicate how the state and transition model, for range management is replacing
19 the classical rangeland succession model as a better means for understanding
20 rangeland vegetation dynamics incorporating multiple stable states.

21 The validity of the two paradigms that evaluate vegetation dynamics in grassland
22 ecosystems has been a source of extensive debate. There are two main models at the
23 core of this debate and these include the range succession model and the state-and-
24 transition model (Ellis and Swift 1988; Laycock 1989; Westoby et al. 1989; Westoby
25 and Noy-Meir 1989; Briske et al. 2003) (Table 1). Despite the long-standing debate

1 Briske et al. (2003) concluded that a paradigm shift has still not taken place within
2 grassland ecology and management. An evaluation of either model or paradigm
3 indicates that neither model is correct enough on its own to interpret the vegetation
4 dynamics with grasslands (Wu and Loucks 1995; Fernandez-Gimenez and Allen-Diaz
5 1999). Briske et al. (2003), concludes that no evidence exists of either the equilibrium
6 or non-equilibrium paradigm being superior in explaining vegetation dynamics within
7 grasslands. “The appropriate question appears to be, when do equilibrium and non-
8 equilibrium dynamics apply? Rather than, do equilibrium or non-equilibrium dynamics
9 apply?” (Briske et al. 2003, pg. 611).

10 Briske et al. (2003, pg. 605) state that “The distinction between the range succession
11 and state and transition models directly reflects their origins in the equilibrium and non-
12 equilibrium paradigms, respectively”. However, the state and transition model was
13 designed to overcome event driven dynamics that were not properly addressed by the
14 range succession model (Briske et al. 2003). In fact, Briske et al (2003) clearly indicate
15 that the state and transition model was not intended to replace the range model and
16 that it can accommodate both equilibrium and non-equilibrium dynamics (Westoby
17 1979; Westoby 1980; Westoby et al. 1989).

18 The state and transition (Westoby et al. 1989), catastrophe (Lockwood and Lockwood
19 1991) and threshold (Laycock 1991) models are all closely related and describe quasi-
20 stable vegetation states (Fernandez-Gimenez and Allen-Diaz 2001). Another model is
21 the non-equilibrium persistent model (Ellis and Swift 1988; Briske et al. 2003) that
22 addresses the effects of abiotic factors on plant communities and animal population
23 changes.

24 Rangelands that exhibit variation in rainfall and are prone to frequent perturbations
25 experience changes in forage availability. These changes are too unpredictable and

1 rapid to be associated with animal populations (Ellis and Swift 1988). In these
2 rangelands biomass production and plant cover do not play a large role in
3 understanding vegetation composition (Fernandez-Gimenez and Allen-Diaz 2001).
4 Such a system would occur in arid rangelands and be referred to as a non-equilibrium
5 system.

1 Table 2. 1: Comparison between the Range Succession and State and Transition
 2 Models (Ellis and Swift 1988; Laycock 1989; Westoby et al. 1989; Westoby and Noy-
 3 Meir 1989; Briske et al. 2003)

Range Model	State and Transition Models
<ul style="list-style-type: none"> Equilibrium paradigm 	<ul style="list-style-type: none"> Can accommodate Non-equilibrium and equilibrium paradigms
<ul style="list-style-type: none"> Continuous and reversible vegetation change 	<ul style="list-style-type: none"> Discontinuous and potentially non-reversible vegetation change
<ul style="list-style-type: none"> Indicates that grazing intensity acts against secondary succession in a continuous manner to change species composition towards a more pioneer dominated state 	<ul style="list-style-type: none"> Indicates that transitions between states are triggered by natural perturbations, management decisions or both.
Criticisms	
<ul style="list-style-type: none"> Thought to be too simple and is ineffective in climatically variable environments 	<ul style="list-style-type: none"> Developed to overcome the limitations of single equilibrium models but may also over emphasize event driven situations

4

1 ***Grasslands and grazing***

2 Sub-humid grasslands are those that receive relatively high rainfall when compared to
3 semi-arid grasslands. Sub-humid grasslands are described as having grass species
4 that are short, medium or tall as a result of species divergent historical selection of
5 their tolerance to grazing (Milchunas et al. 1988, Figure 2, pg. 94). Within these high
6 rainfall grasslands, different intensities of grazing can affect vegetation structure
7 varyingly. For example, when there is no or minimal grazing, tall species can dominate
8 the area and this may further deter grazing due to the large quantity of stem tissue or
9 dead plant tissue present (Milchunas et al. 1988). Under moderate grazing, a mixture
10 of grass species is apparent. This mixture of tall and short grasses, creates a canopy
11 structure that may improve the regrowth potential of short grasses by allowing
12 creeping grasses to spread (Milchunas et al. 1988). Semi-arid grasslands have a
13 shorter history of grazing and are dominated by short to intermediate height grasses.
14 These grasses are can withstand low rainfall conditions as they have less biomass to
15 support and therefore have a high tolerance to drought (Milchunas et al. 1988).

16 Within grassland communities, grazers and browsers assist in maintaining an open
17 canopy and are generally important in these ecosystems (Belsky 1986a). Disturbance
18 is the damaging of a plant or plant community which potentially allows a new plant
19 community to replace the original one (Sousa 1984; Whalley 1994). Without
20 disturbance, successional theory states that the grassland system will move towards
21 the next successional state being shrubland (Clement 1936). Undisturbed grasslands
22 may or may not undergo relatively rapid succession whereby woody plants colonise
23 moving the system towards the climax successional stage of forest (Wiezik et al.
24 2010). Therefore, disturbance is necessary to maintain the vegetation in a grassland
25 state. Disturbance, resulting from the destructive effects of animals, alongside other
26 impacts, such as fire and strong winds can lead to secondary succession according to

1 the range succession model (Clement 1936; Whalley 1994). Removal of animals can
2 severely change the functioning of grassland ecosystems (Belsky, 1986). Therefore,
3 it is unrealistic to expect that grasslands will function effectively with the removal of
4 animals because grasses have coevolved with herbivores (Stebbins 1981; Milchunas
5 et al. 1988). The morphological adaptations of grasses, including low nutritional value
6 and sharp awns, may be linked to their long relationship with large bodied grazers
7 worldwide (Belsky 1986a). These adaptations indicate an antagonistic relationship
8 (Belsky 1986a). Therefore, it is crucial for grassland researchers to investigate
9 herbivore-induced species composition shifts in grasslands because this is an ongoing
10 problem.

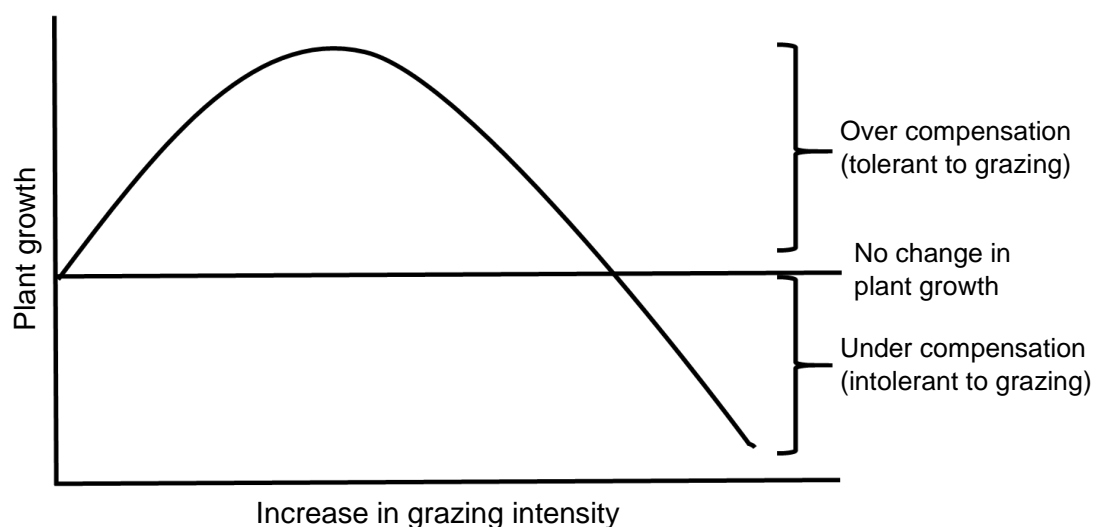
11 ***Effects of defoliation and competition on aboveground biomass***

12 Grazing can result in the injury to individual plants and overall changes of the
13 vegetation within a community (Hobbs and Huenneke 1992). Aboveground biomass
14 of grasses is directly affected by defoliation from herbivores as plants lose
15 photosynthetic tissues, such as leaves, and vital nutrients necessary for growth
16 (Ferraro and Oesterheld 2002). Ferraro and Oesterheld (2002) synthesized the
17 evidence on the effects of defoliation on grass growth and their results revealed that
18 defoliation has severe negative effects on final aboveground biomass (Ferraro and
19 Oesterheld 2002). Total biomass production (includes removed biomass and final
20 biomass) was also reduced due to defoliation (Ferraro and Oesterheld 2002).
21 Furthermore the effect of nitrogen addition affected plant responses by reducing
22 biomass under high nitrogen levels compared to standard nutrient levels (Ferraro and
23 Oesterheld 2002). Positive effects of defoliation on plant productivity also occur and
24 are referred to as herbivore optimization (see Belsky 1986a, pg 873 Figure 2). Studies
25 that report increases in aboveground biomass after defoliation are few (Belsky 1986a)

1 and many of these studies reviewed by Branson (1986) and Jameson (1963) had
2 scientific shortcomings including inadequate replication or lack of controls with little
3 statistical support of findings.

4 Grazing or the lack of grazing may also affect plant species fitness. Species may
5 demonstrate the ability to regrow well after grazing or disappear entirely from a
6 community under no grazing (Belsky 1986a; Belsky 1986b). Work done in the
7 Serengeti, showed that *Themeda triandra* was eliminated from enclosures with no
8 grazing or fire treatment within a period of three years (Belsky 1986a; Belsky 1986b),
9 possibly due to tufts dying off due to a lack of defoliation. This can be explained by the
10 seeds not germinating, as the presence of grazing animals or fire is required for this
11 process (Rowarth et al. 2007).

12 Three broad hypotheses explaining the effect of herbivory on plants exist
13 (McNaughton 1983). The first hypothesis suggests that herbivory is always detrimental
14 to the plant. The second suggests that the plant can withstand low levels of herbivory
15 and its fitness will not be affected and the third hypothesis suggests that moderate
16 levels of grazing will result in growth overcompensation (McNaughton 1983). These
17 three hypotheses and their relationships are incorporated to form the herbivore
18 optimization curve (Figure 2.1).



1

2 Figure 2. 1. Herbivore optimization curve illustrating plant growth/production changes
3 as grazing intensity increases. (Adapted from McNaughton 1983; Belsky 1986a).

4 ***Effect of defoliation and competition on belowground biomass***

5 Aboveground competition involves competition for one resource (light), while
6 belowground competition involves competition for a variety of soil resources (water
7 and space) and soil nutrients (Casper and Jackson 1997). Belowground biomass is
8 less obviously affected by defoliation when compared to aboveground biomass
9 (Ferraro and Oesterheld 2002). However, competition for soil resources is the same if
10 not stronger than for aboveground resources (Casper and Jackson 1997).
11 Generalisations may be made about belowground competition but a clear
12 understanding of it in natural communities is limited as it is challenging to quantify
13 (Cahill 2003). When plants respond to aboveground competition, they may change
14 both root and shoot structure (Aphalo et al. 1999). In general, when plants are
15 competing for belowground resources they can change their fine root growth (Gersani
16 et al. 2001) and the depth of their roots (Wardle and Peltzer 2003) in order to access
17 nutrients and water that are unavailable for surface roots (Estrada-Medina et al. 2012).
18 In order for plant to obtain more of a particular soil resource, more resources would
19 need to be allocated towards growth of belowground structures so that it can uptake
20 the nutrients (Tilman 1985). It would be required for a plant to increase its aboveground
21 growth, particularly leaves in order to increase the rate of photosynthesis (Tilman
22 1985). Tilman (1985) predicts that in areas with resource-poor soil, aboveground
23 biomass would be low and so there would be little light competition whereas in nutrient-
24 rich soils, there would be high biomass production and thus greater aboveground
25 competition. In Tilman's model and field studies, competitive success occurs when a

1 species dominates in an area (Grace 1991). Intraspecific and interspecific competition
2 are considered the tools that determine the effects of light and soil resources on plant
3 evolution (Tilman 1985). There is also the possibility that the level of competition
4 between grass species could be different to competition within a grass species.

5 ***Herbivore impact on grasses***

6 There has been much debate surrounding the impact of herbivores on plants (Belsky
7 1986; McNaughton 1986; Maschinski and Whitham 1989). This debate is centred on
8 two main ideas. Firstly, herbivores are thought to benefit the plants that they feed on
9 in various ways, such as increasing the number of seeds produced (Hendrix and Trapp
10 1981), dispersing seeds (Belsky 1986a), fertilizing soil through dung (Belsky 1986a),
11 increasing biomass production (Savory 1983) and by reducing the size of competing
12 plants (Belsky 1986a). Alternatively, herbivores may negatively affect the plant as they
13 reduce plant production (Parker and Root 1981; Louda 1983). Other studies show that
14 herbivory has no effect on plants, for example the biomass of *Digitaria macroblephara*
15 was found to be unaffected by defoliation in areas with soils with high Phosphorus
16 content (McNaughton and Chapin 1985). This variation in grazing response is caused
17 by the ability of plants to replace biomass lost to herbivory, also called grazing
18 tolerance (Maschinski and Whitham 1989).

19 Whether herbivory is harmful or beneficial, depends on the abiotic and biotic conditions
20 experienced by the plant (Maschinski and Whitham 1989). The major impact of
21 herbivores on vegetation has been well studied (del-Val and Crawley, 2004). Grazing
22 impacts plant growth by influencing photosynthetic processes through a decrease in
23 leaf area (Briske 1991; Briske 1996). The influences of grazing on grass tufts are
24 further influenced by those factors that affect the probability and extent of grazing of a
25 specific tuft experiences (Briske 1996). These include morphological and biochemical

1 attributes, both of which affect tissue accessibility and palatability (Briske 1996). As
2 different species differ in their morphological and physiological properties they respond
3 differently to grazing and this affects the function of populations within communities
4 (Briske 1996). This can then also affect the competitive interactions between plant
5 species.

6 Grazing changes the competitive behaviour of species by removing leaf material and
7 thus reducing leaf area (Briske 1996). This may alter growth rates following a series
8 of defoliation events (Briske 1996). Under management regimes with different
9 defoliation intensities or frequencies, species composition may change. This is
10 because changes in competitive ability may shift the advantage from one species
11 group to another (Briske 1996). This change in species composition may then reduce
12 carrying capacity through a shift towards low forage quality species which will affect
13 livestock production and managerial strategies (Briske, 1996).

14 Even though plant defence mechanisms have been studied extensively, very few
15 studies have focused on plant tolerance. Cullen et al. (2006) compared the defoliation
16 tolerance responses and survival thresholds of perennial grasses over a period of
17 twelve weeks. They measured that ability of the grasses to regrow following severe
18 defoliation (Cullen et al. 2006). To maintain the desired plant species composition and
19 veld productivity, suitable management strategies need to be developed. These
20 strategies need to incorporate the morphological and physiological behaviour of the
21 desired or dominant plant species (Briske, 1996).

22 How species cope with grazing, depends on their ability to reduce the probability of
23 being grazed or being able to replace lost leaf material following grazing (Briske,
24 1996). Compensating for lost biomass reduces the negative effects of grazing –

1 increasing the fitness of the grass (Belsky 1986a). Grasses are morphologically
2 adapted to grazing through the use of increased tillering (Belsky 1986a).

3 Long term survival of a species is dependent on its ability to recruit new tiller growth
4 within the community (Olson and Richards 1989). How a community responds to
5 herbivory may not necessarily be reflected in single plant or species responses (Brown
6 and Archer 1989). Therefore response on the individual level and the community level
7 need to be determined and linked (Brown and Archer 1989). The changes observed
8 in a vegetation community depend on both the season and intensity of grazing and
9 the differences that occur are explained by the plants grazing response (Bullock et al.
10 2001). Understanding the response to grazing is crucial if one is to develop
11 management strategies to achieve a particular vegetation composition.

12 **PLANT SURVIVAL STRATEGIES IN GRAZED COMMUNITIES**

13 Studies on grassland productivity are important in southern Africa due to the
14 importance of grasslands to the commercial and communal farming sectors. Part of
15 these studies include the understanding of the grazing tolerance of the dominant
16 species within a community and relate it to species composition. Unlike avoidance,
17 grazing tolerance has not been extensively studied for the different species
18 categorised as Increasers or Decreasers (Rosenthal and Kotanen 1994; del-Val and
19 Crawley 2004). The limited studies focussed on grazing tolerance reveal different
20 outcomes and this can be explained by the diverse use of defoliation intensities and
21 frequencies in these studies (Noy-Meir 1993). However, the study of these factors
22 alone may not entirely explain what is observed in natural communities and thus
23 investigation of the added effect of competition may be more beneficial. Meuggler
24 (1972) and Alhamad and Alrababah (2008) suggest that competition among plants

1 may be for resources such as water and light and this can affect the growth ability of
2 plants.

3 Studies incorporating grazing tolerance in mesic grasslands of southern Africa are
4 lacking and it is not clear how competition and other factors affect factors influence the
5 ability of Increasers and Decreasers to tolerate defoliation (Morris 2016). However, at
6 least two hypotheses exist that attempt to explain how selective herbivory contributes
7 to species replacement. Firstly, the selective herbivory hypothesis stating that species
8 replacement within grasslands is driven by animals selectively grazing rather than the
9 different abilities of species to regrow following grazing (Anderson and Briske 1995,
10 Moretto and Distel 1997). In contrast to this hypothesis is the tolerance –selective
11 herbivory hypothesis suggesting that there is a balance between herbivory tolerance
12 and selective grazing within communities whereby desirable and high foraging value
13 species retain their dominance (Augustine and McNaughton 1998, Hendon and Briske
14 2002). It must be noted that both hypotheses recognise the importance of species
15 replacement, but differ in the extent to which herbivory tolerance contributes towards
16 species replacement or species dominance (Hendon and Briske 2002).

17 ***Grazing resistance concept***

18 “Grazing resistance is the relative ability of plants to persist in grazed communities”
19 (Briske and Richards 1995). Grazing resistance is divided into two components;
20 avoidance and tolerance (Briske and Richards 1995). Avoidance is when plants
21 reduce their probability of being grazed by herbivores (Briske and Richards 1995).
22 Whilst grazing tolerance consists of mechanisms which allow plants to grow following
23 defoliation (Briske and Richards 1995). For the purposes of the experiments described
24 within this thesis – grazing avoidance was not investigated. The focus of the
25 information presented is specific to grazing tolerance. The recognition of defoliation

1 tolerance as an important factor reducing species replacement/composition shifts is
2 critical to grassland management.

3 ***Tolerance mechanisms***

4 Plant tolerance is the ability of a plant to withstand herbivory, with a reduced loss in
5 growth ability (Tiffin and Rausher 1999). Alternatively, tolerance is the capacity to
6 make-up for tissue loss (Rosenthal and Welter 1995; Stowe et al. 2000). Tolerance
7 mechanisms require resources to replace plant material that has been lost due to
8 herbivory (Ourry et al. 1988). Therefore resources are used directly for plant growth
9 as observed in tolerance mechanisms, unlike avoidance mechanisms where
10 resources are, directed towards mechanisms such as chemical defences (Davidson
11 1993).

12 The resource availability hypothesis states that plants have the ability to alter their
13 growth rate to equal the availability of resources in their particular habitats (Coley et
14 al. 1985; Coley 1988). This suggests that in late-successional dominants, tolerance
15 mechanisms contribute a higher proportion to herbivory resistance than avoidance
16 mechanisms (Briske 1996).

17 Mesic grasslands are generally productive environments that are characterised as
18 having reasonably good rainfall and temperatures patterns. Therefore, grassland
19 dominants found within such environments are referred to as competitive strategists
20 (Grime 1977). These species possess various morphological features such as large
21 structure, fast growth rate and tissue replacement rate (Grime 1977) allowing them to
22 dominate within vegetation communities. This high competitive ability is required for
23 late-successional species to maintain their dominance within grasslands (Tilman and
24 Wedin 1991). An existing hypothesis is that late-successional dominants rely greatly

1 on tolerance strategies for grazing resistance, more so than early- or mid-successional
2 species (Davidson 1993). This is because tolerance strategies are closely correlated
3 to attributes associated with the competitor strategy (Davidson 1993). In contrast to
4 this, avoidance mechanisms that divert resources from growth towards defensive
5 alkaloids and mechanical deterrents (e.g. tough leaves) reduce the competitive ability
6 of the plant (Briske 1996). However, tolerance mechanisms can also be reduced when
7 grazing removes more biomass than the tolerance mechanisms can replace (Briske
8 1996). In this situation, the suppression of the tolerance mechanisms will lower the
9 grazing resistance of the dominant species to a level below that of the early- or mid-
10 successional species which could then influence competitive interactions and
11 contribute to species composition shifts (Briske 1996).

