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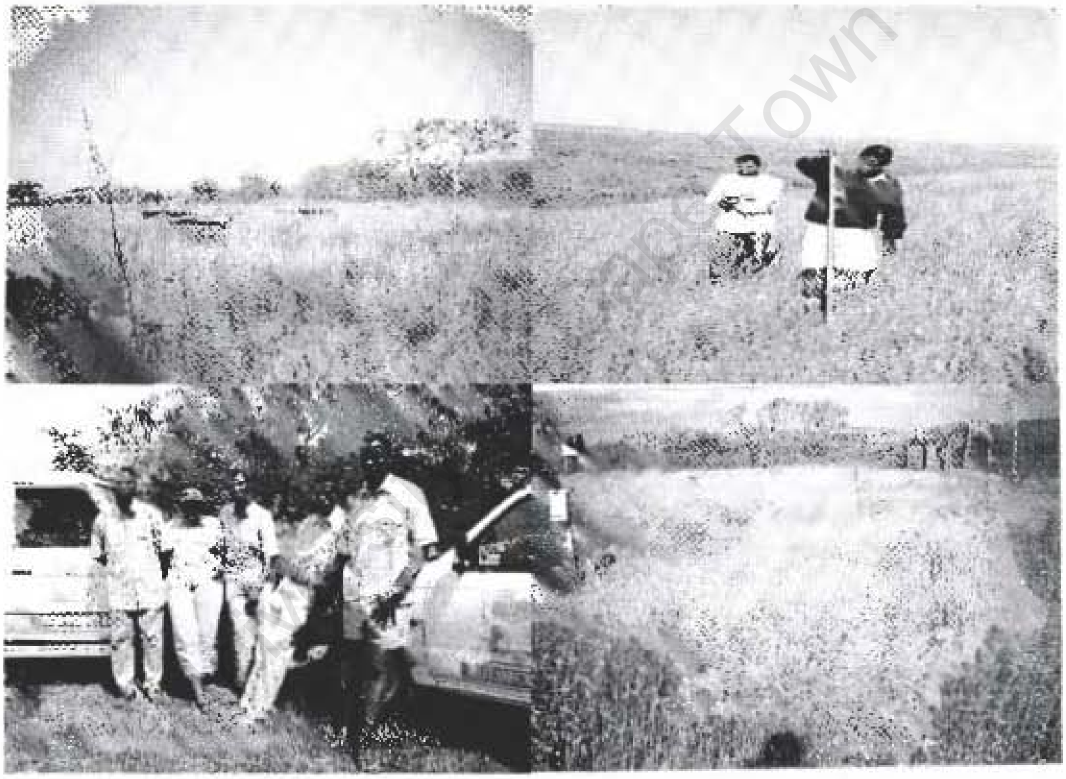
DECOMPOSITION OF GRASSES IN A SOUTH AFRICAN SAVANNA

BY

MMOTO LEONARD MASUBELELE

Submitted in fulfilment of the requirements for a degree of Masters of Science

Supervisors: Prof. WJ Bond and Prof. WD Stock



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April 2007

DECLARATION

I declare that this is my own work. It is being submitted for the degree of Master of Science in the University of Cape Town. It has not been submitted before for any other degree or examination in any other University.

Mmoto Leonard Masubelele

(Signature of candidate)

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ABSTRACT

Tropical and subtropical grasslands ecologists have ignored decomposition, because of the important role it plays in nutrient cycling, in terms of understanding how grass litter gets to the soil during the dry season. The major flaw is in the methods employed to investigate decomposition. In the prairies and steppes, litterbag methods employed investigate decomposition when litter is on the soil, even though the importance of carryover from standing litter is recognized. Standing litter results in high carryover which slows down decomposition thereby hindering productivity in the next growing season. I therefore decided to investigate the processes of photodegradation and microbial decomposition, as well as carryover and also how these processes differ between mesic and semi-arid grasslands. Since previous studies suggest that tallgrass prairies experience more carryover and slower decomposition than shortgrass prairies, I therefore hypothesized in this thesis that mesic grasslands will experience more carryover and slower decomposition than semi-arid grasslands. Results from this thesis showed that standing litter decomposition was slower than surface soil decomposition; hence photodegradation was slower than microbial decomposition. Photodegradation was important in controlling the rate of decomposition among the different grass species standing litter. Different grass species decomposed at different rates. Different plant traits were responsible for decomposition rates of standing litter and surface soil litter. Tensile strength and polyphenolic content were important during initial and final decomposition of standing litter whereas for the surface soil litter the same factors together with C/N ratio and lignin were important. Carryover existed in mesic grasslands but not so much in semi-arid grasslands. This implies that mesic grasslands are phylogenetically designed to burn while semi-arid grasslands are controlled by herbivory.

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Data collection would not have been possible without the help of the Zululand Grassland Project staff. Sue Van Rensburg allowed me to stay in Hluhluwe Research Centre. Krissie Krook taught me how to organise and plan fieldtrips during her stint as the Zululand Grassland Project manager. Matthew Scott Waldram supplied me with the necessary data for the Peak standing biomass used in chapter 2. He also helped me with IT problems and travelling around the park. I cannot thank enough Eric Khumalo and Sinenhlanhla (now working for (SABRE group) for their valuable knowledge and identification of grass species in the park. These two people were always responsible for driving me around the field sites of the Zululand Grassland Project. A little bit of the Zulu language that I have learnt was through talking to the above-mentioned people, the

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CHAPTER 1: INTRODUCTION

South African grasslands (Cowling *et al.*, 1997) like many grasslands in the world, show dwindling productivity over successive growing season. This is due to high carryover of necromass from the previous season (Knapp and Seastedt, 1986). This necromass goes through a series of processes from fragmentation by the sun and other abiotic factors to breakdown by fungi into soil organic matter. Necromass that remains at the start of the new growing season hinders grass productivity (Knapp and Seastedt, 1986). Thus carryover of necromass from one growing season to the next may vary along rainfall gradients with most carryover predicted for mesic (>750mm) and least in semi-arid and arid (<700mm) grasslands.

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Litter decomposition has been extensively studied in woody ecosystems using leaves placed in litterbags (Meentemeyer, 1978; Melillo *et al.*, 1982; Aber *et al.*, 1989). This method mimics the natural process of leaf fall on the soil surface. However in tropical and subtropical grasslands, leaf and stem biomass persists as dead standing material throughout long dry season. Litterbags of grass material placed on the soil surface may give exaggerated rates of decomposition since the rate limiting process may be the conversion of standing dead material to litter in contact with the soil surface. Plant traits that influence the rate of conversion of standing litter to surface litter may be quite different from plant traits that influence decomposition rate once litter is in contact with the soil. For example, resistance of leaf material to photodegradation may be far more important than resistance to microbial breakdown. Thus, to understand litter breakdown in savanna grasses, it is necessary to look separately at the standing litter and surface litter. Differences in carryover of necromass between semi-arid and mesic grasslands, or between and among species in different savannas, may depend on differences in conversion of standing to surface litter, or surface litter to decomposed organic matter or both.

In some grasslands, litter accumulation is so great and the effect on productivity so pronounced, that grass productivity is limited more by litter accumulation than by rainfall (Tilman and Wiedin, 1991). Litter accumulation influences not only productivity but also grass species composition. In South African mesic grasslands, *Themeda* *triandra*, a dominant pasture grass, was reduced from 70% to <10% cover after more than three years of litter accumulation (Uys *et al.,* 2004), probably because of high light requirements for initiation and growth of new tillers. Undecomposed litter accumulates as fuel in many types of grassland. This can increase fuel loads and fire properties from grass production in the previous growing season.

Despite the importance of litter accumulation in grasslands for grass productivity, in terms of shifts in grass species composition or fuel load accumulation when in excess, few studies have analysed decomposition processes in tropical and subtropical grasslands. In South African grasslands, for example, a number of studies have investigated rainfall and other determinants of grass productivity (reviewed in O'Connor and Bredenkamp, 1997) but none have considered litter carryover as a factor limiting grass production. Yet a common objective for prescribed burning in grasslands is removal of moribund material or undecomposed necromass.

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The problem of litter accumulation seems to be particularly of the tropics and subtropics prominent in mesic grasslands dominated by grass with the C4 photosynthetic pathway. In South Africa, the 'sourveld" with higher rainfall regimes is notorious for accumulation of 'moribund' grasses, and fire is extensively used to rejuvenate grass productivity (Tainton, 1999). Fire is much less commonly used in arid and semi-arid ('sweetveld') grasslands, partly because the accumulation of moribund, undecomposed litter is less of a problem. Our grasslands types might therefore be exposed to different abiotic and biotic factors. It is important to explore how carryover influences the dynamics in the different types of grasslands so as to understand the feedback between nutrient cycling and ecosystem stability among grassland types. We know that species in general differ in the way they shape the environment. There also seems to be a different suite of grass species occurring in mesic and semi-arid grasslands.

Grasses that occur in South African grasslands are mostly C4 species (Vogel, *et al.*, 1978; Schulze, *et al.*, 1996). Of the 12 grass subfamilies, Chloridoideae and Panicoideae are dominant in tropical and subtropical regions. Gibbs-Russell and Spies, 1988 and Barkworth and Capels, 2000, both established that there was apparent specialisation at subfamily level for semi-arid versus mesic rainfall areas. The Panicoideae and Chloridoideae grass subfamilies together comprise the great majority of the grass flora of tropical and subtropical regions of the world (Hartley, 1958; Hartley and Slater, 1960; Taub, 2000; Bond *et al.*, 2003; 2005). These subfamilies differ in their distributions across natural precipitation gradients and fire dependence, with species of the Chloridoideae found in drier and less fire prone environments than those of the Panicoideae which are found in mesic and more fire dependent environments, especially the tribe Andropogoneae (Bond *et al*, 2003). Of the Panicoideae tribes the Andropogoneae is the most prominent in mesic tropical regions with the Paniceae prominent in semi-arid tropical regions (Gibbs-Russell, 1986; Kellogg 2000) and closely linked in chromosomes pattern to the Chloridoideae subfamily (Hilu, 2004).

The Andropogoneae species are highly productive (Scholes and Walker, 1993) but lose their nutritional value towards the end of the growing season. This may reduce their decomposition rates resulting in more necromass carryover in successive seasons in species in this tribe (Bond *et al.*, 2003). Another common feature of this tribe is their accumulation of tannin-like substances (Ellis, 1990) at the beginning of the dry season which deters herbivores and slows down decomposition rate. The Chlorideae and Paniceae species on the other hand remain palatable in the dry season and are expected to have higher rate of decomposition than Andropogoneae and hence less carryover (Bond *et al.*, 2003).

Chapter 5 investigates if there are predicted differences in decomposition rates between the three tribes. This section is the core of the whole thesis. Decomposition rates of senescing plant leaves have been shown to vary tremendously (Robertson and Paul, 2000) depending on the structure and chemical composition of the organic matter decomposing. Decomposition rate also depends on the abiotic environment in which decomposition is taking place. Lastly, decomposition rate is influenced by microbial and faunal heterotrophs that the decomposing substrate is exposed to (Swift *et al.*, 1979).

Based on the above-mentioned factors, one might expect to find differences in decomposition rates both within and between mesic and semi-arid grasslands. Robertson and Paul, 2000, suggest that within ecosystem differences in decomposition rates include, for example, differences between standing litter in the canopy layer as well as the surface litter on the soil within a forest. This relationship between surface and standing litter might be important in explaining carryover and decomposition in mesic

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and semi-arid grasslands. We know that mesic grasslands receive more annual rainfall than semi-arid grasslands. Therefore there might be differences in decomposition rate between mesic and semi-arid grasslands. Decomposition is assayed by following mass and nutrient changes of dead litter placed in mesh bags, which are often referred to as litterbags in most papers. The mesh bags are normally placed on the soil surface or embedded in the soil. The litterbags are employed to optimize access of all micro-organisms to the entrained litter while minimizing plant material loss *in situ*. A mass change of the litter *in situ* through time represents the decomposition rate. The changes in nutrient composition of the same litter represent rates of nutrient release, retention and immobilization. Chapter 6 of this thesis investigates the nutrient composition changes in the grass species used in chapter 5. This chapter also explores whether tannin-like substances and other plant traits might be related to decomposition rates in these tribes.

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Thesis structure

In order to explore patterns and determinants of decomposition in South African savanna grasslands I needed to clear four things in understanding nutrient cycling of mesic and semi-arid grasslands.

1. I needed to show if there were differences in peak standing grass biomass and carryover among mesic and semi-arid grassland types and if so what causes the variation in carryover among the different grassland types.
2. I also needed to show whether differences in carryover were linked to decomposition by photodegradation using shading treatments in mesic versus semi-arid grasslands.
3. I also needed to show if there was variation between photodegradation of standing litter and microbial decomposition of surface litter among the dominant species in both savanna grasslands and if so what causes variation in decomposition rates between the different grass types in standing litter versus soil litter? The above question is answered by addressing the following sub-questions.

a) The breakdown of litter by sun (photodegradation) may be important in the long dry seasons of savanna grasslands, yet there is little if any research at all investigating the process. How does photodegradation influence breakdown in the different grass tribes and also the different species within these tribes?

b) Plant traits such as high lignin content and high C/N ratio have been shown to slow down the rate of decomposition. I also explored the importance of a number of additional leaf traits in contributing to decomposition rates of standing and surface litter. These included polyphenolic content, specific leaf area and tensile strength. I also explored plant trait differences between species and grass tribes.

4. I also needed to show how productivity, carryover and decomposition were linked and also what governed the relationship between the three in mesic and semi-arid grasslands.

These five goals mentioned above were organised and reported as 5 chapters in my dissertation. Each section can be seen as a study in its own right but can be linked altogether into one study and thus contributes to my dissertation.

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Thesis outline

Chapter 1: Introduction

Chapter 2: Study area description

Hluhluwe/iMfolozi Park (HiP)'s grassland types are discussed. The rainfall regimes, altitude and vegetation classification of each chosen site is given in this chapter. This chapter outlines the sites used in the study as whole but mostly those used in Chapter 3.

Chapter 3: A comparative study of the impact of carry-over on grass productivity in arid savannas versus mesic savanna. What is the impact of carry-over on grass production in savanna grasslands? Is it as important as has been found in the prairies? There is a rich literature on the impact of carry-over in the prairies. It has been discovered that carry-over can vastly influence grass productivity by suppressing growth in the beginning of the growing season (Knapp and Seastedt, 1986). This chapter explores if similar effects are taking place in our South African grasslands and if so, how they vary among the different grassland types?

Chapter 4: Photodegradation in a field set up versus litterbag breakdown. In this chapter, the impact of photodegradation in the field is tested by using shading nets to see if more sunlight causes more decomposition and less carry-over. Litterbags were also placed under the shading nets to see if there will be a difference in breakdown by the sun. The question here is whether photodegradation is an important factor influencing decomposition over the dry season?

Chapter 5: In this chapter I explore variation in decomposition rates between species of Andropogoneae, Chlorideae and Paniceae in the sun versus on the soil in a series of litterbag experiments in Hluhluwe and Cape Town.

Chapter 6: In this chapter I explored the importance of various leaf traits on decomposition in the sun versus on the soil. The leaf traits include lignin content, C/N ratio, polyphenolic content, tensile strength and specific leaf area of the different species in the three tribes.

Chapter 7: Discussion and conclusions. Here, all the above chapters are discussed in a synthesis on how decomposition occurs in savanna grasslands.

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CHAPTER 2: STUDY AREA

The study was carried out from April 2002 to February 2004. Field studies and plant collections were made at the Hluhluwe/ *i*Mfolozi Park (H*i*P), in the Kwazulu/ Natal Province of South Africa (28°00'S and 28°26'S; 31°43'E and 32°09'E) (figure 2.1). The map below was modified from Archibald's MSc thesis obtained in 2003.

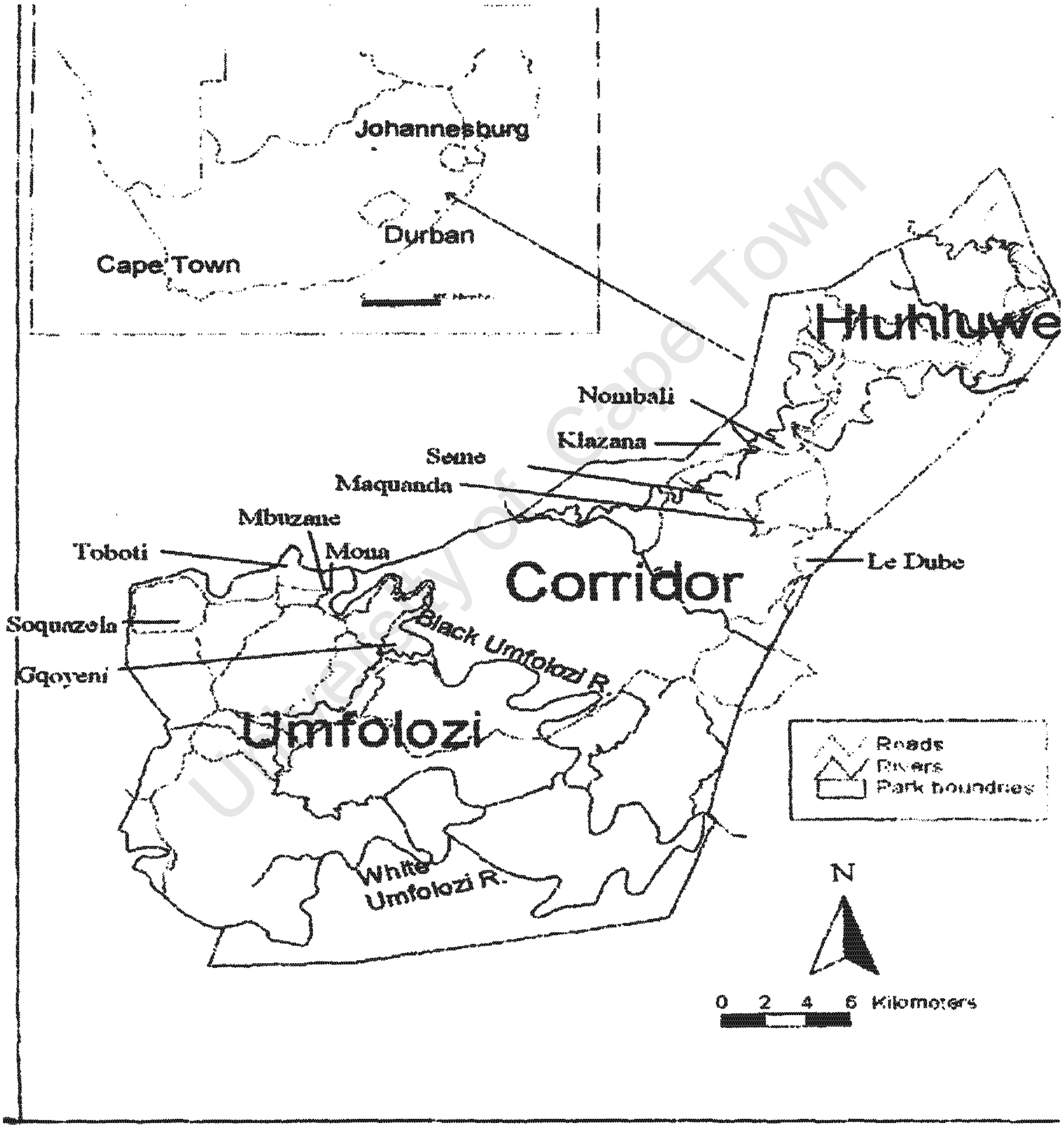

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Figure 2.1: Map showing the location of Hluhluwe iMfolozi Game Reserve in KwaZulu Natal, South Africa. Major rivers, roads, sections of the game reserve and study sites are shown in this map.

2.1. Park History

This park was formerly known as Hluhluwe Umfolozi Park. Hluhluwe *i*Mfolozi Park consists of two reserves, the Hluhluwe Game Reserve (HGR) (225km²) to the north, the *i*Mfolozi Game Reserve (*i*GR) (447km²) to the south and a corridor (227km²) joining the two (Whateley and Porter, 1983). The name for Hluhluwe Game Reserve has not been changed while Umfolozi Game Reserve was changed to *i*Mfolozi Game Reserve. H*i*P has a varied hilly topography with altitudes ranging from 60m to 450m above sea level.

Mean minimum temperature is 13° C and mean maximum temperature is 35° C (Balfour and Howison, 2002). Annually, rainfall shows a unimodal seasonal pattern and the driest time of year is between June and August (Figure 2.3). Rainfall increases with altitude so that Hluhluwe, which is at higher elevations, supports a mesic savanna whereas *i*Mfolozi is a semi-arid savanna. Mean annual rainfall near the highest point in Hluhluwe (Egodeni) is 980 mm (68 year record) with a coefficient of variation of 28.4%. Mean annual rainfall for Gunjaneni, a station in Hluhluwe at altitudes more similar to the study sites, is 755 mm (25 year record) with a coefficient of variation of 33.4%. In *i*Mfolozi, mean annual rainfall at Mpila, an elevated site, is 728 mm (36 year record) with a coefficient value of 29.9%. However most of *i*Mfolozi is at lower elevations and has lower rainfall. At Mbuzane, close to the study sites, rainfall is 658 mm (18 year record) with a coefficient of variation of 26.3%. Hluhluwe *i*Mfolozi Park is typical of Southern African savannas in that it is prone to long-term fluctuations in rainfall. Extended periods of above average rainfall are followed by periods of below average rainfall (Brooks and Macdonald, 1983; Balfour and Howison, 2002) hence the large coefficients of variation in annual rainfall (Coetsee, 2003).

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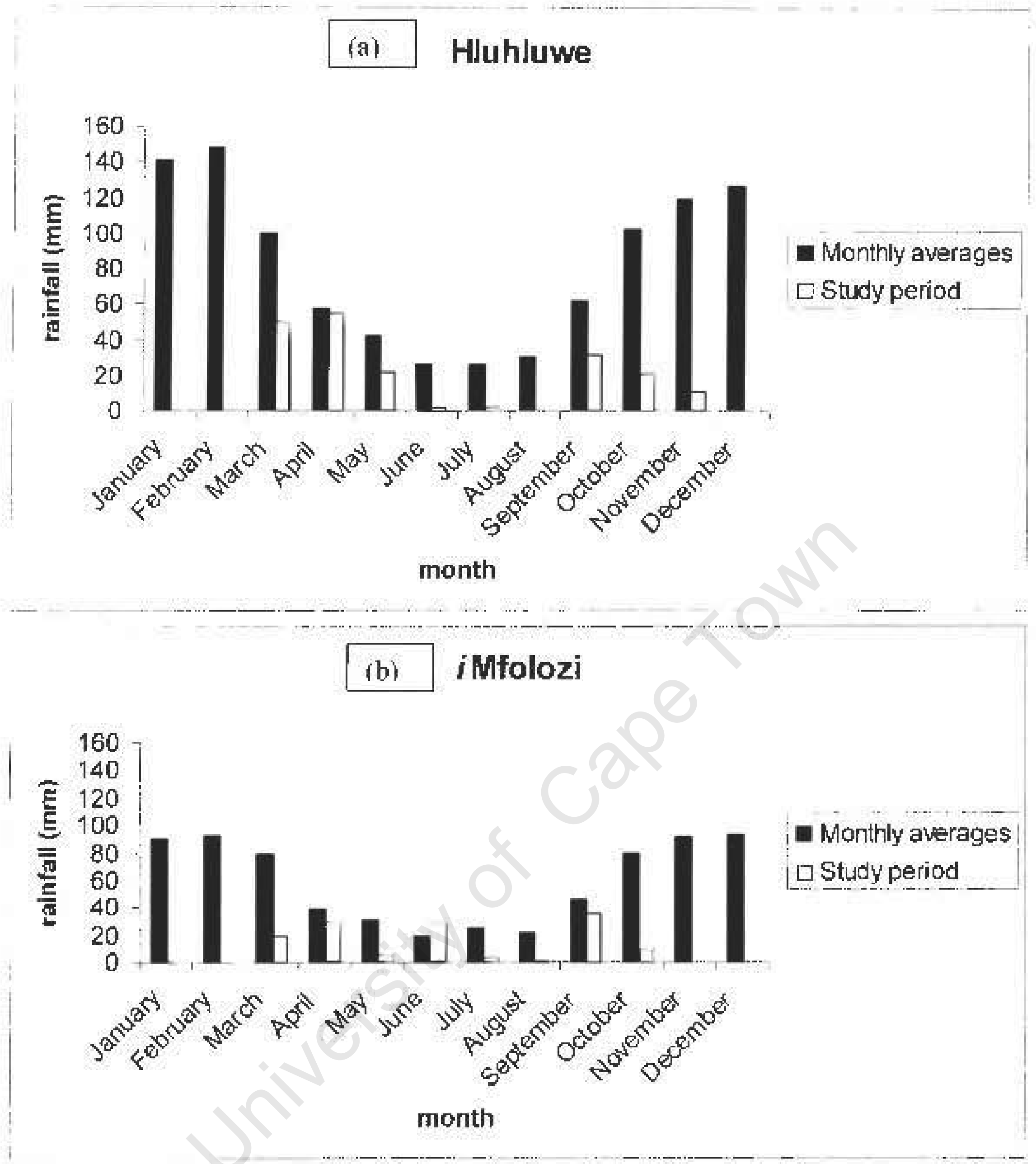

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Figure 2.3: Mean monthly rainfall in mm (bars) for (a) Hluhluwe and (b) *i*Mfolozi. Rainfall data for Hluhluwe is the monthly average rainfall for the period 1964-2001 measured at Memorial gate and for *i*Mfolozi is the average monthly rainfall for the period 1959-2002 measured at Mpila camp (EKZN wildlife data). The study period was from May to October 2003.

The vegetation consists predominantly of the Lowveld subcategory of the Tropical Bush and Savanna Types of Acocks (1956), as well as Zululand Thornveld (Brooks and MacDonald, 1983). The most prevalent grassland types are bunch-grass communities, dominated by members of the Andropogoneae, especially *Themeda triandra.*

Cymbopogon excavatus or *plurinodis*, *Hyparrhenia filipendula*, *Heteropogon contortus* (Downing 1974; Brooks & Macdonald 1983). Other bunch grass communities are also present however, where *Sporobolus pyramidalis* and *Eragrostis curvula* are common. These are members of the Chlorideae tribe (Gibbs-Russell, 1986). Bunch grasses are tall, tussock-forming grasses, which grow very fast, produce a high fuel load (400-700g/m^2), and promote frequent fires. These tall-grass areas do not support high numbers or a high diversity of grazing animals except after fire; only Buffalo (*Syncerus caffer*) was a tall grass specialist at Hluhluwe (Page and Walker, 1978). Bunch grasses are also fairly intolerant of heavy grazing and their growth-form means that their leaves are not protected from grazing, and they cannot reproduce vegetatively (Uys *et al.*, 2004). They are mostly of decreaser/increaser I ecological status (Tainton, 1999). Thus these grass communities are most dominant in areas of frequent fire and relatively low grazing pressure. All the species mentioned above dominate in Hluhluwe Game Reserve landscape.

"Grazing lawns" occupy areas of intensive grazing dominated by grazing-tolerant species at *i*GR (see Plate A below). The grass species in grazing lawns are short-statured, stoloniferous grasses that spread mainly through vegetative growth and are tolerant of, and productive under, heavy grazing. Many of the species are members of the tribe Chlorideae including *Dactyloctenium australe, Chloris gayana, Sporobolus nitens* or members of the tribe Paniceae (sensu Gibbs-Russell and Spies, 1988) such as *Urochloa mosambicensis, Cenchrus ciliaris, Digitaria longifolia* and *Panicum coloratum*. Grazing lawns are grazed by white rhinos (*Ceratotherium simum*), Burchell's zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*) both mixed feeders, and warthog (*Phacochoerus africanus*).

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Plate A: The heavily grazed semi-arid grassland of *i*Mfolozi Park dominated by short grass vegetation

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Plate B: The tall grass dominated vegetation of the mesic grasslands of Hluhluwe Park

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The mesic bunch grassland dominated by Andropogoneae (see Plate B) is fire prone accumulating higher fuel load than semi-arid areas. Both frequencies and sizes of fire are affected by variation in fuel loads during the wet and dry years (Balfour and Howison, 2002). Bond *et al.*, (2001) and Archibald *et al.*, 2005 have showed that there was a decrease in the extent of heavily grazed grasslands, including lawns, since the 1970's and an increase in bunch grass communities dominated by *Themeda triandra* or *Sporobolus pyramidalis*. They attributed this to lower densities of grazing animals, increased rainfall and higher fire frequencies since the 1970s.

2.2. Site descriptions and floristic composition

2.2.1. Site classification

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Field experiments for this study were based on experimental sites set up by the Zululand Grass Project (ZLGP) to test for grazing effects on grassland ecology. There are ten sites in the park (Figure 2.1) at each of which there are three to five fencing treatments excluding different size classes of mammal herbivores. My studies were conducted in the 'hare fence', a 40 x 40 m exclosure with mesh fence excluding all grazers equal to or larger than a hare. The two game reserves had five sites each arranged along a grazing intensity gradient (see Table 2.1 below). The grazing intensity gradient was determined by the proportions of bunch or lawn grass or forbs at each site in both mesic and semi-arid grasslands. The bunch grass sites were Le Dube in Hluhluwe and Soquazela in *i*Mfolozi. Mixed grass sites were Nombali and Maquanda in Hluhluwe while Gqoyeni and Mbuzane were selected for *i*Mfolozi. Grazing lawn sites were Seme and Toboti in Hluhluwe and *i*Mfolozi respectively. The most grazed sites, with a substantial amount of forbs and bare ground, were Klazana (Hluhluwe) and Mona (*i*Mfolozi).

Table 2.1: Site information for the hare exclosures at H*i*P. Grazing gradient is relative grazing pressure defined by proportion of short grasslands at the site. Rainfall is estimated from a regression with altitude (Balfour and Howison, 2001)

Site name	Grazing gradient	Park	E	S	Altitude m	Soil forms	Rainfall mm
Le Dube	1	Hluhluwe	32.02	28.23	270	Bonheim, Cartref	776
Maquanda	2	Hluhluwe	31.98	28.18	210	Valsrivier/Glenrosa	706
Nombali	3	Hluhluwe	32.01	28.15	190	Swartland, Valsrivier	683
Seme	4	Hluhluwe	31.97	28.17	190	Glenrosa, Sepane	683
Klazana	5	Hluhluwe	31.58	28.09	190	Glenrosa	683
Soquazela	1	*i*Mfolozi	31.73	28.28	260	Hutton/Mispah	765
Mbuzane	2	*i*Mfolozi	31.79	28.22	130	Oakleaf/Valsrivier	613
Gqoyeni	3	*i*Mfolozi	31.85	28.27	110	Shortlands	590
Toboti	4	*i*Mfolozi	31.77	28.22	190	Swartland	683
Mona	5	*i*Mfolozi	31.80	28.22	130	Hutton	613

2.2.2. Soils

Soils were classified by Geoff Hughes and colleagues from University of KZN (Pietermaritzburg) using the South African soil taxonomy system (see Table 2.1). The Hluhluwe sites had variable soils with Le Dube being the most complex site. The eastern side of this site has structured clay rich soils (Bonheim, Sepane, Valsrivier, Mayo, and Oakleaf). The western side has sandy soils with some eluviation (indicating seasonally perched water tables: Cartref, Fernwood, Kroonstad)). Most of the control had sandy soils while rhino and hare fence were clay rich. Maquanda has clay-rich structured very dark brown soils (Swartland, Valsrivier). Nombali, Maquanda and Seme have similar clay-rich, structured, very dark brown soils. Klazana has relatively shallow (Glenrosa) soils with some signs of seasonal wetness. These soils were sandier than the other sites (except west of Le Dube).

Soils in *i*Mfolozi were generally red, clay-rich meso- or eutrophic. Soquazela had red apedal mesotrophic clay-rich soils (Hutton), and some shallow rocky soils (Mispah). Gqoyeni has red structured clay-rich soils (non-calcareous). Mbuzane has mostly very dark brown clay-rich structured soils (Valsrivier) with some red apedal (Hutton) soils in the west of the control plot and some calcareous sub-soils. Toboti has clay-rich, very

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dark brown, structured soils (Swartland) with some calcareous sub-soil. Mona was all red apedal sandy clay loam soils (Hutton) that were Eu to meso-trophic.

2.2.3. Vegetation and Species Composition

The dominant species (based on estimate of cover) were recorded annually under disk pasture meter. The disk pasture meter readings were 200 per fence treatment, per site, per annum

Le Dube

The dominant grass species were *Themeda triandra* and *Cymbopogon excavatus* during the 2002 dry season. The other species include *Hyparrhenia filipendula*, *Setaria sphacelata* and *Digitaria eriantha* during that season. The study period was dominated by *Themeda triandra*, *Sporobolus pyramidalis* and *Cymbopogon excavatus*. The dominant tree species was *Acacia nilotica.*

Maquanda

The grass species dominant at the site were *Sporobolus pyramidalis, Digitaria longifolia*, *Eragrostis curvula* and *Panicum maximum*. The dominant tree species were *Sclerocarya birrea, Euclea divinorum* and *Acacia nilotica.*

Nombali

Nombali was dominated by a combination of *D. longifolia* with *Bothriochloa insculpta* and *S. pyramidalis* during 2002 as well as the 2003 peak standing biomass season. The other species found in large quantity were *Eragrostis superba* and *U. mosambicensis.* The trees that were common in the vicinity are *Acacia gerrardii* and *Dichrostachys cinerea*.

Seme

The dominant species during the 2002 dry season were *Dactyloctenium australe* and *Digitaria longifolia,* followed by *P. coloratum* and *B. insculpta*. *Eragrostis plana* and *Eragrostis paspaloides* were also present but in smaller quantities. The dominant species during the study period was *D. longifolia* followed by *E. plana* then *T. triandra* and *Eragrostis curvula*.

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Klazana

Digitaria longifolia was dominant again in Klazana. This was followed by *T. triandra* and *E. superba*. Other species at the site during the 2002 dry season include *Panicum schinzii*, *E. curvula*, *B. insculpta* and *Aristida congesta*. The 2003 dry season was similar in dominant species to the 2002 dry season with an additional species in the form of *Heteropogon contortus*.

Some grass species that are common in Hluhluwe (above) were common in iMfolozi (below) as well. This shows that these species were of major importance in the whole of H*i*P.

Soquazela

Dominant species during 2002 dry season were *B. insculpta* followed by *E. superba*, *P. coloratum*, *T. triandra* and *A. congesta*. *Bothriochloa insculpta* was also dominant in the next dry season with the following species very close, *P. coloratum*, *E. superba*, and *T. triandra*. The grassland forms an understorey in open *Acacia nigrescens* woodlands.

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Gqoyeni

The dominant grass species in 2002 was *T. triandra*. The other species found at this site were *P. coloratum*, *A. congesta*, *U. mosambicensis* and *E. superba*. These species were also present during the 2003 dry season. *Acacia nigrescens* and *Dichrostachys cinerea* were common woody plants at the site.

Mbuzane

This mixed site was dominated by *P. coloratum* followed by *B. insculpta*, *Digitaria argyrograpta*, *U. mosambicensis*, *E. curvula* and *A. congesta* during the previous dry season. The study period was dominated by *U. mosambicensis* supported by *B. insculpta*, *P. maxima* and *E. curvula*. The dominant tree species was *Acacia nigrescens* with *A. grandicornuta* in the vicinity.

Toboti

The most abundant species at this site during the 2002 dry season was *Digitaria argyrograpta* followed by *P. coloratum*, *E. superba*, *H. contortus* and *A. congesta*. The study period was dominated by a combination of *D. argyrograpta*, *E. superba*, *H.*

contortus and *T. triandra*. Other species here include *Sporobolus nitens*, *P. maxima* and *U. mosambicensis*. *Acacia tortilis* and *Acacia nigrescens* were common tree species at this site.

Mona

The last site had *Urochloa mosambicensis* dominant in the previous dry season of study followed by *P. coloratum*, *Tragus berteronianus*, *P. maxima* and *A. congesta*. The study's dry season was completely taken over by *U. mosambicensis* with very little *A. congesta* at the site. Tree species included *Acacia nigrescens, A. grandicornuta,* and *Dichrostachys cinerea* with *Spirostachys africana* thickets in the vicinity.

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CHAPTER 3: PRODUCTIVITY AND CARRYOVER AMONG GRASSLAND TYPES

3.1. INTRODUCTION

Savanna systems are well known to consist of a wide range of habitat and vegetation types. They often are in areas of very variable rainfall and disturbances such as fire and large mammals. There is evidence that H*i*P is a highly dynamic system and that the proportions and distributions of different habitat types (grass and tree communities) are very variable, depending on factors such as fire, rainfall and grazing (Archibald, 2003; Archibald *et al.*, 2005; Bond and Keeley, 2005). Natural fires occur every 1 to 3 years in the mesic savannas but less often, once in a decade in semi-arid South African savannas (Frost 1985; Walker, 1985; Balfour and Howison, 2002). It is very well known that the incidence, intensity and impact of fire depends on the amount of fuel load (grass) present, the prevailing environmental conditions and thus the season of burning (Trollope, 1984; Watson, 2005). The dynamics of fuel accumulation are of vital importance to fire managers because of the relationship between fuel load, fire intensity and potential for fire control (Raison *et al.*, 1983; Trollope, 1984; Cheney, 1996; Govender *et al.*, 2006).

Fuel load is important for fire frequency and intensity in savanna grassland systems (mesic and semi-arid included). There seems to be a huge variation in fuel load accumulation amongst and between mesic and semi-arid grassland sites depending on grass productivity in the previous growing season. Since this variation in fuel load is important in management of these savanna systems this motivated us to pose the question, what causes variation in fuel load or grass productivity among mesic and semi-arid savanna? This might also depend on carryover of litter from the growing season prior to previous growing season (that is, the amount of decomposition). The impact of large herbivores in the dry season is also important in determining the large variations in fuel load during the dry season in savanna grasslands. What role does herbivory play in the variation in fuel load among mesic and semi-arid grasslands? Semi-arid grasslands are associated with heavy grazing due to high numbers of

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herbivores while mesic grasslands are known to have lower numbers of herbivores (McNaughton, 1985; McNaughton *et al.*, 1989; 1993; 1997; Frank and Groffmann, 1998).

Grass productivity and hence accumulation of dry season fuel load varies depending on rainfall (O'Connor and Bredenkamp, 1997; Snyman, 2000). High rainfall has been shown to be related to high production while little rainfall was associated with low production. Some studies have shown that this feedback between rainfall and grass productivity is also influenced by other factors such as temperature (Le Houerou *et al.*, 1988; Long *et al.*, 1992; Hall and House, 1995; Jobbágy *et al.*, 2002; Heisler *et al.*, 2004), soil moisture and nutrients (Briggs and Knapp, 1995; Hector *et al.*, 1999). Grass productivity variation in mesic and semi-arid savanna grasslands also depends on intra-annual rainfall distribution (Sala and Laurenroth, 1982; Briggs and Knapp 1995; Paruelo *et al.*, 1997; Knapp *et al.*, 1998; Xiao *et al.*, 1998; Sala and Austin, 2000; Knapp *et al.*, 2001). This led to the question, is productivity and fuel load associated with rainfall and if so, is there a direct feedback between rainfall and productivity? Lastly, how does this feedback influence carryover?

Another important predictor of grass productivity is grass species composition (O'Connor and Bredenkamp, 1997). Grass species composition of a site or an area differs vastly among mesic and semi-arid grasslands. Could species composition be the cause of variation in fuel load among mesic and arid grasslands? Often mesic grasslands are dominated by one or a few species whereas semi-arid grasslands are dominated by more than several species. The idea here is that sites with grass species that are fast growing will result in high production, and might end up with one dominant species compared with those with slow growing species in which there are more gaps for more species to utilise. Fuel load accumulation may depend on structural and chemical composition of the individual grass species and may differ among phylogenetic groups such as Andropogoneae or Chlorideae or Paniceae species. Just as the chemical and morphological properties of plants make them more susceptible to herbivory, so too some kind of plants are more susceptible to fire than others (Bond, 1997), for example tussock-forming species with unpalatable chemicals are managed by fire since they cannot be consumed by animals. Species with high fibre and specific leaf weight may burn more easily because of their lower moisture content and their slow decomposition.

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But little is known about decomposition of the major grass tribes dominating mesic and semi-arid grassland (see Chapter 4 and 5).

This chapter looks at productivity and carryover in mesic versus semi-arid savanna grasslands. The main question in this study is whether productivity and carryover vary between mesic and semi-arid savannas. The second question looks at the potential feedback of carryover on productivity among the grassland types. Thirdly, the contribution of carryover to dry season fuel loads among mesic and semi-arid savannas is investigated. I expected peak standing biomass and hence carryover to vary according to dominance by Andropogoneae versus Chlorideae or Paniceae grasses with the former decomposing more slowly (as standing litter in the sun) and therefore accumulating more dead biomass.

3.2 METHODS

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Peak standing biomass is an indication of what biomass is left after a season's growth and grazing (Titlyanova, 1988). A comparison of peak standing biomass and carryover of semi-arid and mesic savanna grassland types was carried out in Hluhluwe *i*Mfolozi Park. H*i*P Park consist of two game reserves namely Hluhluwe Game Reserve and *i*Mfolozi Game Reserve. The former is a mesic savanna whereas the latter is a semi-arid savanna (see chapter 2).

Carryover was estimated by following grass production in mobile exclosures over a full year. All the grass swards had been burnt in the dry season before initial biomass sampling commenced. The fires removed any dead litter so that the study follows productivity and accumulation of dead material over the year following a burn. Grass productivity was measured in the presence and absence of large grazers (control vs. hare fence) using mobile exclosures in the former case.

The sampling in this project for biomass started in September 2002 after the sites in both game reserves were burned during the July/August period. Peak standing biomass was sampled around June 2003 when grass species growth was near the maximum before the dry season. At the end of the growing season (June) fixed 1 m^2 plots were clipped in all treatments and sites (replication = 5 per treatment per site). In the mixed grass sites (both lawn and bunch grasses occurring) fixed 1 m^2 plots in both lawn and bunch grass patches were sampled separately (n = 5). Additionally, when bunch grass patches were found within the sampling frame in a lawn grass site, the rule was been set that when their presence was more than 30%, the lawn and bunch grasses were bagged and weighed separately. Similarly, where lawn grasses occurred in bunchgrass sites. Samples were sorted into litter, forbs and grass but all grass can be assumed dead at this time.

Biomass was sampled at ten sites, five in the mesic savanna (Nombali, Seme, Maquanda, Klazana and Le Dube); and five in the semi-arid savanna (Mbuzane, Toboti, Gqoyeni, Mona and Soquazela) (see chapter 2A). At each site, four mobile cages each ca 1m x1m x 1m tall was set up in the control treatment and each was marked (1-4). One square metre matched plots, that were not enclosed, were set up next to each mobile exclosures. The matched plots were set up using large spray-painted nails that were labelled using metal pegs at the corner of each plot. Grass biomass was measured indirectly by a disk pasture meter (DPM) in the mobile enclosures and the paired plots. An additional plot (T1 clip) was selected next to the 4 paired plots. DPM readings were taken and the plot clipped in September 2002 at the end of the growing season. Temporary exclosures and matched plots were sampled from T1 onwards at a monthly frequency after which exclosures were moved to newly selected plots.

Four one square meter plots were selected randomly in the hare fence (all large herbivores excluded) at each date of sampling. Sampling took place once a month from September 2002 to September 2003. The following sampling procedure was adopted starting from October 2002: 5 DPM and vegetation height readings per 1x1 m^2 plot and then the plots were clipped. A sub-sample of the clipped grass material was sorted into leaf, stem and dead material, air dried for 48 hours and weighed. The dead material is the "carryover" from the 2002/2003 growing season to the next (2003/2004)

Rainfall was measured daily from 1st of September 2002 to 31st of October 2003. This was done using a tipping bucket rain gauge. This was done to see how rainfall contributed to productivity at the start of the dry season (peak standing biomass) and also to see how much rainfall was received during the dry season.

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3.3. DATA ANALYSIS

Rainfall data, species composition data and tribes' data were analysed using Microsoft Excel. Site as well species were related using a method which uses multidimensional scaling (MDS), an ordination method, using Bray Curtis similarity measures on square-root transformed weighted frequencies.

I first compared the differences in grass productivity among parks and sites, in terms of total standing grass biomass and carryover. This analysis also showed differences in fuel load accumulation at the different game reserves. Here the average of total grass, litter, total standing dead biomass and total dead biomass in two seasons were compared for the game reserves and sites. Bar graphs and stacked area chart types were constructed in Excel. These displayed the trends of the contribution of each parameter (average of total grass, litter, total standing dead biomass and total dead biomass) over time in months.

The data for monitoring successive productivity, peak standing grass biomass and carryover at the different park sites in the hare fence exclosures were analysed in Excel and Statistica. This was the data from June 2003 to February 2004 dry to early wet seasons. Since we wanted to know how much material of the previous growth season was still in the vegetation at the onset of the next growth we used the first date of harvesting at the start of the dry season and a couple of months after the start of the new rains. Most important was the weight of total dead material and total grass standing biomass (Peak Standing Biomass). Total dead material equals the weight of standing dead plus litter material. The latter parameter was related to total standing grass biomass at the beginning of the dry season to determine whether carry-over was proportional to the total grass biomass or whether other factors were more important in determining the amount of carry over (e.g. species composition). The data was square root transformed to achieve homogeneity of variance ($p>0.05$). The data was analysed using one-way ANOVA to determine if there were significant differences between mesic and semi-arid grassland types.

The second part of data analysis explored variation in peak standing biomass for the 2003-2004 growing season with a disk pasture meter (dpm). The average dpm value per plot was converted to biomass values using the following equation (biomass=12.33 +

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26.12 (dpm value). This was then called the peak standing biomass. The equation was based on 1774 values used to relate biomass and dpm values. This was developed by the ZLGP group. The data was then log transformed to achieve normality.

The data was then analysed using a nested ANOVA with peak standing biomass as the dependent variable (JMP 5). This tested whether sites within the parks, their treatments and grass type were important in determining the variation in peak standing biomass at the end of the growing season. Generalized linear/non linear regressions were used in Statistica to asses the contribution of these factors to peak biomass. Combinations of one-way ANOVA were done to test the site differences under the different herbivore treatments.

3.4 RESULTS

3.4.1. Rainfall and species composition

Rainfall

Rainfall events in Hluhluwe and iMfolozi were different during the study period (see Figure 3.1). The highest amount of rainfall was received in April 2003 for Hluhluwe. The *i*Mfolozi Game Reserve had peak rainfall in February 2003. Hluhluwe had very little rain during the dry season month of June to mid July. The period of no rainfall in *i*Mfolozi during the dry season was the end of July to end of August. The average monthly rainfall over the dry season for Hluhluwe was 9mm whereas *i*Mfolozi had 7mm (July to October 2003).

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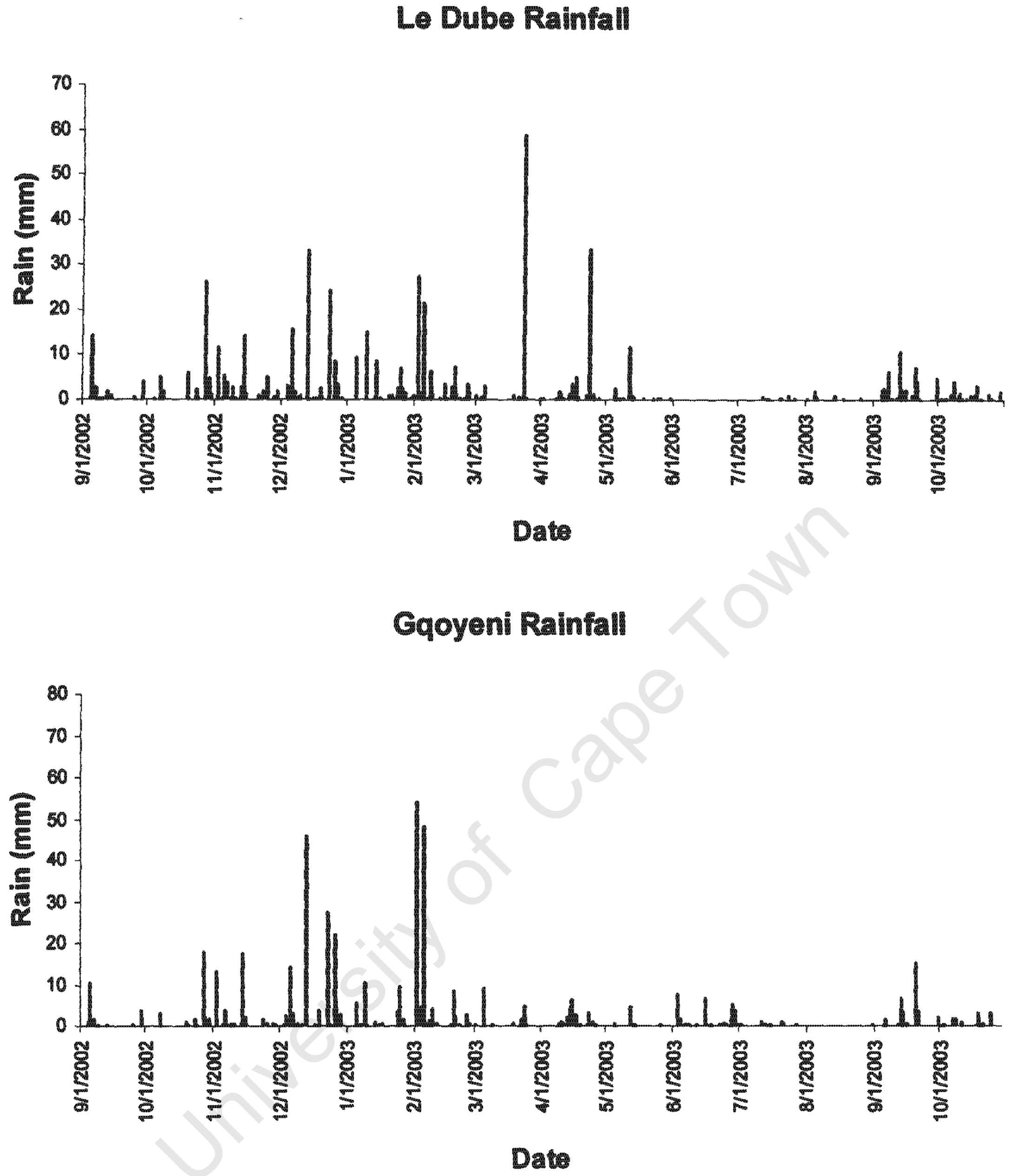

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Figure 3.1: Rain events from September 2002 to November 2003, Le Dube site, Hluhluwe (mesic savanna) and Gqoyeni site, iMfolozi (semi-arid savanna). Rainfall recorded with an automatic tipping bucket rain gauge.

Grass species composition

Themeda triandra was common at all sites except Mona and Maquanda (see Figure 3.5 (a & b)). But it was dominant at Le Dube, Seme, Gqoyeni and Toboti with a higher cover. Mona, Klazana and Maquanda were dominated by *Panicum maximum*. This species was common at all sites in mesic and semi-arid grasslands. *Panicum coloratum* was common only in semi-arid grasslands but dominant at Mbuzane and Soquazela.

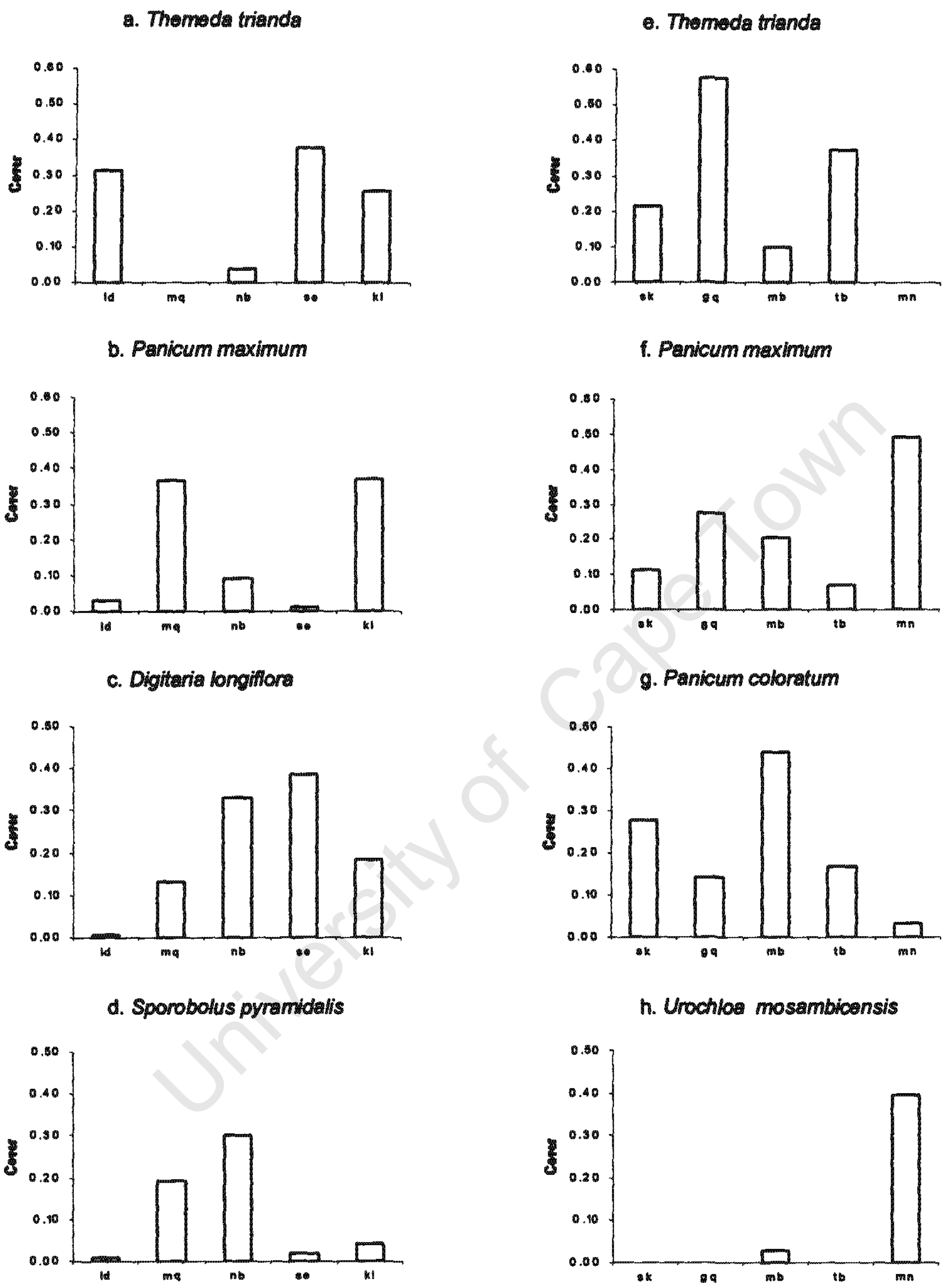

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Figure 3.2: Cover (proportion of total) of dominant grasses in hare fence exclosures at Hluhluwe (a-d) and Imfolozi (e-h). Sites are arranged in order of increased grazing intensity from left to right.

Species like *Digitaria longiflora* and *Sporobolus pyramidalis* were common only in the mesic savanna. The latter was dominant in Nombali while the former was dominant at

Seme and Nombali. *Urochloa mosambicensis* was co-dominant with *Panicum maximum* at Mona but common only in two semi-arid sites.

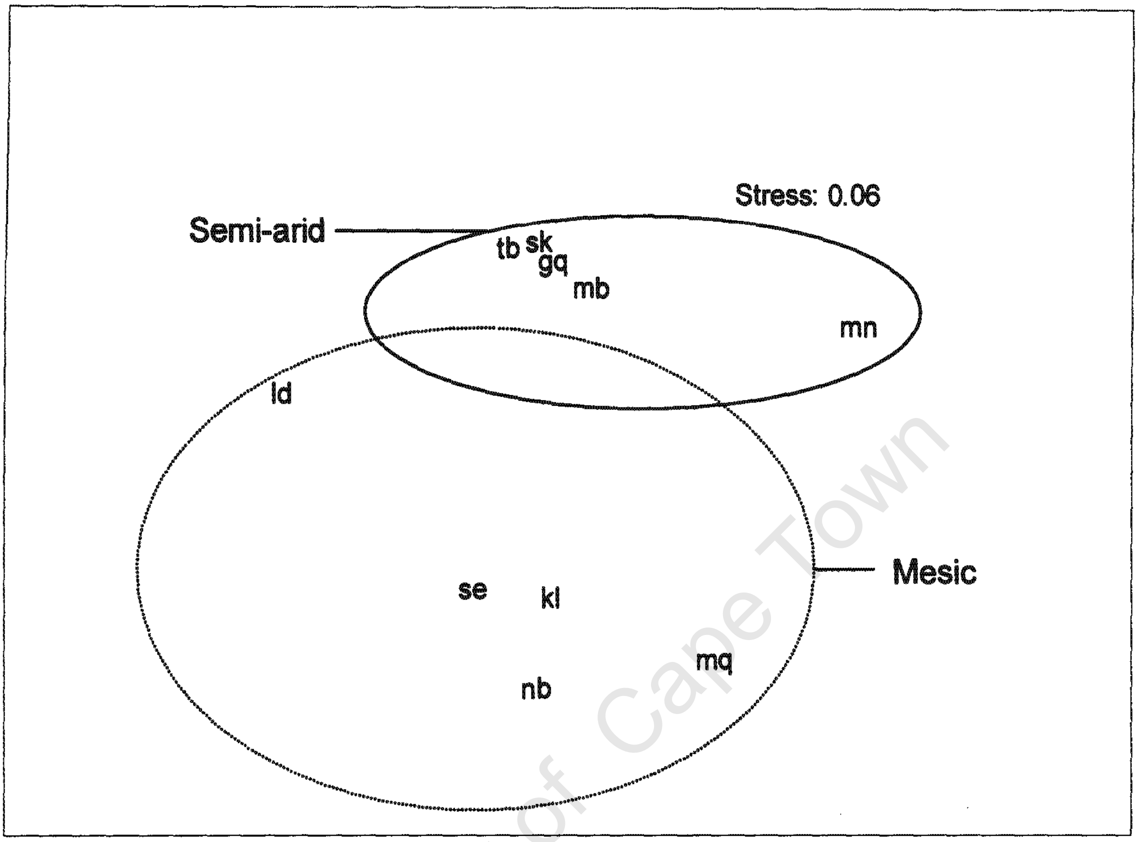

Figure 3.3.1 Ordinations of sites according to grass composition within exclosure sites. Ordination method – multidimensional scaling (MDS) using Bray Curtis similarity measure on square-root transformed weighted frequencies. Sites on (A) are Le Dube (ld), Maquanda (mq), Nombali (nb), Seme (se), and Klazana (kl), all mesic; and Soquazela (sk), Gqoyeni (gq), Mbuzane (mb), Toboti (tb), and Mona (mn), all semi-arid

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The stress is a measure of poorness of fit between the ordination and measured ecological distances. The stress values on figures 3.3.1 and 3.3.2 show the relationship between the similarity in species composition and the closeness in ordination space. The lower the stress value the better the accuracy in grouping. Stress values for both figures are low and therefore ordination is good. The semi-arid sites were clumped together due grass composition while mesic sites were also grouped together (see Figure 3.3.1). Grass composition is important in determining differences in mesic and semi-arid grasslands. Toboti, Soquazela, Gqoyeni and Mbuzane were very similar in grass composition in the semi-arid grassland with Mona slightly less similar to the other four. The mesic sites were grouped at lower end of the graph having few grass species in comparison with the semi-arid sites. Grass species responsible for the differences among mesic and semi-arid grasslands are shown in Figure 3.3.2.