12 ***Availability of meristems***

13 Grass growth is dependent on the presence of intercalary and apical meristems and
14 buds (Briske and Richards, 1995). Leaf growth occurs at a faster rate from the
15 intercalary meristems (Cook and Stoddart, 1953; Briske, 1991) than from the apical
16 meristem (Skinner and Nelson, 1994). These meristematic sources of leaf growth
17 differ among species and are influenced by environmental conditions (Coughenour et
18 al. 1985; Olson and Richards, 1988) which in turn influences grazing tolerance. For
19 example, rhizomatous and caespitose grasses differ in grazing tolerance due to
20 meristematic availability and the time of defoliation (Briske 1996).

21 ***Seed number and viability***

22 Grazing can reduce seed success in grasses by affecting resource availability
23 (O'Connor 1991; Noy-Meir and Briske 1996). This occurs when the microenvironment
24 suitable for seed germination and seed establishment is altered (O'Connor 1991; Noy-

1 Meir and Briske 1996). In environments where grass species rely on seed success to
2 reproduce, heavy grazing can alter the abundance of these species although this may
3 not be the case in mesic grasslands, where species reproduce predominantly by
4 tillering.

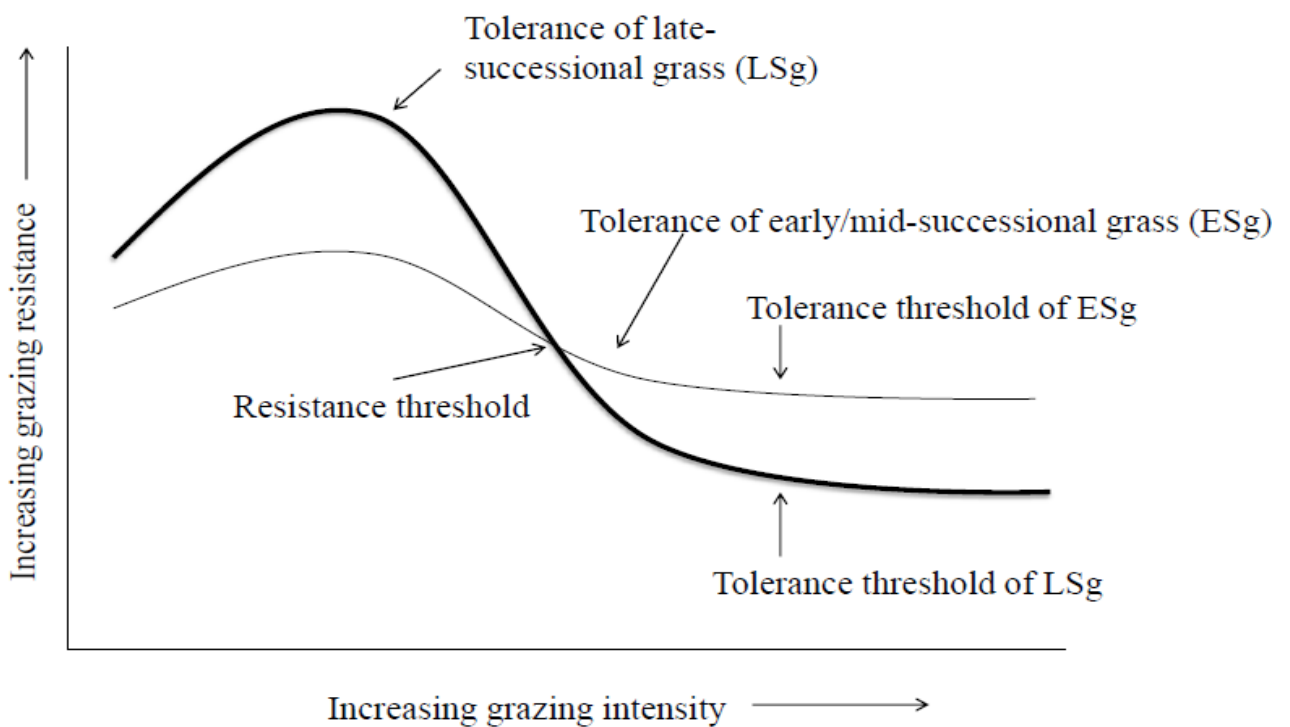
5 ***Compensatory processes and growth***

6 There are several physiological mechanisms that have the potential to increase plant
7 growth after grazing or defoliation has taken place (Briske 1996). These are
8 compensatory processes (photosynthesis, nutrient absorption and resource
9 allocation) and compensatory growth (Briske 1996). The importance of these
10 compensatory processes towards plant growth and community development following
11 grazing is not clear (Briske and Richards 1995). Existing data supports the occurrence
12 of compensatory growth, however they also reveal that the conditions required to
13 obtain these compensatory responses are not well understood (Briske and Richards
14 1995).

15 ***Interpretation of grazing resistance***

16 Replacement of late-successional species by early- and mid-successional species
17 occurs when a resistance threshold is reached (Briske 1996). The hypothesized
18 functional interpretation of species compositional change within mesic grasslands
19 (Figure 2.2 (adapted from Briske 1996 Figure 2.4, pg. 46) indicates that a point exists
20 where the grazing resistance of the dominant species is equal to the grazing
21 resistance of the other sub-dominant species (Briske 1996). With increasing grazing
22 intensity, the grazing resistance of the dominant species will continue to decrease and
23 they will lose their competitive ability (Briske 1996) which will lower the abundance of
24 that species in the community. According to this interpretation, when the grazing

1 resistance of the dominant species is reduced it will have reached a tolerance
2 threshold. At this point, the contribution of the tolerance strategy is no longer
3 functional, the plant experiences photosynthetic limitations and ultimately dies
4 (assuming that the grazing intensity is maintained) (Briske 1996). The practical
5 implications of species replacement are that herbivores will be forced to graze species
6 with a greater expression of avoidance mechanisms (Briske 1996). This could result
7 in herbivores grazing on undesirable, poor quality species which will negatively affect
8 both herbivore health and grassland condition.
9



10

11 Figure 2. 2. Hypothesized functional interpretation of species composition changes in
12 mesic grasslands (Adapted from Briske 1996 Figure 2.4, pg.46).

1 **COMPETITION**

2 Plants are affected by neighbouring plants and how they respond to this interaction
3 will determine their competitive ability. "Competition can be defined as the interaction
4 between individuals and populations which is negative for both" (Weiner 1993, pp.
5 100).

6 ***Asymmetric and symmetric competition***

7 An important part of resource competition among plants is the level of size-asymmetry
8 in the portioning of resources (Weiner 1990; Schwinning and Weiner 1998).
9 Asymmetric competition occurs when a plant has obtains a disproportionately large
10 volume of resources relative to its size, reducing the growth of the surrounding plants
11 (Weiner 1993). However, if a plant is three times as large as another and has three
12 times the ability to obtain resources then competition is symmetrical (Weiner 1993).
13 Competition for resources is size symmetrical when all plants use the same amount
14 per unit biomass and when a single larger plants uses more resources, that is referred
15 to as asymmetrical competition (Weiner 1990; Schwinning and Weiner 1998). For
16 example, when populations are grown in higher densities, they show a greater size
17 variability than populations grown at lower densities (Weiner and Thomas 1986). By
18 contrast, symmetric models of competition predict that populations grown at higher
19 densities will have the same or lower levels of size inequality than populations grown
20 at lower densities or without competition (Weiner 1993).

21 ***Interspecific competition***

22 According to the limited reductionism approach, competition must be examined in
23 whole communities and small subsets of the community but it would be impossible to
24 look at all the multispecies interactions and predict the outcomes. The importance of

1 competition between plants has led many ecologists to ask if “competitive ability”
2 exists in plants and if so, what characteristics are associated with it. It was
3 hypothesized that competitive ability is a heritable trait (Sakai 1961, cited in Keddy
4 and Shipley 1989). Sakai (1961) looked unsuccessfully for correlations between
5 success in competition experiments and measureable traits such as plant height.
6 However, other studies have found that success in plant communities goes to species
7 which establish first, germinate earlier, put up a canopy early and have large seed
8 reserves (Weiner 1993). These results further support the importance of asymmetric
9 interactions in plant communities.

10 Grime (1979) outlined three basic plant strategies, namely: stress tolerant, ruderal and
11 competitive. He hypothesized trade-offs between these strategies. He assumed that
12 competitive ability is a useful concept and plants that are good competitors for one
13 resource will be good competitors for all resources. Alternatively Tilman (1990, 1991)
14 proposed a mechanistic model which indicated that the best competitor is the species
15 which can tolerate the lowest levels of a limiting resource. This is because resource
16 levels are reduced when plants compete. When resources become low, the ability to
17 grow and survive becomes the important issue (Edwards and Edwards 2011). Plants
18 differ in their tolerances for low levels of different resources. For example, a plant that
19 can tolerate low light levels will not be able to tolerate low nitrogen levels. There is no
20 overarching competitive ability; rather a competitive ability for each different resource
21 and competitive relationships will change depending on the levels of the different
22 resources. The difference between the theories described by Grime and Tilman has
23 been difficult to clarify because of their assumptions and terminologies.

24 Goldberg et al. (1992) contributed to the discussion by pointing out that there are a
25 number of parts to competitive interactions. Firstly a competitive effect occurs when

1 an individual lowers the resources available for another individual and secondly a
2 competitive response occurs when an individual responds to the lowered resource.
3 Therefore a good competitor can be one which is effective lowering a particular
4 resource as supported by Grime (1979) or one that has the ability to tolerate the
5 lowered resources as a result of its neighbours as proposed by Tilman (1985).

6 **CONCLUSION**

7 The concept of grazing resistance is largely based on empirical evidence and the
8 theoretical base explaining this concept is limited. This highlights that there is a need
9 for further studies that focus on understanding plant-herbivore interactions to expand
10 the theoretical understanding. The concept of grazing resistance hypothesizes that
11 late-successional dominants tend to rely on tolerance strategies more than early- and
12 mid- successional species. As a result, late-successional dominants have attributes of
13 the competitor strategy. Tolerance mechanisms, unlike avoidance mechanisms, do
14 not divert resources from growth but directly contribute to plant growth. Tolerance
15 strategy is defined by morphological and physiological mechanisms and it emphasizes
16 that many plant attributes are involved when determining the relative grazing
17 resistance among different plant species. These present opportunities for managers
18 to influence plant utilization by animals and then affect plant growth responses among
19 species within plant communities, thus influencing community composition.
20 Successful management of grasslands will require some level of understanding of
21 plant grazing resistance and associated strategies used by plants in response to
22 grazing.

1 **STUDY SPECIES**

2 The four common mesic grassland grasses to be used in this study are *T. triandra*
3 (decreaser), *T. leucothrix* (decreaser), *E. curvula* (increaser) and *E. plana* (increaser).
4 *Themeda triandra* is a dominant species in lightly grazed grasslands and *T. leucothrix*
5 grows alongside *Themeda triandra* in the same habitat. These grasses can be
6 replaced by *E. curvula* and *E. plana* in communities subjected to intensive grazing.
7 Under lightly grazed conditions, decreaser species are considered better competitors
8 and grazing tolerators and as they increase in productivity they can outcompete
9 increaser species.

10 ***Themeda triandra* Forssk.**

11 *Themeda triandra* (red grass) is a perennial grass, reaching a culm height of 1500 mm
12 and belonging to the sub-family Panicoideae (Van Oudtshoorn 2002). It is categorised
13 as a late-successional (climax) decreaser species, which dominates grasslands with
14 well-drained soils that undergo some form of moderate to light non-selective
15 defoliation, such as burning or mowing (Fynn 2004). This grass does not tolerate the
16 litter accumulation occurring when no disturbance takes place (Belsky 1992). It has
17 high forage quality and is an indicator of veld in a good condition and flowers from
18 October to July (Van Oudtshoorn 2002).

19 ***Tristachya leucothrix* Trin. ex Nees**

20 *Tristachya leucothrix* (hairy trident grass) is a tufted grass reaching a culm height of
21 900 mm and grows together with *Themeda triandra* and *Alloteropsis semialata* in the
22 same habitat (Van Oudtshoorn 2002). *Tristachya leucothrix* belongs to the sub-family
23 Panicoideae and is categorised as an Increaser I species as it increases in abundance
24 when veld is infrequently grazed (Foran et al. 1978). However, because in the veld, it

1 declines in abundance under heavy and selective grazing (Morris and Tainton 1992),
2 it can be considered to also behave as a Decreaser species (Morris 2016). It grows
3 well in veld that is underutilized and produces reasonable leaf biomass allowing
4 grazing early in the season. It has high forage quality and flowers from October to
5 March (Van Oudtshoorn 2002).

6 ***Eragrostis curvula* (Schrad.) Nees**

7 *Eragrostis curvula* (weeping love grass) is tall (culm height from 300 – 1200 mm) (Van
8 Oudtshoorn 2002), has narrow leaves, and tends to invade and dominate grasslands
9 that are infrequently burnt (Fynn 2004). This species belongs to the sub-family
10 Chloridoideae and is categorised as an early-successional (pioneer) increaser IIb
11 species (Van Oudtshoorn 2002). This species has average forage quality, establishes
12 rapidly and is important in stabilising exposed soil (Van Oudtshoorn 2002). Its
13 abundance increases when veld is infrequently burnt (Fynn 2004). *Eragrostis curvula*
14 flowers from August to June (Van Oudtshoorn 2002).

15 ***Eragrostis plana* Nees**

16 *Eragrostis plana* (tough love grass) is a short grass (culm height from 400 -1000 mm)
17 that grows in disturbed and trampled places (Van Oudtshoorn 2002). It belongs to the
18 sub-family Chloridoideae and is categorised as a mid-successional (subclimax)
19 increaser IIb species. It has poor forage quality, although it can be utilized late into the
20 dry season in arid areas because the leaves remain green (Van Oudtshoorn 2002).
21 The presence of this grass indicates that the area has been subjected to overgrazing
22 or too frequent burning (Van Oudtshoorn 2002). *Eragrostis plana* flowers from
23 September to March (Van Oudtshoorn 2002).

24

CHAPTER 3: THE DEFOLIATION TOLERANCE OF INCREASER AND DECREASES MESIC GRASSLAND SPECIES

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

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This chapter focuses on firstly, how four grassland species that are common in mesic areas are able to tolerate herbivory (in the form of simulated defoliation/clipping) and secondly, how morphological traits are affected by different combinations of defoliation frequencies and intensities. This experiment is important because the ability of grasses to tolerate defoliation has been recognised for a long time but the extent to which tufts regrow following herbivory is poorly studied. This information can allow for more informed management decisions and for one to anticipate species compositional changes within grassland communities.

In this chapter, Decreasers refer to *Themeda triandra* (*T. triandra*) and *Tristachya leucothrix* (*T. leucothrix*) and Increaseers refer to *Eragrostis curvula* (*E. curvula*) and *Eragrostis plana* (*E. plana*).

ABSTRACT

1
2 Grasses that respond to grazing in a similar manner fall into the same grazing
3 response group. The growth response of two Decreaser and two Increaser
4 species was tested using a pot trial under three levels of defoliation intensity
5 and three levels of defoliation frequency over the summer growing season (150
6 days). Aboveground and belowground phytomass, tuft height, tillering and root
7 to shoot biomass ratios were determined for each tuft. Contrary to expectations,
8 defoliation tolerance was species specific rather than being common to the
9 grazing response groups. None of the measured traits were good predictors of
10 defoliation tolerance. In terms of influencing plant traits, defoliation intensity
11 seemed less important than frequency. Aboveground phytomass was greatest
12 for *E. curvula*, lowest for *T. leucothrix* and similar between *T. triandra* and *E.*
13 *plana*. Severe defoliation reduced aboveground phytomass. *Themeda triandra*
14 and *T. leucothrix*, which co-occur in mesic grasslands, maintained belowground
15 phytomass regardless of defoliation frequency. By contrast the *Eragrostis spp.*
16 had lower root biomass under frequent defoliation, although after a single
17 defoliation *E. plana* showed high root biomass implying that it may be a strong
18 competitor in infrequently defoliated mesic grasslands. Undeveloped tufts were
19 taller than undeveloped tufts. Unexpectedly, tillering was reduced by defoliation,
20 possibly affecting development of new tillers. *Eragrostis plana* had the highest
21 root: shoot ratio (R:S), possibly due to effects of a single defoliation, and *E.*
22 *curvula* had the lowest. This suggests that R:S is driven by root biomass. In
23 making management decisions the current species composition must be
24 considered and a lenient but frequent grazing system applied as results show
25 that desirable species (*T. triandra* and *T. leucothrix*) are tolerant to defoliation
26 and have the potential for compensatory growth. Given the relevance of this

1 **work to mesic grassland management, further research is necessary to better**
2 **understand the broad-scale effects of frequent defoliation and its influence on**
3 **competitive interactions among common grass species.**

4 **Keywords:** humid grasslands, compensatory growth, heavy grazing, resting

5 INTRODUCTION

6 Herbivory is one of the most important disturbances that take place within grasslands
7 (Sala 1988). It affects plants selectively and several studies have shown that grazing
8 can significantly affect species abundance and composition within grassland
9 communities (Augustine and McNaughton 1998). Generally, the presence of particular
10 grasses is favoured by grazing i.e. Increasers, whilst other grasses tend to be lost from
11 the sward because of heavy grazing i.e. Decreasers (Crawley 1990; Bullock et al.
12 2001; Vesk and Westoby 2001).

13
14 Much of the literature on grazing effects compare grazed and ungrazed treatments
15 (Vinton and Hartnett 1992; Spasojevic et al. 2010), although the effects of different
16 levels of grazing are possibly of more importance. Plants do not respond linearly to
17 defoliation frequency or intensity. The optimum capacity of a plant to regrow is
18 observed when plants are exposed to a low or moderate grazing intensity (N'Guessan
19 and Hartnett 2011). This compensatory response is reduced when plants are more
20 severely defoliated (N'Guessan and Hartnett 2011). The capacity to regrow and
21 endure herbivory is referred to as tolerance (Tiffin and Rausher 1999; Fornoni and
22 Nunez-Farfan 2000). Tissue regrowth after herbivory is known as compensatory
23 growth but there are inconsistencies in the literature regarding the drivers and extent
24 of this response, signalling the need to consider the influence of both abiotic and biotic
25 conditions (Morris 2016). In many studies, compensation is analysed by comparing
26 the production of defoliated plants to that of undefoliated plants (Oesterheld and

1 McNauughton 1988; Ovaska et al. 1993; Mabry and Wayne 1997). However, Anten et
2 al. (2003) argue that this method does not directly assess the compensatory
3 responses of plants. A more suitable estimation of compensatory growth response is
4 to compare defoliated plants to the estimated responses of hypothetical plants that
5 have been defoliated but cannot regrow (Anten et al. 2003). Perhaps, it is partially the
6 use of either the classical or iterative approach, in addition to variable environmental
7 conditions, that has resulted in a variety of responses regarding compensatory growth.
8 Factors that may influence the extent to which plants compensate include the timing
9 of defoliation and the interaction of timing, nutrient availability and competition with
10 neighbouring plants (Maschinski and Whitham 1989).

11

12 Defoliation of desirable and undesirable grass species with varying palatability in
13 mesic grasslands is a topic that has been well studied (Rethman and Booyesen 1968;
14 Barnes 1989; Danckwerts and Nel 1989). Plant responses to herbivory are variable
15 and can be influenced by the plant part removed i.e. leaves and inflorescences
16 (Maschinski and Whitman 1989). One common perception is that the removal of
17 leaves will negatively impact the ability of plants to sustain root growth (Crawley 1983).
18 Evidence of this is seen mainly from experiments performed as pot trials (Crawley
19 1983) and not on grazing sites. Milchunas and Lauenroth (1993) performed analyses
20 of a multiple site data set that evaluated species composition, aboveground biomass,
21 root biomass and forage nutrient content between grazed and ungrazed sites and
22 found no relationship between existing shoot biomass and root biomass production.
23 The timing, intensity and frequency of herbivory may also influence plant response
24 and as a result sward dynamics. The selected grass species used in this study differ
25 in morphology and thus were expected to differ in their response to simulated
26 herbivory. Understanding how clipping intensity and frequency interact at a species

1 level is necessary for understanding the effects of herbivory on grass populations and
2 on sward composition. This information will assist in conservation and the sustainable
3 use of grassland ecosystems.