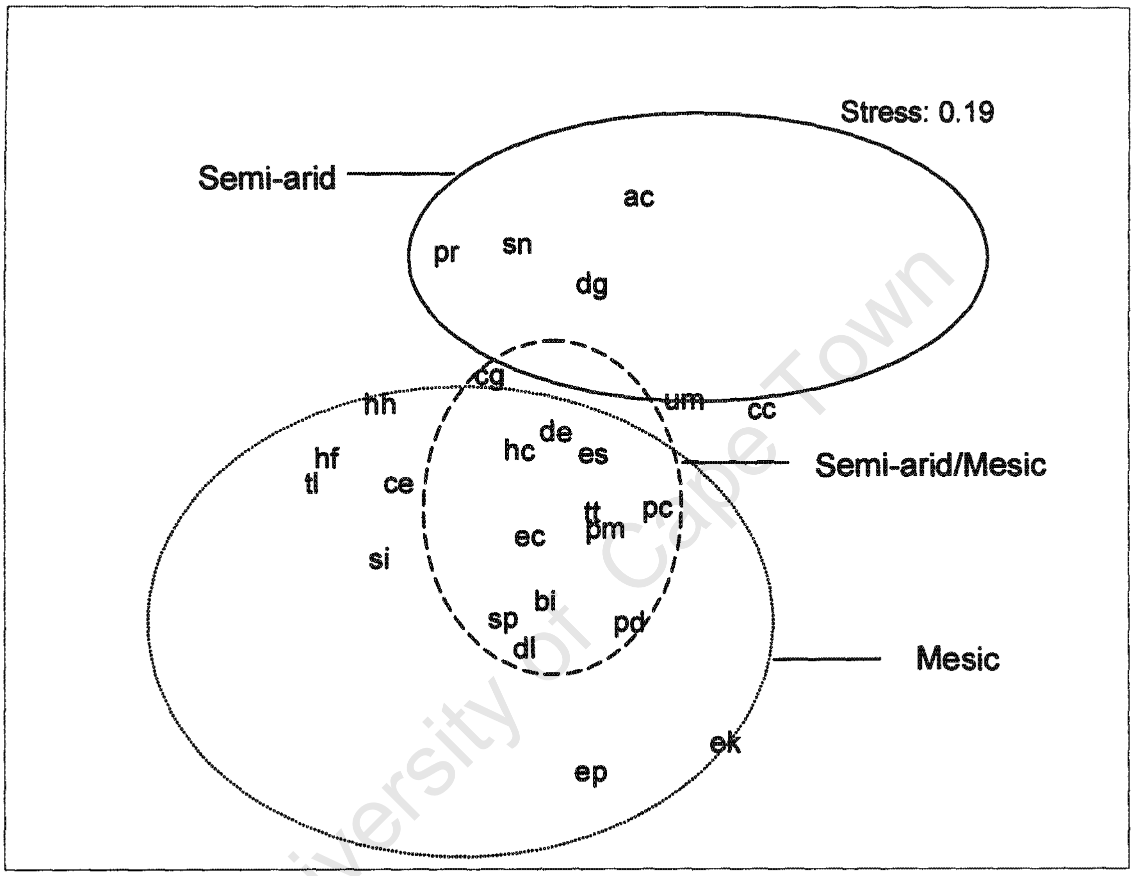

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Figure 3.3.2 Ordinations of grass species within exclosure sites. Ordination method – multidimensional scaling (MDS) using Bray Curtis similarity measure on square-root transformed weighted frequencies. The species codes used represents the following species, *Aristida congesta* (ac), *Sporobolus nitens* (sn), *Panicum repens* (pr), *Digitaria argyrograpta* (dg), *Digitaria eriantha* de, *Chloris gayana* (cg), *Hyparrhenia hirta* (hh), *Hyparrhenia filipendula* (hf), *Urochloa mosambicensis* (um), *Cenchrus ciliaris* (cc), *Digitaria longifolia* (dl), *Heteropogon concortus* (hc), *Eragrostis superba* (es), *Cymbopogon excavatus* (ce), *Panicum coloratum* (pc), *Themeda triandra* (tt), *Panicum maximum* (pm), *Eragrostis curvula* (ec), *Bothriochloa insculpta* (bi), *Sporobolus pyramidalis* (sp), *Eragrostis capensis* (ek), *Eragrostis plana* (ep), *Tristachya leucothrix* (tl), *Setaria nigrirostris* (si) and *Panicum deustum* (pd).

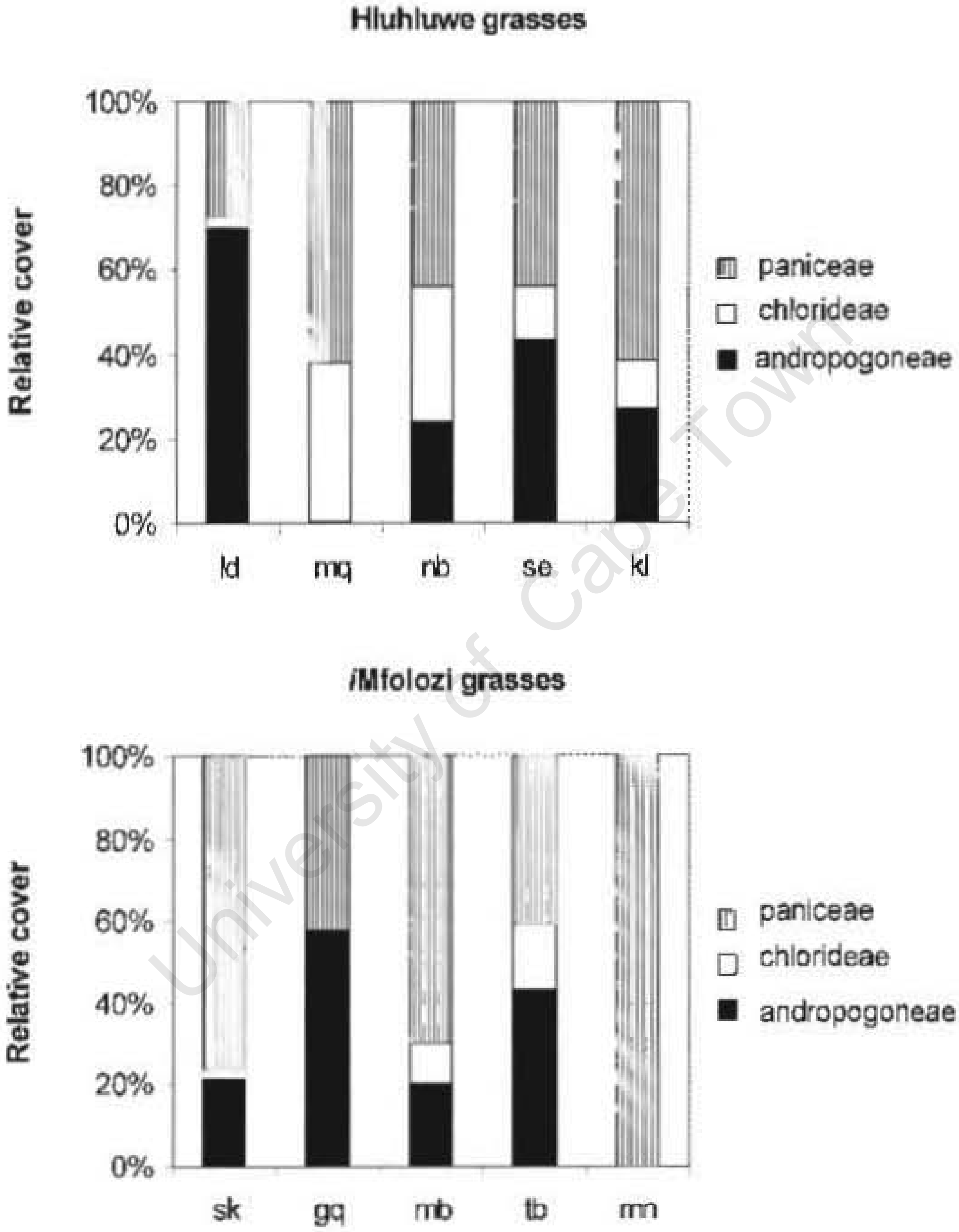

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Figure 3.4: Composition of grass layer according to tribe in Hluhluwe (above) and iMfolozi (below). Sites are arranged along a gradient of increasing grazing intensity from left to right. The proportion of total cover made up of species in each tribe is shown.

Paniceae was dominant in most grassland sites, Maquanda and Klazana in mesic grasslands as well as Soquazela, Mbuzane and Mona in semi-arid grasslands. Le Dube and Seme in mesic grasslands as well as Gqoyeni and Toboti in semi-arid grasslands were dominated by Andropogoneae. Mona and Maquanda did not have grasses belonging to the tribe Andropogoneae.

3.4.2. Productivity and Carryover from harvested biomass

From figure 3.5 one can see a sharp decline from the time of the highest biomass accumulation until the end of the dry season. Peak standing biomass ranged from maximum of 381 g/m^2 in Toboti to the minimum of 102 g/m^2 in Mona.

The peak standing grass biomass values indicated are net productivity until the end of the growing season and signify the amount of biomass that will go through the process of decomposition. From figure 3.6 (A) it was evident that Toboti although higher in peak standing biomass was not significantly different from other sites except Maquanda, Klazana and Mona. Mona with the least peak standing biomass was significantly different from four sites with the highest biomass, that is, Toboti, Gqoyeni, Nombali and Mbuzane. The ANOVA results in table 3.1 confirm that the variation in peak standing biomass among mesic and semi-arid grasslands sites was slightly significant at the lawn grass and forb site compared to the bunch and mixed sites. The mesic savanna of Hluhluwe had similar peak standing biomass and hence productivity to the semi-arid savanna of *i*Mfolozi.

Carryover ranged from the maximum of 215 g/m^2 in Nombali to a minimum of 24g/m^2 in Mona. Le Dube burnt accidentally so there is no data. Gqoyeni was heavily infested by harvester termites therefore data on carryover is excluded form the analyses. The variation in carryover is shown in figure 3.6 (B) across all the different sites in mesic and semi-arid grasslands. It can be noticed from the graph for example that Nombali had higher carryover than all the other mesic and semi-arid sites. The results from ANOVA in table 3.2 show that the determinants of variation in carryover among mesic and semi-arid grasslands were highly dependant on the site composition as well as the park. Mesic grasslands had significantly higher carryover than semi-arid grasslands.

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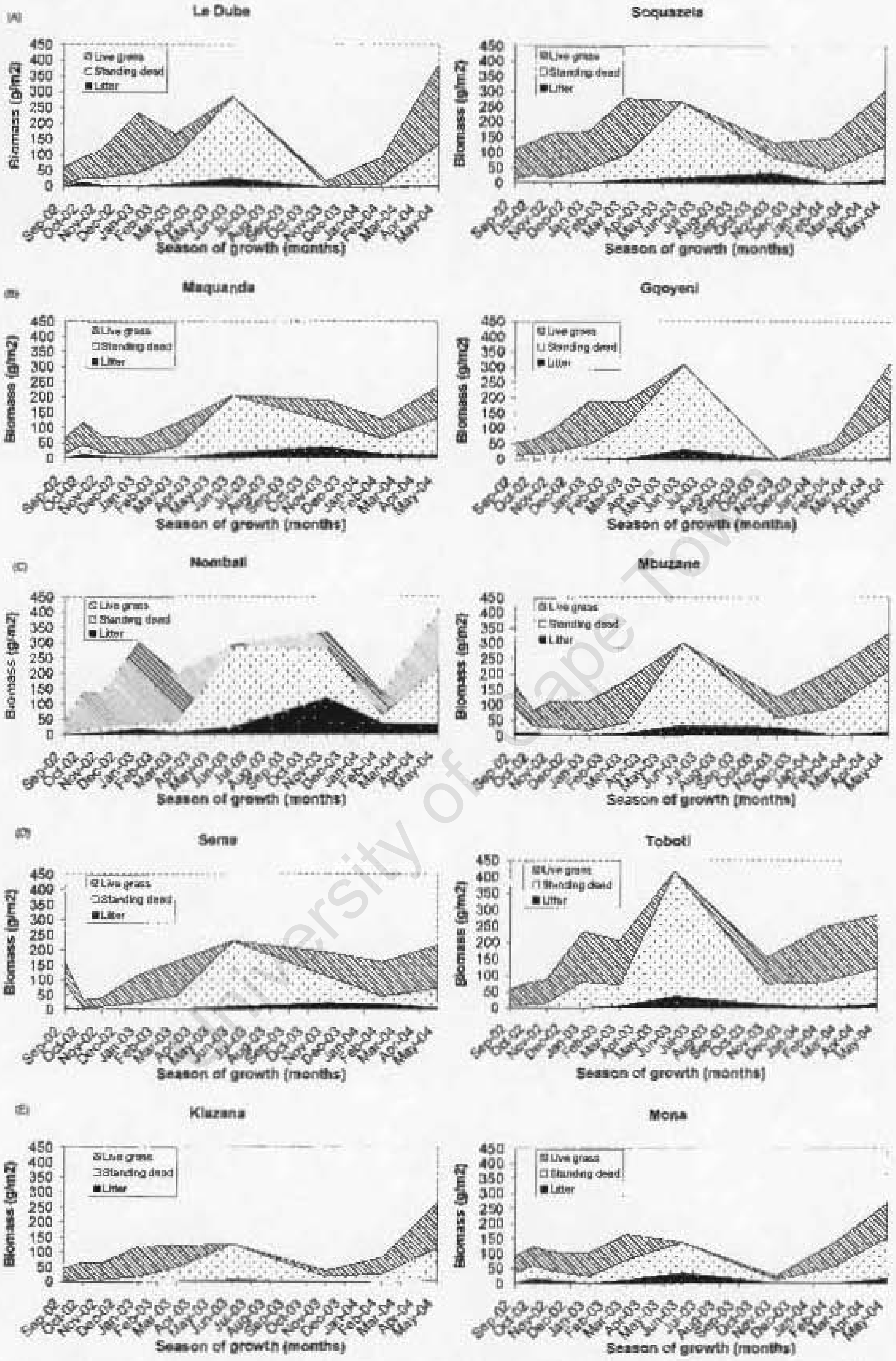

Figure 3.5: Productivity based on biomass collection of grasses in mesic (right) and semi-arid (left) grasslands sites with herbivore excluded. Total grass biomass equals to live grass + standing dead + litter. Sites in both parks are arranged from low (A) to high (E) grazing gradient.

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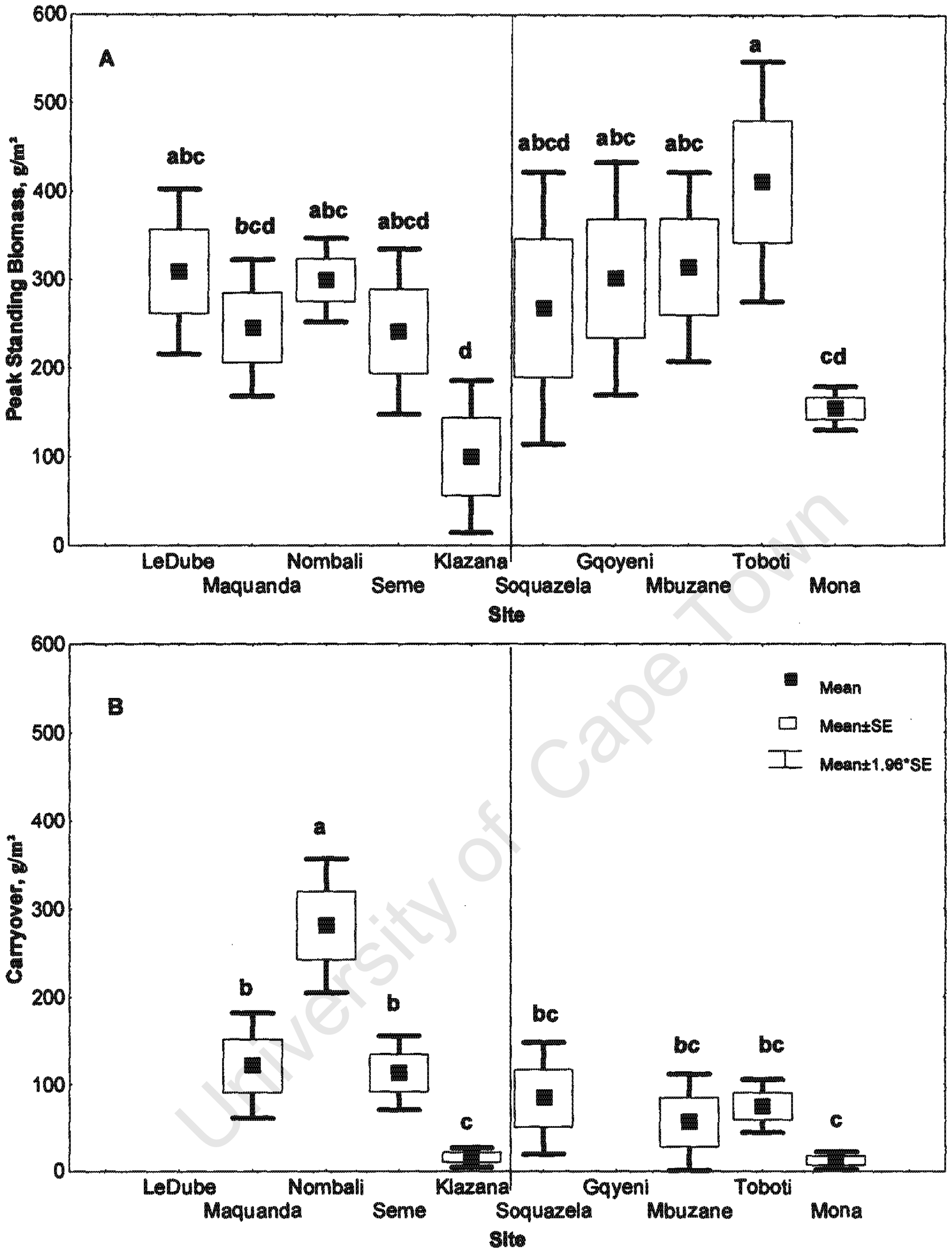

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Figure 3.6: Peak standing biomass (A) and Carryover (B) among the 5 mesic sites on the left and semi-arid sites on the right. Peak standing biomass was harvested in June 2003 while the carryover was the total dead material recorded for the harvests in November, 2003. Le Dube was burnt accidentally and Gqoyeni (Gqyeni on the graph) was infested with termites, therefore no carryover readings.

Table 3.1 Results of a Nested ANOVA on the potential determinants of variation in the peak standing biomass harvested using log transformed data. Park= mesic vs. semi-arid. Homogeneity tests showed that p>0.05. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
Park	1	0.043	0.74	0.39
Site (Park)	8	1.117	2.42	**0.03**

Table 3.2 Results of a Nested ANOVA on the potential determinants of variation in carryover using log transformed data. Park= mesic vs. semi-arid. Homogeneity tests showed that p>0.15. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
Park	1	1.09	9.52	**0.001**
Site (Park)	6	5.21	7.60	**0.001**

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To determine how fast carryover disappears from an individual site in the wet season the amount of dead material in the first months after the rain was compared (see Figure 3.5). The period investigated was between November 2003 and February 2004. This gave us a decomposition rate for the carryover during the early wet season. The percent dead material remaining after the early wet season was obtained by dividing the dead material present in February, 2004 by total dead in November, 2003. The percent dead material remaining after the early wet season was higher in Nombali at 84.2% and least in Klazana at 43.3%. Hluhluwe had an average of 60.4% of the dead material remaining after the early wet season while iMfolozi had 50.6%. The dead material remaining after early wet season was not significant for the two parks (p>0.1).

When carryover was related to peak standing biomass, it was established that there was a positive relationship (see Figure 3.7 below). Peak standing biomass affected carryover in mesic grasslands differently to semi-arid grasslands. In mesic grasslands, low biomass resulted in low carryover with high biomass sites having high carryover. Semi-arid grasslands, whether higher or lower in peak standing biomass, had low carryover.

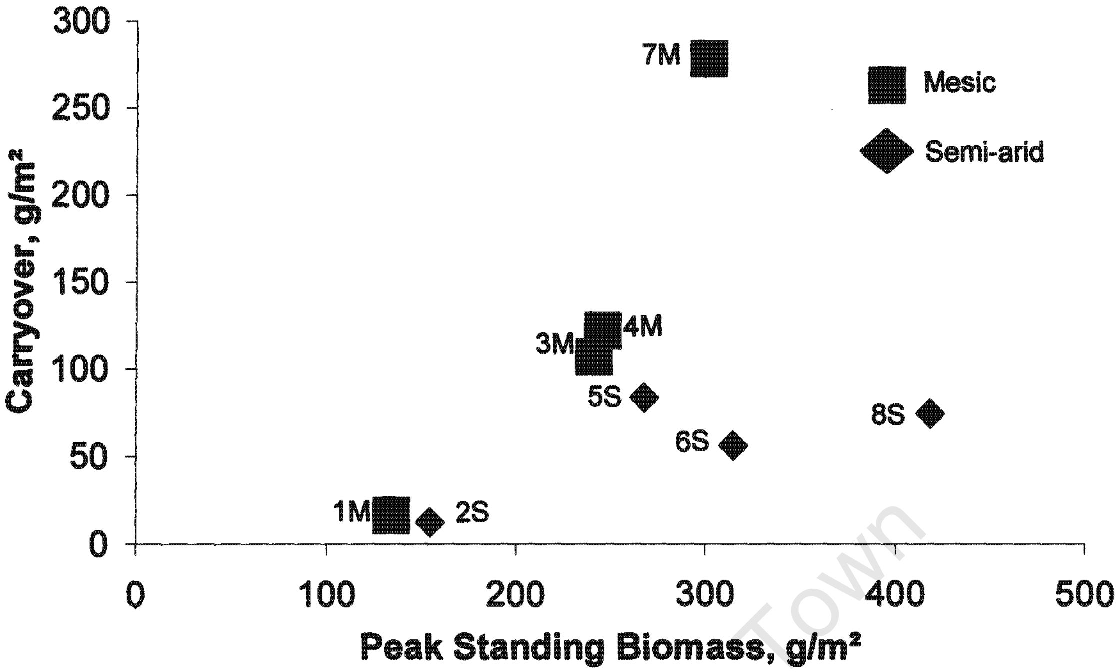

Figure 3.7: The relationship between carryover after first rain versus peak standing grass biomass during the June-November 2003 dry season. Sites are: 1, Klazana; 2, Mona; 3, Seme; 4, Maquanda; 5, Soquazela; 6, Mbuzane; 7, Nombali; and 8, Toboti. Data points with symbol M is for mesic savanna whereas S is for semi-arid savanna. Gqoyeni had biomass removal by termites while Le Dube got burnt accidentally and therefore could not be used in this analysis.

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3.4.3. Peak standing grass biomass (DPM converted) during the 2002-2003 growing season between the Hare fence and the Control of H*i*P.

Grassland productivity differences due to herbivory

This section refers to biomass measured by disk pasture meter, rather than clipping. Disk pasture meter measurements are a better measure of variation in grass biomass across each treatment. Table 3.3 below show that peak standing biomass was not significantly different between the parks. The sites within the two parks were very important in determining how much peak standing biomass was achieved at the end of the growing season. It also was evident that herbivory contributed to large variation between sites within the park. When large herbivores were excluded in the Hare fence, the variation in fuel load among sites in both parks was significant (see Figure 3.8 (A)).

The presence of large herbivores resulted in large variations in peak standing biomass among highly grazed sites and sites with low grazing in both mesic and semi-arid grasslands (see Figure 3.8 (B)).

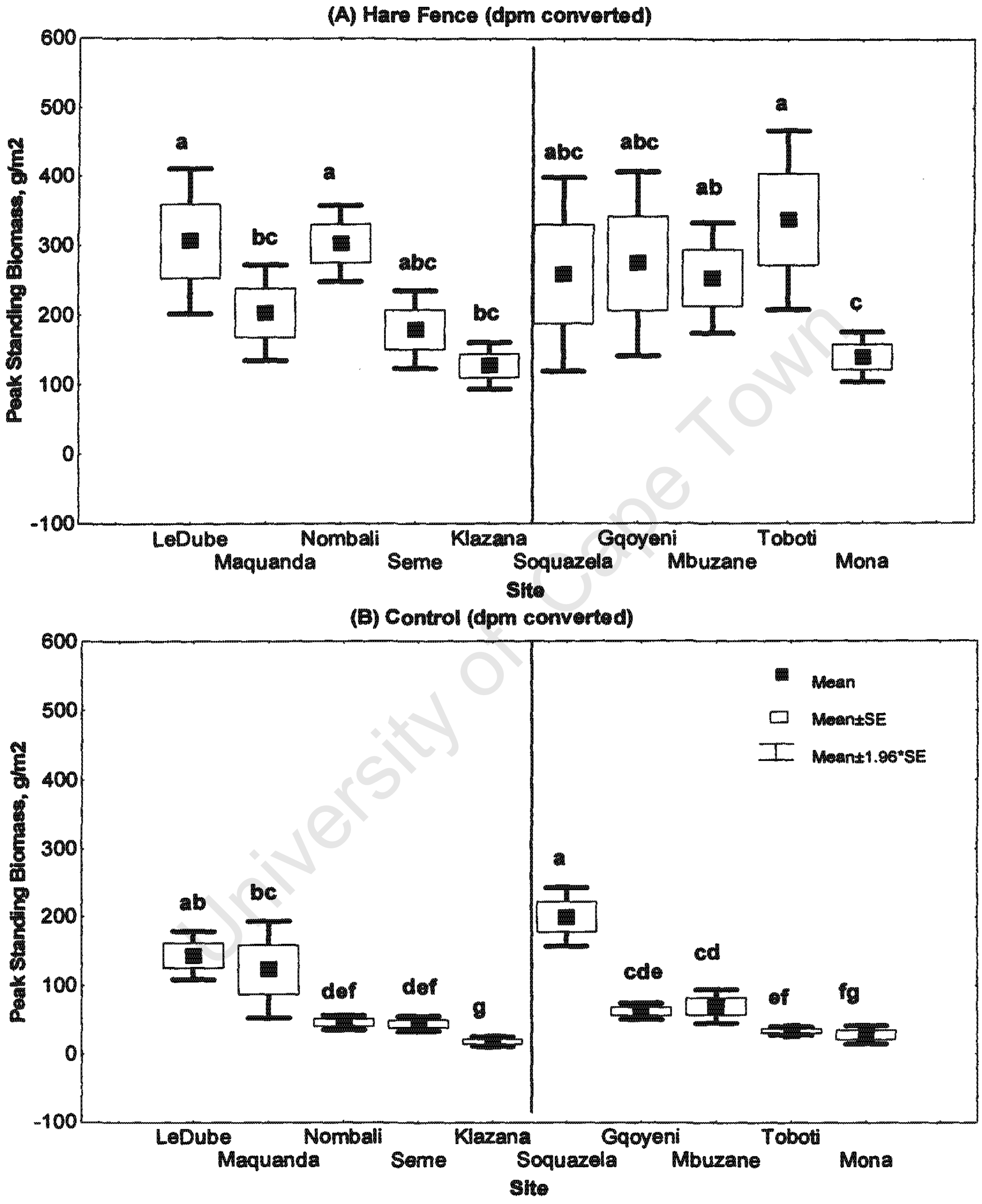

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Figure 3.8: Peak standing biomass from DPM measured in the Hare fence (A) and the control (B).

Table 3.3 Results of an ANOVA on the potential determinants of variation in the peak standing biomass using log transformed DPM averages. Park= mesic vs. semi-arid. Treatment= control vs. hare fence. Homogeneity tests showed that p>0.05. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
Park	1	0.04	0.58	0.45
Site (Park)	1	3.85	6.93	**0.001**
Treatment	6	11.7	168	**0.001**

Variation among sites in peak standing biomass measured by clipping in the Hare fence (see Figure 3.6 (A)) were similar to those measured by the DPM with Nombali, Le Dube and Toboti were significantly higher only to Maquanda, Klazana and Mona.

3.5. DISCUSSION

There seems to be little variation in productivity and hence fuel load among mesic and semi-arid grasslands. In this study, there was very little variation in peak standing biomass among mesic and semi-arid grasslands (see Figure 3.2 (B)) as well as Figure 3.4 (A) when large herbivores were excluded. The mesic savanna was not significantly different to the semi-arid savanna (Tables 3.1 and 3.3). The high variation among the grassland types within the parks was due to the fact that tallgrass sites and mixed sites naturally had more peak standing biomass than shortgrass and forb sites. This can be further be shown by the fact that the shortgrass site in mesic savanna, Klazana was similar to the one in the semi-arid savanna, Mona (see Figure 3.2 (B) and 3.4 (A)).

The amount of grass biomass at the beginning of the dry season starting the process of decomposition is therefore similar between mesic and semi-arid savanna grasslands. This led to the question how does carryover vary among mesic and semi-arid grasslands. Here we wanted to understand how much of the production that goes through senescence is left at the different grassland types during the start of the new growth season. In this study, unlike productivity (peak standing biomass), carryover was significantly different between and among mesic and semi-arid grasslands. Mesic grasslands had very high carryover compared to semi-arid grasslands when large

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herbivores are excluded. The variation in carryover was even higher among the different sites within the different parks (mesic vs. semi-arid), with the least carryover in fenced treatments.

These results led to us to see how production was linked with carryover among mesic and semi-arid grassland. The variation in peak biomass might be related to variation in carryover among mesic and semi-arid grasslands. Here we checked to see whether high production necessarily meant high carryover or vice versa. From figure 3.3 it was evident that some sites with high production had high carryover while others with little biomass had little carryover. What was noticed from the graph was that grass productivity and carryover in mesic grasslands responded differently from semi-arid grasslands. High productivity does not necessarily mean high carryover. In mesic grasslands, low productivity resulted in low carryover and high productivity in high carryover. Semi-arid grasslands on the other hand had low carryover with higher or lower productivity.