4

5 The focus of this chapter will be to determine how four grasses, common in mesic
6 grasslands, respond to simulated herbivory by clipping. This response to herbivory is
7 demonstrated by tolerance and is reflected in the final biomass produced by the plant
8 (McNaughton 1983; Augustine and McNaughton 1998). Categorising grass species
9 into grazing response groups, assumes that all species in a certain response group
10 will respond to herbivory in a similar manner and this may not necessarily be true
11 (Tainton 1999 cited in Ford 2015). This supports further investigation of the importance
12 of the effect of species identity when understanding herbivory tolerance. There are
13 essential factors that influence tolerance including plant structure and biomass
14 allocation between roots and shoots (Chapin and Slack 1979; Marquis 1996,
15 Oosterheld and McNaughton 1991). Therefore, the understanding of grass
16 morphological traits and their response to defoliation might assist in creating predictors
17 for certain levels of tolerance.

18

19 The aim of this experiment was to determine how four Increaser and Decreaser grass
20 species common in mesic grasslands respond to different frequencies and intensities
21 of herbivory. The first objective was to determine the difference in defoliation tolerance,
22 in terms of aboveground phytomass production, of Decreaser and Increaser species.
23 The second objective was to determine the difference in defoliation tolerance between
24 individual species, regardless of grazing response group. These objectives address
25 the question, how does defoliation tolerance differ in Decreaser and Increaser mesic
26 grasses relative to undefoliated plants? It was hypothesized that differences in

1 defoliation tolerance would be greater between Decreasers and Increasers than
2 between species within each group. The third objective of this study was to understand
3 the morphological responses (cumulative growth, tuft structure and resource
4 allocation) of those species differing in grazing tolerance to various levels of defoliation
5 frequency and intensity. The first research question associated with this objective was
6 to determine how defoliation frequency, intensity, and their interaction affect the
7 cumulative growth (above- and belowground) of mesic grasses? It was hypothesized
8 that frequent and severe defoliation would reduce cumulative growth of grazing-
9 tolerant grasses less than that of grazing-sensitive grasses. The second research
10 question was how does defoliation frequency, intensity, and their interaction affect the
11 tuft structure of mesic grasses? It was hypothesized that frequent and severe
12 defoliation will reduce tuft height and tillering in grazing-sensitive grasses. The third
13 research question was how does defoliation frequency, intensity, and their interaction
14 affect resource allocation? It was hypothesised that frequent and severe defoliation
15 would decrease resource allocation to belowground growth, resulting in a reduced
16 root:shoot biomass ratio in grazing-sensitive grasses.

17

18

METHODS

19 In order to investigate the defoliation tolerance of Decreaser and Increaser grass
20 species, various clipping frequencies and intensities were applied under controlled
21 conditions.

22

23 Four grass species, common in the mesic grasslands of KwaZulu-Natal in South
24 Africa, were used for this experiment. These four species included two Decreaser
25 species (*Themeda triandra* and *Tristachya leucothrix*) and two Increaser II species
26 (*Eragrostis curvula* and *Eragrostis plana*). Decreaser grass species are abundant in

1 grassland in good condition and their abundance is reduced under conditions of heavy
2 grazing or under grazing (van Oudtshoorn 2002). Increaser II grass species are
3 abundant in grasslands that are heavily grazed (Van Oudtshoorn (2002). *Tristachya*
4 *leucothrix* is categorized as an Increaser 1 species, a species which increases in
5 abundance in veld that is infrequently defoliated (Foran et al. 1978), but is known to
6 grow in close association with *Themeda triandra* (Morris and Tainton 1992) and
7 declines or becomes eliminated in heavily or selectively grazed grasslands (Morris et
8 al. 1992). Morris (2016) defends the need to classify *Tristachya leucothrix* as a
9 Decreaser supporting the decision made in this experiment.

10

11 This study was a pot trial where the size of the plastic pots were as follows: diameter
12 – 280 mm, circumference of the pot – 890 mm, height – 350 mm. The plastic pots
13 consisted of eight holes (each having a diameter of 20 mm) located 30 mm from the
14 base of the pot. Sand was used because of a lack of nutrients. This allowed for
15 Hoagland's solution to be added to each pot, to control for nutrient level per pot. All
16 pots received approximately the same amount of sand however sand drying was not
17 done to assure pots received the same amount of sand. This pot trial was performed
18 in a shade house under light shade cloth (20%). The experiment was arranged in a
19 randomized complete block design with six replications of each treatment combination.
20 Two treatments were established; defoliation intensity and defoliation frequency.
21 Defoliation intensities, with three levels; no defoliation, 50 mm (intense) and 100 mm
22 (lenient), were applied at three defoliation frequencies (one, two or three occasions).
23 An undefoliated control was established for each species. Grass tufts for all species
24 were established from material collected from patches of managed, natural grassland
25 at Ukulinga Research Farm. Approximately 8 – 10 tillers per pot were planted in sand
26 for each individual experimental tuft. These tufts were monitored for three to four

1 weeks to assess the condition of the plants. All plants were irrigated every second day
2 and Hoagland's nutrient solution (see Appendix A, Table 5.1) was applied once a week
3 when plants were not irrigated. A total of 168 of the most well established plants were
4 selected for inclusion in the experimental trial (42 per species). The variables that were
5 measured throughout the growing period were clipped aboveground phytomass, tuft
6 height and number of tillers. Tuft height measurements and an initial count of tillers
7 were done at the start of the trial. Aboveground phytomass was clipped, bagged and
8 weighed after every defoliation. For the duration of the trial all pots were well watered
9 with 40 % Hoagland's nutrient solution (Hoagland and Arnon 1950) (Table 5.1) every
10 week and were flushed to remove dried salt accumulation every other week. The
11 results of this experiment are from a single growing season, similar to previous studies
12 (see Morris and Tainton 1993). The trial was run from 24 December 2015 to 26 June
13 2016 (150 days plus the harvesting of plants). This period was selected because the
14 majority of the growing season grazing in mesic grasslands occurs within these dates
15 (O'Connor and Pickett 1992) with the growing season defined as falling between
16 September to March, with late precipitation up to the end of April (see Knapp et al.
17 2006). After 150 days final measurements were taken and the plant roots were washed
18 to remove excess sand. Shoot i.e. aboveground phytomass was separated from root
19 biomass. For each pot, the separated root material was placed onto a tray and water
20 was used to wash out the sand from the root material. No sieve was used and no
21 attempt was used to distinguish between the live and dead roots. All phytomass was
22 dried at 60 °C for a period of 48 hours and weighed. The final s biomass was added
23 to the dry biomass recorded from each clipping for each pot to produce a single
24 cumulative biomass value for each pot. Cumulative biomass for the unclipped control
25 pots was represented by the final shoot biomass value alone.

26

1 **Data analysis**

2 *Defoliation tolerance*

3 To address the first objective, defoliation tolerance was determined as a percentage
4 using cumulative shoot biomass for each species from the control and treatment pots
5 using equation below (similar to Del-Val and Crawley 2005):

6

$$7 \text{ Defoliation tolerance (\%)} = \frac{\text{Aboveground phytomass of pot (g)} - \text{Mean aboveground phytomass of control (g)}}{\text{Mean aboveground phytomass of control (g)}} * 100$$

8

9 Defoliation tolerance data was analysed in GenStat 18. To determine the difference in
10 defoliation tolerance between the two response groups – Decreaser and Increaser,
11 the data were analysed using an Independent Sample T-test once the assumptions of
12 normally distributed data and equality of variances were met. To determine if there
13 were species specific differences in defoliation tolerance a one-way analysis of
14 variance (ANOVA) was used. This was performed after testing the assumptions of
15 normal distribution of residuals and equal variances of the residuals among the
16 treatments. When the ANOVA revealed significant differences, a Fisher's test (LSD)
17 was used to separate the means.

18

19 *Morphological responses*

20 Aboveground phytomass was determined from the cumulative aboveground
21 phytomass over the growing season. Belowground phytomass was obtained from the
22 final harvest, where roots were separated from aboveground phytomass at ground
23 level. Height was determined from the final plant height per individual. Root to shoot
24 biomass ratio was calculated by dividing the final root biomass by the cumulative shoot
25 biomass. Tillering was defined as the change in tiller number as a percentage of the
26 initial tiller number (Bullock et al. 1994 see Figure 1, pg. 334). Hence, tillering was
27 determined from the following formula;

1
$$\text{Tillering}(\%) = \frac{\text{No.of tillers (final)} - \text{No.of tillers (initial)}}{\text{No.of tillers (initial)}} * 100$$

2

3 All variables were analysed in GenStat 18. A general analysis of variance (ANOVA)
4 was used to assess the effects of grass species, clipping intensity and clipping
5 frequency on grass productivity as well as their interaction, on (1) biomass based on
6 cumulative aboveground and belowground phytomass, (2) tuft structure based on
7 height and tillering and (3) resource allocation based on the root to shoot biomass
8 ratio. Final tuft height met the assumptions of ANOVA (normal distribution and
9 homogeneity of variances) while aboveground phytomass, belowground phytomass
10 and tillering data were subjected to square root transformations and root to shoot
11 biomass data were subjected to a double log transformation to meet the assumptions
12 of ANOVA. When the ANOVA revealed significant differences, a Fisher's test (LSD)
13 was used to separate the means for the main effects and a Tukey's test (HSD) was
14 used for the two-way and three-way interaction effects.

15

RESULTS

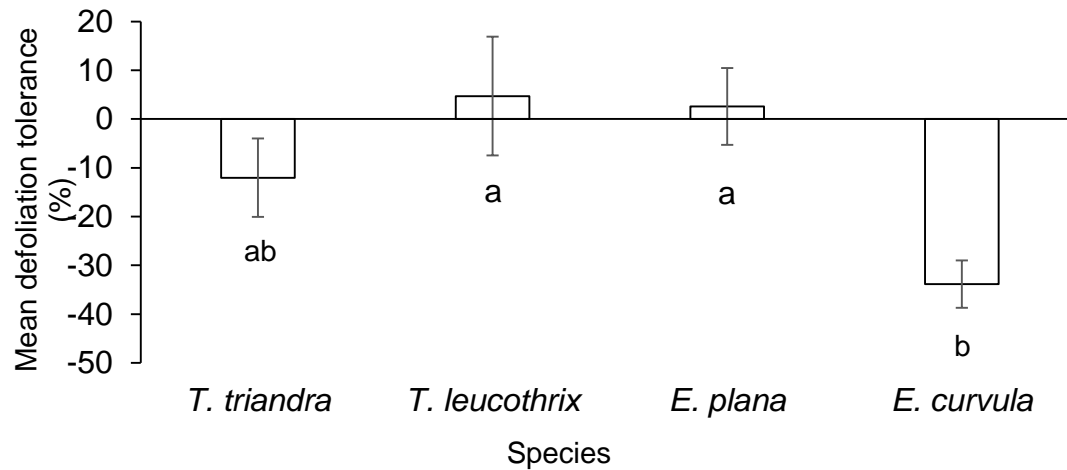
16 **Defoliation tolerance**

17 There was no significant difference ($t_{142} = 1.36$ $p = 0.176$, $n = 144$) in defoliation
18 tolerance between the two grazing response groups.

19

20 Defoliation tolerance differed significantly between grass species ($F_{3, 140} = 4.330$, p
21 $= 0.006$, $n = 144$). The two species that were able to slightly overcompensate and
22 tolerate defoliation were *T. leucothrix* ($4.716 \pm 11.920\%$) and *E. plana* ($2.581 \pm$
23 7.860%), *T. triandra* ($-12.040 \pm 8.051\%$) showed little to no response, while *E. curvula*
24 ($-33.870 \pm 4.852\%$) was significantly less tolerant than *T. leucothrix* and *E. plana*
25 showing a general suppression of biomass as a result of defoliation (Figure 3.1).

26



1

2 Figure 3. 1. Mean defoliation tolerance (%) (\pm SE) of four common mesic grassland
 3 species. Percentages above zero indicate overcompensation and below zero
 4 indicate under compensation resulting from loss of shoot biomass (aboveground
 5 biomass).

6 **Morphological responses – Cumulative growth**

7

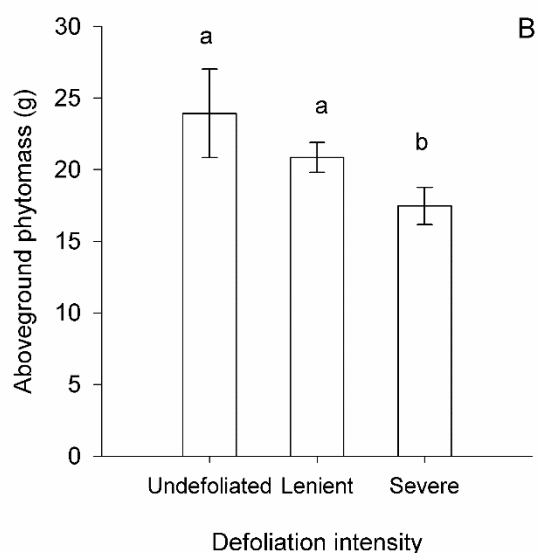
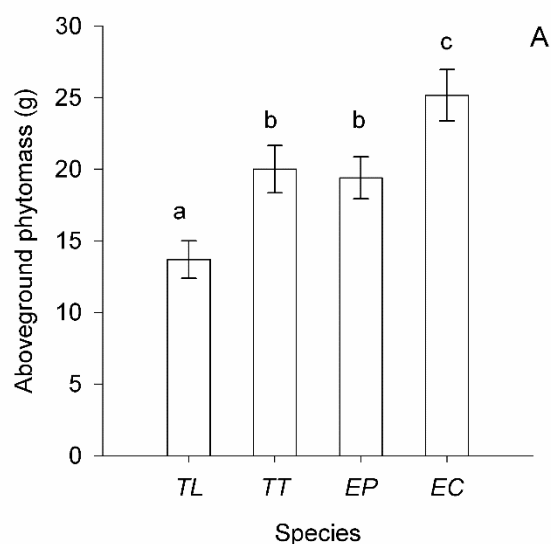
8 **Aboveground phytomass**

9 Species differed in their aboveground phytomass ($P < 0.001$, $F_{1,133} = 9.6$, Table 3.1)
 10 with *T. leucothrix* having the least aboveground phytomass (13.690 ± 1.309 g), *E.*
 11 *curvula* producing the highest (25.160 ± 1.790 g) and *T. triandra* and *E. plana*
 12 producing intermediate but similar mass of 20.000 ± 1.655 g and 19.400 ± 1.463 g
 13 respectively (Figure 3.2 A). Defoliation intensity also affected aboveground phytomass
 14 ($P = 0.023$, $F_{1, 133} = 5.28$). Leniently defoliated plants (20.850 ± 1.041 g) and
 15 undefoliated plants (23.920 ± 3.085 g) produced significantly greater aboveground
 16 phytomass than severely defoliated plants (17.460 ± 1.294 g) (Figure 3.2 B).

1 Table 3. 1: Results of analysis of variance of the main effects and interactions of
 2 defoliation frequency and intensity on the aboveground phytomass of *T. leucothrix*,
 3 *T. triandra*, *E. plana* and *E. curvula*. Data were square root transformed. The
 4 degrees of freedom (d.f), sum of squares (s.s.), mean squares (m.s.) F-ratio and p-
 5 values are shown, with significant values in **bold***

Source of variation	d.f	s.s	m.s	F-ratio	p-value
Control	1	1.413	1.413	0.990	0.322
Species	3	41.289	13.763	9.600	<0.001*
Control.Intensity	1	7.565	7.565	5.280	0.023*
Control.Frequency	2	0.390	0.195	0.140	0.873
Control.Species	3	7.039	2.346	1.640	0.184
Control.Intensity.Frequency	2	1.065	0.532	0.370	0.690
Control.Intensity.Species	3	1.366	0.455	0.320	0.812
Control.Frequency.Species	6	10.018	1.670	1.170	0.329
Control.Intensity.Frequency.Species	6	14.332	2.389	1.670	0.134
Residual	133	192.016	1.433		
Total	160	271.451			

6
7
8



1
 2 Figure 3. 2. Mean \pm SE aboveground phytomass for A) species ($F_{3, 133} = 9600$, P
 3 < 0.001) and B) defoliation Intensity ($F_{1, 133} = 5.280$, $P < 0.001$). Letters in common
 4 indicate non-significance ($P > 0.05$). Graphs shown are from untransformed data.
 5 Abbreviations: TL – *Tristachya leucothrix*, TT – *Themeda triandra*, EP – *Eragrostis*
 6 *plana* and EC – *Eragrostis curvula*.

7

8 Belowground phytomass

9 The main effect of species affected belowground phytomass ($P < 0.001$, $F_{3, 133} = 17.18$,
 10 Table 3.2) where *E. plana* produced the most roots (6.287 ± 0.920 g) and the other
 11 three species produced less (Figure 3.3 A). Defoliation frequency also influenced

1 belowground phytomass ($P < 0.001$, $F_{2, 133} = 8.25$, Table 3.2 B). Belowground
 2 phytomass was greatest when tufts were defoliated once during the growing season
 3 (5.482 ± 0.913 g) (Figure 3.3 B). Undeveloped tufts (3.428 ± 0.736 g) and those
 4 defoliated twice (2.519 ± 0.366 g) and three times (2.731 ± 0.300 g) during the growing
 5 season produced similar belowground phytomass (Figure 3.3 B). There were no
 6 species specific effects of defoliation on mass but general differences between
 7 species were apparent in undeveloped plants ($P = 0.031$, $F_{3,133} = 3.04$, Figure 3.3 C).

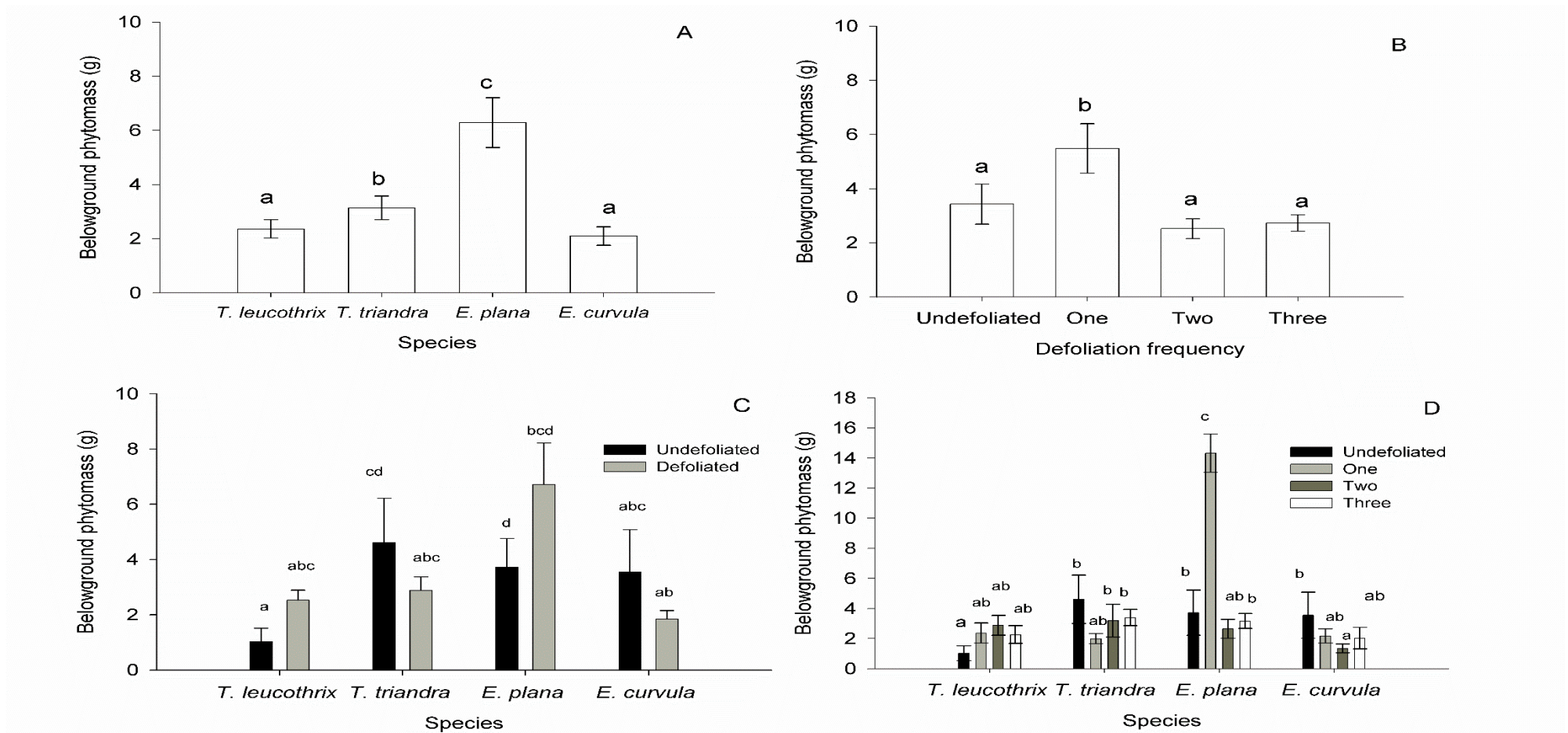
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9 Table 3. 2: Results of analysis of variance of the main effects and interactions of
 10 defoliation frequency and intensity on the belowground phytomass of *T. leucothrix*, *T.*
 11 *triandra*, *E. plana* and *E. curvula*. Data were square root transformed. The degrees
 12 of freedom (d.f), sum of squares (s.s.), mean squares (m.s.) F-ratio and *P*-values are
 13 shown, with significant values in **bold***

Source of variation	d.f	s.s	m.s	F-ratio	p-value
Control	1	0.241	0.241	0.540	0.464
Species	3	23.114	7.705	17.180	<0.001*
Control.Intensity	1	0.031	0.031	0.070	0.793
Control.Frequency	2	7.399	3.699	8.250	<0.001*
Control.Species	3	4.084	1.362	3.040	0.031*
Control.Intensity.Frequency	2	2.301	1.150	2.570	0.081
Control.Intensity.Species	3	1.711	0.570	1.270	0.287
Control.Frequency.Species	6	30.367	5.061	11.290	<0.001*
Control.Intensity.Frequency.Species	6	1.282	0.214	0.480	0.825
Residual	133	59.640	0.448		
Total	160	128.914			

14

1



2

3 Figure 3. 3. Mean \pm SE belowground phytomass for A) species ($F_{3, 133} = 17.180$, $P < 0.001$), B) defoliation frequency ($F_{2, 133} = 8.250$, $P < 0.001$),
 4 C) each species in a defoliated and undeveloped state ($F_{3, 133} = 3.040$, $P = 0.031$) and D) each species at four different defoliation frequencies
 5 ($F_{6, 133} = 11.290$, $P < 0.001$). Graphs shown are from untransformed data. Letters in common indicate non-significance ($P > 0.05$).

1 **Morphological responses – Tuft structure**

2 **Final tuft height**

3 As expected, height differed among species with *T. leucothrix* being the shortest
4 (26.080 ± 2.676 cm) and *E. curvula* being the tallest (57.710 ± 4.189 cm) ($P < 0.001$,
5 $F_{3, 133} = 33.430$, Table 3.3, Figure 3.4 A). In general, undefoliated tufts (67.230 ± 6.496
6 cm) were taller than defoliated tufts (36.860 ± 1.621 cm) ($P < 0.001$, $F_{1, 133} = 76.28$,
7 Table 3.3, Figure 2.4 B). A prominent decrease in height was observed with an
8 increase in defoliation frequency ($P < 0.001$, $F_{2, 133} = 26.04$, Table 3.3, Figure 3.4 B).
9 Only *T. triandra* tuft height was unaffected by defoliation, all other species were shorter
10 after defoliation ($P < 0.001$, $F_{3, 133} = 8.430$, Table 3.3, Figure 3.4 C). Overall, the tallest
11 tufts were observed under no defoliation ($P = 0.044$, $F_{2, 133} = 3.2$, Table 3.3, Figure 3.4
12 D). At each level of defoliation, frequency there was no difference in height between
13 lenient and severe defoliation. Under lenient defoliation tufts were tallest when cut
14 once and shortest when cut three times during the growing season, while under severe
15 defoliation only three cuts during the growing season reduced tuft height (Figure 3.4
16 D).

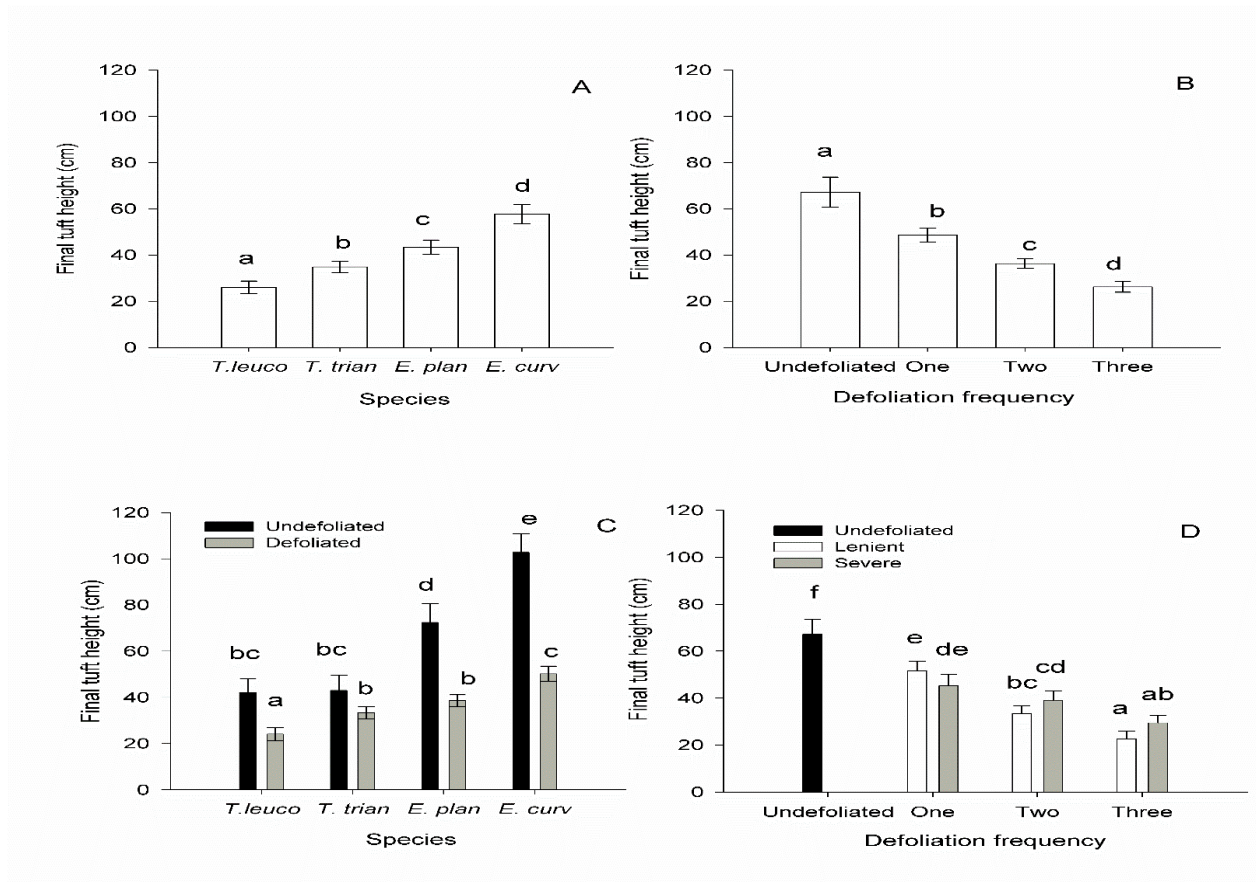
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1 Table 3. 3: Results of analysis of variance of the main effects and interactions of
 2 defoliation frequency and intensity on the final tuft height of *T. leucothrix*, *T. triandra*,
 3 *E. plana* and *E. curvula*. The degrees of freedom (d.f), sum of squares (s.s.), mean
 4 squares (m.s.) F-ratio and *P*-values are shown, with significant values in **bold***

Source of variation	d.f	s.s	m.s	F-ratio	p-value
Control	1	16767.800	16767.800	76.280	<0.001*
Species	3	22044.100	7348.000	33.430	<0.001*
Control.Intensity	1	167.300	167.300	0.760	0.385
Control.Frequency	2	11450.600	5725.300	26.040	<0.001*
Control.Species	3	5557.400	1852.500	8.430	<0.001*
Control. Intensity. Frequency	2	1405.300	702.700	3.200	0.044*
Control.Intensity.Species	3	359.200	119.700	0.540	0.653
Control.Frequency.Species	6	1478.600	246.400	1.120	0.353
Control.Intensity.Frequency.Species	6	743.000	123.800	0.560	0.759
Residual	133	29456.600	219.800		
Total	160	88196.900			

5

1



2

3 Figure 3. 4. Mean \pm SE final tuft height for A) species ($F_{3, 133} = 33.430$, $P < 0.001$), B) defoliation frequency ($F_{2, 133} = 26.040$, $P < 0.001$), C) each
 4 species in a defoliated and undefoliated state ($F_{3, 133} = 8.430$, $P < 0.001$) and D) lenient and severe defoliation at three defoliation frequencies
 5 ($F_{2, 133} = 3.200$, $P = 0.044$). Graphs shown are from untransformed data. Letters in common indicate non-significance ($P > 0.05$). Labels: *T. leuco*
 6 (*Tristachya leucothrix*), *T. trian* (*Themeda triandra*), *E. plan* (*Eragrostis plana*), *E. curv* (*Eragrostis curvula*).

1 **Tillering**

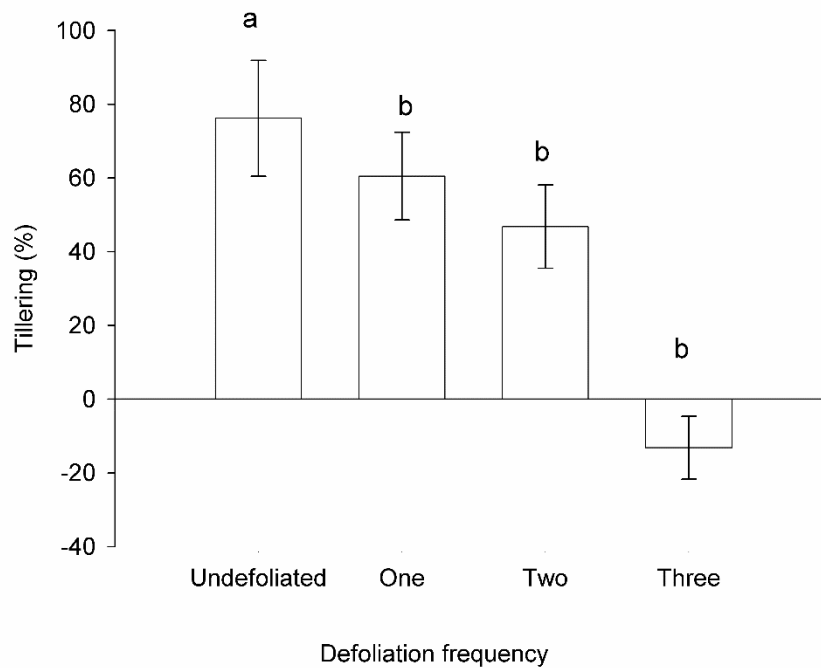
2 Tillering was lower under defoliation ($77.770 \pm 3.800\%$) than no defoliation ($97.400 \pm$
3 7.800%) ($P = 0.029$, $F_{1, 82} = 4.960$, Table 3.4). This trend continued when examining
4 defoliation frequency, with defoliation reducing tillering rates, regardless of frequency
5 ($P < 0.001$, $F_{2, 82} = 18.180$, Table 2.4, Figure 3.5).

6

7 Table 3. 4: Results of analysis of variance of the main effects and interactions of
8 defoliation frequency and intensity on tillering of *T. leucothrix*, *T. triandra*, *E. plana*
9 and *E. curvula*. The data were square root transformed. The degrees of freedom
10 (d.f), sum of squares (s.s.), mean squares (m.s.) F-ratio and *P*-values are shown,
11 with significant values indicated in **bold***

Source of variation	d.f	s.s	m.s	F-ratio	p-value
Control	1	0.583	0.583	4.960	0.029*
Species	3	0.215	0.716	0.610	0.611
Control.Intensity	1	0.018	0.018	0.150	0.699
Control.Frequency	2	4.280	2.140	18.180	<0.001*
Control.Species	3	0.716	0.239	2.030	0.117
Control.Intensity.Frequency	2	0.493	0.247	2.100	0.129
Control.Intensity.Species	3	0.526	0.176	1.490	0.224
Control.Frequency.Species	6	0.461	0.077	0.650	0.688
Control.Intensity.Frequency.Species	6	0.224	0.045	0.380	0.860
Residual	82	9.6514	0.118		
Total	108	14.236			

12



1
 2 Figure 3. 5. Mean \pm SE tillering for untransformed data ($F_{2, 82} = 18.180$, $P < 0.001$).
 3 Letters in common indicate non-significance ($P > 0.05$).
 4

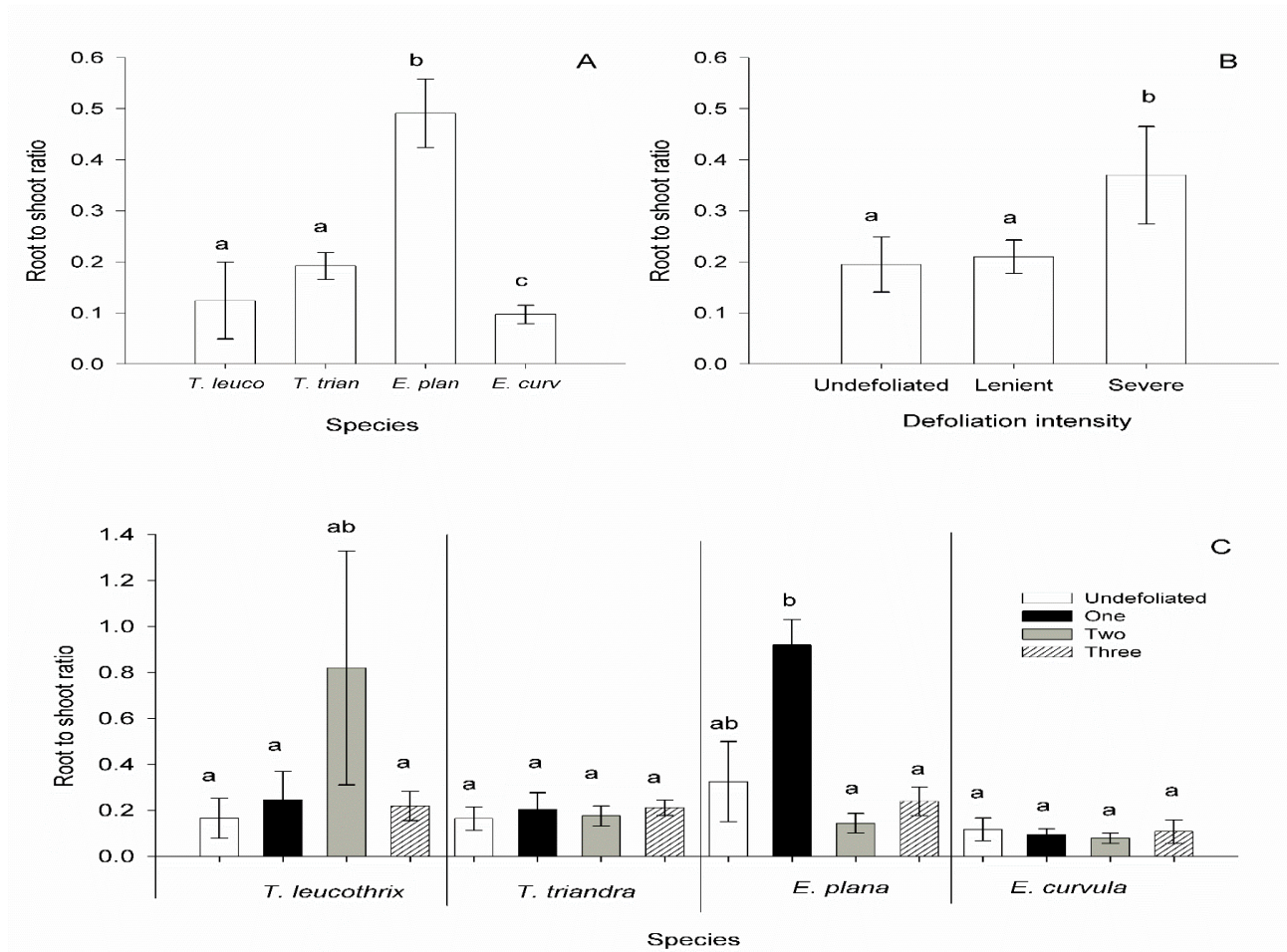
5 **Morphological responses – Resource allocation**
 6 **Root to shoot biomass ratio (based on the aboveground and belowground**
 7 **phytomass)**

8 The main effect of species indicated that *E. plana* (0.421 ± 0.067) had the greatest
 9 ratio, indicating large root biomass, with *T. leucothrix* (0.124 ± 0.075) and *T. triandra*
 10 (0.192 ± 0.029) being similar and *E. curvula* (0.097 ± 0.018) having the least, indicating
 11 large shoot biomass ($P < 0.001$, $F_{3, 133} = 11.6$, Table 3.5, Figure 3.6 A). Root to shoot
 12 allocation was similar under lenient and no defoliation (0.210 ± 0.033 and $0.195 \pm$
 13 0.054 respectively) and significantly greater under severe defoliation (0.370 ± 0.095)
 14 ($P = 0.031$, $F_{1, 133} = 4.47$, Table 3.5, Figure 3.6 B). Only root to shoot ratios of *E. plana*
 15 were affected by defoliation frequency, with a single defoliation during the growing
 16 season increasing the root to shoot biomass ratio (Figure 3.6 C).
 17

1 Table 3. 5: Results of analysis of variance of the main effects and interactions of
 2 defoliation frequency and intensity on the root to shoot biomass ratio of *T. leucothrix*,
 3 *T. triandra*, *E. plana* and *E. curvula*. Data were double log transformed. The degrees
 4 of freedom (d.f), sum of squares (s.s.), mean squares (m.s.) F-ratio and *P*-values are
 5 shown, with significant values in **bold***

Source of variation	d.f	s.s	m.s	F-ratio	p-value
Control	1	0.029	0.029	1.000	0.320
Species	3	1.006	0.335	11.600	<0.001*
Control.Intensity	1	0.137	0.137	4.470	0.031*
Control.Frequency	2	0.113	0.057	1.960	0.145
Control.Species	3	0.015	0.005	0.180	0.912
Control.Intensity.Frequency	2	0.167	0.083	2.880	0.059
Control.Intensity.Species	3	0.041	0.135	0.470	0.706
Control.Frequency.Species	6	0.878	0.146	5.060	<0.001*
Control.Intensity.Frequency.Species	6	0.240	0.040	1.380	0.227
Residual	133	3.843	0.0290		
Total	160	6.455			

6



1

2 Figure 3. 6. Mean \pm SE root to shoot biomass ratio for A) species ($F_{3, 133} = 11.600$, $P < 0.001$), B) defoliation intensity ($F_{1, 133} = 4.470$, $P = 0.031$)
 3 and C) each species at four levels of defoliation frequency ($F_{6, 133} = 5.060$, $P < 0.001$). Graphs shown are from untransformed data. Letters in
 4 common indicate non-significance ($P > 0.05$). Labels: *T. leuco* (*Tristachya leucothrix*), *T. trian* (*Themeda triandra*), *E. plan* (*Eragrostis plana*), *E.*
 5 *curv* (*Eragrostis curvula*).

DISCUSSION

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Findings for this study revealed that grazing response groups may not be adequate in explaining defoliation tolerance within grasslands. This contrasts statements reported in Del-Val and Crawley (2005) indicating that grass species response to repeated defoliation is associated with its grazing response group. Therefore, the hypothesis that differences in defoliation tolerance would be greater between Decreasers and Increasers than between species within each group was rejected as tolerance differed between species and not between response groups. This supports the need to investigate the importance of species identity in determining defoliation tolerance and the response of various morphological traits.

Many studies have investigated or grouped grass species into response groups and this has resulted in generalisations in terms of responses to herbivory, which have significantly influenced grassland management practices (Danckwerts and Stuart-Hill 1987; Everson et al. 1988; Trollope et al. 1989; Crawley 1990; Bullock et al. 2001; Del-Val and Crawley 2005; Morris 2016). This allocation of species into response groups is based on how species react to grazing impact but few studies have investigated how individual species respond and how variable the responses are within these grazing response groups (Hurt et al. 1993). Morris (2016) supports the findings of this study stating that grazing tolerance is not necessarily explained by response groups and differences can be observed at a species level. Differences in response may also be influenced by resource availability and plant interactions (Borer et al. 2014; Morris 2016). In this study, the results indicate that slight overcompensation is possible for *T. leucothrix*

1 and *E. plana* but not exhibited by *T. triandra* and *E. curvula*. However, there was no
2 difference in defoliation tolerance between *T. leucothrix*, *T. triandra* and *E. plana*. This
3 implies that *T. leucothrix*, *E. plana* and *T. triandra* are grazing tolerant whereas *E. curvula*
4 is grazing intolerant. The inability of *T. triandra* to overcompensate for lost aboveground
5 phytomass may be caused by continued intense defoliation over the growing season.
6 Similar observations have been made by Snyman et al. (2013) who indicated that *T.*
7 *triandra* may disappear completely under intense disturbance. Interestingly, the high
8 compensation and tolerance of *E. plana* may be attributed to its morphological plasticity
9 as related to its ability to grow laterally and produce more leaves when defoliated
10 compared to undefoliated tufts. Given that these results were obtained under controlled
11 conditions some variability may be seen in the field as a plants ability to compensate for
12 lost tissue may be influenced by soil nutrient status, environmental conditions, the timing
13 of defoliation, the type of herbivore and competition from the surrounding sward
14 (McNaughton and Chapin 1985; Maschinski and Whitham 1989; Vinton and Hartnett
15 1992).