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As mentioned in the introduction, rainfall is known to be important in governing grass productivity in grasslands. Because of the low variation in peak standing biomass among sites with different rainfall, one would suggest that rainfall effects were not entirely important in explaining productivity in mesic as well as semi-arid grasslands. Rainfall might still be important in decomposition of litter carryover at the start of the new growing season. There is very little information on how rainfall influences carryover. Early rains at the start of new growth season might be important in removing dead litter during that time, for example by the physical impact of rain drops. The variation in carryover might be due to rainfall differences at the different grassland types. However, the decomposition rate of carryover for mesic grasslands was slower than for semi-arid grasslands. For example, mesic grasslands had on average 60.4% of dead material remaining after early wet season compared to 50.6% for semi-arid grasslands in hare fence exclosures.

Herbivory is also known to be important in determining production at the end of the dry season. The results in this study have also supported that idea. Table 3.3 confirms that differences in productivity were determined by site differences as well as herbivory.

Grass species composition at an individual site might be responsible for differences in productivity and carryover among mesic and semi-arid grasslands. For example, Seme and Toboti were mixed short grassland sites but there was a high accumulation of *Themeda triandra* at both sites resulting in high peak standing biomass during the study period. The most biomass of these sites was mostly contributed by *D. longifolia* of the Paniceae tribe and *B. insculpta* belonging to Andropogoneae while Chlorideae species like *Sporobolus pyramidalis*, *Eragrostis plana* and *Eragrostis curvula* were also responsible. The more biomass a site had the more carryover was happening depending on whether the grassland type was in mesic or semi-arid savanna. Semi-arid sites also seem to depend on species composition dominating the site but this factor seems to be not very specialised as species that accumulate more biomass has reasonably speedy disappearance of standing litter. This can be seen from the fact that although Toboti had the highest peak standing biomass, it still has very quick biomass disappearance. The sites with the highest carryover were the mesic sites although a couple of *Themeda triandra* dominated semi-arid grasslands were also higher in carryover, for example, Toboti and Soquazela. Grass species composition, therefore may contribute to variation in carryover in mesic versus semi-arid grasslands.

Most of the semi-arid sites, although having more aboveground biomass than the mesic grasslands, had less carryover than the mesic grasslands. I therefore suggest that decomposition in the semi-arid sites was influenced by different parameters than decomposition in mesic grasslands. The other possibility might be that the same factors influence the species composition in these savanna grasslands differently resulting in the differences in carryover. I suspect that differences in photodegradation by the sun might be responsible for the less carryover and speedy decomposition rates of grass species in semi-arid savanna grasslands.

Peak standing biomass and carryover was determined by site differences. The factors that differentiated between the sites included altitude, rainfall, soil type, grazing gradient and grass species composition. When one looks at sites like Seme and Klazana which have similar rainfall, altitude and soil type, one might conclude that it is not the three factors determining peak standing biomass and hence carryover. The results from this chapter have shown that species composition was very important.

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3.6 CONCLUSION

The semi-arid sites, despite their high peak standing biomass, had low carryover implying fast decomposition rates. The mesic sites on the other hand had medium peak standing biomass but high carryover, and hence slower decomposition rates. Low carryover is also presumably due to higher levels of grazing relative to mesic sites with Gqoyeni excluded.

Carryover and litter disappearance amongst the sites showed most mesic grasslands to have slow carryover disappearance rates after early rainfall at the start of the new season semi-arid sites. This implies that carryover interfered more with growth and hence productivity as formerly found by Knapp and Seastedt in 1986 at the prairies of the US, and hence affect mesic savanna grasslands more than semi-arid ones. Hence there will be a high accumulation of carryover that will occupy space and shade new growth from receiving maximum sunlight during the growing season in mesic grasslands. Phylogenetically mesic grasslands are designed to burn since fire will remove accumulated carryover.

All of the above differences between mesic and semi-arid grasslands appear to be governed by the species composition at both grassland types. To further understand the differences in carryover among the two grassland types due to species composition, the dominant species at both grassland types were tested in a litterbag experiment (Chapter 4 and 5) to see whether there were definitely differences in decomposition rates among the species occupying these grasslands. The later stages of the thesis explain what caused the differences in carryover and decomposition rates among the grassland species and types

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CHAPTER 4: PHOTODEGRADATION AND CARRYOVER AMONG MESIC AND ARID GRASSLANDS

4.1. INTRODUCTION:

The positive relationship between rainfall and grass productivity is well known (Snyman and Fouche, 1991; Lauenroth and Sala, 1992; Silvertown *et al.*, 1994; Briggs and Knapp, 1995; Scholes and Walker, 1993; O'Connor and Bredenkamp, 1997; Lane *et al.*, 1998; Rutherford *et al.*, 1998, Snyman, 1998; Reynolds *et al.*, 1999; Snyman, 1999; Xiong and Nilsson, 1999; Snyman, 2000; Knapp and Smith, 2001; Knapp *et al.*, 2002; Fay *et al.*, 2003; Wiegand *et al.*, 2003). However, grass productivity can be strongly reduced by undecomposed grass litter, "carryover", accumulated over previous season (Knapp and Seastedt, 1986). Therefore, understanding the relationship between decomposition rate and grass productivity is important in different grass ecosystems. The grass layer of semi-arid savannas experiences a long dry sunny winter and there is little accumulation of necromass (Chapter 2) while the tallgrass in mesic savanna grasslands on the other hand seems to accumulate necromass. Carryover of biomass from one growing season to the next may inhibit productivity by shading the current year's production (Knapp and Seastedt, 1986) in mesic savanna grasslands but not semi-arid savanna grasslands.

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In this experiment I tried to establish whether photodegradation during the long dry season was a factor causing the difference in necromass accumulation between the moist and dry savanna grasslands. I tested the impact of photodegradation on litter accumulation in the field using shade nets to see whether reduced sunlight decreased physical breakdown resulting in more carry-over. If photodegradation has no effect on decomposition in wet and dry grasslands I expected to find the amount of biomass carryover over a dry season to be similar in both grassland types and in shaded treatments relative to the control of unshaded plots. But if photodegradation affects decomposition in these grasslands, then I expected the amount of biomass carryover to be higher in mesic grasslands than in semi-arid grasslands with more carryover in the shaded treatments relative to the control.

To test the effect of shading on decomposition, I measured biomass loss from standing grass biomass from the beginning to the end of the dry season. I also placed litterbags under the shade nets to see if there was a difference in breakdown by the sun between field decomposition and litterbag decomposition. I also wanted to test whether weight loss from litterbags is a good predictor of decomposition. If litterbags are good predictors of decomposition I expected to see similar weight loss for litterbag decomposition and decomposition of standing grass biomass. This study helps to establish both the importance of photodegradation in the amount of litter that was carried over to the next season and whether there was a difference in litter carry-over between mesic and arid grasslands.

4.2. METHOD:

The study was carried out in large mammal exclosures set up as part of the ZLGP project in Hluhluwe *i*Mfolozi Park (H*i*P). The exclosures were 40 by 40m and constructed of mesh fencing excluding all mammals larger than a rat. Four sites were used, two in Hluhluwe Park (HP) and two in *i*Mfolozi Park (*i*P). The former is a mesic savanna whereas the latter is an arid savanna. The four sites used were Nombali, a site dominated by *Sporobolus pyramidalis* (Chlorideae); Seme, a site dominated by *Themeda triandra* (Andropogoneae); Mona, a site dominated by *Urochloa mosambicensis* (Paniceae); and finally Gqoyeni, a site dominated by *Themeda triandra* (Andropogoneae). Nombali and Seme are located in the mesic savanna, Hluhluwe Game Reserve, whereas Mona and Gqoyeni are in *i*Mfolozi Game Reserve, the arid savanna.

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4.2.1. Climate data during the experiment

The two parks experience a similar seasonal rainfall regime, with more rain in summer (Figures 2.3a and 2.2). The study took place in the dry season but the rainfall data shows that there is slight rainfall during that time; hence it is not completely dry. Annual rainfall averages for the past 71 years, shows that there was slightly more average monthly rainfall during the dry season in Hluhluwe than in *i*Mfolozi. The mean annual rainfall in Hluhluwe is 984 mm/year whereas iMfolozi is 706 mm/year. The sites though experienced lower mean annual rainfall in the region of 780 mm/year in mesic and 590 mm/year in arid grasslands. Rainfall was confirmed to be higher at the start of the growth season in Hluhluwe than in iMfolozi but was higher during the dry season in iMfolozi than in Hluhluwe.

4.2.2. Carry-over measurements

Shade treatments were set up to reduce the intensity of solar radiation over the dry season from May 2003 to October 2003. The three treatments used were 80% shading net, 40% shading net and a control that had no shading net. The shading nets were 1.5 by 1.5 m covering a plot of 1.3 by 1.3m and set up 10cm above the grass canopy. The grass canopy was uniform in height of grass cover for each plot. Three replicates were selected for each treatment within a site. Treatments were randomly allocated to each of the plots.

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Grass biomass was recorded non-destructively using a disc pasture meter (Bransby and Tainton, 1977). This is a simple round metal disc, attached to a hollow metal rod. Within this hollow rod is another metal pole with height calibrations (cm). Knowing the height of the disc (as determined by the vegetation) and the biomass under the disc one can calibrate the height of the disc to standing biomass. With time this allows for a non-destructive estimation of standing biomass. The Disc pasture meter, developed by Bransby and Tainton (1977), is used to estimate grass fuel loads in African grasslands and savannas. The DPM has a very small flaw, that of flattening the grass cover as measurements are taken. But the grass cover gets back to normal standing position after a while. Six Disk Pasture Meter (DPM) readings were taken under each roof at the beginning and end of the experiment. The DPM readings were measured at the same spots on each occasion. The shade nets were removed at the beginning of October. The plots were clipped at the end of the experiment and biomass samples were taken and sorted into green and dead matter.

4.2.3. Litterbag experiment

The litterbag experiment was set up under the similar shading treatments to test how well the litterbags estimate rate of decomposition. Two species of Andropogoneae, *Themeda triandra* and *Cymbopogon excavatus* and one Paniceae, *Urochloa mosambicensis* and one Chlorideae, *Chloris gayana* were used. One Chlorideae or

Paniceae species was paired with one of the Andropogoneae species under each treatment. *C. gayana* was paired with *T. triandra* while *U. mosambicensis* was paired with *C. excavatus*. There were 20 litterbags each containing 3 grams of dry leaves under each shade treatment, with ten litterbags per species. The litterbags were simulating standing litter since they were put on top of a metal table mesh about 20cm above the grass cover. Five litterbags for each species were treated with a fungicide and the other 5 with no fungicide. The total number of litterbags that were used was 720. The litterbags were removed a few days before the plots were clipped.

4.3. DATA ANALYSIS

The following assessments were determined when comparing the rates of biomass loss between Andropogoneae and Chlorideae or Paniceae sites at HiP. I used carryover as my dependent variable to establish the relationship between mesic and semi-arid grasslands. This was based on the conversion of DPM values using the linear equation established by the ZLGP group at HiP. The equation was total biomass=12.33 +26.12(DPM value) where DPM is the disk pasture meter height measurements. The number of samples measured for calibration was 1745. This relationship had an R-squared of 0.72 with a p-value of less than 0.001. The DPM values measured in my study were converted to total standing biomass readings (g/m2). The DPM at the beginning (May readings) and DPM at the end (October readings) were both converted to total standing biomass values. Carryover was determined as the total grass standing biomass converted from DPM readings obtained in October divided by the total grass standing biomass converted from DPM readings obtained in May.

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I used dead material sampled in October to quantify carryover in mesic versus dry grasslands at the beginning of the wet or growing season. Generalized linear models were used to analyse carryover occurring at different sites and the different species involved. A fit model in JMP 5.0.1 statistical package was used to analyse carryover in this instance. A nested ANOVA was performed for the 4 sites nested within the 2 parks. Total standing grass biomass converted from DPM readings obtained in May was used as a covariate in the analysis. For the litterbag experiment, percent litter carryover was the independent variable and represented the decomposition rate. Dependent variables included park, site, tribe, shading treatment, and species name and fungicide treatment.

Correlations were done in JMP using a Bivariate fit from Fit Y by X to analyze the litterbags predictive power to determine decomposition as compared to biomass loss in a natural environment.

4.4. RESULTS

The fact that termites reduced a lot of carryover at Gqoyeni, but were excluded in the litterbag experiment, might have contributed to increased carryover accumulation at this site.

Litter carryover measurements from shading

It is important to notice that tall grassland sites had higher total standing biomass than short grassland sites. Total biomass estimated from the DPM readings at the start of the experiment were similar ranging between 300 g/m² and 400 g/m² in May 2003, except for the 80% shade treatment at Gqoyeni with higher total standing biomass at 550 g/m² than all the other treatments in all the sites. There was a decrease in total standing biomass at all sites over the dry season (Figure 4.3).

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Mona showed the least carryover over the dry season (see Figure 4.4). It was followed by Gqoyeni then Nombali and finally Seme. The arid sites at *i*GR, namely Gqoyeni and Mona, showed less carryover than the mesic sites, Nombali and Seme at HGR. Gqoyeni and Mona although not significantly different from each other, were significantly lower than Nombali and Seme (Figure 4.5).

The shade treatments at Andropogoneae sites in both Parks, Gqoyeni and Seme, had an interesting order of carryover. The 80% treatment showed less carryover than the 40% treatment, while the control treatment led to the greatest carryover for these Andropogoneae sites. The Chlorideae or Paniceae sites showed the least carryover in the control and the 80% shading.

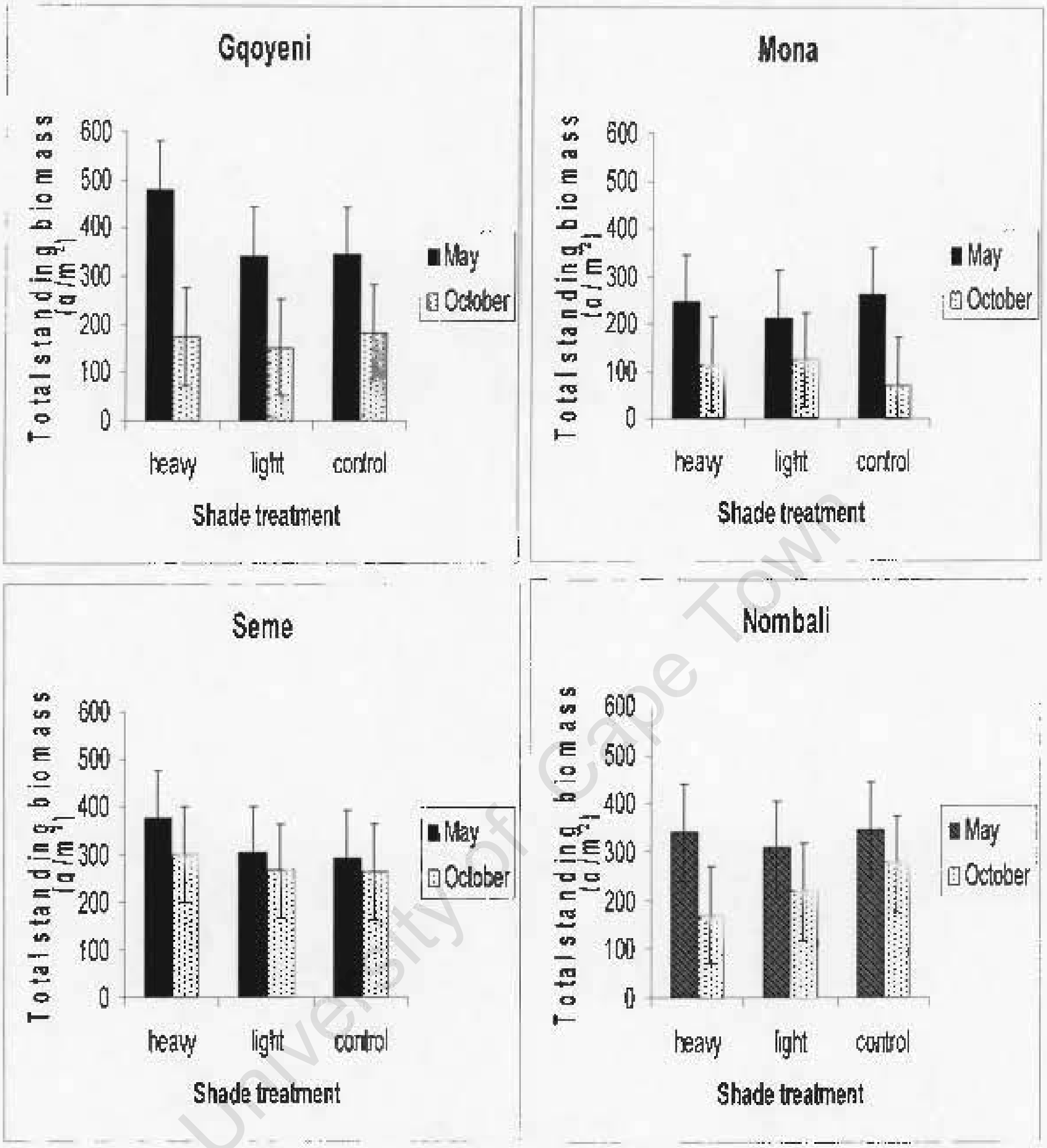

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Figure 3.3: Bar graph showing the relationship between total grass standing biomass (g/m2) at the beginning (May 2003) and the end (October 2003) of the experiment under different shade treatments at the 4 different sites in HiP. Shade treatments were: Heavy-80% shade net, Light-40% shade net, control-no shade

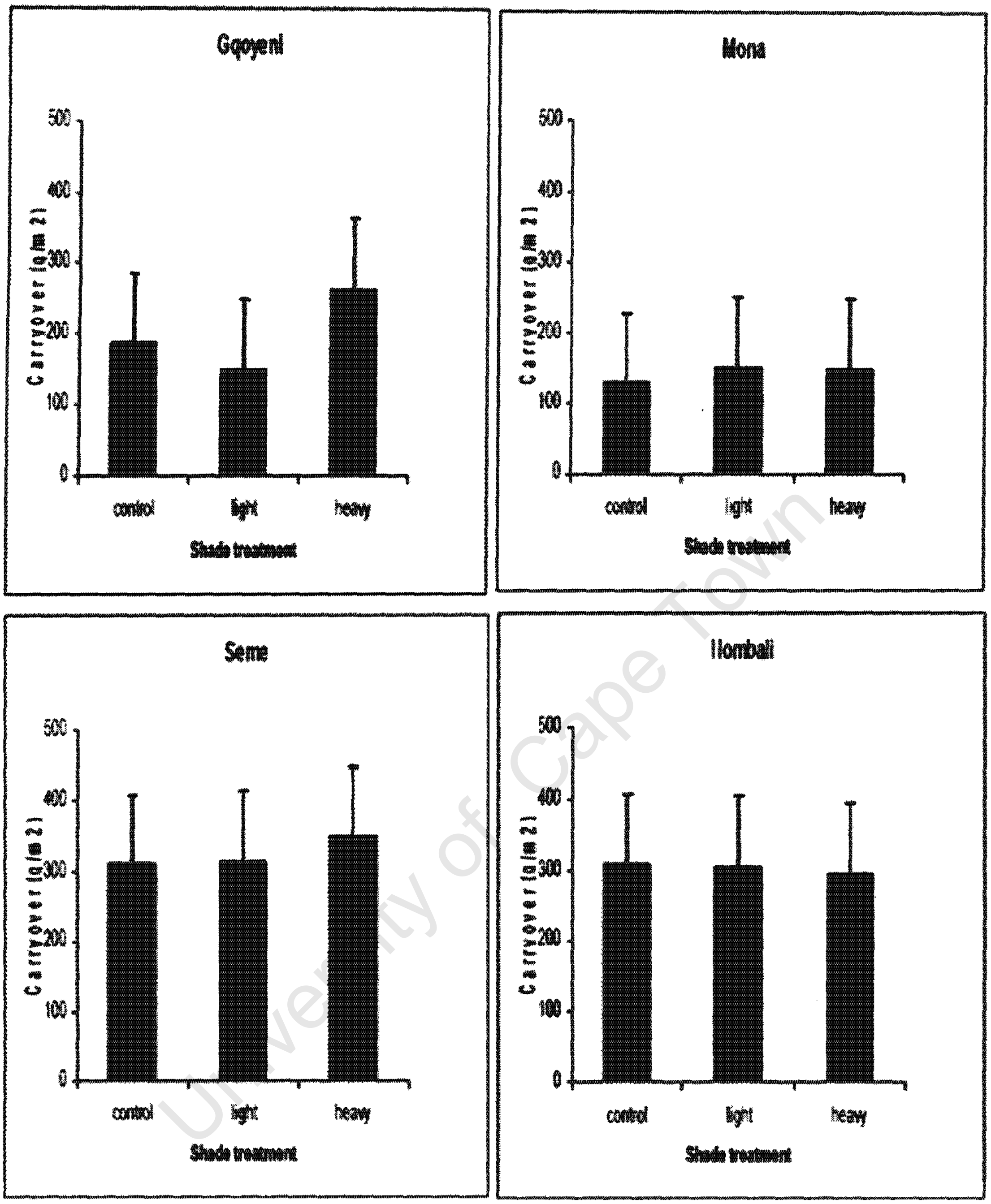

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Figure 4.4: Bar graph showing carryover under different shade treatment at the four different sites during the period May to October 2003 in H*i*P. Shade treatments were Control=no shade, Light=40% shade net, and Heavy=80% shade net

Carryover at all sites except Mona showed no significant differences between the shading treatments (Figure 4.5). The only significant difference obtained at Mona was between the control treatment and 40% shade treatment with the control treatment having significantly lower carryover than the 40% shade treatment.

Carryover to the start of the growing season

Carryover, measured as dead material in plots clipped in October, varied among sites and treatments. Mona had the lowest carryover in the control (26.11 g/m²). This was significantly lower in dead grass accumulation than all the sites. Carryover (49.65 g/m²) was higher in the 40% shade treatment than in the 80% treatment (39.39 g/m²) and both were greater than the control treatment (26.11 g/m²). The shade treatments within Gqoyeni and Mona were not significantly different from each other (Figure 4.5).

Seme had the highest carryover (354.64 g/m²) followed by Nombali (244.64 g/m²) (Figure 4.4 and 4.5). At Seme and Nombali carryover was significantly different between the control, the 40% and 80% shade treatments (Figure 4.5). At these sites the control had significantly less carryover than the 80% shade treatment ($p<0.02$) in Seme whereas those at Nombali showed contrasting results with the control having significantly more carryover than the 80% shade treatment. The two mesic sites also had the highest amount of dead material under the control treatments. Though they were not significantly different from each other, they were certainly significantly higher in dead grass accumulation than the arid sites.

At *i*Mfolozi sites, the shade treatments were not significantly different from each other. The sites at Hluhluwe showed contrasting results, with the control having significantly higher dead grass material than the 80% shaded treatment in Nombali and the 80% shaded treatment significantly higher than the control in Seme. The two treatments were not significantly different from the 40% shaded treatment

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Table 4.1 Summary of a Nested ANOVA on the potential determinants of variation in carryover $((B_{oct}-B_{may})/B_{oct})$ among mesic and semi-arid savanna grasslands using JMP statistical package. Total standing biomass in May (TSB (May)) was used as a co-variate. Carryover=127.4+0.001(total standing biomass), R=0.84, p<0.0001, Based on N=35. Park= mesic vs. semi-arid. Homogeneity tests showed that p<0.01. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
TSB (May)	1	18482	12.98	**0.010**
Park	1	189692	133.2	**0.001**
Site (Park)	2	7264.3	2.55	0.090
Shade Treatment	2	1816.8	0.64	0.540

Table 4.2 Summary of a Nested ANOVA on the potential determinants of variation in carryover (dead material clipped) among mesic and semi-arid savanna grasslands using JMP statistical package. Total standing biomass in May (TSB (May)) was used as a co-variate. Carryover=214.6+0.12(total standing biomass), R=0.73, p<0.0001, Based on N=35. Park= mesic vs. semi-arid. Homogeneity tests showed that p>0.21. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
TSB (May)	1	2514.86	0.67	0.420
Park	1	159484	42.7	**0.001**
Site (Park)	2	114473	15.3	**0.001**
Shade Treatment	2	2268.96	0.30	0.740

Carryover derived from DPM values (see Table 4.1) confirms what the equation in Figure 4.5 showed that the park difference was the major determinant of carryover at the end of the dry season. The mesic savanna had more carryover than the semi-arid savanna. Secondly, the sites within the parks were also different, and contributed to variation in carryover among mesic and semi-arid grasslands. Lastly, the shade

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treatments were not important in explaining the variation in carryover among mesic and semi-arid grasslands.

For carryover due to dead material clipped (Table 4.2), the total standing biomass was not an important determinant. The first influential determinant was the Parks, with the mesic savanna having more dead material than the semi-arid savanna. Thirdly, the sites within the parks were also different, and explained a lot of variation in dead material among mesic and semi-arid grasslands. Lastly, the shade treatments were not important in explaining the variation in dead material among mesic and semi-arid grasslands.

Litterbag decomposition

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The litterbag decomposition rate was measured as weight loss. At all sites, the weight loss was greater in the control and least in the 80% shade treatment. Figure 4.6 shows that weight loss was higher under the control followed by the 40% shade treatment then the 80% shade treatment at Gqoyeni. The 40% and 80% shade treatments were not significantly different from each other but both were significantly less than the control treatment. The treatments at Mona decreased in the same order as those in Gqoyeni with greater weight loss in the control followed by the 40% shade treatment then the 80% treatment. At Mona weight loss was not significantly different between the control and 40% shade treatment but both were significantly different from the 80% shade treatment. There were no significant differences between the shade treatments at Seme. The control treatment was only significantly different from the 80% shade treatment at Nombali.

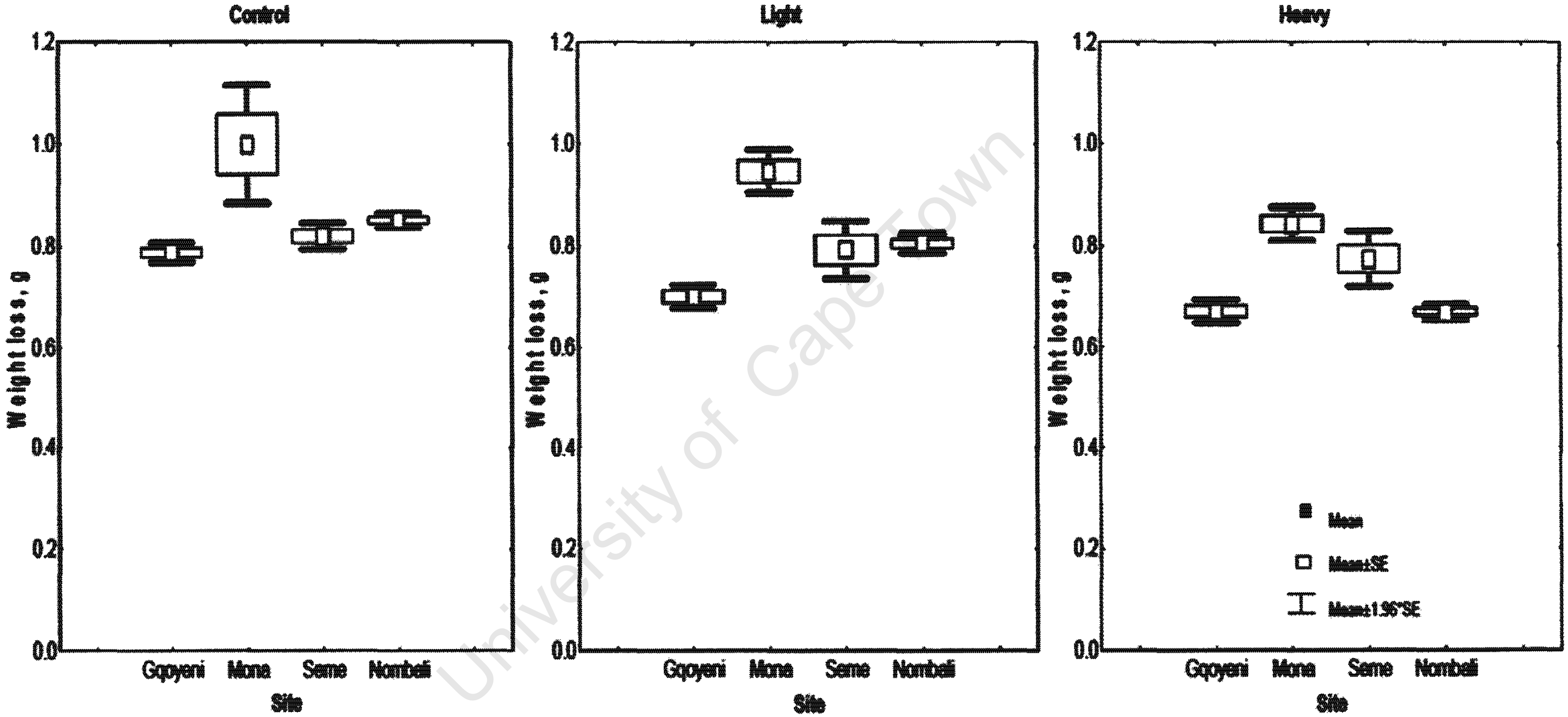

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Figure 4.6: Weight loss from litterbags placed at the four sites under different shade treatments

Table 4.3 Summary of a Nested ANOVA on the potential determinants of variation in weight loss from litterbags among mesic and semi-arid savanna grasslands using JMP statistical package. Intercept=1.13, R=0.59, p<0.0001, Based on N=191. Park= mesic vs. semi-arid. Homogeneity tests showed that p<0.01. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
Park	1	1.12	86.1	**0.001**
Site (Park)	2	0.60	21.8	**0.001**
Shade Treatment	2	3.51	128	**0.001**
Species	3	8.59	208	**0.001**
Fungicide Treatment	1	1.72	125	**0.001**

From the table above, there are significant differences in weight loss between mesic and semi-arid grasslands with semi-arid grasslands having higher decomposition rates. The differences were largely due to species dominating these grasslands types. Photodegradation was important since shade treatments were significantly different from each other with the control significantly higher than the 40% shade treatment which was significantly higher to the 80% shade treatment. Fungicide treatment reduced decomposition.