16

17 Cumulative growth response was not affected by whether a grass was grazing tolerant or
18 grazing sensitive, therefore the second hypothesis was rejected. Aboveground
19 phytomass was significantly affected by species and defoliation intensity with decreasing
20 mass associated with increasing defoliation intensity. Similar findings were observed by
21 Del-Val and Crawley (2005) where shoot biomass was significantly different across
22 species regardless of intensity and frequency of damage. In general the grazing-tolerant
23 species produced less aboveground phytomass than grazing-sensitive species over the

1 growing season. Grazing-tolerant *T. leucothrix* produced the least aboveground
2 phytomass and grazing-sensitive *E. curvula* produced the most aboveground phytomass.
3 *Tristachya leucothrix* was observed overall, to be a slow growing species which, although
4 defoliation-tolerant, seemd to become more sensitive to the clipping treatments towards
5 the end of the growing season (personal observation). Peddie et al. (1995) suggested
6 that *T. leucothrix* tufts tend to grow rapidly at the beginning of the growing season and
7 reduce herbage growth by March. This could have negatively affected how this species
8 further adapted to the simulated herbivory experiment. Of particular interest was the
9 persistence of *T. triandra* to grow and produce the similar aboveground phytomass as *E.*
10 *plana*. Considering it grows with *T. leucothrix* in the natural environment the two species
11 could be expected to respond similarly. It has been suggested that *T. triandra* is a species
12 relatively sensitive to defoliation (Coughenor et al. 1985) especially heavy grazing (Lock
13 and Milburn 1971, Morris and Tainton 1993). However, *T. triandra* can tolerate light to
14 moderate levels of grazing (Morris and Tainton 1993) which supports findings of this
15 study. The ability of *T. triandra* to produce sufficient shoot biomass may increase its
16 competitiveness within natural communities given that tufts with greater leaf area are
17 capable of greater photosynthetic rates (Gastal and Leimaire 2015), thus affecting sward
18 structure in the long term. Grass tufts of all species left undefoliated or leniently defoliated
19 were significantly more productive than severely defoliated tufts, in terms of shoot
20 biomass. This suggests that lenient levels of defoliation may indeed be necessary for
21 species to maintain aboveground phytomass.

22

1 Root growth is generally reduced by defoliation (Crider 1955; Jameson 1963; Davidson
2 and Milthorpe 1966) and this view has been accepted by some ecologists (Belsky 1986,
3 Painter and Belsky 1990 McNaughton et al. 1998). Although findings of this pot study do
4 not support this view. Field studies reveal that defoliation may have no effect on (Cargill
5 and Jeffries 1984, Milchunas and Lauenroth 1989) or possibly increase root biomass
6 (Sims and Singh 1978, van der Maarel and Titlyanova 1989). The results of this study
7 support studies indicating that defoliation has no effect on belowground phytomass,
8 however significant effects are observed between different species due to morphology.
9 This difference between species is also not a good predictor for grazing tolerance and
10 this is because root measurements are difficult to perform. In addition to this difference,
11 Moron Rios et al. (1997) indicate that defoliation may reduce belowground carbohydrate
12 storages reserves further affecting belowground growth rates (Oesterheld 1992). This
13 may have implications in natural communities when species are competing for
14 belowground resources and further promote species composition shifts, favouring
15 competitive and grazing - tolerant individuals over less competitive and grazing –
16 intolerant individuals. Studying root growth for plants growing in the field is not an easy
17 task (Richards 1984) given that the techniques are destructive and there is the possibility
18 of collecting and studying the incorrect root system. Hence, the decision to plant in pots
19 and carefully separate, remove and wash the plant material to obtain root biomass.
20 Results of this study did not support the hypothesis that the belowground phytomass of
21 grazing-tolerant grasses would be reduced less than that of grazing-sensitive grasses.
22 Belowground phytomass production was lowest for grazing-sensitive *E. curvula* and
23 grazing-tolerant *T. leucothrix* and highest for grazing-tolerant *E. plana*. This may be as a

1 result of differing resource allocation strategies between species. It is possible that *E.*
2 *curvula* allocated more resources towards aboveground growth than belowground growth
3 because its shoot biomass was the highest. Species morphology may also explain this
4 difference because *E. curvula* generally grows taller than the other species, reaching
5 heights of 1200 mm (Van Oudtshoorn 2002). This may explain *E. curvula's* high
6 aboveground phytomass production. This trend was not true for *T. leucothrix* because
7 both belowground and aboveground phytomass were the lowest, possibly because the
8 species is a short (ranging from 150- 900 mm in culm height) (Van Oudtshoorn 2002).

9
10 In the present study, root biomass was the same for undefoliated and plants defoliated
11 twice or three times during the growing season. Plants defoliated once produced more
12 belowground phytomass. However, it is possible to assume that a reduction in
13 belowground growth will affect uptake of nutrients and storage abilities (Thornton and
14 Millard 1996). The differences in belowground phytomass can be explained by the
15 morphology or architecture of the grass species selected in this study. In addition roots
16 are sensitive to shading experienced by the leaves (Langer 1972). The results show the
17 opposite effect, a reduction in root biomass, when *T. triandra*, *E.plana* and *E. curvula* are
18 defoliated when compared to undefoliated tufts. Light is an important factor in plant
19 competition. A stressed tuft in a dense sward will experience suppressed root growth
20 which would reduce its capability to absorb water and minerals. The results of this study
21 suggest that increased defoliation frequency does not affect all species by significantly
22 reducing the root biomass, but instead this effect is species specific. Belowground
23 phytomass of *T. triandra* and *T. leucothrix*, two species known to grow together in mesic

1 grasslands was not affected by frequent defoliation. In contrast, the *Eragrostis spp.* that
2 showed the greatest root biomass under no defoliation (*E. curvula*) and a single
3 defoliation (*E. plana*). This implies that *E. plana* may indeed become a stronger
4 competitor for belowground resources than *E. curvula* within lightly defoliated mesic
5 grasslands. For *E. plana* specifically this contradicts reports by Davidson and Milthorpe
6 (1966) indicating that declines in nutrient absorption and respiration following defoliation
7 are related to defoliation intensity. Furthermore, *E. curvula*'s decline in belowground
8 phytomass when defoliated may be explained by carbohydrate supply, which is the main
9 reason why root growth rates decline when leaves are defoliated. Clement et al. (1978)
10 indicate that the perennial pasture grass *Lolium perenne* demonstrated declined
11 absorption rates of nitrate (NO₃⁻) after 70% of its shoot biomass had been removed. To
12 summarise the findings – defoliation frequency has a little effect on root biomass,
13 differences were noticeable between species and this may be linked to morphology.

14
15 It is suggested that *T. triandra* is a species relatively sensitive to defoliation (Coughenor
16 et al. 1985) especially heavy grazing (Lock and Milburn 1971, Morris and Tainton 1993)
17 however this study contradicts these suggestions. This study confirms that *T. triandra* can
18 tolerate moderate levels of grazing, similar to reports by Morris and Tainton (1993), with
19 a decreased potential of compensating for loss material when compared to *T. leucothrix*
20 and *E. plana*. Complications associated with the use of “moderate grazing” are twofold,
21 firstly, how does one define the term moderate and secondly, under which grazing
22 regimes is moderate grazing most applicable and beneficial to the farmer. To investigate
23 part of this issue, four defoliation frequencies were used in this experiment. Results

1 indicate that severe (defoliated to a height of five centimeters) and frequent (defoliated
2 three times during the growing season) defoliation affects tuft structure by reducing height
3 and tillering, thus accepting the third hypothesis. This was more evident for tuft height
4 than tillering. As expected defoliation frequency significantly affected tuft height with
5 undefoliated tufts being the tallest and tufts defoliated three times being the shortest. Tuft
6 height is not always related to the degree to which a tuft is grazed (O'Connor 1992). This
7 statement is debateable because tuft height may not mean that herbivores will only feed
8 on tall species and avoid shorter species. Selective herbivores such as sheep may prefer
9 shorter species like *T. leucothrix* due to its reasonable leaf production and nutritional
10 value (Van Oudtshoorn 2002). Foliage density will decrease with tuft height suggesting
11 that a logistic relationship between the two morphological traits (Wade and Carvalho
12 2000), supporting the results of this study.

13

14 Evidence indicating that tuft exposure to increased light intensity leads to increased
15 tillering (Cullen et al. 2006). Therefore, it is expected that undefoliated plants would be
16 shaded and receive less intense light than defoliated plants and this would reduce tillering
17 within these individual tufts. Unexpectedly, undefoliated tufts produced more tillers than
18 defoliated tufts in this study. The Red: Far Red ratio decreases when light passes through
19 leaves, inhibiting tillering in plant communities with tall dense plants (Cullen et al. 2006).
20 Cullen et al. (2006) report that in all species, undefoliated individuals produced more tillers
21 than defoliated individuals. This is possibly due to plants not having enough recovery time
22 to produce new tillers before the next clipping. These findings are similar to the results of
23 this study. The results indicate reveal that frequent and severe defoliation reduces

1 tillering. Defoliation should result in the sharing of resources between mature intact tillers
2 and defoliated tillers (Marshall and Sagar 1965; Ryle and Powell 1975; Cullen et al. 2006).
3 It is possible that this did not occur in this experiment because tufts were intensely
4 defoliated, leaving very little if any leaf material on the tuft. Resting time may also have
5 not been sufficient to allow new leaves to develop to support tiller development. Cullen et
6 al. (2006) stated that mature tillers cannot support defoliated tillers indefinitely.
7 Carbohydrate resources are reduced by shading (Ong and Marshall 1979), repeated and
8 severe defoliation (Fulkerson 1994) resulting in tiller reduction or plant mortality (Cullen
9 et al. 2006). An important implication of the results of this experiment is that frequent and
10 severe defoliation negatively affects tillering and this may be more harmful to younger
11 developing plants, if resting of veld is not implemented as part of the grazing regime.

12
13 Severe defoliation increased the root to shoot biomass ratio with no species specific
14 effects. Infrequent defoliation increased the root to shoot biomass ratio of grazing-tolerant
15 *E. plana*, while grazing-sensitive *E. curvula* was unaffected. The effects of defoliation
16 frequency revealed that *T. triandra* and *E. curvula* were able to maintain root to shoot
17 biomass regardless of defoliation frequency. In contrast to this, *T. leucothrix*, maintained
18 root to shoot biomass but had greater belowground biomass when undefoliated. Ratios
19 were maintained up until defoliation frequency was increased to two and three times
20 within the growing season for *E. curvula*. For *E. plana* a single defoliation decreased root
21 to shoot biomass ratio but no defoliation and defoliating twice or three times resulted in a
22 shift in resources being allocated towards root growth. Thus, the fourth hypothesis that
23 frequent and severe grazing reduces the root to shoot biomass ratio in grazing-sensitive

1 species was rejected. In this study, root to shoot ratios were significantly different between
2 species, indicating a strong influence of root biomass on root to shoot ratio biomass
3 allocation. Similarly, a study on eight British grasses (four Increaser and four Decreaser
4 species) revealed differences in root: shoot ratios among species (see Table 2, Del-Val
5 and Crawley 2005). The present results indicate that *E. plana* had the highest root: shoot
6 ratio and *E. curvula* had the lowest. Monk (1966) suggests that high root to shoot biomass
7 ratios indicate that belowground competition is high. It is therefore beneficial to assess
8 root to shoot biomass in plants grown with competition with low and high nutrient
9 availability as this may influence plant interactions. In general, the species do not follow
10 the response patterns of the ecological grazing groups of Decreasers and Increasers or
11 the grazing tolerance patterns revealed in this study (*T. leucothrix*, *T. triandra* and *E. plana*
12 vs *E. curvula*). Although root to shoot biomass ratios can be useful estimators of plant
13 response, generalisations are difficult to make considering that these estimates tend to
14 be highly variable (Synman et al. 2013). These estimates of root: shoot ratios may be
15 influenced by factors such as the way in which the roots were extracted and the point
16 during the growing season when the roots were extracted (Ingram and Leers 2001).

17 **CONCLUSIONS**

18 Responses of grass species to repeated defoliation are not explained by grazing
19 response groups. In fact, different defoliation tolerances were observed for species within
20 the same response groups, suggesting that ecological classification of grazing response
21 may not be useful in determining how species tolerate grazing. Under- compensation was
22 observed for *T. triandra* and *E. curvula* and slight overcompensation for *T. leucothrix* and
23 *E. plana*, in terms of aboveground phytomass and none of the morphological responses

1 measured were good predictors of defoliation tolerance. Given that the four species
2 studied did not respond in the manner typical of their grazing response groups, their
3 individual response in terms of aboveground phytomass production may be as a result of
4 their morphology. Many experiments focussing on defoliation have not considered
5 recovery time as a variable, ignoring its important role in how plants respond to defoliation
6 (Oosterheld and McNaughton 1988). Plants defoliated three times had little time to
7 recover, suggesting that time for regrowth or resting is an important factor that needs to
8 be considered when applying a grazing regime. In terms of changes in species
9 composition, the results did not support the hypothesized functional model proposed by
10 Briske (1996). A typical change in mesic grasslands is for unpalatable species to replace
11 palatable species, decreasing forage quality, and quantity and as a result reducing
12 livestock health. Veld managers need to consider their current species composition and
13 apply a lenient but frequent grazing system as results show that desirable species (*T.*
14 *triandra* and *T. leucothrix*) are tolerant to moderate defoliation and have the potential for
15 compensatory growth. However, understanding grazing tolerance in a sward while
16 experiencing competition may provide valuable insight to develop effect management
17 regimes. Findings in this chapter support the need to assess tolerance of two species that
18 grow in competition in mesic grasslands that have been identified as grazing tolerant (*T.*
19 *triandra*) and grazing intolerant (*E. curvula*).

1 **CHAPTER 4: THE EFFECT OF DEFOLIATION AND COMPETITION ON**
2 ***THEMEDA TRIANDRA* WHEN COMPETING WITH *ERAGROSTIS CURVULA***
3

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

5
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9
10
11 This chapter focuses on the effect of defoliation and competition on *Themeda triandra*
12 when competing with *Eragrostis curvula*. The relevance of competition between/among
13 plants has been realised for a long time, however the magnitude of its effect on species
14 performance has long been debated (Grime 1973; Tilman and Wedin 1991). This
15 supports the need for additional experimental studies that test the effect of competition
16 and simulated herbivory on two important grass species that interact in South African
17 mesic grasslands.

ABSTRACT

1
2 Understanding effects of defoliation and competition on palatable and less
3 palatable grass species is important in order to make informed decisions when
4 managing mesic grasslands. The responses of a highly palatable grass species,
5 *Themeda triandra*, to two levels of defoliation (no defoliation and defoliation) and
6 three levels of competition (none, partial and full competition) with a less palatable
7 species, *Eragrostis curvula*, over the summer growing season were investigated
8 using a pot trial. *Themeda triandra* was able to over-compensate and tolerate
9 defoliation under no competition and partial competition (with the competitor
10 defoliated) but was intolerant under full competition. When the competitor was
11 defoliated it did not matter if the target was defoliated or not because the
12 competitive suppression experienced by the target was the same. In contrast, when
13 the competitor was undefoliated then defoliation of the target plant caused
14 competitive suppression while undefoliated target plants experienced facilitative
15 effects. Overall, a greater competitive suppression was experienced by *T. triandra*
16 under conditions of selective defoliation than non-selective defoliation.
17 Unexpectedly, frequent defoliation and competition did not affect tillering but
18 increased the tuft height of *T. triandra*. Under non-selective defoliation conditions,
19 *T. triandra* was able to grow taller than under selective grazing. This implies that *T.*
20 *triandra* is more productive under conditions of lenient, non-selective defoliation
21 when it is competing with *E. curvula*. These results need to be considered as a
22 basis to understand how *T. triandra* swards respond at the tuft-tuft scale and

1 further investigations are necessary to validate the broader impact on natural
2 communities.

3 **Key words:** Humid grassland, red grass, herbivory, neighbouring plants

4

5

INTRODUCTION

6 *Themeda triandra*, commonly known as red grass in South Africa, dominates grasslands
7 and savannas in many parts of the world including southern and eastern Africa and the
8 Middle East (Snyman et al. 2013). The presence of *T. triandra* indicates that a grassland
9 is in good condition and it declines in abundance when heavily grazed or ungrazed
10 (Everson and Tainton 1985, Van der Westhuizen et al. 2001).

11

12 The main factors that determine grassland species composition are how the species are
13 able to compete (Aarssen and Turkington 1985), grazing regimes (Tallowin et al. 1989)
14 and the interaction of grazing and competition (Crawley and Ross 1990). Mature grass
15 tufts will not respond in the same way to competition from the surrounding sward (Tedder
16 et al. 2011). The ability of grasses to respond to competition may be affected by
17 availability of resources, which influences biomass production and tillering (Tedder et al.
18 2011). Through resource provision, soil type also affects the competitive advantage one
19 species may have over another, affecting species distribution and sward composition
20 (Fynn et al. 2005).

21

22 Herbivore induced changes in species composition may be explained by two possible
23 scenarios (Anderson and Briske 1995). Firstly, through the limited ability of late-seral
24 dominant species to replace lost tissues following herbivory, suggesting their inability to

1 tolerate intensive herbivory and secondly, when late-seral plants are selectively foraged
2 by animals as a result of avoidance mechanisms exhibited by other species (Anderson
3 and Briske 1995). It is suggested that species that are grazed less severely, recover better
4 after defoliation, thus possessing a combination of tolerance and avoidance mechanisms
5 resulting in a competitive advantage (Caldwell et al. 1981; Briske 1991).

6
7 The response of plants towards competition may be affected by factors including inter-
8 plant distance and methods of resource acquisition (Frecklelton and Watkinson 2001).
9 Competitive interactions can be symmetric or asymmetric (Weiner 1988). Symmetric
10 competition refers to resources being shared among plants equally, while asymmetric
11 competition is the unequal sharing of the available resources where larger plants may
12 have an added advantage over smaller plants (Weiner 1993; Freckleton and Watkinson
13 2001).

14
15 Defoliation affects different plant traits in various ways (Ferraro and Oesterheld 2002). A
16 study on how two grass species (*Briza subaristata* Lam. and *Stipa baviensis* Speg.)
17 respond to defoliation revealed the ability of these grasses to maintain shoot biomass
18 regardless of defoliation intensity (Oesterheld 1992). However, this is only achieved when
19 sufficient time is given for the plant to recover (Oesterheld and McNaughton 1988). The
20 way a study is conducted is also known to affect the outcome of the results. For example,
21 experimental studies examining shoot and root biomass allocation performed on potted
22 plants may be biased and negatively affected by pot size (limiting root growth)
23 (Oesterheld 1992).

1 Competition and herbivory are two very important factors that affect plant growth and can
2 strongly influence phenotypes (Painter and Belsky 1993). As the intensity of grazing
3 increases, shorter plant species tend to do better than tall species (Bradshaw 1959,
4 possibly because taller plants become more visible and accessible to grazers when the
5 veld is patchy with tufts varying in height. When animals graze selectively, plant
6 competitiveness and production of preferred species is reduced, resulting in a change in
7 species composition (Teague et al. 2016). In addition to selective grazing, weather
8 conditions such as drought may magnify the negative impacts on preferred species (Scott
9 1979; Fowler 1986; Briske 1991).

10

11 The relationship between herbivory and biomass production has received very little
12 attention from researchers in general (Bonser and Reader 1995), and even less so in
13 South Africa. Those experimental studies on herbivory and biomass production that have
14 been conducted have also shown inconsistent results (Bonser and Reader 1995),
15 suggesting a need for further work.

16

17 The aim of this experiment was to determine the response of *Themeda triandra* to
18 defoliation and interspecific competition with *Eragrostis curvula*. The first objective was to
19 determine the defoliation tolerance, in terms of the aboveground phytomass production,
20 of *T. triandra* when growing with clipped and unclipped *E. curvula*. This objective
21 addressed the question, is *T. triandra* tolerant to defoliation when interacting with
22 defoliated and undefoliated tufts of another species? It was hypothesized that tolerance
23 to defoliation would be reduced by the presence of another species. The second objective

1 was to determine how *T. triandra* responds to different levels of competition from *E.*
2 *curvula* (defoliated and undefoliated). The second research question was, what is the
3 effect of defoliation of *T. triandra* on the interactions between *T. triandra* and *E. curvula*?
4 It was hypothesized that defoliation would cause *T. triandra* to experience greater
5 competitive suppression. The third objective was to understand the morphological
6 responses (tillering and tuft height) of *T. triandra* to various levels of defoliation and
7 competition. The third objective addresses the question, how do defoliation and
8 competition affect the morphological structure (tillering and tuft height) of *T. triandra*? It
9 was hypothesized that defoliation and competition would reduce tillering rate and tuft
10 height of *T. triandra*.