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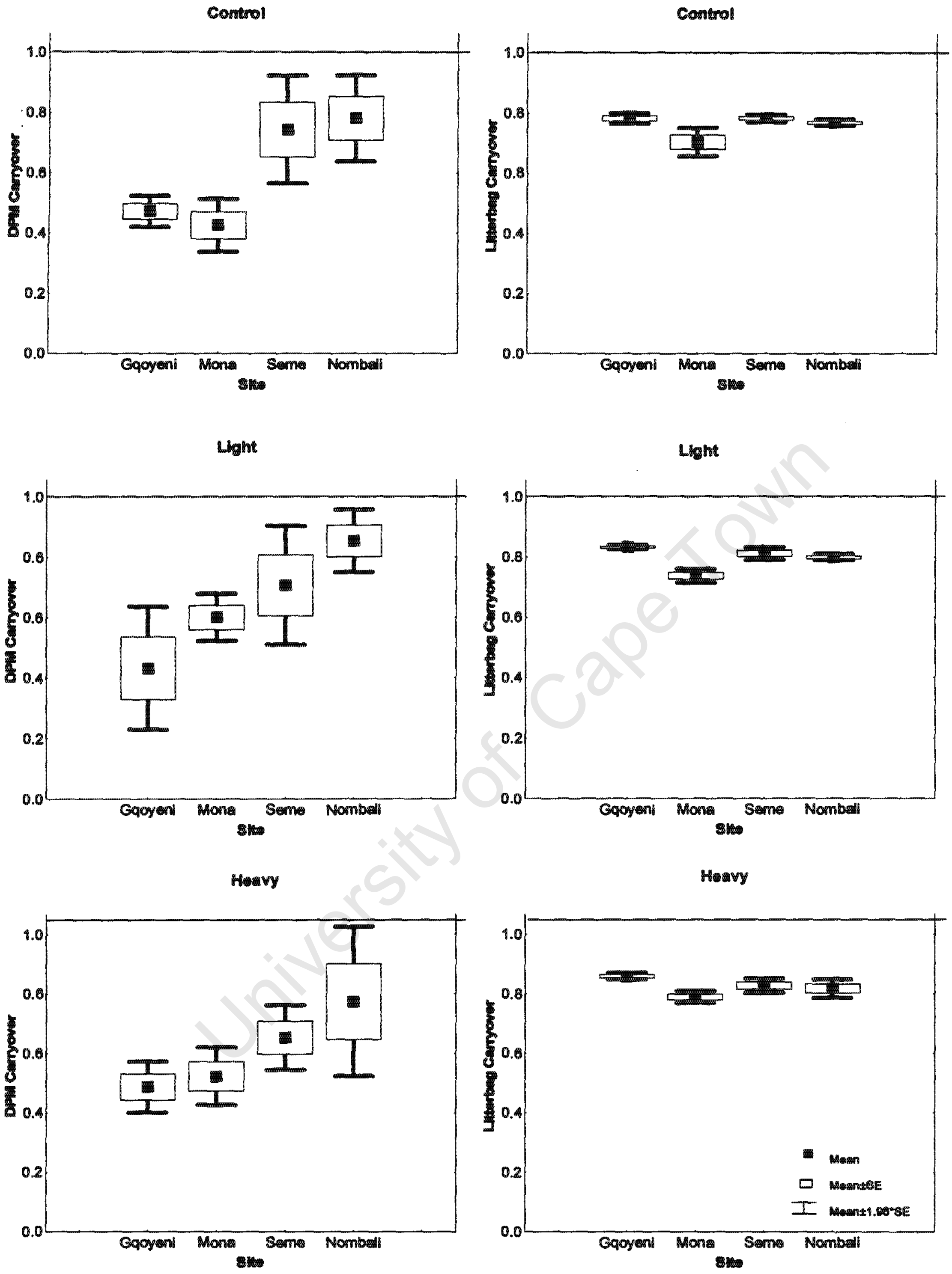

Figure 4.7: Left: The proportion of Carryover measured with DPM obtained from the equation ((Boct-Bmay)/Boct) across the sites. Right: Dead material harvested by clipping the plot. Shade treatments start with the control at the top followed by the light (40%) shade in the middle then heavy (80%) at the bottom. Semi-arid sites are Gqoyeni and Mona while Seme and Nombali are mesic sites.

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Figure 4.7 shows that litterbag carryover unlike dpm carryover (Figure 4.5 and Table 4.2) was influenced by shading, with significant differences between the shade treatments in mesic and semi-arid grasslands. There were differences in carryover due to litterbags versus carryover by dpm, for example the rates of carryover by litterbag had very high rates compared to the dpm values. The most different predictor was shade treatment with lower carryover under no shade and in lower shade treatments. Shade or photodegradation was important as can be seen in table 4.3. Mesic grasslands as was the case in dpm carryover had significantly higher carryover in mesic grasslands than in semi-arid grasslands. The other similar important predictor was the grass species at the sites within the parks. Andropogoneae dominated sites had higher carryover than Chlorideae or Paniceae sites.

4.5. DISCUSSION

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The main question to be answered in the experiment was whether carryover of litter was different between mesic versus semi-arid savannas due to photodegradation. As was the case in Chapter 2, carryover was higher in mesic sites than in semi-arid sites. Secondly, I wished to determine whether photodegradation was an important factor influencing decomposition and carryover over the dry season in both grasslands. I hypothesized that litter carryover between mesic and semi-arid savanna grasslands was similar during the dry season. If photodegradation had no effect on decomposition in moist and dry grasslands I expected to find carryover to be similar in grassland types, sites and shade treatments. But if the opposing prediction holds, where photodegradation affects decomposition in these grasslands, then I expected carryover to be higher in mesic grasslands than in semi-arid grasslands. I also expected the shaded treatments to have less change in grass cover than the control. Site differences should be witnessed in this case with Andropogoneae dominated sites having more carryover than Chlorideae or Paniceae dominated sites. The shading treatments were not significantly different from each other implying that photodegradation had little influence on carryover in mesic versus semi-arid grasslands under dpm measurements and clipping harvests.

Land cover change is likely to influence key ecosystem processes in grasslands, which in some regions alters carbon cycling and feedbacks to climate change (Norby *et al.*, 2001). Our results show that mesic savannas had less loss of grass biomass and hence higher carryover than dry savannas. Thus the experimental sites in Hluhluwe (Seme and Nombali) started their next growing season with more dead material carried over than the sites at iMfolozi. As noted by Knapp and Seastedt, 1986, primary productivity would decrease in these sites as a result of shading by moribund grasses.

The second question tries to show the importance of photodegradation in mesic and semi-arid grasslands. Figure 4.5a suggests that shading had little effect on decomposition rate and carryover from DPM measurements. However, there are some trends. For example if one looks at the dead material clipped under different treatments at Mona (figure 4.5b), there seems to be more biomass carried over when shaded than the control consistent with photodegradation. However, Seme in the mesic savanna showed the opposite trend. To answer the other half of the question, which involves how different is photodegradation between the two grassland types, it was evident that different mechanisms are involved since the plots without shading nets in HGR had less biomass loss than those with shading nets. The opposite phenomenon occurred at IGR where plots covered with shading nets had less biomass loss than the controls except those in Gqoyeni. Termites were visibly active at this site but not at the other sites. Shading nets seemed to favor termite activity at Gqoyeni. So, one can say that photodegradation appeared to decrease carryover by accelerating decomposition in semi-arid savanna grasslands but not the mesic grassland sites.

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Weight loss using litterbags showed decreasing rates between the controls and shading treatments. This supports the idea that photodegradation was an important part of decomposition in savanna grasslands (see Chapter 4). The different dominant tribes from these environments decompose at different rates with Chlorideae or Paniceae having more loss than Andropogoneae. When a comparison was made between decomposition using litterbags and biomass loss from the natural situation, it was evident that these two were going in different directions. Litterbag decomposition predicted that more weight loss should be taking place in mesic savanna grasslands than in arid savanna grasslands whereas natural decomposition showed the opposite phenomenon. I think this difference between litterbag and natural decomposition was due to the fact that litterbags at mesic sites experienced more rain. When rain beats the litter in the litterbags the litter would be more likely to fall out of the bags onto the ground. Mesic grasslands had lower decomposition rate and hence higher carryover than semi-arid grasslands when the two techniques were compared. It was also interesting to have the same kind of site ranking for some sites when using the different techniques. Therefore one can say that, though the litterbag technique exaggerates decomposition, it was a good predictor of qualitative trends in decomposition rate but not quantitative litter decomposition.

The flaws in the project could be due to the fact that shortgrass and tallgrass species were compared and it was difficult to quantify the structural differences between the two growth forms. It might also be due to factors like rainfall that can override the minor effect that photodegradation might have on mesic versus arid savannas with the former receiving more rainfall than the latter. Soil organisms could not be excluded. For example, termite presence at Gqoyeni was high resulting in severe grass biomass loss in the treatments and the whole area.

4.6. CONCLUSION

Photodegradation had less impact on decomposition and hence fuel load between mesic and semi-arid grasslands. However, mesic grasslands had significantly lower biomass loss and hence higher carryover than semi-arid grasslands, as it was shown in chapter 3. Shading had little impact on biomass loss and carryover. So, photodegradation was not a good predictor of biomass loss and carryover between mesic and semi-arid grasslands. Shade treatment effects were not consistent between sites. For example *T. triandra* decomposed faster under shading than when exposed to full sunlight in mesic grasslands while in semi-arid grasslands the opposite happens, that is, more decomposition in the sun exposed than under shading.

Carryover was higher in mesic sites than in arid grasslands when using DPM, as was the case in Chapter 3. Clipping experiment showed more dead material in mesic sites than in semi-arid sites. Gqoyeni had higher dead material than Mona even when the dead material there was harvested by termites. Mesic grasslands had lower decomposition rate and hence higher carryover than semi-arid grasslands when the two techniques were compared. Litterbag technique as well had similar differences between mesic and semi-arid savannas. Therefore one can say that the litterbag technique was a good predictor of the direction of differences in decomposition rate but not the rate of decomposition.

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The study suggests that phylogenetic grouping matters since all the Andropogoneae dominated sites had more dead material than Chlorideae or Paniceae dominated sites. Some Paniceae and Chlorideae species decomposed faster than others. However, Andropogoneae species had high carryover in both parks. Hluhluwe Game Reserve had significantly higher carryover than *i*Mfolozi game Reserve. Therefore photodegradation might be important in determining carryover and hence decomposition rates of savanna grasses.

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CHAPTER 5: VARIATION IN DECOMPOSITION RATES BETWEEN PHOTODEGRADATION AND SOIL BREAKDOWN

5.1. INTRODUCTION

Grass litter may break down through physical effects of solar radiation or microbial decomposition. Most studies tend to focus on microbial decomposition and plant traits and environmental conditions that influence microbes. That is, grassland ecologists tend to focus on factors like lignin content, C/N ratio (Melillo *et al.*, 1982) and abiotic factors like rainfall and temperature (Meentemeyer, 1978; Gil *et al.*, 2003), but not solar radiation, as determinants of plant decomposition. However some studies have shown that solar radiation, such as ultraviolet light, can have a fairly large impact on decomposition of plant materials (Tevini *et al.*, 1983; Teramura and Tevini, 1989; Aber *et al.*, 1989; Milchanus *et al.*, 2004; Austin and Vivanco, 2006; Gallo *et al.*, 2006).

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Decomposition rate in this study represent the rate at which grass litter experiences weight or mass loss. The causes of differences in decomposition rates among the different savanna grasses is not yet understood in spite of the fact that a couple of studies (Morris *et al.*, 1978; Scholes and Walker, 1993) have been made to relate decomposition rate to a number of factors. No studies in South Africa have compared decomposition rates of standing dead litter on the soil for different grass species. This chapter is the strength of the whole thesis and more emphasis will be made in the synthesis and discussion chapter.

Photodegradation is the breakdown of litter or any living organism by light (Morrison, 1992; Morrison and Nelson, 1994; Rozema, 199; Austin and Vivanco, 2006; Gallo *et al.*, 2006). Photodegradation is likely to be important in the long dry seasons encountered in many savanna grasslands (see Chapter 3). For example, Austin and Vivanco, 2006 concluded that photodegradation is a dominant control on the aboveground litter decomposition in the semi-arid Patagonian steppe. Because mesic and semi-arid savanna grasslands are dominated by the different tribes as explained in Chapter 1, I therefore decided to compare the relative rates of decomposition by photodegradation versus soil breakdown and to test whether these rates differ between Andropogoneae and Chlorideae or Paniceae. This chapter also explores whether photodegradation is a rate controlling step in decomposition of grasses and more of this point is explained by plant traits analysis in Chapter 6.

The decomposition process starts the moment plant material goes into senescence. Thus, before the material gets to the ground it has already experienced the first period of breakdown, part being through physical causes (light, UV, drying) and part biotic (fungi and bacteria). The standard protocol for studying decomposition rates uses litterbags placed on the soil (Witkamp and Crossley, 1966; Meentemeyer, 1978; Morris *et al.*, 1978; Melillo *et al.*, 1982; Austin and Vivanco, 2006; Gallo *et al.*, 2006). However, savanna grasses persist as standing dead material for many months in the dry season. The rates at which this material reaches the ground are ignored in litterbag studies because most studies (Morris *et al.*, 1978; Meentemeyer, 1978; Moorhead and Reynolds, 1989; Scholes and Walker, 1993; Norby *et al.*, 2001; Schadler *et al.*, 2003) investigate decomposition by placing litterbags on the soil.

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In some grasslands standing litter accumulates to such an extent that new growth is suppressed by undecomposed grass litter at the beginning of the growing season (Everson *et al.*, 1988; Knapp and Seastedt, 1986; Knapp, *et al.*, 1989; Tilman and Wedin, 1991). The suppression of grass productivity by undecomposed litter seems to be associated with mesic savannas which are dominated, world-wide, by members of the tribe Andropogoneae (Chapter 1). In South African savannas, semi-arid savannas do not seem to accumulate litter (Chapters 3 and 4). Members of the tribe Andropogoneae are rare in semi-arid savannas whereas members of the tribe Chlorideae or Paniceae tend to dominate semi-arid grasslands in South Africa (Gibbs-Russell, 1988; Gibbs-Russell *et al*, 1990) and elsewhere in the world (Hartley, 1954; Hartley and Slater, 1960; Taub, 2000; Hilu, 2004). I hypothesized that Andropogoneae decompose more slowly in the sun than Chlorideae and Paniceae (based on differences in fuel accumulation from year to year).

In this chapter, I compare decomposition rates in litterbags placed above the ground, simulating standing litter versus litterbags placed on the soil, which is the standard procedure. To help determine the relative importance of physical and biological processes in comparing standing litter to surface litter on the soil, I therefore placed litterbags at different angles of incidence to the sun and treated some of the litterbags with fungicide. Decomposition rates are known to vary among species with different litter properties, but experimental evidence has been limited to soil placed litterbags. I therefore compared decomposition rates in the sun and on the soil among a number of species representing different phylogenetic groupings (Andropogoneae versus Chlorideae or Paniceae), and also functional grouping (lawn versus bunch grasses). If the relative ranking of species was similar for decomposition in the sun versus the soil, then similar leaf traits may determine conversion of standing litter to surface litter on the soil. If decomposition rates are not correlated between the sun and soil treatments, then different decomposition processes and different traits may be governing this stage of grass decomposition in savannas.

5.2. METHOD AND MATERIALS

Two litterbag experiments were conducted, one in the savanna region of KwaZulu-Natal Province at H*i*P and one in the summer dry season at the University of Cape Town in the Western Province. The decomposition study in Hluhluwe *i*Mfolozi Park began with collection of leaf litter harvested in April 2002 at the end of the 2001-2002 growing season, prepared during the winter and placed in the field the following spring August 2002 and removed after one month in the same year. Grass species used in the study, their growth form and taxon grouping, are listed in Table 4.1. These grass species were air dried for more than 48 hours and then stored at room temperature during the preparation period in winter. The grass leaf blades were used in this instance. Hluhluwe samples were put out in August 2002 for a month while the Cape Town samples were also air dried for 48 hours packed and transported to Cape Town where they were sorted at room temperature and finally put out in December 2002 until the end of April 2003.

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Table 5.1: List of grass species, their species codes, growth forms and tribes used in the litterbag experiments in Cape Town and at HiP. Andropogoneae together with Paniceae are tribes belonging to the subfamily Panicoideae. Chlorideae is a tribe belonging to subfamily Chloridoideae.

Species code	Species name	Tribe	Growth type
bi	*Bothriochloa insculpta*	Andropogoneae	Lawn
ce	*Cymbopogon excavatus*	Andropogoneae	Bunch
cl	*Chloris gayana*	Chlorideae	Bunch
da	*Dactyloctenium australe*	Chlorideae	Lawn
dl	*Digitaria longifolia*	Paniceae	Lawn
ec	*Eragrostis curvula*	Chlorideae	Bunch
hf	*Hyparrhenia filipendula*	Andropogoneae	Bunch
pc	*Panicum coloratum*	Paniceae	Lawn
tt	*Themeda triandra*	Andropogoneae	Bunch
sn	*Sporobolus nitens*	Chlorideae	Lawn
sp	*Sporobolus pyramidalis*	Chlorideae	Bunch
um	*Urochloa mosambicensis*	Paniceae	Lawn

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Litterbags used for both experiment were made of metal mesh used for mosquito netting and did not rust and could last for more than 4 months out in the field. The mesh size was 2mm with dimensions of 20x20 cm. The litterbags were made not to be flat but oval-shaped to allow the grass species material to be loose in the bag. A table was designed to simulate standing litter facing the sun horizontally using chicken wire fencing with a mesh size of 5cm to allow the litter material to fall out freely to the ground. The top mesh of the table was more than 20cm above the soil. For simulating standing litter facing the sun vertically a line designed using a thin wire was used to hang litterbags vertically between two metal rods. This design was like hanging clothes on washing line but was also 20cm above the soil. For Hluhluwe samples, one Andropogoneae grass species in the form of *Themeda triandra* and two Chlorideae grass species in the form of *Sporobolus pyramidalis* and *Sporobolus nitens*, as well as a Paniceae grass species in the form of *Urochloa mosambicensis* were used. Leaves of these four species were collected in Hluhluwe/Imfolozi Park. Leaf material was inserted into litterbags and placed in an open "lawn grass" patch 20 cm above the ground at the Nombali exclosure site (Plate 5). The amount of leaf material inserted in the litterbag was 1.5 grams. There were 30 litterbags in total per species all containing 1.5 grams of leaf material. Five t0 samples were also measured out for each species.

Three treatments were used. Two simulated decomposition of standing litter. One treatment contained 10 litterbags per species hung vertically 5cm from each other and the other treatment contained 10 litterbags per species hung horizontally on a chicken mesh table. In the third treatment, 10 litterbags were placed on the soil to simulate decomposition of litter in contact with the soil. Litterbags hung vertically to the sun relative to those hung horizontally to the sun since the latter were exposed to more sun breakdown since the whole leaf blade was exposed. Five of the 10 litterbags per species per treatment were treated with a fungicide from Bayer Folicur. The fungicide was sprayed to reduce microbial breakdown. There were 40 litterbags per treatment placed at Nombali giving a total of 120 litterbags. All the litterbags were removed in September 2002, weighed, then dried at 80 °C for 48 hours and thereafter weighed again to obtain the dry weight.

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In the Cape Town experiment decomposition was again simulated for standing litter exposing litterbags to the sun above the ground and compared with weight loss of litterbags placed on the soil surface. I was particularly interested in explaining species differences in decomposition rates for simulated standing litter versus surface litter on the soil. The following grass species were used; *Themeda triandra(tt)*, *Hyparrhenia filipendula (hf)*, *Sporobolus pyramidalis (sp)*, *Eragrostis curvula (ec)*, *Bothriochloa insculpta (bi)*, *Cymbopogon excavatus (ce)*, *Panicum coloratum (pc)*, *Digitaria longifolia (dl)*, *Urochloa mosambicensis (um)* and *Dactyloctenium australe (da)*. Dry leaves of these ten species were collected in Hluhluwe/Imfolozi Park in June 2002. Leaf material was air dried and then sorted at room temperature. Equal amounts of 2.5 grams were inserted into litterbags at the University of Cape Town. Twenty litterbags of each species were placed on a table and the other 20 on the ground except *D. australe* and *D. longifolia* that had 15 litterbags per treatment giving a total of 390 litterbags.

Decomposition rate was obtained by removing five litterbags for each species on the ground and on the table every month during the dry season from December 2002 moving into the wet season of April 2003 on a grass patch in Cape Town. The litterbag contents were removed and weighed using Mass Balance. These contents were ground into powder for chemical analysis in the laboratory every time the litterbags were removed (see Chapter 6 for results).

5.3. ANALYSIS

Decomposition was measured as weight loss as well as the decomposition constant (*k*). k is obtained from the equation $B_t = B_0 e^{-kt}$, where B_0 is the initial dry mass, B_t is the mass at time t, and *k* is the decomposition constant. The decomposition constant was obtained by relating the average weight (g) in the litterbags with the date of collection of the litterbags (in months). The average weight at T0 on the first day was 2.5g (the weight put out at the start) for the Cape Town litterbags. The other four data points were the average weight in the litterbag on the month of collection. An exponential curve was fitted to the data with the exponents providing the *k* values.

Data were analysed in a number of ways (mentioned below) mostly using weight loss as the dependent variable to determine whether there was variation in decomposition rates between Andropogoneae, Chlorideae and Paniceae. Decomposition constant was sometimes used. All data were first tested for homogeneity of variance (using Bartlett's tests) and data transformations applied where appropriate. Data were analysed using the general linear model routines of the JMP and Statistica statistical software packages. In JMP 5.0.1 a Nested ANOVA was applied to the data with grass species nested within the tribe. Mann Whitney's tests were used to analyse the data that were not normally distributed according to homogeneity tests even after the data was transformed. Significant results are reported for the rates in H*i*P and Cape Town.

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5.4. RESULTS

5.4.1. Weight loss in Hluhluwe Imfolozi Park

Grass litter showed increased weight loss from vertically placed to horizontally placed litterbags in the sun and then on the soil (Figure 5.2.1). It was difficult to compare the four species in terms of subfamily since two Chlorideae species were compared against one Andropogoneae, *T. triandra*, and one Paniceae, *U. mosambicensis*.

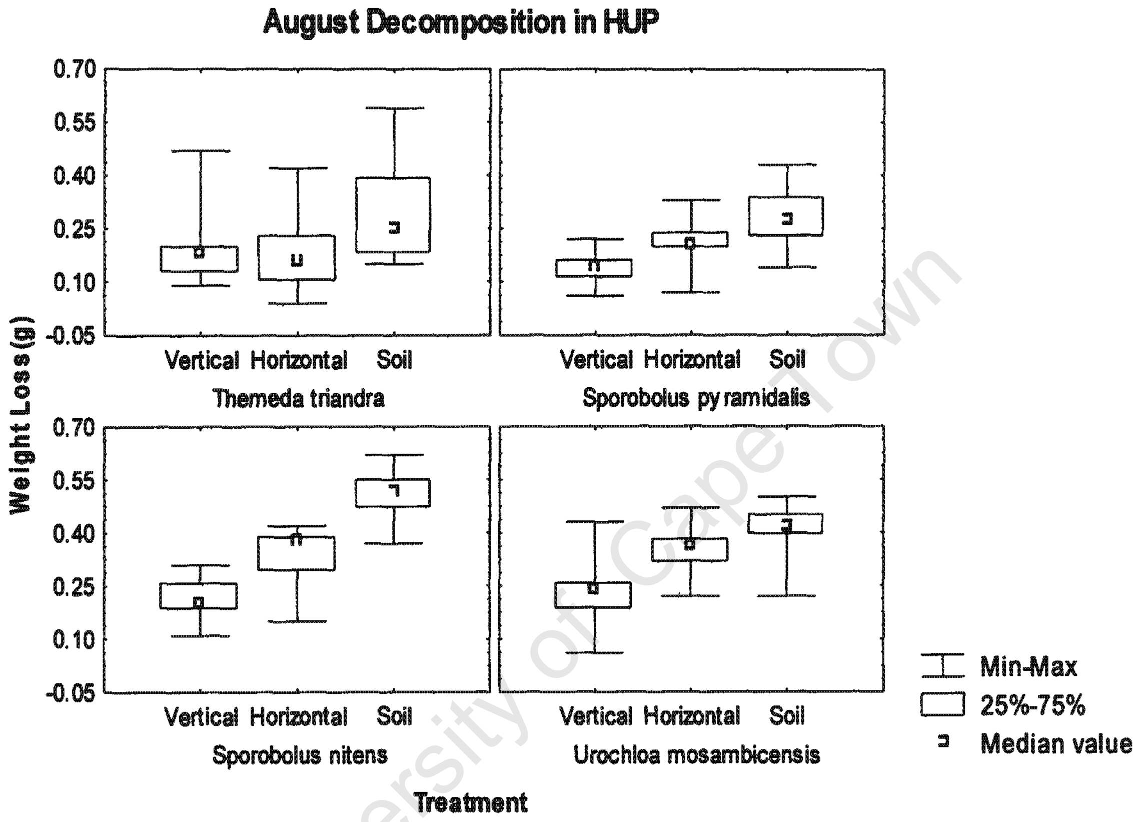

Figure 5.2.1: Results from a box whisker plot showing weight loss of four grass species at HiP for litterbags placed in the sun vertically versus sun horizontally versus soil surface. Litterbags were left in the field for 31 days in the hare exclosure in Nombali. N=30

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When basing assessment on bunch versus lawn grasses, the lawn grasses decomposed faster than bunch grasses. Lawn species that is *U. mosambicensis* and *S. nitens* decomposed faster than *S. pyramidalis* which is a bunch grass. The one lawn Paniceae showed significantly greater weight loss than the two bunch grass species in all the treatments except *S. nitens* placed vertically in the sun (Figure, 5.2.1).

Table 5.2: Results of an ANOVA on the potential determinants of variation in weight loss among four species for standing litter versus surface litter on the soil. Treatment= sun vertical vs. sun horizontal vs. soil surface. Homogeneity tests showed that p>0.12. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
Treatment	2	0.65	38.91	**0.001**
Species	3	0.46	18.57	**0.001**
Species*Treatment	6	1.72	125	**0.020**
FungicideTreatment	1	0.01	0.79	0.380

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From table 5.2 it was shown that variation in weight loss or decomposition rate was determined mostly by the treatment, with losses from the sun being significantly slower than surface soil litterbags. The second most important predictor was the species subjected to decomposition. Interaction between species and the treatments was also important. Fungicide treatment did not matter much in determining the variation in weight loss, with the effects being small relative to position alteration in litter decomposition (see Table 5.2).

Table 5.2 is further supported the results from a Post Hoc analysis, which show that the weight loss of *T. triandra* and *S. pyramidalis* was significantly slower than *S. nitens* ($p<0.001$) and *U. mosambicensis* ($p<0.001$) when the litterbags were placed horizontally. For the vertical treatment all species ($p>0.05$) were not significantly different from each other except *U. mosambicensis* and *S. pyramidalis* ($p<0.02$). In the soil treatment, however, all the species were significantly different from each other ($p<0.05$) except *T. triandra* and *S. pyramidalis* ($p>0.55$). The rates of weight loss for the grasses on the soil were double the rates in the sun placed vertically (Figure 5.2.1).

5.4.2. Weight loss in Cape Town

As at Hluhluwe, all species had a greater decomposition rate in the soil treatments than in the sun (see Figure 5.3). This was similar for weight loss, with the soil samples having doubled the amount of weight loss than the sun samples. Table 5.3 shows significant differences between Andropogoneae in the sun and Chlorideae and Paniceae in the sun with Chlorideae and Paniceae decomposing more rapidly. The results for the litterbags in Cape Town were also assessed to determine whether the ten grass species differed in decomposition rates when placed in the sun versus on the soil.

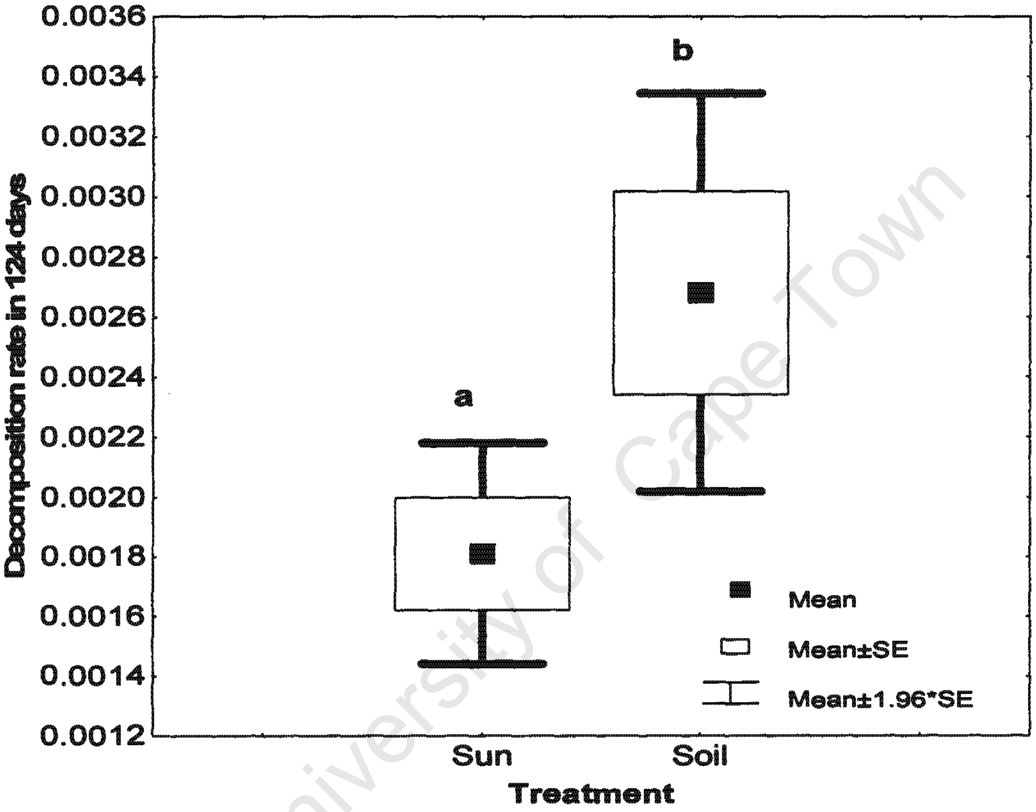

Figure 5.3: Box whisker plot for mean decomposition rate in 124 days for 10 species placed in the sun or on the soil surface in the month of April 2003 in Cape Town. Decomposition rate, *k*, was obtained from the equation $B_t=B_ie^{-kt}$

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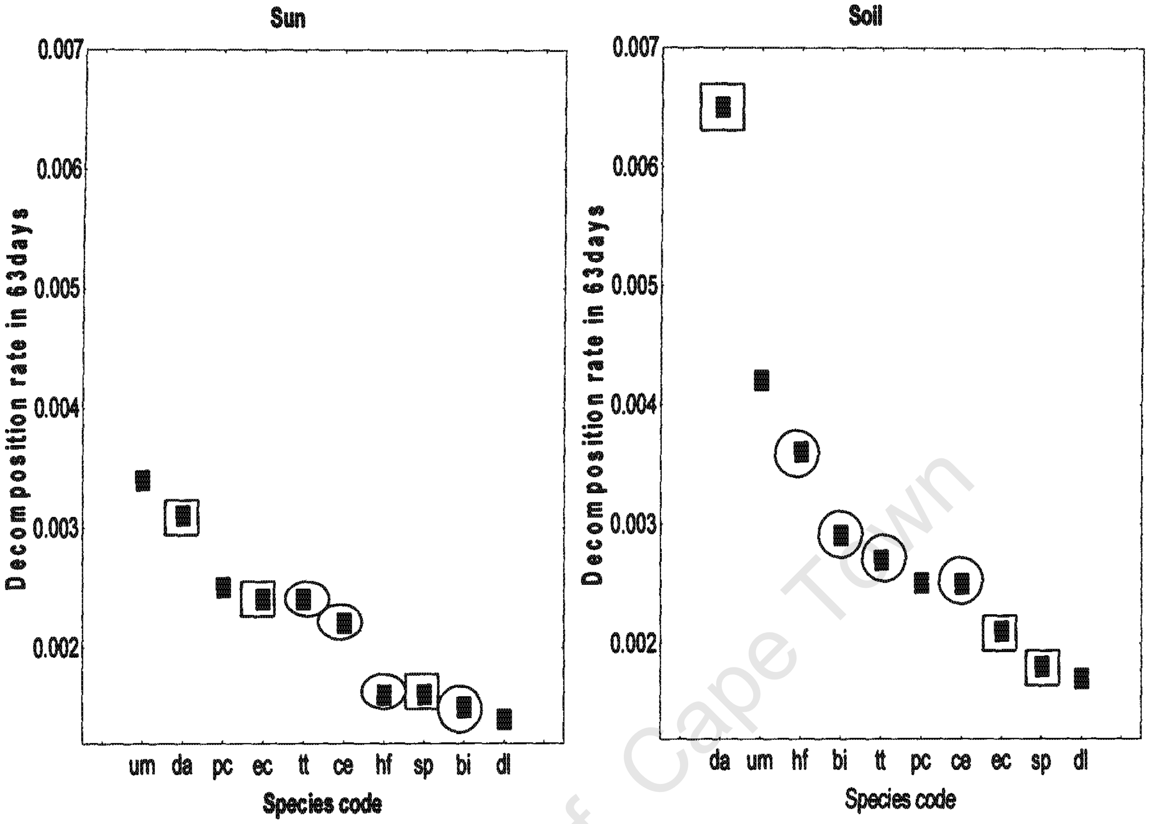

Figure 5.4: Mean decomposition rate of the grass species in the sun and the soil ranked from the highest to the lowest over 63 days. Full names for the symbols used for the species are listed in Table 4.1. The circled symbols represent the tribe Andropogoneae; the rectangle encased symbols represent the tribe Chlorideae while the loose symbols represent Paniceae.

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Individual grass species varied greatly in decomposition rates, with *U. mosambicensis* and *D. australe* having the most weight loss of all species in the soil (figure 5.4). It is interesting to note that both species are chloridoids. Decomposition rate was significantly different among species (Table 5.3). Tukey Kramer HSD comparison showed that *D. australe* was significantly different from all species in the sun and on the soil except *U. mosambicensis* on the soil. *U. mosambicensis* was significantly different from all the other species in the sun and on the soil for all the months of exposure to the sun. The species with the least weight loss were *S. pyramidalis* and *D. longiflora.*

Not all the Chlorideae species decomposed quickly when exposed to the sun. Chlorideae with a bunch grass growth form decomposed more slowly *S. pyramidalis* being an example. However, there was no significant difference in decomposition rates between lawn and bunch grass species. For example, *B. insculpta* a lawn grass decomposed less in the sun and the soil than *C. excavatus*, a bunch grass in this situation. *Panicum colaratum*, a lawn grass member of the Paniceae had intermediate decomposition rates.

Tribes comparison:

Weight loss from the sun was significantly less than weight loss from the soil (Tables 5.2 and 5.3) after two months of exposure. The Andropogoneae were more resistant to photodegradation than Chlorideae and Paniceae. Weight loss was 40% greater in the soil than in the sun treatment for Andropogoneae and 29% greater for Chlorideae and Paniceae. The treatments were significantly different for all the months that the samples were left in the field. Chlorideae and Paniceae had higher decomposition rates than Andropogoneae. The tribes were not significantly different from each other for all the months (Table 5.3). Differences in decomposition rate among the tribes were governed by individual species within the tribes. The difference between standing versus soil surface litter was the most important factor explaining the major differences in decomposition in this study.

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Table 5.3: Summary of an analysis of decomposition rate after four months between Andropogoneae, Chlorideae and Paniceae standing litter versus surface litter on the soil. This was obtained using a NESTED ANOVA in JMP statistical package. Treatment= sun vertical vs. sun horizontal vs. soil surface. DF= degrees of freedom

Predictor	DF	Sum of Squares	F Ratio	p
Treatment	1	0.000004	19.8	**0.001**
Species (Tribes)	7	0.000012	8.28	**0.010**
Treatment*Tribes	6	0.0000002	0.43	0.670
Tribes	1	0.0000004	1.07	0.390

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Figure 5.5 below shows the relationship between decomposition in the sun and decomposition on the soil for Andropogoneae, Paniceae and Chlorideae. Though decomposition in the soil was correlated with the rate in the sun for Chlorideae and Paniceae species, there was no apparent correlation in the Andropogoneae species

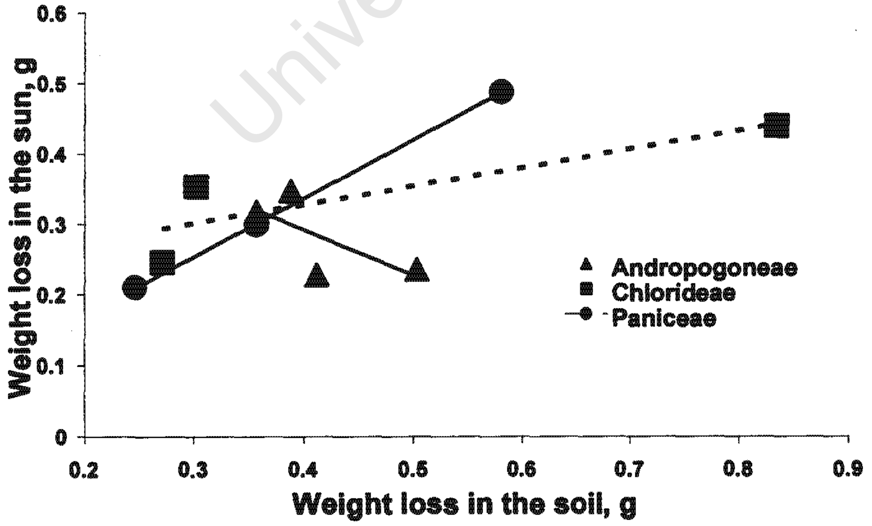

Figure 5.5: Correlation between weight losses in the sun versus on the soil surface.

This suggests that traits that influence decomposition in the sun are not playing a similar role in the soil for Andropogoneae. The Chlorideae decomposition rates in the soil were correlated (weakly) with the rates in the sun meaning that traits promoting litter decomposition in the soil are similar to the traits involved in photodegradation. There was a strong correlation for Paniceae, resulting in decomposition in both the sun and the soil surface being promoted by similar leaf traits. The fact that decomposition in the soil for Andropogoneae was not correlated to decomposition in the sun suggests that sun breakdown might be a rate controlling step. Further analysis to determine the factors influencing decomposition is reported in Chapter 6.

5.5. DISCUSSION

There were significant differences in decomposition rates among the different grass species used in this study. For example, *U. mosambicensis* had higher decomposition rates than *S. nitens*, *S. pyramidalis* and *T. triandra* in the 1 month experiment in August at H*i*P's Nombali site (Figure 5.2.1). For the Cape Town experiment *U. mosambicensis* and *D. australe* always decomposed at greater rates than the other species used in the experiment (Figure 5.4).

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The different treatments at Nombali were also significantly different from each other (Figure 5.2.1). Decomposition in the sun was significantly slower than decomposition in the soil averaging about half the rate of weight loss in the soil. These results imply that previous studies based only on decomposition rates in soil litterbags, have exaggerated decomposition rates in savanna grasslands. Standing litter first has to reach the soil and this is a slow process. Photodegradation appears to alter the rate at which plant litter will reach the soil. The fact that sun decomposition was significantly slower than soil decomposition implies that microbial decomposition occurs at much faster rates than photodegradation. Photodegradation is important in controlling the rate of decomposition in grass species by influencing the rate at which standing litter reaches the soil surface. Species that breakdown rapidly in the sun should decompose at a reasonable pace. Species with protection mechanism against sun breakdown would have very slow decomposition rates. This suggests that different factors are operating in the sun and on the soil. In general sun decomposition rate would be much slower than soil decomposition in the soil, so the litterbag technique exaggerates the decomposition rate.

Fungal treatment had a minor effect relative to sun vertical versus sun horizontal or sun versus soil. This further implies that physical rather than biological processes are responsible for converting standing litter to surface litter on the soil. Species comparisons show different decomposition rates among species from the soil (well known) and sun. So different species will decompose at different rates from standing to soil position.

Photodegradation helps to disintegrate plant material especially at the beginning of the process of decomposition when plant material is still standing at the start of the dry season. It becomes less important towards the end of the decomposition of grass species. Once litter has reached the soil, grass species decomposed at a faster rate than when in the sun. This can be seen from the fact that *S. pyramidalis* which had the slowest loss rate in the sun in the Cape Town experiment had significantly faster decomposition rates on the soil. The same can be said for *B. insculpta*. In general, Chlorideae and Paniceae species decomposed faster than Andropogoneae in the soil as was also the case in the sun. It was interesting to observe that most Andropogoneae species were in middle of the extremes, that is, Chlorideae either had very high decomposition rates (for example, *D. australe*) or low decomposition rates (*S. pyramidalis*). The same can be said for Paniceae, for example *U. mosambicensis* had very high rates whereas *D. longifolia* had the lowest rates.

This study has shown that within a functional group, decomposition rate may vary considerably. For example, decomposition rates of lawn grasses like *U. mosambicensis* and *D. australe* were more than twice those of bunch species like *E. curvula* and *S. pyramidalis*. Decomposition rates of an Andropogoneae lawn grass like *B. insculpta* was half that of Andropogoneae bunch grasses like *H. fillipendula*, *C. excavatus* and *T. triandra*.

This implies that the functional type of grass is not good predictor of decomposition since lawn Chlorideae and Paniceae were faster than bunch Chlorideae whereas bunch Andropogoneae were faster than lawn Andropogoneae. The other fact was that the three dominant tribes in grasslands were decomposing differently since the lawn to bunch grass differences were opposing as mentioned above (see Figure 5.5).

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5.6. CONCLUSION

Decomposition of grass litter in the sun was half the rate of decomposition on the soil in both experiments, though litterbags are known to exaggerate decomposition rates. Species differ in decomposition rates in the sun and soil. When grasses are still standing in the field, photodegradation is more important than the microbial process. There was no evidence for functional type differences (i.e. lawn versus bunch grass) in decomposition rates.

The phylogeny of grass species seems to account for decomposition speed of grass species though there were some exceptions for instance *S. pyramidalis*. One can suggest that Andropogoneae are generally more resistant to sun or soil breakdown than Chlorideae and Paniceae. However there are marked exceptions (such as *Sporobolus pyramidalis*). Chapter 6 will explore the factors that cause variation in litter decomposition rates among grasses.

Decomposition rates were not always correlated for the sun versus soil. This implies that different factors are operating. This further suggests conversion of standing to surface litter is not the same process as conversion of surface litter to humus.

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CHAPTER 6: LEAF TRAITS AND DECOMPOSITION RATES OF SAVANNA GRASSES

6.1. INTRODUCTION

Chapter 4 has established that there are differences in decomposition rates within and between Andropogoneae, Paniceae and Chlorideae grass tribes. The decomposition of plant litter is influenced by physical and chemical factors (Swift, *et al.*, 1989; Gahrooee, 1998; Schuurman, 2005). The previous chapter touched on the physical factor that is often ignored namely the sun or the process of photodegradation. In this chapter the leaf attributes influencing photodegradation and microbial decomposition were examined.

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Plant traits determine the productive capacity of the vegetation and the rates of decomposition and nutrient mineralization (Chapin, 2003; Eviner and Chapin, 2003). Litter decomposition is an important process in all terrestrial ecosystems because it controls the recycling of nutrients (Couteaux *et al.*, 1991; 1995; Kavvadias *et al.*, 2001; Quested *et al.*, 2003). Both environmental factors, and litter properties, affect rates of litter decomposition. Of the environmental factors, soil moisture (Meentemeyer, 1978) and soil temperature have been shown to be important in determining decomposition rate (Sing and Gupta, 1977). Important plant traits include C/N ratio and lignin (Meentemeyer, 1978; Morris *et al.*, 1978; Schädler *et al.*, 2003), leaf thickness, tannin or polyphenolic content of decomposing material (Gil *et al.*, 2003). C/N ratio, lignin and lignin/nitrogen ratio have been reported as most important in studies from Australia (Christie, 1979), New Zealand (Wardle *et al.*, 2002) and America (Mellilo *et al.*, 1982; Hobbie, 1992). As mentioned in the previous chapter decomposition is generally measured using litterbags with many studies on forest litter decomposition (Mellilo *et al.*, 1982, Hobbie, 1992, Cornellisen, 1996; Cornellisen *et al.*, 2004). There are fewer reports on decomposition rates of standing litter from highly fibrous grasslands and especially of how standing litter reaches the ground.

The main question I addressed in this chapter was which of the different leaf properties were the best predictors of savanna grass decomposition. I measured a number of leaf traits from samples collected at the start of the litterbag experiments discussed in the previous chapter. I determined the best predictors of decomposition rates using regression analyses with *k*, the decomposition constant, as the dependent variable. I was particularly interested in whether decomposition in the sun was determined by the same plant traits as decomposition in the soil. Finally, I asked whether decomposition in the different tribes was influenced by the same leaf attributes.

6.2. METHODS AND MATERIALS

Variables sampled were polyphenolic content, carbon to nitrogen ratio and lignin, which have previously been shown to play a major role in decomposition in all terrestrial ecosystems. In addition, I measured tensile strength and specific leaf area (SLA) for each species. The dependent variable for this study was the decomposition constant (k) at 2, 3 and 4 months period as determined by the method described in Chapter 4.

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6.2.1. Carbon to nitrogen ratio analysis

Carbon to nitrogen has been shown to be a major determinant in decomposition of terrestrial ecosystems (Jensen, 1974). All the samples were analyzed for C/N ratio using the CHN analyses at the Archeology Department at the University of Cape Town. The method was adopted from Chimpango *et al* (2003). Concentrations of Carbon (C) and Nitrogen (N) in all the different grass leaves were measured as %C and %N using a Carlo Erba NA 1500 elemental analyzer (Fisons Instruments SpA, Strada Rivoltana, Italy) coupled to a Finniggan MAT 252 mass spectrometer (Finniggan MAT GmbH, Bremen, Germany) via a Conflo II open-split device. The amount of C and N per grass leaf was estimated from the product of %C and %N and the dry matter weight.

6.2.2. Lignin

For lignin determination the ANKOM method was used. This is a stepwise procedure that starts by removing proteins, then hemi-cellulose, cellulose, crude fibre and lastly acid lignin. This was done using the ANKOM Fibre Analyzer. The last step of this method involves ashing the samples to determine the loss at ignition. A comprehensive description of the method can be found in the ANKOM website (www.ankom.com). The method was similar to that used by Rowland and Roberts, (1994).

6.2.3. Polyphenolic content

Bernays *et al.*, (1989), found that light levels profoundly influence foliar phenolic levels including polyphenolic content (Ellis, 1990). Mole *et al.*, (1988) realized that there was a very close positive correlation between light intensity and polyphenolic content in tropical rainforest leaves (Nocolai, 1988). Based on these findings abiotic factors might be more important than herbivores in determining concentrations of polyphenolic content in tannin-producing plants. Polyphenolic content and flavonoids are often thought only to defend the leaf from herbivores (Robbins *et al.*, 1987). However since there is a close link between litter decomposability and vegetation response to herbivory (Wardle *et al.*, 2002), polyphenolic content may influence decomposition rate. Studies conducted by Gil *et al.*, (2003), have shown the potential of polyphenolic content for reducing decomposition by the sun. The Prussian blue assay method (Hagermann *et al.*, 1998) was used to assay polyphenolic content of the different grass species in this study. All the ten species were analyzed for their polyphenolic content by this method.

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6.2.4. Tensile strength

Studies on the mechanical properties of grass leaves have elucidated much useful information such as the relationship of leaf tensile strength and stem flexibility to palatability to livestock (Theron and Booysen, 1968), digestibility, resistance to trampling (Sun and Liddle, 1993), and more recently, drought tolerance (Balsamo *et al.*, 2003; 2005). It was the last relationship of tensile strength versus drought tolerance that prompted me to use tensile strength as a potential determinant of decomposition rate. It suggested that, because a grass species with a high tensile strength will tolerate drought, breakdown by the sun might be at lower rates than grass with a low tensile strength.

Instruments for measuring tensile strength have been through a revolution starting from the early work by Beaumont *et al.*, (1933) to work by Kneebone (1960), Theron and Booysen (1966), Martens *et al.*, 1968, and more recently Balsamo *et al.*, (2003; 2005). The tensile strength of the grass leaves of each species was measured in the laboratory.

A Tensiometer was constructed using 50 Newton (N) Pesola scales (Baar, Switzerland), a mounting bracket, clamps, weather stripping, metal beaker, a duct tape, and a Retort stand (Balsamo *et al.*, 2003; 2005). Tensile strength was calculated by dividing the failure load by the cross-sectional area of the leaf blade. The leaf materials used in this experiment were air-dried green leaves collected as t0 samples at the start of the litterbag experiment described in Chapter 4.

6.2.5. Specific leaf area

The specific leaf area (SLA) is the projected leaf area per dry mass. It has become a key variable in comparative plant ecology because it can be correlated with a wide range of attributes that affect the ecology of different species (Poorter and Garnier, 1999). Westoby (1998) has developed a new classification of plant strategies in which SLA was one of the key plant traits. As in Schädler *et al.* (2003), SLA in our study implies the ratio of leaf area to leaf dry weight. The leaf area of thirty leaves per species for the experiment in HIP was measured using the LI-3000 Area Meter (LI-COR inc., Lincoln, Nebraska, USA). It was then divided by the dry weight measured using a mass balance. The dry leaves collected as t0 samples for the experiment in Cape Town were used to establish SLA, which was then correlated with decomposition rate (see Results).

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6.3. DATA ANALYSIS

Meentemeyer (1978), Mellilo *et al.*, (1982) and other scientists investigating ecosystem dynamics have explored determinants of decomposition rates by correlating the decomposition rate with plant traits like carbon to nitrogen ratio and lignin to nitrogen ratio. This study used these and other traits as discussed above to explore determinants of the rate of decomposition. I was particularly interested in whether the same or different traits determine soil decomposition rates versus sun breakdown rates.

The following statistical tests were used for the analysis of the data using JMP 5 and STATISTICA 6 statistical software. The decomposition rate, k, was the dependent variable (multiplied by 10000 to adjust it to be close to the means of the predictor variable). A regression analysis was performed to determine which variables best predicted decomposition either in the sun or on the soil. The variables were first tested for normality, and were corrected if necessary using logarithmic and square root transformations. Comparing predictor variables using Pearson correlation coefficients checked multicollinearity between the variables. Five predictor variables were used for this analysis, that is, lignin, polyphenolics, C/N ratio, SLA and tensile strength. Polyphenolics were also adjusted by dividing values by 1000. Generalized linear models, stepwise regressions (James and McCulloch 1990; Mac Nally, 2000; and Quinn and Keough, 2002) and other multiple linear regressions (Mac Nally, 2000; Quinn and Keough, 2002) were employed to predict the best possible model that predicts decomposition rate in this study.

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Generalized linear models with a log link function were used to obtain the best sub-set regression models in Statistica. I ran best sub-sets model with the Akaike Information Criterion. The Akaike Information criterion (AIC; Akaike, 1983, Burnham and Anderson, 2002) was used to select the best model. The estimated variable coefficients in the selected model were then used in the back prediction procedure to create potential predictors of decomposition rate in savanna grasslands. One can use this method to work out which variables are most consistently entered into the best models that have $\Delta AIC<4$ and therefore most likely to be involved in the decomposition process. The species were compared within their tribes and could not be compared among themselves because their averages were used for analysis.

6.4. RESULTS

6.4.1. Trait differences among the different species and tribes

The species used in this experiment had different chemical and physical leaf traits at the beginning of the experiment (Table 6.1.1). Chemical traits include lignin, polyphenolic content and C/N ratio. The species that had the highest mean lignin content by far was *Sporobolus pyramidalis* with *Digitaria longifolia* having the least mean lignin content. *Themeda triandra* had the highest mean polyphenolic content followed by *Bothriochloa insculpta* with *Urochloa mosambicensis* having the least polyphenolic content.

Eragrostis curvula had the highest C/N ratio with *Dactyloctenium australe* having the lowest C/N ratio.

Table 6.1.1 Plant trait differences among the different species used in this project. Mean values are shown. Units are: lignin, mg/g; polyphenolics, µg/nm; SLA, cm^2/g; and tensile strength, N/cm^2.

Species name	Lignin	Polyphenolics	C/N ratio	SLA	Tensile
Themeda triandra	0.502	**35604.3**	51.85	98.89	21.07
Sporobolus pyramidalis	**0.674**	19238.1	59.27	62.35	33.11
Panicum coloratum	0.441	24217.3	40.74	102.90	***12.91***
Urochloa mosambicensis	0.540	***5610.1***	44.25	**147.26**	13.08
Hyparrhenia filipendula	0.402	22941.5	64.30	68.14	39.31
Eragrostis curvula	0.463	11274..6	**74.06**	***32.08***	35.23
Cymbopogon excavatus	0.477	24429.2	72.33	57.43	24.94
Bothriochloa insculpta	0.468	33473.4	57.43	93.80	13.23
Digitaria longifolia	***0.310***	15154.5	60.22	74.15	**66.02**
Dactyloctenium australe	0.409	17536.9	***18.07***	97.49	20.02

Note: The largest values are in bold type while the smallest values are in bold and italics.

Physical leaf traits included specific leaf area and tensile strength. The highest mean specific leaf area was obtained for *U. mosambicensis*. It was followed by *Panicum coloratum* and the lowest mean specific leaf area was found in *E. curvula*. Tensile strength of some species exceeded the tensiometer's force; the values for *S. pyramidalis*, *E. curvula* and *C. excavatus* could actually be double the obtained values. The highest mean tensile strength was obtained in *D. longifolia* followed by *H. filipendula*, *E. curvula* and *S. pyramidalis*.

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Table 6.1.2 Plant trait differences between the three tribes at the beginning of the experiment. Mean values are used with standard errors in brackets. Units for the predictors are lignin, g/g; polyphenolics, μg/nm; SLA, cm^2/g; and tensile strength, N/cm^2.

Predictor	Andropogoneae	Chlorideae	Paniceae
Lignin	0.462 (0.21)	0.515 (0.81)	0.430 (0.66)
Polyphenolics	29110.5 (3.18)	16022.4 (2.42)	14991.6 (5.37)
C/N ratio	61.47 (4.42)	50.46 (16.75)	48.40 (5.99)
SLA	79.57 (9.99)	63.98 (18.90)	108.1 (21.26)
Tensile strength	24.64 (5.46)	29.45 (4.76)	30.67 (17.68)

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Table 6.1.2 demonstrates that the most important plant trait separating the major tribes was polyphenolic content. Andropogoneae had significantly higher polyphenolic content than the Chlorideae and Paniceae. Andropogoneae also had a higher C/N ratio than Chlorideae and Paniceae although means were not significantly different. Chlorideae had higher lignin content and specific leaf area but were also not significantly different.

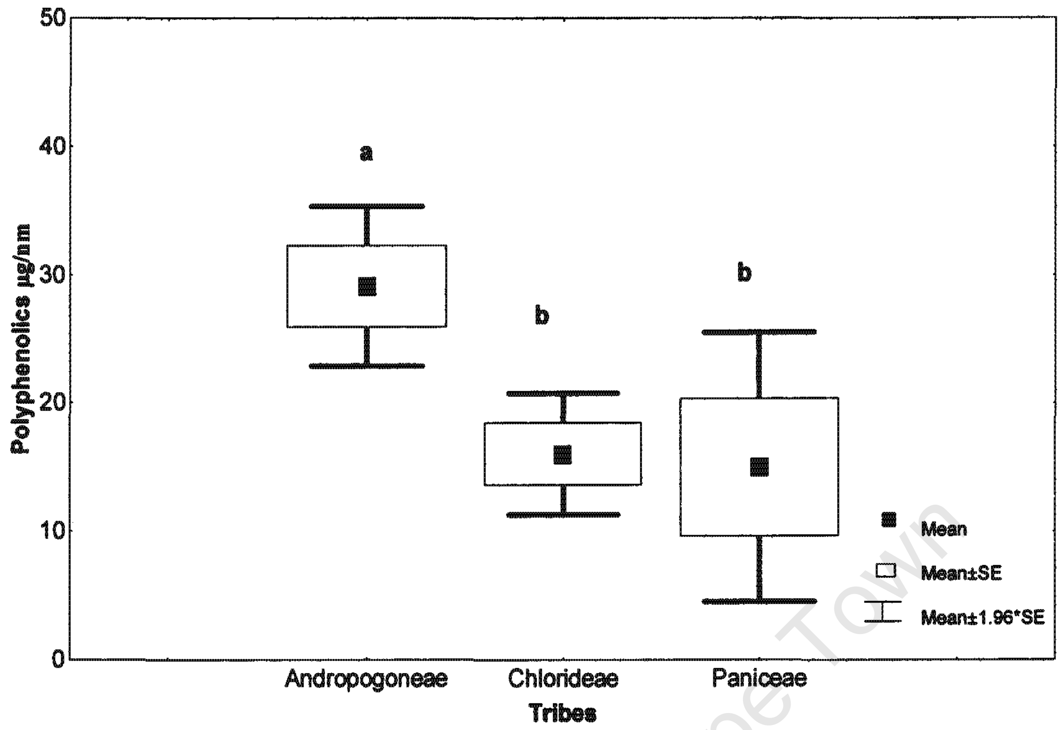

Figure 6: Box whisker plot showing polyphenolic content differences among the three tribes.

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6.4.2. Decomposition rate comparison between Paniceae, Chlorideae and Andropogoneae

From Chapter 5 there were no significant differences between decomposition rates of the three tribes in the soil. In the sun, the mean decomposition rate of Chlorideae and Paniceae was higher than the mean decomposition rate of Andropogoneae (Table 5.3). However there was considerable variation among species within a tribe and the differences were only weakly significant ($p<0.1>0.05$). The H*i*P litterbags could not be compared since there were two Chlorideae species versus one Paniceae versus one Andropogoneae.

To understand this difference in decomposition rate between the three tribes, the predictor variables were compared between Andropogoneae and Chlorideae or Paniceae. Decomposition rates are discussed starting with the rates measured in the Cape Town experiment.

6.4.3. Correlation of Plant traits with decomposition rate

6.4.3.1. Cape Town Correlations

Decomposition was modelled for different stages of decomposition starting first with predictor variables most important during the first two months of weight loss. I ran GLIM models and GLZ models from Statistica to determine the best predictors and best regressions for explaining decomposition rate in grasslands. My predictor variables were lignin, polyphenolics, specific leaf area (SLA), tensile strength and carbon to nitrogen ratio. The tests were done to see if the variables responsible for predicting decomposition rate in the soil were also responsible for decomposition in the sun.

A correlation matrix for the predictor variables was done. Tensile strength was significantly correlated with specific leaf area (R^2=0.54), and specific leaf area with carbon to nitrogen ratio (R^2=0.68). The impact of correlated predictor variables on the estimates of parameters and hypothesis testing can cause computational problems, which makes the determinant of the matrix of the predictor variables close to zero. So dividing by a determinant that is close to zero results in the matrix being very sensitive to small differences that in turn gives unstable regression slopes. When there is collinearity, we are not confident in our estimates of model parameters (Quinn and Keough, 2002). In our case, the correlation between the abovementioned predictor variables was not detrimental in this study. The accepted predictor variables in the model included tensile strength; polyphenolics and C/N ratio which were not strongly correlated, although C/N ratio and tensile strength were related to specific leaf area that did not form part of best sub-sets in the linear regression models except the sun model over 124 days.