11

12

METHODS

13 In order to investigate the effect of defoliation and competition on *T. triandra*, a single
14 intense clipping was applied every 2.5 weeks to the tufts using a pot trial experiment.
15 Data were collected only for the target species, *T. triandra*.

16

Study species

18

19 Two grasses, of differing palatability, that are common in South African mesic grasslands
20 were selected to investigate competitive interactions in the presence of defoliation. *T.*
21 *triandra* is classified as a Decreaser species and it dominates grasslands with well-
22 drained soils that undergo some form of moderate to light non-selective defoliation, such
23 as burning or mowing (Fynn 2004), and *E. curvula* is classified as an Increaser 1 species

1 and the presence of this grass indicates that the area has been subjected to overgrazing
2 or too frequent burning (Van Oudtshoorn 2002). *Themeda triandra* is unable to withstand
3 frequent and intense defoliation and can be replaced by increaser grass species, such as
4 *E. curvula*. In mesic grasslands dominated by these grasses, the competitive ability and
5 biomass production of these species has received little attention. The defoliation
6 tolerance of *T. triandra* and its morphological responses when defoliated and competing
7 with *E. curvula* was investigated to provide insight for refining veld management
8 strategies.

9

10 **Experimental design**

11 The experiment was performed in a shade house at the NM Tainton Arboretum, University
12 of KwaZulu-Natal, Pietermaritzburg in South Africa. Tufts of *T. triandra* and *E. curvula*
13 were collected from Ukulinga Research Farm, Pietermaritzburg. Within a day of collection
14 each tuft was separated into 8 or more smaller tufts, depending on the quality of the roots,
15 which were transplanted into individual pots. These were planted as soon as possible
16 after collection to avoid drying out of plants and possible transplant stress. The grass tufts
17 were planted in sand and supplemented with a nutrient solution (Hoagland's solution)
18 (Hoagland and Arnon 1950).

19

20 This study was a pot trial where the size of the plastic pots were as follows: diameter –
21 280 mm, circumference of the pot – 890 mm, height – 350 mm. The plastic pots consisted
22 of eight holes (each having a diameter of 20 mm) located 30 mm from the base of the
23 pot. Sand was used because of a lack of nutrients. This allowed for Hoagland's solution
24 to be added to each pot, to control for nutrient level per pot. All pots received

1 approximately the same amount of sand however sand drying was not done to assure
2 pots received the same amount of sand. This pot trial was performed in a shade house
3 under light shade cloth (20%). Each pot included one tuft of the target plant planted in the
4 centre of the pot and those allocated to the competition treatment included four competitor
5 tufts surrounding the target plant. The four competitor tufts were planted 100 mm away
6 from the single target tuft. Target plant refers to *T. triandra* and competitor plant refers to
7 *E. curvula*. The treatments consisted of a 3 x 2 factorial design. This experiment consisted
8 of two factors, firstly target defoliation and secondly competition. Target defoliation had
9 two levels of defoliated and undefoliated. Competition had three levels of no competition,
10 competitor defoliated and competitor undefoliated. In total there were six treatment
11 combinations; 1) target defoliated + alone, 2) target defoliated + competitor undefoliated,
12 3) target defoliated + competitor defoliated, 4) target undefoliated + alone, 5) target
13 undefoliated + competitor undefoliated and 6) target undefoliated + competitor defoliated.

14

15 There were two control treatments (1) with the target species growing alone undefoliated
16 and (2) with the target species growing alone defoliated. The remaining four treatment
17 combinations consisted of pots where the target and the competitor species were grown
18 together as follows: 1) target undefoliated + competitor undefoliated, 2) target
19 undefoliated + competitor defoliated, 3) target defoliated + competitor undefoliated and
20 4) target defoliated + competitor defoliated.

21

22 The trial was arranged in a completely randomised design and plants were watered every
23 other day and twice a day on extremely hot days. After the trial had been planted the tufts

1 were given 14 days to establish before clipping treatments were applied. Initially, all plants
2 were cut to a standing height of approximately 150 mm to make sure that the tufts were
3 physically similar at the outset of the trial. Thereafter, assigned treatments were clipped
4 to a height of 100 mm above sand surface every 2.5 weeks. After each clipping the clipped
5 biomass was bagged, oven dried (80 °C) for 48 h and weighed. Final aboveground
6 phytomass was added to previous clippings to determine cumulative aboveground
7 phytomass for each pot. Aboveground phytomass was measured but belowground
8 phytomass was not due to the difficulty associated with separating the roots of the two
9 species.

10

11 **Data analysis**

12 *Defoliation tolerance*

13 To address the first objective, defoliation tolerance was determined as a percentage using
14 cumulative shoot biomass for each individual pot. The mean from the control was then
15 subtracted from each cumulative shoot biomass per pot using equation below (similar to
16 Del-Val and Crawley 2005):

17

$$18 \text{ Defoliation tolerance (\%)} = \frac{\text{Aboveground phytomass of pot (g)} - \text{Mean aboveground phytomass of control (g)}}{\text{Mean aboveground phytomass of control (g)}} * 100$$

19

20 Defoliation tolerance data was analysed in GenStat 18. To determine the difference in
21 defoliation tolerance between the three levels in the competition treatment. To determine
22 if there were treatment differences in defoliation tolerance a two-way analysis of variance
23 (ANOVA) was used. This was performed after testing the assumptions of ANOVA of
24 normal distribution of residuals and equal variances of the residuals among the

1 treatments. When the ANOVA revealed significant differences, a Fisher's test (LSD) was
2 used to separate the means.

3

4 *Relative Interaction Index*

5 Relative interaction indices (RII) were calculated for cumulative shoot biomass (Armas et
6 al. 2004). RII represents the net loss or gain of a measurable trait as a result of the inter-
7 specific interaction relative to the value of the trait when there is no inter-specific
8 interaction. The index is calculated using the formula below:

$$9 \quad RII = (Bw - Bo)/(Bw + Bo)$$

10 Where BW represents the shoot biomass of the tuft growing with interspecific interaction
11 and Bo represents the shoot biomass of tufts growing without interspecific interaction
12 (Armas et al. 2004). The calculated value of the ratio range from -1 to 1. The negative
13 values indicating competition, zero indicate symmetry and positive values suggest
14 facilitation is occurring (Armas et al. 2004).

15

16 The RII data was analysed in GenStat 18. To determine the difference in RII for the main
17 and interaction effects of target defoliation and competitor defoliation an analysis of
18 variance (ANOVA) was used. This was performed after testing the assumptions of
19 ANOVA of normal distribution of residuals and equal variances of the residuals among
20 the treatments. When the ANOVA revealed significant differences, a Fisher's test (LSD)
21 was used to separate the means.

22

23

1 *Cumulative and morphological responses*

2 Aboveground phytomass was determined from the cumulative aboveground phytomass
3 over the growing season. Tiller numbers were calculated as a percentage of the initial
4 numbers (Bullock et al. 1994 see Figure 1, pg. 334). Hence, tillering was determined from
5 the following formula;

6

7
$$\text{Tillering} = \frac{\text{No. of tillers (final)} - \text{No. of tillers (initial)}}{\text{No. of tillers (initial)}} * 100$$

8 A general analysis of variance (ANOVA) was used to assess the effects of defoliation and
9 competition on tillering and tuft height of *T. triandra*. All variables were analysed in
10 GenStat 18. Each variable was analysed separately. This was performed after testing the
11 assumptions of ANOVA of normal distribution of residuals and equal variances of the
12 residuals among the treatments. Tillering were subjected to square root transformations
13 to meet the assumptions of ANOVA. Height data were not transformed as data met the
14 assumptions of ANOVA. When the ANOVA revealed significant differences, a Fisher's
15 test (LSD) was used to separate the means for the main effects and a Tukey's test (HSD)
16 was used for the two-way interaction effects.

17

18 **RESULTS**

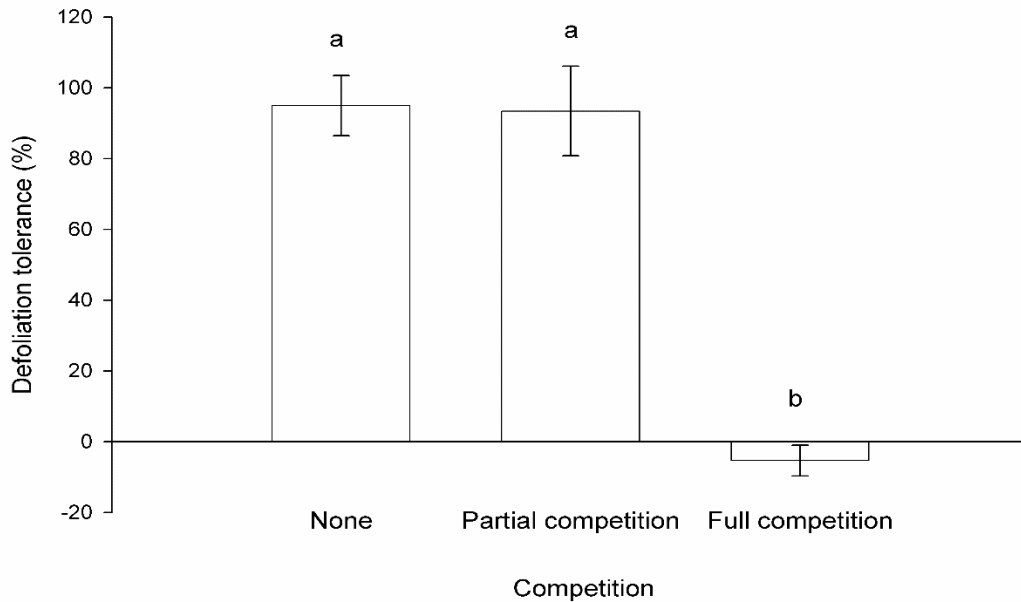
19

19 *Defoliation tolerance*

20

21 There was a significant difference ($F_{2, 27} = 39.420$, $p < 0.001$, $n = 30$) in defoliation tolerance
22 among the treatments. *Themeda triandra* was able to over compensate and tolerate
23 defoliation under no competition ($94.400 \pm 8.493\%$) and partial competition ($93.400 \pm$

1 12.670%), while under compensation was observed under full competition ($-5.370 \pm$
2 4.343%) (Figure 4.1).



3
4 Figure 4. 1. Mean defoliation tolerance (%) (\pm SE) of *T. triandra* ($F_{2, 27} = 39.420$, $P < 0.001$).
5 Percentages above zero indicate overcompensation and below zero indicate under
6 compensation resulting from loss of shoot biomass (aboveground phytomass). Letters in
7 common indicate non-significance ($P > 0.05$). Graphs shown are from untransformed
8 data.

9 *Relative Interaction Index (RII)*

10

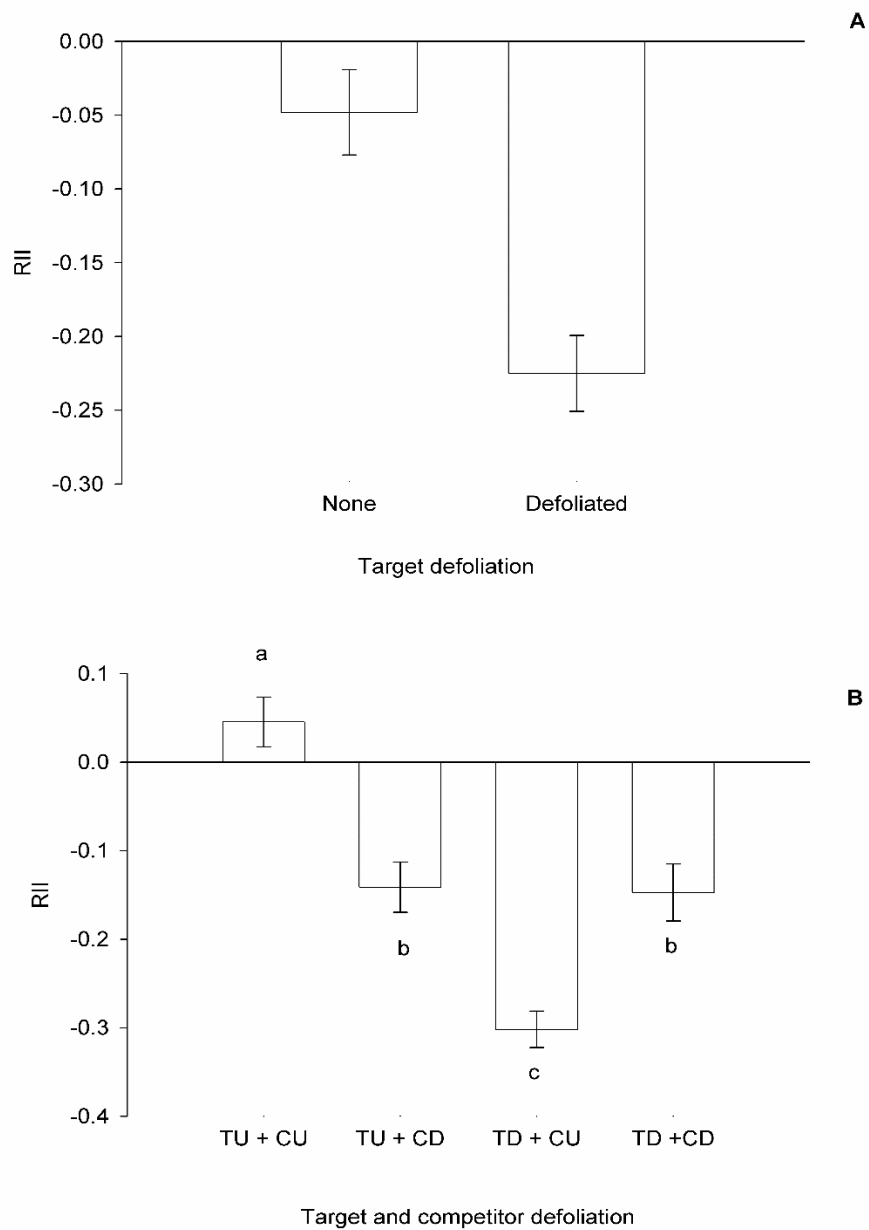
11 The main effect of RII was significant for target defoliation ($F_{1, 36} = 40.740$, $p < 0.001$, $n =$
12 40) (Table 4.1), with *T. triandra* experiencing a greater competitive suppression when
13 defoliated (-0.225 ± 0.026) compared to when it is undefoliated (-0.049 ± 0.029) (Figure
14 4.2 A). The main effect of competitor defoliation was non-significant ($F_{1, 36} = 0.330$, p
15 $= 0.571$, $n = 40$) (Table 4.1). The interaction effect of target and competitor defoliation was

1 significant ($F_{1,36}=38.080$, $p < 0.001$, $n = 40$) (Table 4.1). When the competitor is defoliated
 2 it does not matter if the target is defoliated (-0.141 ± 0.029) or undefoliated ($-0.147 \pm$
 3 0.032) because the competitive suppression experienced by the target is the same
 4 (Figure 4.2 B). In contrast, when the competitor is undefoliated it makes a significant
 5 different if the target is defoliated (-0.302 ± 0.021) or undefoliated (0.045 ± 0.028) because
 6 the competitive suppression experienced by the target greater and a facilitative effect is
 7 observed respectively (Figure 4.2 B).

8 Table 4. 1: Results of analysis of variance of the main effects and interactions of
 9 defoliation and competition for the relative interaction indices of *Themeda triandra*. The
 10 degrees of freedom (d.f), F-ratio and p-values are shown, with significant **bold***

	d.f	s.s	m.s	F- ratio	p-value
Target defoliation (T)	1	0.312	0.312	40.740	< 0.001*
Competitor defoliation (C)	1	0.002	0.003	0.330	0.571
T.C	1	0.291	0.291	38.08	< 0.001*
Residual	36	0.275	0.008		
Total	40				

11



1

2 Figure 4. 2. Mean RII (\pm SE) calculated from cumulative shoot biomass of a) the main
 3 effect of *T. triandra* defoliation ($F_{1, 36} = 40.740$, $P < 0.001$) and b) interaction of target and
 4 competitor defoliation effect ($F_{1, 36} = 38.080$, $P < 0.001$). Letters in common indicate non-
 5 significance ($P > 0.05$). Graphs shown are from untransformed data. Key: TD (target
 6 defoliated), TU (target undefoliated), CD (competitor defoliated) and CU (competitor
 7 undefoliated).

1 *Tuft Morphology – Tillering*

2

3 There was no significant effect of target defoliation, competitor defoliation or their
4 interaction on the tillering of *T. triandra* (Table 4.2).

5 Table 4. 2: Results of analysis of variance of the main effects and interactions of
6 defoliation and competition for tillering of *Themeda triandra*. Data was square root
7 transformed. The degrees of freedom (d.f), F-ratio and p-values are shown.

	d.f	s.s	m.s	F- ratio	p-value
Target defoliation (T)	1	558.500	558.500	2.830	0.098
Competitor (C)	2	1097.400	548.700	2.780	0.071
T.C	2	251.600	125.800	0.640	0.533
Residual	54	10665.200	197.500		
Total	60				

8 *Tuft Morphology –Final tuft height*

9

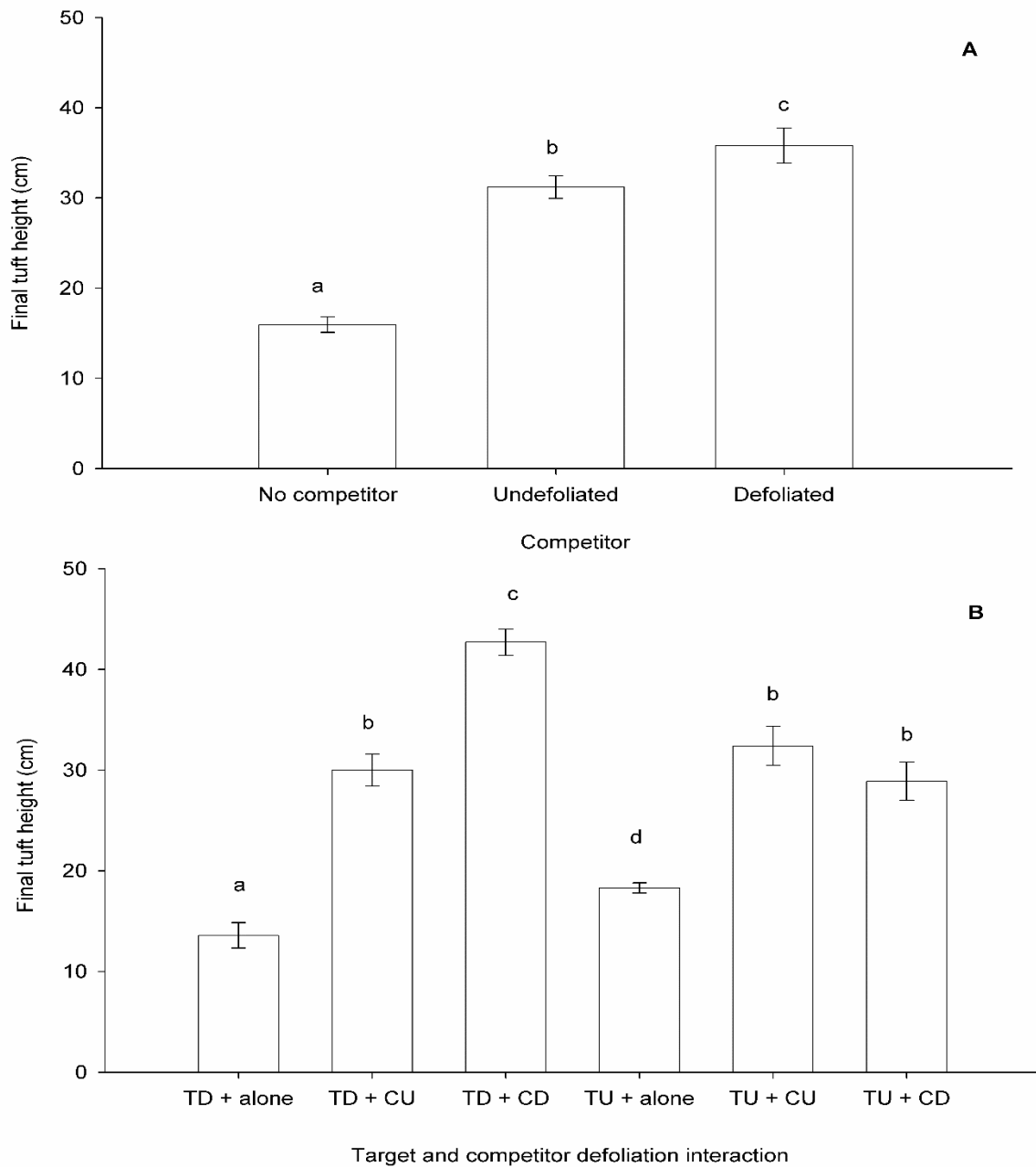
10 There was no main effect of target defoliation on tuft height ($F_{1, 54} = 3.350$, $P = 0.073$, $n =$
11 60) (Table 4.3). When the competitor was defoliated it resulted in taller *T. triandra* tufts
12 (35.800 ± 1.938 cm) compared to when the competitor was not defoliated (31.200 ± 1.252
13 cm) and no competitor present (15.950 ± 0.851 cm) ($F_{2, 54} = 96.690$, $P < 0.001$, $n = 60$)
14 (Table 4.3) (Figure 4.3 A). Target and competitor defoliation interaction significantly
15 affected tuft height of *T. triandra* ($F_{2, 54} = 22.760$, $P < 0.001$, $n = 60$) (Table 4.3). Tufts were
16 tallest when both the *T. triandra* and the competitor were defoliated (42.700 ± 1.300 cm)
17 ($F_{2, 54} = 22.760$, $P < 0.001$) (Table 4.3) (Figure 4.3 B) and shortest when *T. triandra* was
18 defoliated in the absence of a competitor (13.600 ± 1.258 cm) ($F_{2, 54} = 22.760$, $P < 0.001$)

1 (Table 4.3) (Figure 4.3 B). When the competitor is undefoliated, the defoliation regime
2 imposed on the target is not important because tuft height was the same (Figure 4.3 B).