Decomposition over 2 months (63 days)

Sun

Results for the GLIM analysis of variables influencing initial decomposition in the sun are shown in Table 6.3. This pointed to tensile strength, followed by tannin content, as

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the only significant predictor variables. For decomposition in the sun after two months, polyphenolic content and tensile strength had a negative relationship with decomposition rate. The best regressions for these factors are given in Table 6.4.

Table 6.3 General linear model best predictor variables of decomposition rate (*k*) over 2 months with tribes and leaf traits as predictor variables in the sun. Tribe=Andropogoneae versus Chlorideae versus Paniceae

Variables	DF	Wald	p
Intercept	1	16.22	0.001
Lignin	1	0.43	0.505
Polyphenolics	1	3.69	**0.049**
C/N ratio	1	1.26	0.610
SLA	1	0.55	0.460
Tensile strength	1	3.17	**0.069**
Tribes	2	0.10	0.951

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The best regression model selected had the second lowest AIC values. The results were based on the findings from Burnham and Anderson, 2002. They showed that when using AIC's to predict the best linear regression model, the model with the smallest value and the fewest variables that is selected is the 'best' model. The Mallow's Cp results were also checked to see if they produced similar best sub-set regressions to the Akaike Information criterion. A two factor model, number 1 in table 6.4 including polyphenolic content and tensile strength, was the best predictor of decomposition rate in the sun over 63 days. This model had the highest predictive power with the lowest ΔAIC value. No other two-factor model had comparable predictive power. Models 2-10, which include various combinations of the other three plant traits, were also acceptable predictors (ΔAIC < 4, Burnham and Anderson 2002). Polyphenolics and tensile strength were the only variables consistently appearing in all the models with delta AIC < 4.

The estimated regression coefficients for model 1 were -0.46 (polyphenolics) and -0.31 (tensile strength). The estimated standard errors for the regression parameters were 0.09 and 0.16 respectively. The selected model had an R^2 value of 0.69 and a p value of 0.002.

Table 6.4. The best 10 models for k in the sun over 63 days selected from the multiple linear regression using an information theoretic approach (Akaike 1983, Burnham and Anderson 2002, Archibald et al. 2005)

	Variable included in the model								
Model	Lignin	Polyphenolics	C/N ratio	SLA	Tensile strength	df	AIC	Delta AIC	*w* (AIC)
1		X			X	2	59.36	0.00	0.06
2		X		X	X	3	59.82	0.79	0.04
3		X	X		X	3	59.92	1.02	0.04
4	X	X			X	3	60.66	1.45	0.03
5		X	X	X	X	4	61.07	1.86	0.03
6	X	X		X	X	4	61.81	2.10	0.02
7		X	X			2	61.90	2.13	0.02
8	X	X	X		X	4	62.33	2.19	0.02
9		X	X		X	3	64.46	2.58	0.02
10	X	X	X	X	X	5	64.94	3.00	0.01

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Soil

Table 6.5 shows the results of a GLIM analysis of predictors of decomposition rate in the soil. According to this analysis, polyphenolic content, C/N ratio, tensile strength, SLA and lignin were all significant predictors of initial (63 days) decomposition rate in the soil. The main important predictor variable was tribe. The best plant trait predictor was polyphenolic content followed by C/N ratio. Tensile strength was also important followed by lignin. Table 6.6 shows the results of best sub-set regression analysis of determinants of initial decomposition in the soil. Polyphenolic content, carbon to nitrogen ratio, tensile strength, SLA and lignin were the predictor variables consistently included in all of the two best-fit regression models.

Table 6.5 General linear model best predictor variables of decomposition rate (*k*) over 2 months with tribes and leaf traits as predictor variables in the soil. Tribe=Andropogoneae versus Chlorideae versus Paniceae

Variables	DF	Wald	p
Intercept	1	1009.7	0.001
Lignin	1	**4.126**	**0.040**
Polyphenolics	1	**1396.8**	**0.001**
C/N ratio	1	**377.21**	**0.001**
SLA	1	**31.54**	**0.001**
Tensile strength	1	**172.18**	**0.001**
Tribes	2	**2009.1**	**0.001**

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For decomposition rate in the soil after 63 days, a five-factor model, number 1 in table 6.6 including Polyphenolics, C/N ratio, tensile strength, SLA and lignin was the best model. This model had the highest predictive power by far with the lowest ΔAIC value. No other model had comparable predictive power. Model 2, which include various combinations of the other plant traits, were also acceptable predictors (ΔAIC < 4, Burnham and Anderson, 2002). The estimated regression parameters for model 1 were -3.81 (lignin), -0.33 (Polyphenolics), -0.52 (C/N ratio), 0.1 (SLA) and -0.28 (tensile strength). The estimated standard errors were 4.64, 0.43, 0.27, 0.14 and 0.32 respectively. The selected model had an R^2 value of 0.67, p= 0.01.

Table 6.6. The best 10 models for k in the soil over 63 days selected from the multiple linear regression using an information theoretic approach (Akaike 1983, Burnham and Anderson 2002, Archibald et al. 2005)

	Variable included in the model								
Model	Lignin	Polyphenolics	C/N ratio	SLA	Tensile strength	df	AIC	Delta AIC	*w* (AIC)
1	X	X	X	X	X	5	25.58	0.00	0.05
2		X	X	X	X	4	27.04	1.46	0.03
3	X	X	X		X	4	37.82	12.24	0.02
4		X	X		X	3	49.29	23.22	0.02
5		X	X			2	50.30	23.71	0.02
6	X	X	X			3	51.26	24.72	0.01
7		X	X	X		3	51.83	25.68	0.01
8	X	X	X	X		4	53.07	27.49	0.01
9	X	X		X	X	4	60.74	35.15	0.01
10	X	X		X		3	61.81	36.23	0.01

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Decomposition over four months (124 days)

Sun

The same predictor variables were examined for litterbags left in the sun and on the soil for four months. Generalized linear models and generalized regression models were used as in the case with the two months litterbags. The tests to predict what plant traits were responsible for decomposition after 124 days under different treatments were done and this yielded the results below. Tribe contributed the most in explaining decomposition in the sun after four months. The main predictor plant traits were tensile strength, polyphenolic content and lignin (Table 6.7). Specific leaf area was slightly important and contributed the least.

Table 6.7 General linear model best predictor variables of decomposition rate (*k*) over 4 months with tribes and leaf traits as predictor variables in the sun. Tribe=Andropogoneae versus Chlorideae versus Paniceae

Variables	DF	Wald	p
Intercept	1	100.13	0.001
Lignin	1	**3.85**	**0.049**
Polyphenolics	1	**8.70**	**0.001**
C/N ratio	1	0.04	0.840
SLA	1	2.74	0.092
Tensile strength	1	**11.41**	**0.001**
Tribes	2	**14.92**	**0.001**

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The variable most often appearing in best sub-set regression analysis was tensile strength, followed by polyphenolic content, lignin then SLA (table 6.8). A four factor model, number 1 in table 6.8 including lignin, polyphenolic content, SLA and tensile strength, was the best predictor of decomposition rate in the sun over 124 days. This model had the lowest AIC value. Models 2-5 also had comparable predictive power and were also acceptable predictors (ΔAIC < 4, Burnham and Anderson, 2002). The estimated regression equation was *k*=intercept-2.02 (lignin)-0.26 (tensile strength)-0.25 (polyphenolics)+0.1 (SLA). The estimated standard errors for the regression parameters were 1.39, 0.10, 0.14, and 0.05, respectively. The selected model had an R^2 value of 0.74, p= 0.02.

Table 6.8. The best 10 models for k in the sun over 124 days selected from the multiple linear regression using an information theoretic approach (Akaike 1983, Burnham and Anderson 2002, Archibald et al. 2005)

	Variable included in the model								
Model	Lignin	Polyphenolics	C/N ratio	SLA	Tensile strength	df	AIC	Delta AIC	*w* (AIC)
1	X	X		X	X	4	56.74	0.00	0.39
2		X	X		X	3	56.92	1.45	0.19
3	X	X	X	X	X	5	57.01	1.96	0.15
4	X	X	X		X	4	57.29	2.51	0.11
5		X	X	X	X	4	57.58	3.37	0.07
6		X	X	X		3	57.84	6.18	0.02
7	X		X	X	X	4	57.90	6.19	0.02
8	X	X		X		3	57.97	6.26	0.02
9	X	X		X	X	4	58.02	6.66	0.01
10	X	X			X	3	58.11	6.84	0.01

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Soil

The GLM analysis showed C/N ratio and tensile strength as well as polyphenolic content as the only significant predictor variables. The variable most often appearing in best sub-sets was C/N. The second closest variables were tensile strength and polyphenolic content (table 6.9). The presence of polyphenolic content was also important with a p-value of less than 0.05. Lignin followed tensile strength and polyphenolic content although not significant with a p-value of 0.15.

Table 6.9 General linear model best predictor variables of decomposition rate (*k*) over 4 months with tribes and leaf traits as predictor variables in the soil. Tribe =Andropogoneae versus Chlorideae versus Paniceae

Variables	DF	Wald	p
Intercept	1	84.93	0.001
Lignin	1	**7.97**	**0.010**
Polyphenolics	1	**7.55**	**0.010**
C/N ratio	1	**9.13**	**0.001**
SLA	1	1.36	0.240
Tensile strength	1	**8.28**	**0.001**
Tribes	2	4.65	0.090

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Table 6.10. The best 10 models for k in the soil over 124 days selected from the multiple linear regression using an information theoretic approach (Akaike 1983, Burnham and Anderson 2002, Archibald et al. 2005)

	Variable included in the model								
Model	Lignin	Polyphenolics	C/N ratio	SLA	Tensile strength	df	AIC	Delta AIC	*w* (AIC)
1	X	X	X		X	4	56.04	0.00	0.12
2	X	X	X	X	X	5	56.08	1.18	0.07
3	X		X		X	3	56.31	1.89	0.05
4				X	X	2	56.40	2.58	0.03
5	X		X	X	X	4	57.20	2.60	0.03
6	X		X	X		3	57.37	3.75	0.02
7	X	X	X			3	58.65	3.77	0.02
8			X	X	X	3	58.68	4.16	0.02
9		X	X		X	3	58.70	4.32	0.01
10	X			X	X	3	60.23	4.49	0.01

A four factor model number 1 in the table 6.10 including C/N ratio, tensile strength, polyphenolics and lignin was the best predictor of decomposition rate in the soil over 124 days. This model had the lowest AIC values. Models 2-7, might have equally good predictive power as model 1. All the Models from model 8, which include a combination of the plant traits, were not acceptable predictors (ΔAIC > 4, Burnham and Anderson, 2002). The estimated regression equation for model 1 was k=intercept-0.42 (C/N ratio)-0.31 (tensile strength)-0.24 (tannins)+0.25 (lignin). The estimated standard errors for the regression parameters were 0.09, 0.08, 0.14 and 1.53, respectively. The selected model had an R^2 value of 0.94, p= 0.000.

The AIC weights in table 6.11 summarize the relative importance of the predictor variables for all the models for decomposition in savanna grasslands throughout the whole 4 months of decomposition. The table lists the sum of the Akaike weights for all models in which the variables appeared. Larger values demonstrate that a variable contributed more to the best sub-set regression models than variables with smaller values (Burnham and Anderson, 2002).

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Table 6.11 Evidence for the plant traits important in decomposition in multiple linear regressions based on the sums of the Akaike weights (*wi*) over the models in which variables occurs.

	Sum of *wi* for the 4 different decomposition rate models			
Predictor	*k* sun 63	*k* soil 63	*k* sun 124	*k* soil 124
Lignin	0.26	*0.89	*0.70	*0.66
Polyphenolics	*0.86	*0.98	*0.91	*0.75
C/N ratio	0.48	*0.98	0.55	*0.96
SLA	0.35	*0.75	*0.69	0.48
Tensile strength	*0.89	*0.92	*0.94	*0.92

Notes: * shows predictor variables included in the selected model (see Tables 6.4, 6.6, 6.8 and 6.10). *k* sun 63 represents decomposition rate in the sun over 63 days, *k* soil 63 represents decomposition rate in the soil over 63 days, *k* sun 124 represents decomposition rate in the sun over 124 days and *k* soil 124 represents decomposition rate in the soil over 124 days.

Species differences

The observed decomposition rates for the different species were related to the predicted values derived from the regression equation established at the different months under different treatments. Figure 6.1 below show observed versus predicted values for each species using the best sub-set regression for each analysis.

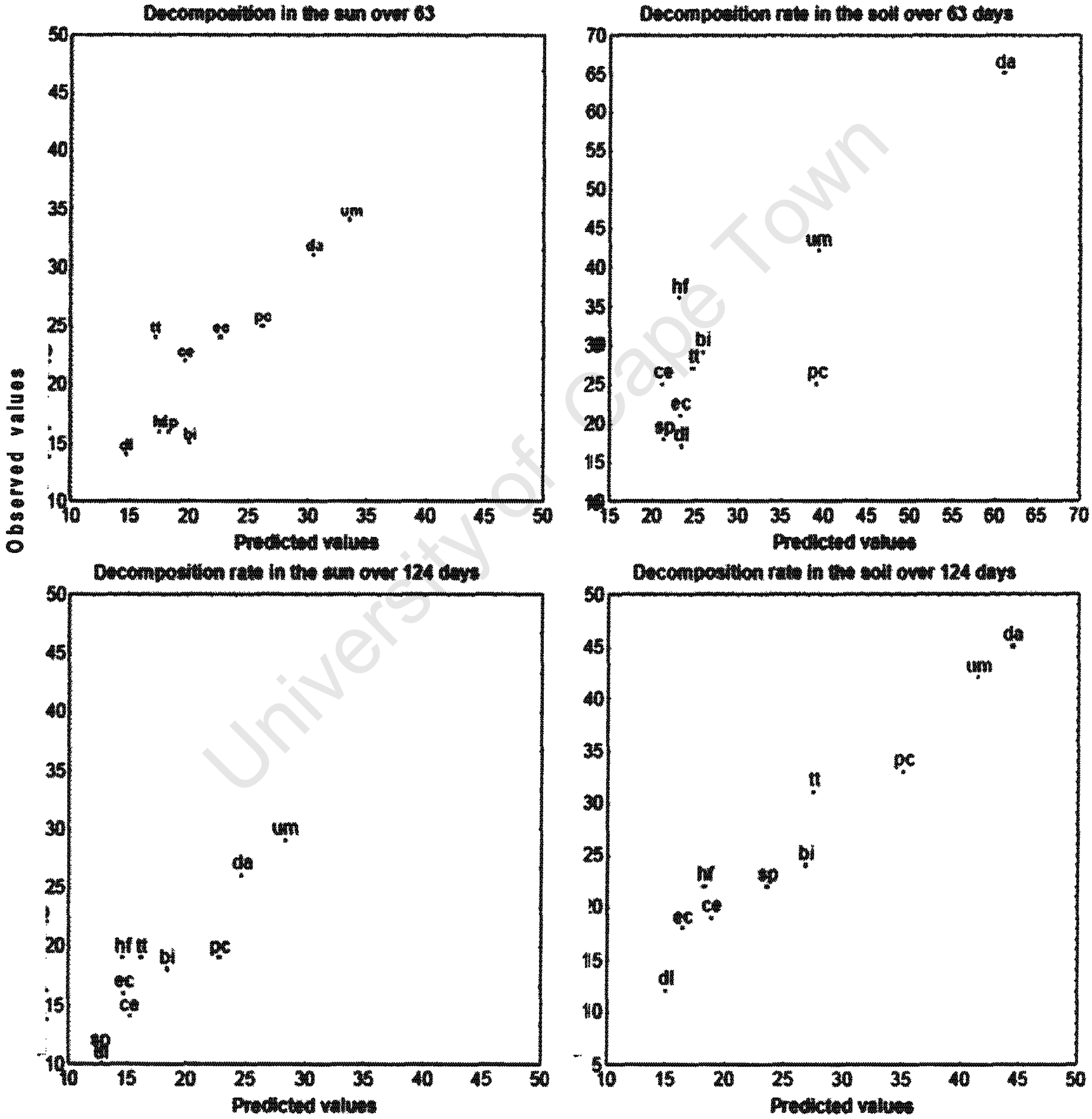

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Figure 6.1: The observed *k* values versus the predicted *k* values of the different grass species.

From the graph above, decomposition rate of litterbags held vertically in the sun at H*i*P was negatively correlated with polyphenolics. There was no relationship for horizontally placed litterbags and also for the soil litterbags. Polyphenolics appear to be important in determining decomposition in the sun.

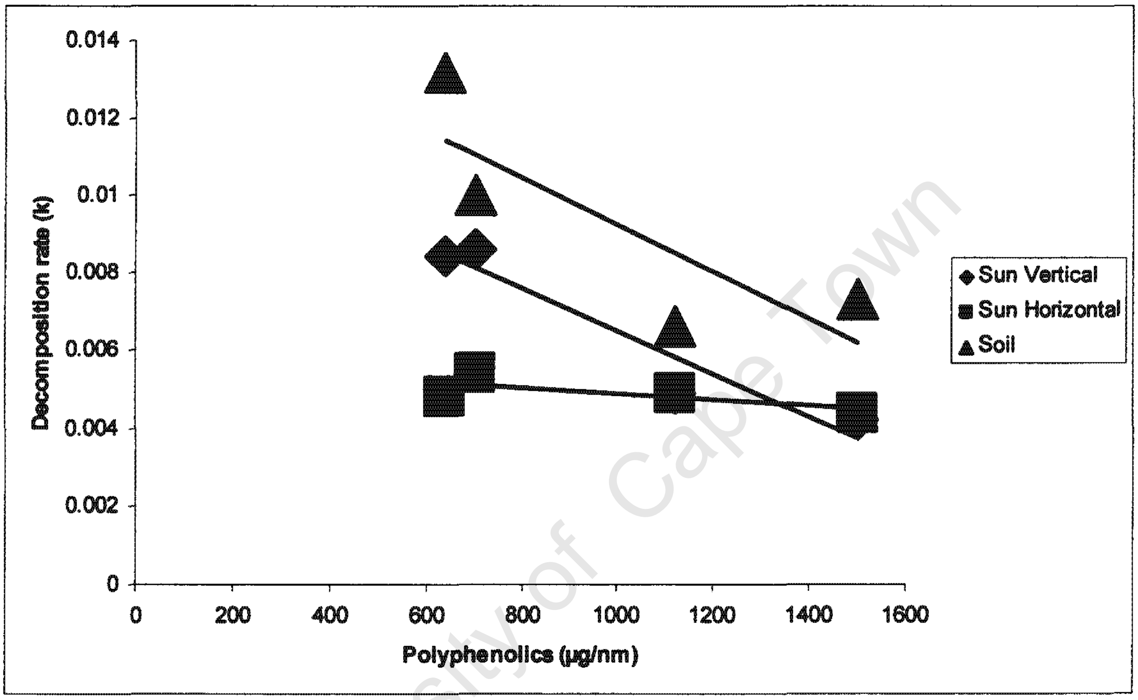

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Figure 6.2: Relationship between polyphenolic content (µg/nm) and decomposition rate (*k*) measured in the soil, sun vertical and sun horizontal in 1 month at HiP.

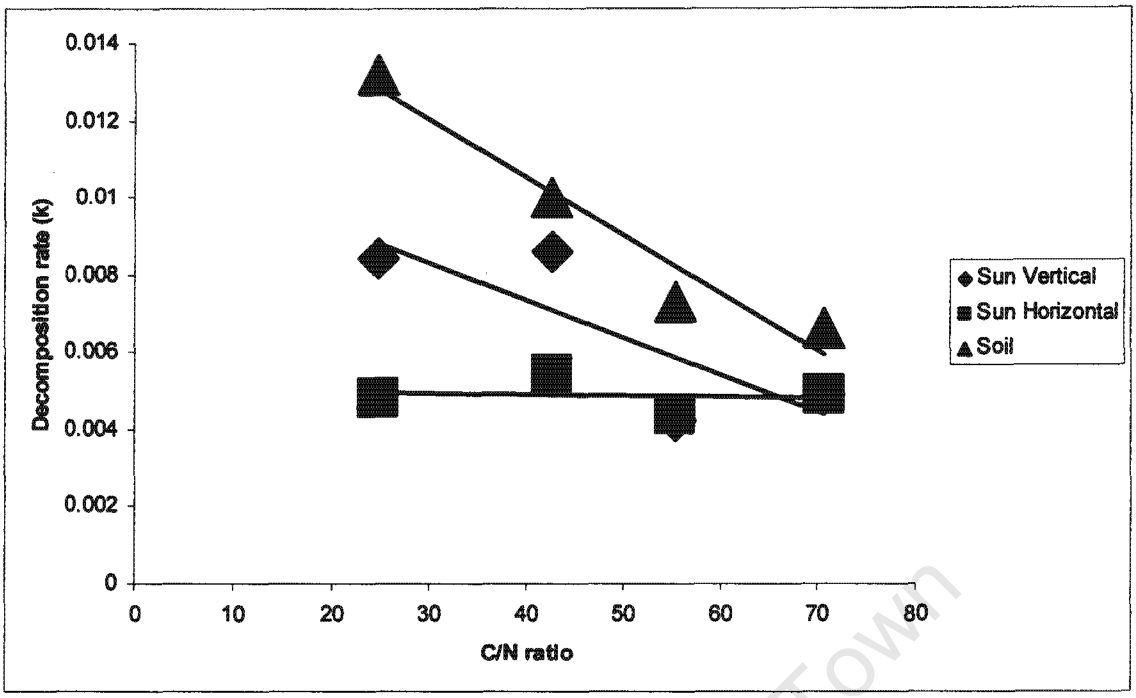

Figure 6.3: Relationship between carbon to nitrogen ratio and decomposition rate (*k*) measured in the soil, sun vertical and sun horizontal in 1 month at HiP.

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The decomposition rate in the diagram above shows a relationship between C/N ratio and the different decomposition treatments at H*i*P. The C/N ratio was the variable that determined decomposition rate on the soil. The relationship was only significant in the soil but not in the sun treatments. Although decomposition rate was not significantly different between the three tribes (previous chapter), there was a puzzling pattern in polyphenolic content differences between the three tribes. When all the plants traits were analyzed to see which plant traits differ between tribes, only polyphenolic content was significantly different (Figure 6).

H*i*P Model in One month

The data for decomposition from H*i*P could not be used to determine traits that best predicted decomposition because there were only four species used in the analysis. I therefore used the regression models obtained from the Cape Town experiment to predict decomposition in the sun (*k*=40.32-0.45(polyphenolics)-0.31(tensile strength) or the soil (*k*=66.71-0.67(C/N ratio)) treatments after 63 days exposure to see if they ranked decomposition rates correctly for the H*i*P experiment. The model for predicted decomposition rate in the sun (for leaves oriented in either a vertical or horizontal position) ranked the species reasonably well with *U. mosambicensis* (33 vs. 86) and *S. nitens* (31 vs. 84) correctly predicted to decompose most rapidly and *T. triandra* (26 vs. 42) and *S. pyramidalis* (24 vs. 49) predicted to have lower decomposition rates. However the latter two species were ranked in the opposite order from the observed values at H*i*P. Predicted species ranking for decomposition in the soil, also produced a reasonable fit to the observed rankings *S. nitens* (50 vs. 132) in the soil had higher predicted k followed by *U. mosambicensis* (38 vs. 100), *T. triandra* (29 vs. 73) then *S. pyramidalis* (19 vs. 66). This suggests the dominance of C/N ratio as a predictor of decomposition rate in the soil.

6.5. DISCUSSION

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Species differences in leaf trait composition play an important role in understanding how individual species influence productivity and decomposition. This is evident in this study as the grass species differed greatly in leaf traits and decomposition rate. The differences in traits of the plant species involved might either be structural or chemical resulting in different responses of the individual species to environmental variables influencing decomposition rates.

Leaf chemistry has long been recognized as an important contributor to variation in decomposition rates among species (Meentemeyer, 1978). For example, it has been demonstrated that litter of species rich in recalcitrant degradable chemicals such as lignin and tannins decompose at a very slow rate, and hence result in accumulation of dead biomass in the ecosystem. So, understanding the species differences in chemical and structural traits is important as this determines the litter quality within the grassland ecosystem.

Major chemical leaf traits important in decomposition include C/N ratio, lignin content and tannins in trees or polyphenolic content (only investigated in this study) in grasses. C/N ratio has been shown to be the prime chemical plant determinant during the process of decomposition. It is interesting to note how the different species vary in C/N ratio rates (see Table 6.1.1) and to see how this influences decomposition rates while the grasses are still standing or when the grasses are on the soil. Lignin and polyphenolic content were also investigated.

Structural leaf traits like tensile strength and specific leaf area have been shown to be important in some ecosystems especially in the US (Wardle *et al.*, 1999; 2002; Gil *et al.*, 2003). Tensile strength was a strong predictor of decomposition in this study. Because of its relationship with lignin content the impact of having a high tensile strength becomes more pronounced in this grassland ecosystem resulting in slow decomposition of grass species with high tensile strength.

The decomposition of plant litter was divided into two phases, with an early and a later stage. Decomposition has been shown to be in two phases with high initial decomposition rate followed by slower rates towards the end of the process. This might be related to the fact that recalcitrant chemicals like lignin are hard to breakdown at later stages of decomposition.

Initial decomposition of standing grass litter was influenced by tensile strength and polyphenolic content. This implies that grass species that were less brittle took longer to breakdown under the influence of the sunlight, and therefore will accumulate more standing dead biomass, resulting in higher carryover. Decomposition rate decreased with increasing tensile strength. Theron and Booysen 1968 suggested that tensile strength of grasses was a function of several contributory factors and that it was determined by the percentage strengthening tissue. In most cases lignin has been found to be the strengthening tissue. It was also related to tensile strength in this experiment but was not important in standing litter at initial decomposition. Many studies have shown that plant species that produce large quality of polyphenolic content deter herbivores and save themselves from being heavily grazed (Coley, 1983; Zucker, 1983; Grime *et al.*, 1997; Schädler *et al.*, 2003). In forest soils, chemical factors like polyphenolic content interfere with the enzymatic functioning or decomposer metabolism resulting in reduction of litter decomposition rate (Palm and Sanchez, 1991). But in this instance, polyphenolic content may be responsible for the blockage of sunlight and therefore slower decomposition in the sun, rather than interfering with microbial decomposition. The species that were heavily armoured with polyphenolic content decomposed at a very slow rate. The sunlight as an herbivore was deterred by

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polyphenolic content, which is quite reasonable considering the long sunny dry season that grass species had to contend with. During initial decomposition, standing grass litter with high polyphenolic content and tensile strength will get to the soil surface at slower rate than those with low polyphenolic content and tensile strength.

Initial decomposition on the soil was governed by tribe differences, with Paniceae and Chlorideae having faster rates than Andropogoneae. The major plant traits were polyphenolic content followed by carbon to nitrogen ratio. Tensile strength and lignin were also important for decomposition of surface litter. Surface grass litter with high polyphenolic content decomposed at a slower rate than one with low polyphenolic content. This was probably due to the fact that polyphenolic content interfered with enzymatic functioning or decomposer metabolism and this is known to reduce decomposition rate (Palm and Sanchez, 1991). Grass species with high C/N ratio decomposed at a slower rate than those with low C/N ratio. This implies that there was less nitrogen for microbes to use on the soil when there was a high C/N ratio. Nitrogen has been determined to be very crucial for microbial organisms on the soil so it makes sense when greater availability of nitrogen in the litter speeds up the decomposition rate. Nitrogen content was positively correlated to decomposition rate whilst carbon content was negatively correlated. High nitrogen content promotes decomposition rate. This was similar to results found by other ecologists investigating decomposition and nutrient cycling in terrestrial ecosystems (Waring *et al.*, 1985; Norby *et al.*, 2001; Schädler *et al.*, 2003). This implies that a loss of carbon from the plant litter leads to an increase in decomposition rate especially when microbes feed on plant litter. For example, *D. australe* with a high nitrogen content or low C/N in its litter showed greater decomposition rates than *S. pyramidalis* with its low nitrogen litter or high C/N when the litter was on the soil surface. Chapin *et al.*, 2002 reported the same trend of litter decomposition in association with nitrogen content. Chapin *et al.*, 2002 also reported that this was caused by the fact that microbes were seldom nitrogen limited below a carbon to nitrogen ratio of 25:1. The nitrogen in excess of microbial demands for growth was released into the soil where it becomes available to plants (Cornellissen, 1996). Surface litter decomposition was also predicted by tensile strength, with tougher litter decomposing at a slower rate than brittle litter, and hence is difficult to break for microbes. This will often result in greater carryover of surface litter. Several authors have shown a negative linear relationship between initial lignin concentration and the

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rate of mass loss during litter decomposition (Cromack, 1973; Mellilo *et al.*, 1982; Berg and Agren 1984). Some authors have found that decomposition at the later stages was determined by lignin (Berg and Meentemeyer, 2002). However, lignin content contributed significantly to initial decomposition rate of surface soil litter in this study.

Standing litter at the later stage of decomposition was governed by tribe differences unlike early decomposition which was controlled exclusively by tensile strength and polyphenolic content. The two traits (tensile strength and polyphenolic content) were also important at a later stage of decomposition of standing litter. But the importance of lignin in standing litter was most pronounced at this stage in decomposition. Specific leaf area, which plays a major role in the understanding of many ecosystem processes, was slightly important at a later stage of decomposition of standing grass litter.

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Surface soil litter decomposition at a later stage was governed by the same plant traits as at initial decomposition. But unlike at early decomposition, polyphenolic content and tribe importance was less than C/N ratio and tensile strength at later decomposition of surface litter. The relationship between polyphenolic content and decomposition rate in the soil was not pronounced at a later stage of decomposition. This confirms the fact echoed by Chuyong *et al.*, 2004, that there was no simple relationship between decomposition and polyphenolic content.

What is more interesting was that my models clearly showed that decomposition in the sun was influenced by different traits from those in the soil. For my sun model, early decomposition in grasses was governed by tensile strength and polyphenolic content. The soil model, in contrast, included Polyphenolic content, C/N ratio, tensile strength and lignin. Final stages of decomposition in grasslands in the sun were determined by polyphenolic content, tensile strength, lignin and specific leaf area. The soil decomposition rates were determined by C/N ratio, tensile strength, polyphenolic content and lignin at a later stage. The C/N ratio is important for soil break-down but not for conversion of standing litter to soil litter.