3 Table 4. 3: Results of analysis of variance of the main effects and interactions of
4 defoliation and competition for final tuft height of *Themeda triandra*. The degrees of
5 freedom (d.f), F-ratio and p-values are shown, with significant **bold***

	d.f	s.s	m.s	F- ratio	p-value
Target defoliation (T)	1	74.820	74.820	3.350	0.073
Competitor (C)	2	431.830	2159.150	96.690	< 0.001*
T.C	2	1016.630	508.320	22.760	< 0.001*
Residual	54	1205.900	22.330		
Total	60				

6



1
 2 Figure 4. 3. Mean tuft height (\pm SE) of *Themeda triandra* for A) the main effect of
 3 competitor ($F_{2,54} = 96.690$, $P < 0.001$) and B) the interaction between target defoliation and
 4 competitor ($F_{2,54} = 22.760$, $P < 0.001$). Graphs shown are from untransformed data. Key:
 5 TD (target defoliated), TU (target undefoliated), CD (competitor defoliated) and CD
 6 (competitor undefoliated).

DISCUSSION

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The main results in this study reveal that defoliation tolerance was the same for *T. triandra* tufts growing under no competition and partial competition, and over-compensatory growth was observed under these conditions. In fact the tested hypothesis was not rejected. *Themeda triandra* was less tolerant of defoliation under full competition and demonstrated under-compensation in terms of shoot biomass. Morris (2016) states that compensation or over-compensation tend to occur when resources are limiting in the environment or plants are under intensive competitive pressure. Oosterheld and McNaughton (1991) further add that compensation most likely occurs when plants are experiencing the least amount of stress. The results of this study are attributed to changes in competitive pressure because nutrients and water were controlled and not limiting. The findings of *T. triandra*'s tolerance to defoliation disputes claims that it is a species sensitive to artificial defoliation or grazing (Coughenour et al. 1985; Morris 2017). In addition, many authors have shown that *T. triandra* is unable to withstand heavy grazing and that its growth is suppressed by intensive grazing (Heady 1964; Lock and Milburn 1971; Foran et al. 1978; Snyman et al. 2013). Based on the defoliation tolerance results from chapter 3, *E. curvula* was determined to be a grazing intolerant species and this may partially explain how *T. triandra* could remain tolerant to defoliation and competition against *E. curvula*. Plant recovery and tolerance following defoliation is influenced by competition exerted by more grazing tolerant neighbouring plants (Caldwell and Richards 1986; Cottam 1986; Crawley 1990) and this further supports the importance of assessing species tolerance in light of defoliation and competition.

1 The hypothesis associated with competition was also not rejected. *Themeda triandra*
2 experienced a greater competitive suppression when defoliated. Furthermore, a greater
3 competitive suppression was experienced by *T. triandra* under conditions of selective
4 defoliation than non-selective defoliation. These results are important because of the
5 different styles of management used to manage grasslands. A common belief is that
6 continuous grazing results in rangeland deterioration and in contrast rotational grazing
7 maintains good rangelands. However, Briske et al. (2008) reviewed empirical evidence
8 from the past sixty years and found rotational grazing to be no better than or equal to
9 other grazing systems in terms of plant production and animal production per head per
10 area. Universally there is a debate surrounding the efficiency of rotational grazing
11 systems and their ability to improve rangeland conditions (Briske et al. 2011; Briske et al.
12 2013; Monbiot 2014). The available evidence does not show a rotational grazing regime
13 to be superior to a continuous grazing regime in terms of vegetation and soil cover
14 (O'Reagain and Turner 1992; Briske et al. 2008). However, changes in semi-natural and
15 natural grasslands are induced by selective herbivory (Anderson and Briske 1995; Grant
16 et al. 1996). Selective herbivory may change species composition by reducing the
17 competitiveness and reproductive ability of preferred species (Teague et al. 2016). In
18 support, the results of this study reveal that *T. triandra* was negatively affected by
19 selective defoliation because the competitive effect exerted at the point was be high. This
20 implies that *T. triandra* may not be a good competitor under selective pressure from
21 grazers. However, to clarify this, further investigations of the RII and tolerance of the
22 competing species would need to be performed. Certain animals such as sheep known
23 to be more selective feeders than larger animals' herbivore like cattle (Rook et al. 2014)

1 and this may further affect how *T. triandra* responds to selective grazing. Findings of
2 experiments using cattle and sheep may therefore differ from simulated herbivory
3 experiments.

4
5 As stocking densities, frequencies or severity increase, *T. triandra* becomes negatively
6 affected and its regrowth vigour is reduced (Kirkman and Moore 1995; Kirkman 2002).
7 This may be accompanied by reduced tiller numbers and tuft height (Kirkman 2002). In
8 contrast to this statement, frequent defoliation and competition did not affect tillering but
9 increased the tuft height of *T. triandra* in this study. It was expected that tillering would be
10 affected by defoliation and competition because *T. triandra* requires defoliation to
11 stimulate vegetative growth and in the absence of defoliation tufts become moribund
12 (Danckwerts and Stuart-Hill 1987).

13
14 This study revealed that under non-selective defoliation conditions, *T. triandra* was able
15 to grow taller than under conditions selective defoliation. This implies that *T. triandra* is
16 more productive under conditions of non-selective defoliation when it is competing with
17 *E. curvula*. In support of this finding, Fynn et al. (2005) reports, based on a long-term
18 defoliation trial, that mowing an entire grassland non-selectively in the summer growing
19 season allows *T. triandra* to persist in mesic grasslands. Furthermore, an alternative form
20 of management may be used to maintain *T. triandra* abundance, such as burning in the
21 early wet season (Fynn et al. 2005). Different to non-selective grazing is controlled
22 selective grazing where the aim is to maximise the utilisation of desirable grasses and
23 avoid undesirable grasses, which allows them to eventually grow moribund and die out

1 (Booyesen 1969). This idea supports the observations made during this experiment
2 whereby, the competing undefoliated *E. curvula* plants began to senesce and lose their
3 leaves (personal observation), meanwhile the defoliated *T. triandra* plants remained
4 green for a longer. The concept of non-selective grazing is more beneficial towards tuft
5 height growth of *T. triandra* than selective grazing according to this study. This suggests
6 *T. triandra* possibly allocates more resources towards growing taller in competitive
7 environments than when left undefoliated.

8

9 O'Reagain and Turner (1992), report that lenient defoliation should increase forage
10 quality and intake by animals, allowing animal production to be relatively greater than
11 when compared to non-selective grazing (O'Reagain and Turner 1992). However the
12 implementation of selective grazing management may be difficult as it would require
13 extensive control of animal movement which may not be feasible for all farmers. There is
14 also doubt about whether undesirable species really die out through under or no utilisation
15 (O'Reagain and Turner 1992). The assumption that neighbouring plants can reduce target
16 plant fitness (overall productivity) (Aphalo and Ballare 1995) was rejected as results did
17 reveal no effects or enhanced morphological growth responses of *T. triandra*. However,
18 the results of this study are limited to *T. triandra* and *E. curvula* swards. The implication
19 of possibly using only two species in this study is a common occurrence in experiments
20 but may not be used as a generalisation for all species, particularly given the diversity of
21 mesic grasslands (Weiner 1993).

22

CONCLUSION

1
2 Common thought is that the vigour of tufts that are defoliated frequently and severely
3 during the growing season will be relatively less than undefoliated tufts. The regrowth
4 potential of defoliated tufts is also thought to be further negatively affected by the added
5 effects of competition and resulting in species composition changes within plant
6 communities. *Themeda triandra* may be able to tolerate grazing if the grazing is lenient
7 but frequent and competition is present, but not intense. The severe competitive pressure
8 on *T. triandra* under selective grazing is likely linked to it being an uncompetitive species
9 when compared to its neighbouring plants. With this in mind, farmers would need to
10 carefully consider the type of animals stocked to understand what impact this may have
11 on the species composition. A *Themeda triandra* dominated sward will suffer extensively
12 from grazing by sheep when compared to grazing by cattle due to the greater level of
13 selectivity exhibited by sheep.

14
15 Generally speaking, grasslands dominated by *T. triandra* and few *E. curvula* tufts should
16 be leniently grazed every other year with rest applied following a growing season, to allow
17 *T. triandra* tufts to regrow. A non-selective grazing system should be adopted by farmers
18 during the growing season to lower the competitive pressure exerted on *T. triandra* tufts
19 and to enhance morphological growth. These results need to be considered as a basis to
20 understand how *T. triandra* swards respond on a smaller scale and further investigations
21 are necessary to validate impact on natural communities.

1 **CHAPTER 5: SYNTHESIS AND RECOMMENDATIONS**
2 **FOR FURTHER RESEARCH**

3
4 For years, rangeland managers have been forced to make decisions regarding
5 management with little supporting empirical data to guide these decisions (O'Reagain and
6 Turner 1992). This has led to many managers relying on their intuition and observations
7 when deciding how their rangelands should be managed (O'Reagain and Turner 1992).
8 Although many researchers have claimed that certain management practices are superior
9 to others, debates continue worldwide as to which management is best suited for
10 rangelands. Some management regimes may have applicability in certain regions of the
11 world but may need support from empirical evidence. This supports the need to
12 synthesize the available empirical evidence and highlight the specific recommendations
13 that can be made from the experiments explained in chapters three and four of this
14 dissertation.

15
16 The results and recommendations of these experiments are limited to the grass species
17 used and thus grasslands that are dominated by them. The focus was on their persistence
18 or lack thereof in mesic grasslands.

19 **Aim**
20

21 The main aim of the research was to determine how Increaser and Decreaser grass
22 species common in mesic grasslands tolerate defoliation and competition.

SYNTHESIS

1
2 Grasslands are very important ecosystems that support a large number of animals, but
3 they can be completely transformed as a result of herbivory (Huntly 1991; O'Connor and
4 Bredenkamp 2004). A general pattern of change in mesic grasslands is for grazing to
5 negatively affect the dominance of grazing-sensitive grasses by replacing them with
6 grazing-tolerant grasses, often resulting in the decline of more palatable species and
7 forcing animals to forage on less palatable and undesirable species (Milchunas et al.
8 1998; Briske 1996). This change in species composition has to be recorded and
9 monitored for managers to assess the condition of their veld. A number of different
10 methods to assess veld condition have been described and used in KwaZulu-Natal. Veld
11 condition assessments are useful in determining the "health" of the vegetation (Hardy and
12 Hurt 1999). The methods proposed include the Benchmark Method (BM) (Hardy and Hurt
13 1999), Ecological Index Method (EIM) (Vorster 1982; Hurt and Bosch 1991), Degradation
14 Method (DM) (Mentis 1983) and the Weighted Key Species Method (WKSM) (Hardy and
15 Hurt 1999). The use of these methods will depend on the type of grassland being
16 assessed, and the expertise and resources available. One of the criticisms of these
17 methods is their use of response groups to categorize species based on how the species
18 responds to grazing. This categorisation into Decreasers and Increaser species may not
19 be the most suitable method in determining veld condition in the mesic grasslands of
20 KwaZulu-Natal. The Increaser-Decreaser model indicates that a decline in carrying
21 capacity would result from over-utilization or under-utilization (Tainton 1981; Danckwerts
22 et al. 1993). This model also over emphasizes the effects of grazing and does not
23 incorporate the effects of other factors, such as fire (Trollope 1989), which are extensively

1 used as a form of management in mesic grasslands. A more research-driven
2 management model may be more suitable in mesic grasslands. The findings of the
3 experiments in this dissertation suggest that species identity is more important in
4 determining species grazing tolerance than grazing response groups. Understanding the
5 grazing tolerance of grass species within the veld is important because it will allow
6 managers to apply a more suitable grazing regime that will maintain the species
7 composition or change it to meet the requirements of the animals. Findings show that
8 veld managers need to consider their current species composition and apply a lenient
9 (grazing tufts to a height of 10 cm) but frequent (apply 3 grazing sessions) grazing system
10 because highly palatable species (*Themeda triandra* and *Tristachya leucothrix*) are
11 tolerant to moderate defoliation and have the potential for compensatory growth. Grazing
12 management must also incorporate resting as this benefits growth following grazing.
13 Furthermore, empirical evidence suggests that recovery periods should cover the entire
14 growing season, to allow maximum nutrient mineralisation (Scholes and Sanchez 1990;
15 Fierer and Schimel 2002). Grazing systems that do not provide a sufficient recovery
16 period of an entire growing season may not provide the best recovery period (Fynn et al.
17 2017). Understanding species composition is also crucial because species interactions
18 may affect how species respond to grazing. Such interactions may include competition
19 between species. The regrowth potential of defoliated swards can be further negatively
20 affected by the added effects of competition and resulting in species composition changes
21 within plant communities. Results suggest that grasslands dominated by *T. triandra* and
22 few *E. curvula* tufts should be leniently grazed every other year with rest applied following
23 a growing season, to allow *T. triandra* tufts to regrow. A management strategy including

1 a non-selective grazing system should be adopted during the growing season to lower
2 the competitive pressure exerted on *T. triandra* tufts and to enhance growth.

3 **RECOMMENDATIONS**

4

5 A change in the frequency and intensity of grazing may change the species composition
6 and condition of the grassland (Hart et al. 1993). Defoliation frequency and intensity are
7 two different factors that should not be used interchangeably. Frequency refers to how
8 many times over a specified period of time a rangeland/plant is grazed, and intensity
9 refers to the amount of plant material that is removed during grazing. Results indicated
10 that these two factors may impact differently on cumulative productivity and morphological
11 structures. However, frequency of defoliation was revealed to have a more prominent
12 negative impact than intensity. A factor not investigated in these experiments is the
13 potential of invasion by exotic plant species. Durrough et al. (2004) showed that exotic
14 species can invade even under low grazing frequencies. This invasion by exotic species
15 may further affect the growth of palatable grasses by increasing competition for
16 resources. Although *T. triandra* was tolerant to defoliation under partial competition, it was
17 not grazing-tolerant under full competition and this could reduce its ability to regrow. This
18 signal a need to possibly consider or monitor how many times in a season animals spend
19 grazing a particular grassland. However, this does not indicate that the level of intensity
20 should be ignored. It is recommended that constant monitoring of both factors to be done
21 and changes that best suit the veld to be adopted by farmers.

22

23 Categorising grass species into grazing response groups i.e. Decreasers and Increasesers
24 and using this information to infer how species can tolerate defoliation is questionable.

1 This implies that generalisations made about Decreasers and Increasers within mesic
2 rangelands may be challenged. It may possibly not be sufficient for rangeland managers
3 to make assumptions about how these groups respond to grazing, especially when *T.*
4 *triandra* and *T. leucothrix* are dominant. Perhaps testing the tolerance of more than two
5 Decreaser species may yield different results to those already mentioned. However, pot
6 trials using simulated herbivory as a substitute for grazing may provide different results
7 to field experiments. However, pot trials do allow scientists to control for other conditions
8 such as nutrients, allowing for single or more factors to be tested. The tolerance of a
9 particular species may also be highly variable depending on the management system
10 adopted. Based on the results of this experiment, it is recommended for managers to
11 adequately understand their sward structure and grazing tolerance of the main species
12 as this may affect their persistence in grasslands.

13
14 Grazing has a lagged effect on the productivity of grasslands (Fynn et al. 2017) and
15 numerous studies in southern African grasslands have demonstrated this (Barnes and
16 Dempsey 1992; Peddie et al. 1995; Kirkman 2002; Mudongo et al. 2016). With this in
17 mind, the effects of the grazing system used in one growing season will affect the
18 condition of the grassland in the next growing season. Grassland management is an
19 important issue that has received much attention but degradation still occurs as a result
20 of mismanagement. Certain climatic conditions such as droughts may further exacerbate
21 the vulnerability of our grasslands. The amount of grass productivity available for livestock
22 is affected by rainfall (Deshmukh 1984; Fritz and Duncan 1994) and by stocking rates
23 (Sandland and Jones 1975; Briske et al. 2008). This is evident in the reduction of forage
24 available under high stocking rates (Sandland and Jones 1975) especially in periods of

1 low rainfall (Walker et al. 1987; Fritz and Duncan 1994). This was witnessed recently
2 during the 2015/16 South African drought where monthly rainfall was markedly reduced
3 throughout South Africa (see Appendix B). Events such as this may heighten the negative
4 effects of intensive grazing, affecting the persistence of palatable grass species in mesic
5 grasslands. A possible reason explaining why farmers allow intensive grazing to occur is
6 “over-optimism” whereby stock farmers will stock as many animals as they need to
7 maintain a certain level of profits. The consequences of over-optimism include soil erosion
8 which results in veld deterioration mainly caused by high grazing capacity or because of
9 poor advice given to farmers (Meissner et al. 2013). It is also possible for farmers to
10 underestimate their carrying capacity and this may also change species composition. The
11 results highlighted in chapter 4 showed a reasonable *T. triandra* biomass production over
12 the growing season when undefoliated. In mesic grasslands, under-grazing or no grazing
13 may change species composition through replacement of palatable species by less
14 palatable species. Grass productivity is negatively affected by aging leaves and litter
15 accumulation under conditions of no grazing or low intensity grazing conditions as this
16 prevents new growth due to shading of leaves and meristems (Knapp and Seastedt
17 1986). In this dissertation, *T. triandra*'s growth was reduced under no defoliation
18 compared to under conditions of frequent defoliation and competition. Supporting other
19 studies indicating that *T. triandra* declines in productivity in grasslands that are not grazed
20 or burnt (Belsky 1992; Fynn et al. 2005; Eby et al. 2014). Furthermore there may be little
21 benefits derived from not grazing an area as Leriche et al. (2003) indicate that biomass
22 available for grazers is higher in grazed areas as compared to ungrazed areas. The
23 benefits of grazing are supported by several studies providing evidence of compensatory

1 growth in grazed swards (McNaughton 1979; Hilbert et al. 1981; Danckwerts and Nel
2 1989; Hik and Jeffries 1990; Frank et al. 1998). It is recommended that farmers or
3 managers to first determine their goals and objectives before pursuing or adopting a
4 certain management strategy as these differ from those of a communal farmer to that of
5 a commercial beef farmer.

6
7 The effects of not adjusting livestock numbers to the availability of natural resources is
8 problematic and explains part of the degradation seen in our grasslands. In general,
9 palatable grasses will reduce productivity whereas less palatable grasses will increase in
10 response to competition (Barnes and Dempsey 1992; Kirkman 2002). In chapter 4, the
11 results revealed that frequent selective defoliation of *T. triandra* can increase the
12 competitive effect exerted on it by neighbouring undefoliated tufts when compared to
13 conditions of non-selective defoliation. If selective grazing of *T. triandra* continues
14 extensively this could result in selective overgrazing which can damage veld more than
15 when veld is grazed non-selectively. It is recommended that animals are managed in such
16 a way that they feed on most of the grasses present to create a short grazing lawn. This
17 is important because as grasses increase in tuft height, an increase in indigestible
18 structural tissue (cellulose and lignin) occurs, lowering the digestibility (Hobbs and Swift
19 1988; Wilmshurst et al. 2000; Owen-Smith 2002). In this case, the majority of grass
20 species will be short and competition will decrease among species in the absence of tall,
21 ungrazed grasses. Therefore a carefully determined stocking rate is required to create a
22 short grazing lawn with the inclusion of paddocks for rotation.

1 **Challenges**

2 The first challenge associated with this research included the 2015/2016 South African
3 drought that negatively affected conducting field experiments. As a result, experiments
4 had to be redone the following year under controlled conditions using a pot trial. The
5 growing season of 2015 was negatively affected by the decrease in rainfall. Transplanting
6 grass tufts from the natural veld into the experimental field was difficult as plants dried out
7 too quickly and could not adapt to the changes including soil type. The severity of the
8 drought is shown in the monthly differences in rainfall (mm) in South Africa which are
9 shown in Appendix B. These maps compare the monthly rainfall of November (2014/15),
10 December (2014/15) and January (2015/16). A remarkably decline in rainfall in
11 Pietermaritzburg is observed in December, when comparing 2015 and 2016. The drought
12 had a negative effect on the fisheries, forestry and agricultural sectors. The provinces
13 declared disaster areas were KwaZulu-Natal, Mpumalanga, Limpopo, North West, Free
14 State and the Northern Cape. Production was reduced with about 189 707 livestock
15 farmers being negatively affected, including approximately 3.6 million livestock units
16 (South African Yearbook 2015/16).

17

18 Secondly, when designing the experiments, it was challenging to decide how one would
19 define defoliation frequency and defoliation intensity. In an attempt to overcome this, four
20 defoliation frequencies and three intensities were imposed on the plants to compare
21 across the range.

22

23 The third challenge is the use of artificial defoliation through clipping to represent the
24 action of animals grazing. The use of simulated defoliation has been supported by many

1 studies as it allows researchers assess how the plants themselves respond to defoliation
2 regardless of other conditions. However, the findings may be limited in that the grazing
3 action of animals is much more complicated and certain factors such bite size, trampling
4 and animal type might produce different results.

5 **Further research**

6

7 There are many future research opportunities available for this research that may
8 enhance our understanding of how grass species respond to grazing and competition.
9 Some of these include more field based studies involving livestock, manipulating stocking
10 rates, understanding the effects of belowground competition, microorganisms and
11 nutrient absorption.

12

13 It may be valuable to consider if there is a relationship between veld condition and plant
14 diversity of grasslands in southern Africa. This would expand on work by Scott-Shaw and
15 Morris (2008) that revealed that some forb species are increased in abundance and
16 others are not favoured by grazing pressure. The research done on rangeland biodiversity
17 in South Africa has been mainly focused on commercial livestock farming (O'Connor et
18 al. 2010). This is probably because of the problems associated with communal
19 rangelands including transformation of land into peri-urban human settlements (O'Connor
20 et al. 2010). An interesting focus for further studies would be to determine the most
21 effective grazing system that can be applied on commercial farms and on communal
22 grazing areas, with a particular focus on species grazing tolerance, overall biodiversity,
23 species composition and impact on animal condition.

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APPENDIX A

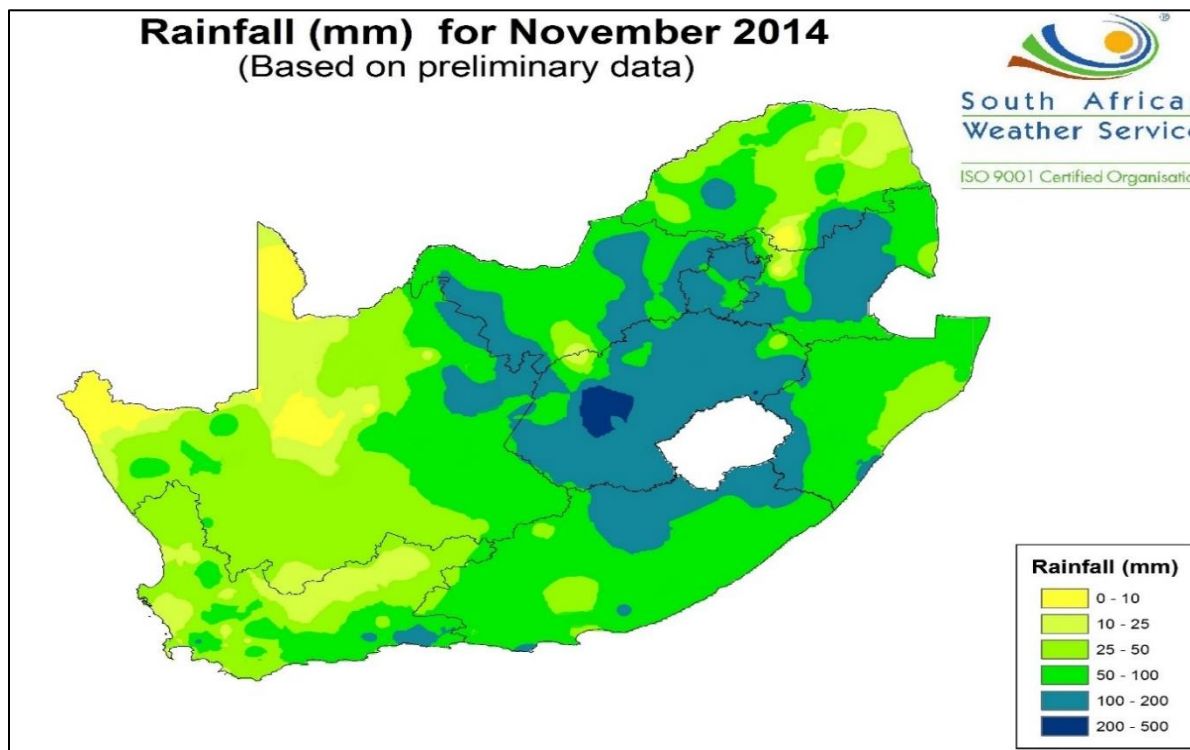
1
2 Table 5. 1: Hoagland's solution

Element	Full concentration g/1000 L
Calcium nitrate	1181.00
Potassium nitrate	505.50
Monopotassium phosphate	136.10
Magnesium sulfate	4.93
Boric acid	2.86
Manganese chloride	1.81
Zinc sulfate	0.22
Copper sulfate	0.08
Molybdic acid	0.02
Ferric sodium EDTA	10.00

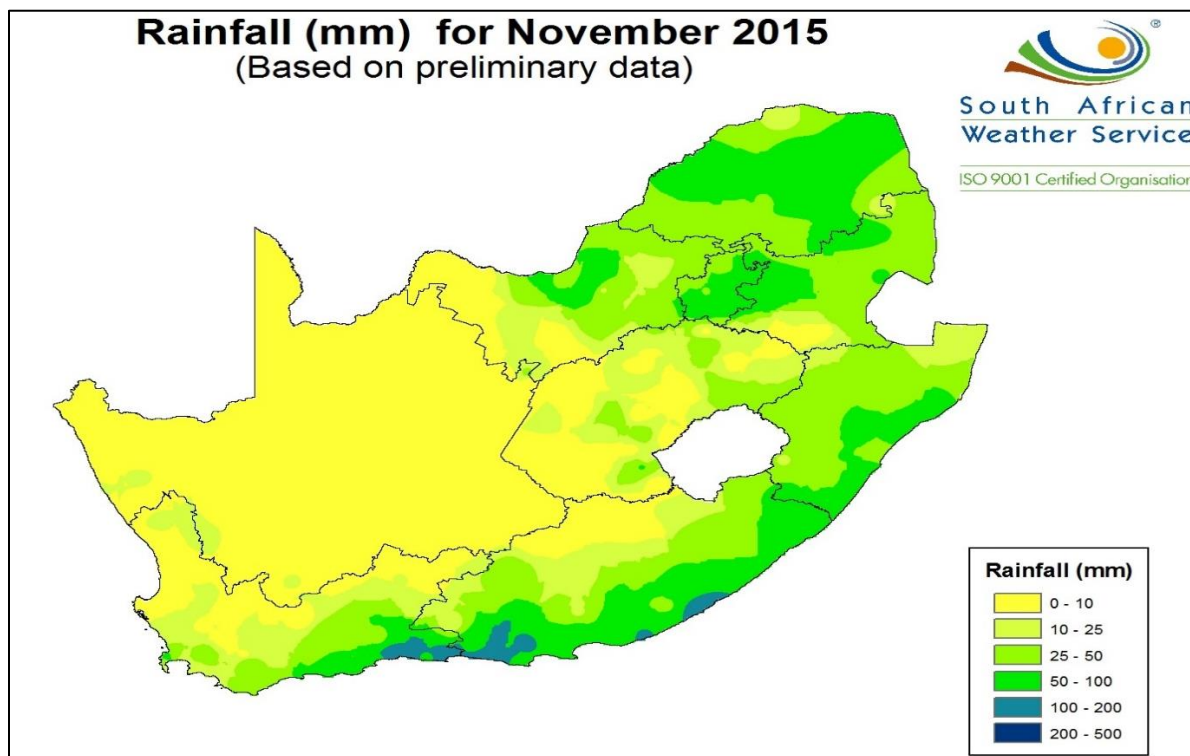
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APPENDIX B

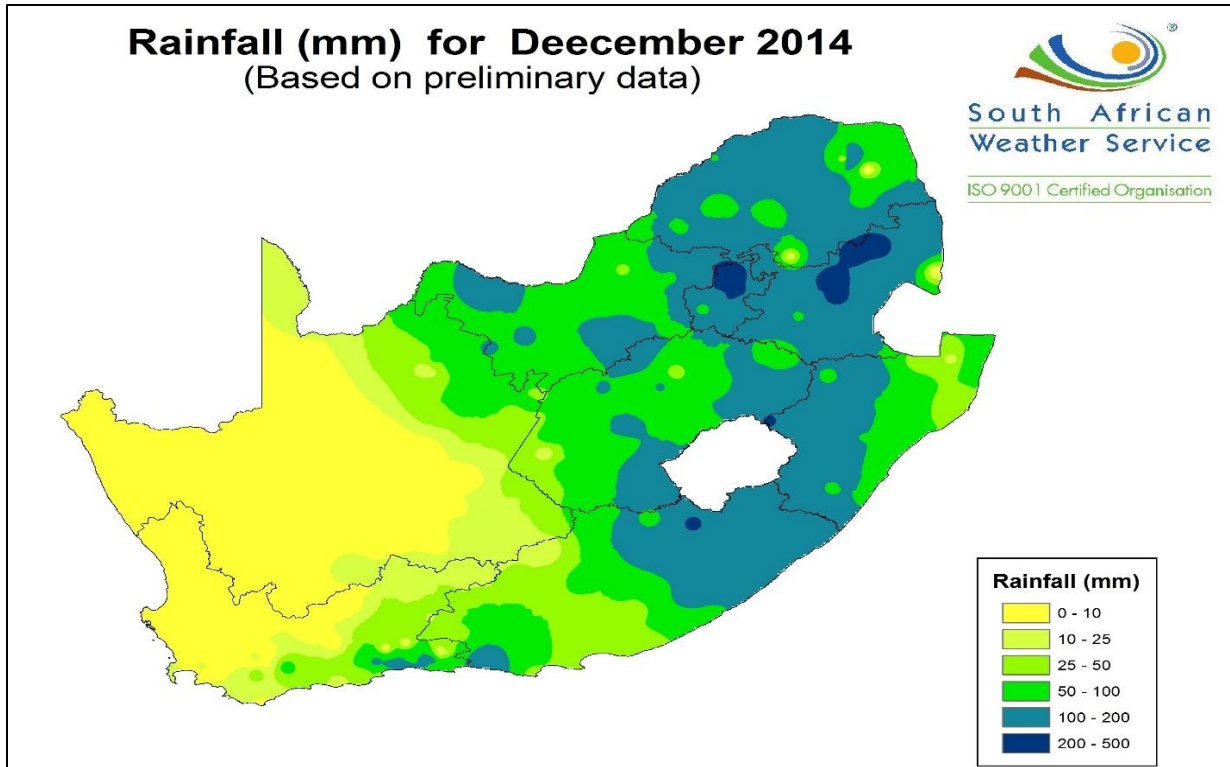


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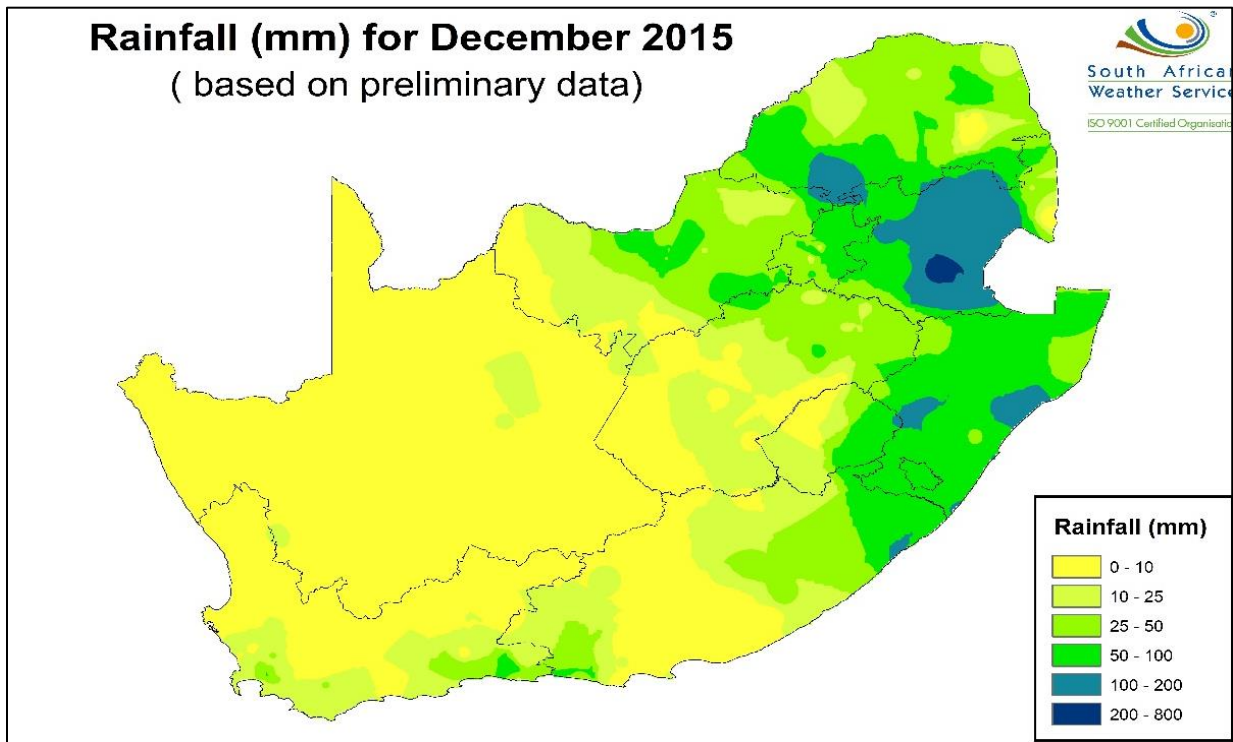


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4 Figure 5. 1. Comparisons between the monthly rainfall between November 2014 and
5 November 2015.



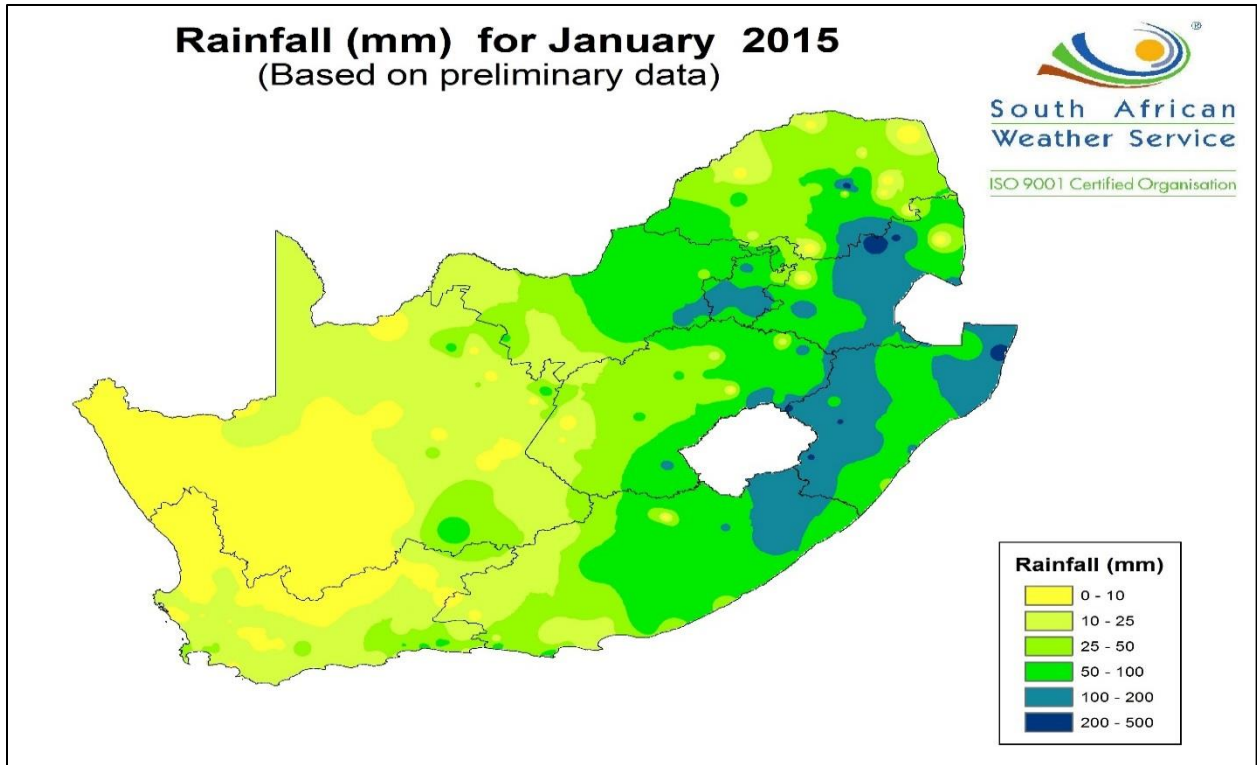
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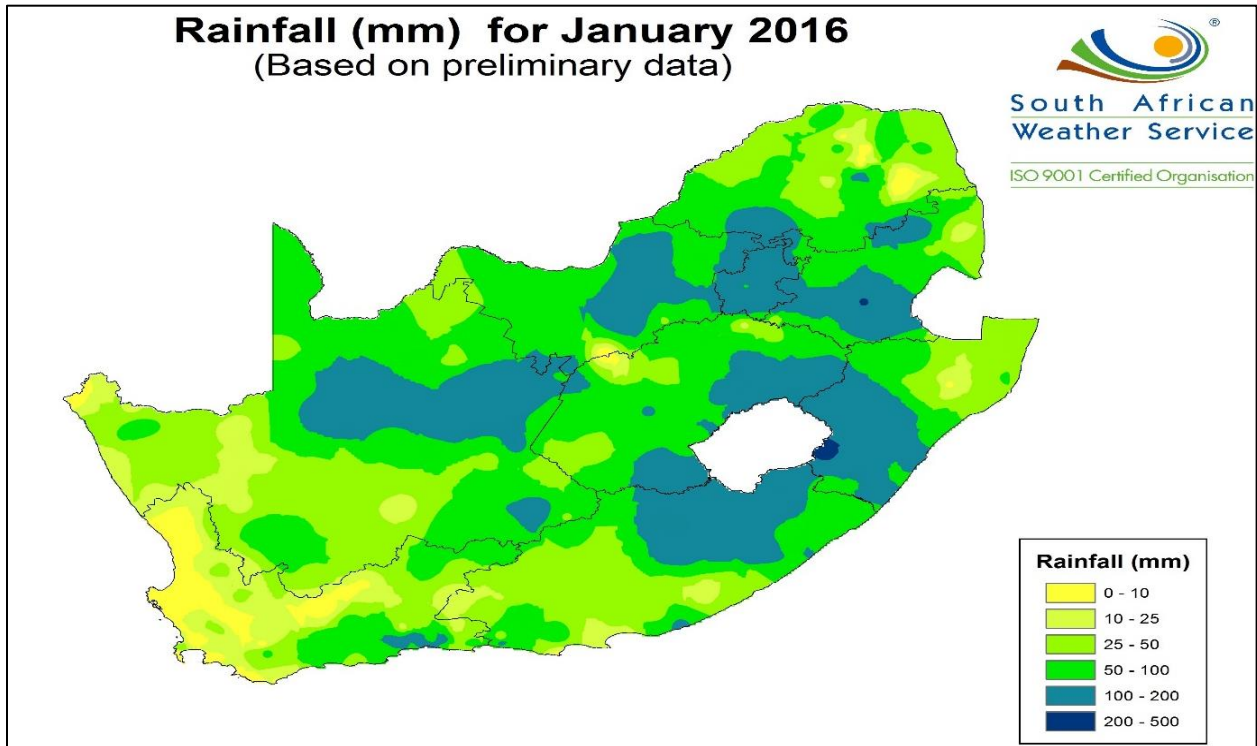
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4 Figure 5. 2. Comparisons between the monthly rainfall between December 2014 and
5 December 2015.



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3

4 Figure 5. 3. Comparisons between the monthly rainfall between January 2015 and
 5 December 2016.