When grass litter is still standing in the sun, decomposition rates of Chlorideae and Paniceae were faster than Andropogoneae. This appears to be due to the fact that Andropogoneae have more polyphenolic content than Chlorideae or Paniceae (Figure 6), and hence slow decomposition rates. Most of the Chlorideae and Paniceae species had faster decomposition rates than their Andropogoneae counterparts. For example *U. mosambicensis* a Paniceae and *D. australe* a Chlorideae had higher rates than all Andropogoneae species (figure 6.3). *S. pyramidalis* and *Digitaria longifolia* were an exception since they were Chlorideae and Paniceae species respectively, with tough, fibrous leaves with high tensile strength hence slow decomposition rate.

The dominance of savanna grasslands by Andropogoneae influences the microclimate through the quantity and structure of litter layer. This results in an insulating litter layer that reduces the average temperature and the magnitude of temperature fluctuations (Knapp and Seastedt, 1986). The chemical properties of polyphenolic content in the Andropogoneae might influence many chemical properties of the soil that are critical to ecosystem functioning. Standing litter can also shade out new growth of grasses and cause a decline in productivity. This has been observed in a number of Andropogoneae in different parts of the world (Knapp and Seastedt, 1986, Knapp *et al.*, 1998, Wand *et al.*, 1999, Fynn *et al.*, 2004).

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6.6. CONCLUSION

Photodegradation was governed by different leaf traits from those predicting microbial decomposition in the soil. These traits include polyphenolic content and tensile strength for photodegradation; and polyphenolic content, tensile strength, C/N ratio and lignin for the microbial decomposition. It is interesting to see that different leaf traits influenced the initial rate of decomposition (over the first two months). For the sun, best predictors were tensile strength and polyphenolic content. However for the soil, polyphenolic content, tensile strength, C/N ratio and lignin remained the most important plant traits by far.

The rates of decomposition were higher in H*i*P than in Cape Town. Decomposition rates also remained constant in the soil throughout the whole experiment and were influenced by similar plant traits at later stages of surface litter decomposition. The sun rates were slower towards the end of the experiment. Andropogoneae had significantly higher polyphenolic content than Paniceae and Chlorideae, and hence decomposed at slower rate resulting in high carryover of grasslands dominated by this tribe.

CHAPTER 7: SYNTHESIS, IMPLICATIONS AND CONCLUSIONS

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Research on decomposition has been restricted to woody ecosystems (Mellilo *et al.*, 1982; Aber *et al.*, 1989; Kavvadias et al., 2001; Quested *et al.*, 2003) while another important aspect of nutrient cycling called litter carryover is restricted to tallgrass prairies (Knapp and Seastedt, 1986). Carryover is not well-studied in South African savanna grasslands. In the prairies it common knowledge that tallgrass prairies tend to experience higher litter carryover than shortgrass prairies. The moribund grass litter hinders grass productivity (Knapp and Seastedt, 1986), hence this carryover results in slow litter decomposition rates. This type of grass litter locks essential plant compounds necessary for nutrient cycling from reaching the soil where it can be incorporated into the soil organic matter.

Not much is known about patterns and determinants of decomposition and carryover in tropical and subtropical ecosystems. The methods employed in woody ecosystems involve putting litter in mesh bags in the soil. The few studies that are there in grassland ecosystems employ similar methods to indicate what happens to surface litter but ignores standing litter. There are many unanswered questions in terms of understanding grass decomposition and nutrient cycling in general.

In this context I set out in this thesis to try and answer the major question namely; how do savanna grasses decompose or how do they get to the soil? What are the patterns, processes and determinants of decomposition as well as carryover in the tropical and subtropical grasslands? Results from this thesis, Chapter 5 showed that when grass litter is still standing the method employed was efficient in predicting the direction in which decomposition rate will be, that is, fast or slow grass species or tribes in tropical and subtropical grasslands. When grass litter is still standing photodegradation is important in that context. I also showed in this thesis that microbial decomposition was faster than photodegradation. But photodegradation was a very important process in terms of controlling the rate at which grass litter decomposes when litter is still standing, thereby dictates what happens on the soil since standing litter which decompose slowly under photodegradation will take time to get to the soil.

The other part of the question which involves determinants of decomposition rates in savanna grasslands is answered by results in chapter 6, which shows that there are different grass traits responsible for microbial decomposition compared to photodegradation. Plant chemical traits and structural traits are commonly used to explain the differences in decomposition rates among plant species. In addition to the common microbial decomposition traits like lignin and C/N ratio; specific leaf area, polyphenolic content and tensile strength are used for the first time in grass species. Grass species early in decomposition were influenced by tensile strength and polyphenolic content when they were still standing. Grass species with high polyphenolic content and tensile strength decomposed at much slower rates than those with less, and remained standing for longer periods in grasslands thereby contributing to carryover. Because of this point photodegradation is important in influencing carryover in semi-arid versus mesic grasslands.

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The different grass species found in mesic and semi-arid grasslands decomposed at different rates both as standing litter as well as surface litter, hence the importance of grass species composition in mesic and semi-arid grasslands carryover. Grass species used here belong to three tribes of grasses namely Andropogoneae, Chlorideae and Paniceae. All the tribes occurred in mesic as well as semi-arid grasslands, but majority of Andropogoneae species were in mesic grasslands while Chlorideae species were common in both savanna grasslands. Paniceae had majority of species in semi-arid grasslands. Paniceae and Chlorideae species decomposed at a faster rate than Andropogoneae species. Therefore phylogeny of grass species seems to account for decomposition rate though there were some exceptions, for instance *Sporobolus pyramidalis* (Chlorideae) and *Digitaria longifolia* (Paniceae) had slowest decomposition rates.

At this point Andropogoneae species with their higher polyphenolic content are expected to decompose slowly and remain standing in the vegetation. Chlorideae and Paniceae species with high tensile strength will also remain standing. Tensile strength and polyphenolic content also play a role in standing litter at the later stages of decomposition as well. Lignin content became important as well later on together specific leaf area at this stage. The tribe differences in decomposition were evident for standing litter later in decomposition, with Andropogoneae slower than Chlorideae and Paniceae.

Initial microbial decomposition was influenced by polyphenolic content, C/N ratio, tensile strength and lignin. Polyphenolic content and tribe differences contributed massively to decomposition on the soil followed by C/N ratio. Polyphenolic content interfered with microbes hence resulting with slower rates in Andropogoneae than in Chlorideae and Paniceae. Because of its high C/N ratio as well Andropogoneae species decomposed slowly because microbes had too much carbon to utilise, thereby using very little. Tensile strength and lignin was important as well with tough surface litter decomposing at slower rates on the soil. The same factors were important at the later stages of decomposition with C/N ratio becoming more important than polyphenolic content and other traits. Therefore this thesis clearly showed how grass species traits influenced how the grass will decompose when still standing and after it reaches the soil. The other point was that most semi-arid grassland species belonged to the tribe Paniceae and decomposed at faster rates than Chlorideae and Andropogoneae, hence low carryover in semi-arid than in mesic savanna grasslands. This can be seen from the fact that fire is commonly used in mesic grasslands to unlock nutrients from moribund grass litter into the soil. The litter carryover acts as fuel load that can only be removed using fire since herbivory is very low. The high toxins in these grasses deter herbivores from grazing further enhancing the accumulation of fuel load and the use of fire.

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The other question asked in this thesis was to show whether there are differences in carryover between mesic and semi-arid grasslands? Results from this thesis in chapter 3 and 4 have shown that mesic grasslands had higher carryover than semi-arid grasslands. The differences between mesic and semi-arid grasslands in carryover were not due to grass productivity as it were the case in tallgrass prairies. Despite mesic grasslands having more rainfall than semi-arid grasslands there were no differences in grass productivity. This is the first study to record the similarities in grass production between mesic and semi-arid grasslands.

In terms of the link between grass productivity and litter carryover between mesic versus semi-arid grasslands in this thesis, litter carryover was strongly related to grass productivity in mesic grasslands than in semi-arid grasslands. That is, high grass productivity in mesic grasslands results in high carryover and low grass productivity with low carryover, while high or low grass productivity in semi-arid grasslands results with low carryover. This further implies that litter carryover disappearance was different between mesic and semi-arid grasslands. Of course the rate of litter carryover disappearance was faster in semi-arid than in mesic savanna grasslands. Further implications are that litter carryover is not a factor in semi-arid grasslands but is important in mesic grasslands. Like in case of tallgrass prairies, litter carryover slowed down grass productivity at the start of a new season in mesic grasslands due to the slow rates of litter carryover disappearance. This carryover occupies space thereby allowing very few grass tillers to grow at the base of the moribund litter. Essential water from the rain is trapped in the litter before reaching the soil. These tillers die off quickly due to the fact that they are shaded from light by the moribund grass litter. The tillers increases fuel load thereby increasing further carryover in the mesic grasslands at the start of the new season unless a fire is applied to recycle nutrients in the form of ash into the soil.

After all this, I conclude this thesis by highlighting that species composition determines how much decomposition and carryover will happen in our grasslands and hopefully around the world. The root of high accumulation of carryover and slow decomposition rates stems from high polyphenolic content and tensile strength when grass litter is still standing. Bearing in mind that the two plant traits mentioned above have been shown to deter herbivores, very little biomass removal by herbivores will further results in more carryover. So, it seems the problem is for grass species to allow for sun breakdown and reach soil since rates of breakdown are higher in the soil and all species used in this study decomposition faster in the soil even though here C/N ratio, tensile strength and lignin were very important as well. I may finally say that mesic grasslands are phylogenetically designed to burn while semi-arid grasslands are for grazing by herbivores.

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REFERENCES

Aber JD, Melillo, JM, Nadelhoffer, KJ, Pastor, J and Boone, RD. 1989. Factors controlling N cycling and N saturation in northern temperate forest ecosystems. *Ecological Applications* 1: 303-315

Acocks, JPH. 1956. *Veld types of South Africa.* 3rd Edition. Botanical Research Institute, South Africa.

Akaike, H. 1983. Information measures and model selection. *Bulletin of the Statistical Institute* 50: 277-290

Allen, SE. 1989. *Chemical analysis of ecological materials.* Blackwell Scientific, Oxford

Archibald, S. 2003. *Effects of frequent burning on grass-grazer interactions in a mesic savanna.* Masters 127 pages. Botany Department, University of Cape Town, Cape Town.

Archibald S, Bond WJ, Stock WD and Fairbanks DHK. 2005. Shaping the Landscape: Fire-Grazer interactions in an African savanna. *Ecological Applications* 15 (1): 96-109

Austin, AT and Vivanco, L. 2006. Litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 442 (7102): 555-558

Balfour, DA and Howison, OE. 2002. Spatial and temporal variation in a mesic fire regime: responses to variation in annual rainfall. *African Journal of Range and Forage Science* 19: 43-55

Balsamo, RA, Vander Willigen, C and Farrant J. 2003. *Relating leaf tensile properties to drought and desiccation tolerance for selected species of Eragrostis.* 4th

University of Cape Town

International Plant Biomechanics Conference, July 20-25, 2003. Michigan State University, Lansing MI, USA in Press

Balsamo, RA, Van der Willigen, C, Boyko, W and Farrant, J. 2005. Retention of mobile water during dehydration in the dessication-tolerant grass *Eragrostis nindensis*. *Physiologia Plantarum* 124 (3): 336-342

Barkworth, ME and Capels, KM. 2000. *The Poaceae in North America: A Geographic Perspective*. Pp. 327-346 in *Grasses: Systematics and Evolution* (Editors), J, Jacobs SWL and Everett. CSIRO pp 331–35, Melbourne, Australia

Beaumont, AB, Stitt, RE and Snell, RS. 1933. Some factors affecting the palatability of pasture plants. *Journal of American Society of Agronomy* 25:123–128.

Berg, B and Agren, G. 1984. Decomposition of needle litter and its organic-chemical components-theory and field experiments. Long-term decomposition in a scots pine forest III. *Canadian Journal of Botany* 62: 2880-2888

Berg, B and Meentemeyer, V. 2002. Litter quality in a northern European transect versus carbon storage potential. *Plant and Soil* 242: 83-92

Bernays, EA, Cooper-Driven, G and Billener, M. 1989. Herbivores and plant tannins. *Advances in Ecological Research* 19: 263-302

Bond, WJ. 1997. Fire. In Cowling, RM and Richardson, DM (editors), *Vegetation of southern Africa* (p 421-446). Cambridge University Press, Cambridge

Bond, WJ, and Keeley, JE. 2005. Fire as global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387-394

Bond WJ, Midgley GF, Woodward FI. 2003. The importance of low atmospheric CO2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* 9: 973–982

University of Cape Town

Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525 -538

Booysen, Martens and Theron. 1968. A tensilemeter for the measurement of the tensile strength of grass leaf blades. *Proccedings of Grassland Soceity of South Africa* 3: 51-56

Bransby, DI and Tainton, NM. 1977. The disc pasture meter: possible applications in grazing management. *Proceedings of the Grassland Society of Southern Africa* 12: 115-118

Briggs, JM and Knapp, AK. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82: 1024-1030

Brooks, PM and Macdonald, IAW. 1983. *The Hluhluwe-Umfolozi Reserve: An ecological case history*. In: Owen-Smith, R.N. (ed.) *Management of large mammals in African conservation areas*, pp. 51-77. Haum Educational Publishers, Pretoria

Burnham, KP and Anderson, DR. 2002. *Model selection and inference: a practical information-theoretical approach*. Second Edition. Springer-Verlag, New York, USA

Chapin III, FS. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany* 91: 455-463

Chapin III, FS, Matson, PA and Mooney, HA. 2002. *Principles of terrestrial ecosystem ecology*. Springer-Verlag, New York

Cheney, NP. 1996. *The effectiveness of fuel reduction burning for fire management*. Proceedings of the conference held 8-9 October 1994. Biodiversity Unit, Dept of the Environment, Sport and Territories: Canberra Paper No.8 pp 9-16. *Fire and Biodiversity: The effects and effectiveness of fire management. Melbourne.*

University of Cape Town

Chimphango, SBM, Musil, CF and Dakora, FD. 2003. Effects of ultraviolet-B radiation on plant growth, symbiotic function and concentration of metabolites in three tropical legumes. *Functional Plant Biology* 30: 309-318

Christie, E.K. 1979. Ecosystem processes in semi-arid grasslands. Litter production, decomposition and nutrient dynamics. *Australian Journal of Agricultural Research* 30: 29-42

Chuyong, GB, Newberry, DM and Songwe, NC. 2004. Rainfall input, throughfall and stemflow of nutrients in a central African rainforest dominated by ectomycorrhizal trees. *Biogeochemistry* 67 (1): 73-91

Coetsee, C. 2003. *Interactions between herbivores, vegetation and nitrogen in Hluhluwe-iMfolozi Park*, South Africa. Masters. Botany Department, University of Cape Town, Cape Town.

Coley, ED. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209-233

Cornelissen, JHC 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84: 573-582

Cornelissen, JHC, Quested, HM, Gwynn-Jones, D, Van Logtestijn, RSP, De Beus, MAH, Kondratchuk, A, Callaghan, TV and Aerts, R. 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology* 18 (6): 779-786

Couteaux, MM, Bottner, P and Berg, B. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10: 63-66

Couteaux, MM, Mousseau, M, Celerier, ML and Bottner, P. 1991. Increased atmospheric CO2 and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos* 61: 54-64

University of Cape Town

Cowling, RM, Richardson, DM and Pierce, SM. 1997. *Vegetation of Southern Africa.* Cambridge University Press, Cambridge

Cromack, K. 1973. *Litter production and decomposition in a mixed hardwood watershed and a white pine watershed at Coweeta Hydrologic Station, North Carolina.* PhD Dissertation. University of Georgia, Athens. 160 pp

Downing, TE. 1974. *Irrigation and Moisture - Sensitive Periods: A Zapotec case in Irrigation's impact on Society*, ed. Theodore E. Downing and M. Gibson, Tucson: University of Arizona Press: 113-122

Ellis, RP. 1990. Tannin-like substances in grass leaves. *Memoirs of Botanical Survey of South Africa* 59. National Botanical Garden, South Africa

Everson, CS, Everson, TM and Tainton, N.M. 1988. Effects of intensity and height of shading on the tiller initiation of six grass species from the highland sourveld of Natal. SouthAfrican *Journal of Botany* 54: 315–318

Eviner, VT and Chapin III, FS. 2003. Functional Matrix: A Conceptual Framework for Predicting Multiple Plant Effects on Ecosystem Processes. *Annual Review of Ecology Evolution and Systematics* 34: 455-485

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL. 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulations shelters. *Ecosystems* 3: 308-319

Frank, DA and Groffman, PM. 1998. Denitrification in a semi-arid grazing ecosystem. *Oecologia* 117: 564–569

Frost, PGH. 1985. *The responses of savanna organisms to fire. In Ecology and Managament of the World's Savannas*, edited by Tothill, JC and Mott, JJ, pp 232-237. Canberra: Australian Academy of Science, Australia

University of Cape Town

Fynn, RWS, Morris, CD and Kirkman, P. 2004. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. *Journal of Ecology* 93 (2): 384-394

Gahrooee, FR. 1998. Impact of elevated atmospheric CO2 on litter quality, litter decomposability and nitrogen turnover rate of two Oak species in a Mediterranean forest ecosystem. *Global Change Biology* 4: 667-577

Gallo, ME, Sinsabaugh, RL and Cabaniss, SE. The role of ultraviolet radiation in litter decomposition in arid ecosystems. *Applied Soil Ecology* 34:82-91

Gibbs-Russell, GE. 1986. Significance of different centres of diversity in subfamilies of Poaceae in southernAfrica. *Paleoecology of Africa* 17: 183-192

Gibbs-Rusell, GE. 1988. Distribution of Subfamilies and tribes of Poaceae in southern Africa. *Monographs in Systematic Botany from the Missouri* Botany 25: 555-556

Gibbs-Russell, GE and Spies, JJ. 1988. Variation in important pasture grasses: I. Morphological and geographical variation. *Journal of Grassland Soceity of South Africa* 5 (1): 15-21

Gibbs-Rusell, GE, Watson, L, Koekemoer, M, Smook, L, Barker, NP, Anderson, HM and Dallwitz, MJ. 1990. Grasses of Southern Africa. *Memoirs of the Botanical Survey of South Africa* 58: 1-437. National Botanical Institute, Pretoria.

Gil, R, Silva, FJ, Zientz, E, Delamotte, F and González-Candelas F. 2003. *The genome sequence of Blochmannia floridanus: comparative analysis of reduced genomes*. Proceedings of the National Academy of Sciences, USA 100: 9388–9393

Govender, N, Trollope, WSW and van Wilgen, BW. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensities in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748-758

University of Cape Town

Grass Phylogeny Working Group. 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden* 88: 373-457

Grime, JP, Hodgon, JG, Hunt, R, Thompson, K, Hendry, GAF, Campbell, BD, Jalili, A, Hillier, SH, Diaz, S, and Burke, MJW. 1997. *Functional types: testing the concept in Northern England.* Pages 122-152 in Smith, TM, Shugart, HH, and Woodward, FI, eds. *Plant functional types*. Cambridge University Press, Cambridge

Hagermann, AE, Reidl, KM, Jones, GA, Sovik, KN, Ritchard, NT, Hartzfeld, PW and Reichel, TW. 1998. High molecular weight plant polyphenolics (tannins) as biological antioxidants. *Journal of Agricultural Food Chemistry* 46: 1887-1892

Hall, DO and House, J. 1995. *World Energy Council, Survey of Energy Resources Series Title: Chapter 10: Bioma*ss (other than Wood), pp 197-206.

Hartley, W. 1958. Studies on the origin, evolution and distribution of the Gramineae. I. The tribe Andropogoneae. *Australian Journal of Botany* 6: 116–128

Hartley, RD and Jones, EC. 1977. Phenolic components and degradability of cell walls of grass and legume species. *Photochemistry* 15: 1157-1160

Hartley, RD and Slater, CS. 1960. Studies on the origin, evolution and distribution of the Gramineae. III. The tribes of the subfamily Eragrostoideae. *Australian Journal of Botany* 8: 256–276

Hector, A, Schmid, B, Beierkuhnlein, C, Caldeira, MC, Diemer, M, Dimitrakopoulos, PG, Finn, JA, Freitas, H, Giller, PS, Good, J, Harris, R, Hogberg, P, Huss-Danell, K, Joshi, J, Jumpponen, A, Korner, C, Leadley, PW, Loreau, M, Minns, A, Mulder, CPH, O'Donovan, G, Otway, SJ, Pereira, JS, Prinz, A, Read, DJ, Scherer-Lorenzen, M, Schulze, ED, Siamantziouras, SD, Spehn, EM, Terry, AC, Troumbis, AY, Woodward, FI, Yachi, S and Lawton, JH. 1999. Plant Diversity and Productivity Experiments in European Grasslands. *Science* 286: 1123-1127

University of Cape Town

Heisler, JL, Briggs, JM, Knapp, AK, Blair, JM and Seery, A. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* 85 (8): 2245-2257

Hilu, K. W. 2004. Phylogenetics and chromosomal evolution in the Poaceae (grasses). Australian Journal of Botany 52: 13-2

Hobbie, SE. 1992. Effects of plant-species on nutrient cycling. *Trends in Ecology and Evolution* 7: 336-339

James, FC and McCulloh, CE. 1990. Multivariate analysis in ecology and systematics: panaceae or Pandora's box? *Annual Review of Ecology and Systematics* 21: 129-166

Jobbágy E, Sala OE, Paruelo JM. 2002. Patterns and controls of primary production in the Patagonian steppe: a remote sensing approach. *Ecology* 83: 307-319

Kavvadias, VA, Alifrais, D, Tsiontsis, A, Brofas, G, and Stamatelos, G. 2001. Litterfall, litter accumulation and litter decomposition rates in four forest ecosystems in northern Greece. *Forest Ecology and Management* 144: 113-127

Kavvadias, VA, Alifragis, D, Tsiontsis, A, Brofas, G, and Stamatelos, G. 2001. Litterfall, litter accumulation and litter decomposition rates in four forest ecosystems in northern Greece. *Forest Ecology and Management* 144 (1-3): 113 – 127

Kellogg, EA. 2000. The grasses: a case study in macroevolution. *Annual Review of Ecology and Systematics* 31: 217-238

King, L. 1970. The geology of Hluhluwe Game Reserve. *Petros* 2: 16-19

Knapp, AK and Seastedt, TR. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36: 662-668

University of Cape Town

Knapp, AK, Briggs, JM, Blair, JM and Turner, CL. 1998. *Patterns and controls of above-ground net primary production in tallgrass prairie. Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (eds A.K. Knapp, J.M. Briggs, D.C. Hartnett & S.C. Collins), pp. 193–221. Oxford University Press, Oxford

Knapp AK, Briggs JM, Koelliker JK. 2001. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* 4: 19-28

Knapp AK, Fay PA, Blair JM , Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, and McCarron JK. 2002. Rainfall Variability, Carbon Cycling, and Plant species Diversity in a Mesic Grassland. *Science* 298: 2202-2205

Knapp AK and Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291: 481-484

Kneebone, WR. 1960. Tensile strength variations in leaves of weeping lovegrass (Eragrostis curvula) and certain other grasses. *Agronomy Journal* 52: 539-542

Lane SJ, Azuma A, and Higuchi, H. 1998. Wildfowl damage to agriculture in Japan. *Agriculture, Ecosysystem and Environment* 70: 69-77

Lauenroth, KW and Sala, OE. 1992. Long-term forage production of North American steppe. *Ecological Applications* 2: 397-403

Le Houerou HN, Bingham RL, Skerbek W. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environment* 15: 1-8

Long, SP, Jones, MB and Roberts, MJ. 1992. *Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics*. Chapman and Hall, Londonl

Martens, PO and Booysen, P de V. 1968. A Tensilmeter for the measurement of the tensile strength of grass leaf blades. *Proccedings of Grassland Soceity of South Africa* 3: 51-56

University of Cape Town

MacNally, R. 2000. Regression and model building in conservation biology, biogeography and ecology: the distinction between and reconcicliation of 'predictive' and 'explonatory' models. *Biodiversity and Conservation* 9: 655-671

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55: 259-294

McNaughton SJ, Banyikwa, FF and McNaughton, MM. 1997. Promotion of the Cycling of Diet-Enhancing Nutrients by African grazers. *Science* 278: 1798-1800

McNaughton SJ, Oesterheld M, Frank, DA and Williams, KJ. 1989. Ecosystem level patterns of primary production and herbivory in terrestrial habitats. *Nature* 341: 142-144

McNaughton SJ, Sala OE, Oesterheld M. 1993. *Comparative ecology of African and South American arid to subhumid ecosystems. Biological relationships between Africa and South America*, pp 548-567 edited by P, Goldblatt. Yale University Press, New Haven, N.J

McCulley, RL and Burke, IK. 2004. Microbial Community Composition across the Great Plains. Soil *Science Society of America Journal* 68: 106-115

Meentemeyer, V. 1978. Microclimate and lignin control of litter decomposition rates. *Ecology* 59: 465-472

Melillo, JM, Aber, JD, Muratore, JF. 1982. Nitrogen and lignin control of hard wood leaf litter decomposition dynamics. *Ecology* 63: 621-626

Milchanus, DG, King, JY, Mosier, AR, Moore, JC, Morgan, JA, Quirk, MH and Slusser, JR. 2004. UV Radiation Effects on Growth and Forage Quality in a Shortgrass Steppe Ecosystem. *Photochemistry and Photobiology* 79 (5): 404-410

University of Cape Town

Mole, SJ, Ross, AM and Waterman, PG. 1988. Light-induced variation in phenolic levels in foliage of rain-forest plants. I. Chemical changes. *Journal of Chemical Ecology*. 14: 1-21

Moorhead, DL, and Reynolds, JF. 1989. Mechanisms of surface litter decomposition in the northern Chihuahuan desert: A reinterpretation. *Journal of Arid Environments* 16:157-163

Morris, JW, Bezuidenhout, JJ, Ferrar, P, Horne, JC and Judelman, M. 1978. A first savanna decomposition model. *Bothalia* 12: 547-553

Morrison, W. L. 1992. Phototherapy and photochemotherapy. *Advances in Dermatology* 7: 255-270

Morrison, W and Nelson, J. 1994. Environmental triggers in multiple sclerosis. Fact or fallacy? *Axone* 16: 23-6

Nocolai, V. 1988. Phenolic and mineral content of leaves influences decomposition in European forest ecosystems. *Oecologia* 75: 575-579

Norby, RJ, Cotrufo, MF, Ineson, P, O'Neill, EG and Canadell, JG. 2001. Elevated CO2, litter chemistry, and decomposition: a synthesis. *Oecologia* 127: 153-165

O'Connor, TG and Bredenkamp, GJ. 1997. Grassland. Vegetation of Southern Africa, pp 615 edited by Cowling, RM, Richardson, DM and Pierce, SM. Cambridge University Press, CambridgeRaich, JW, Russell, AE and Vitousek, PM. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawaii. *Ecology* 78: 707-721

Page, B.R. and Walker, BH. 1978. Feeding niches of four large herbivores in the Hluhluwe Game Reserve, Natal. *Proceedings of the Grassland Society of Southern Africa* 13: 117-122

University of Cape Town

Palm, CA and Sanchez, PA. 1991. Nitrogen release from some tropical legumes as affected by lignin and polyphenol content. *Soil Biology and Biochemistry* 23: 83-88

Paruelo, JM, Epstein, HE, Lauenroth, WK and Burke, IC. 1997. ANPP estimates from NDVI for the Central Grassland Region of the United States. *Ecology* 78: 953-958

Poorter, H and Garnier, E. 1999. *Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire FI, Valladares F, eds. Handbook of functional plant ecology.* New York, NY, USA: Marcel Dekker Inc., 81–120

Quested, HM and Cornelissen, JHC. 2003. Litter decomposition of sub-arctic plant species with differing nitrogen economies: the potential functional role of hemiparasites. *Ecology* 84: 3209-3221

Quinn, GP and Keough, MJ. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge

Raich, JW, Russell, AE and Vitousek, PM. 1997. Primary productivity and ecosystem development along an elevation gradient on Mauna Loa, Hawaii. *Ecology* 78: 707-721

Raison, RJ, Woods, PV and Khanna, PK. 1983. Dynamics of fine fuels in recurrently burnt eucalypt forests. *Australian Forestry* 46: 294-302

Robbins, CT, Hagerman, AE, Austin, PJ, McArthur, C and Hanley, TA. 1991. Variation in mammalian physiological responses to condensed tannins and its ecological implications. *Journal of Mammals* 72: 480-486

Robertson, GP and Paul, EA. 2000. *Decomposition and soil organic matter dynamics*. Pages 104-116 in Osvaldo, ES, Jackson, RB, Mooney, HA, and Howarth, RW, eds. Methods in Ecosystem Science. Springer Verlag, New York, USA

University of Cape Town

Rowlands, AP and Roberts, JD. 1994. Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods. *Communications in Soil Science and Plant Analysis* 25: 269-277

Rozema, J. 1999. *UV-B radiation and terrestrial ecosystems: processes, structure and feedback loops. Stratopheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems*, pp 101-1114 edited by Rozema, J. Leiden. Blackhuys Pubilshers, The Netherlands

Rutherford, MC, Midgley, GF, Bond, WJ, Powrie, LW, Roberts, R and Allsop, J. 1999. *Plant biodiversity: vulnerability and adaptation assessment. South African country study on climate change*. National Botanical Institute, Cape Town, South Africa

Sala, OE and Austin, AT. 2000. *Methods of estimating aboveground net primary productivity. Methods in Ecosystem Science*, pp 31-43 edited by Sala, OE, Jackson, RB, Mooney, HA and Howarth. Springer, New York

Sala, OE & Laurenroth, WK. 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53: 301 -304

Schädler, M., Jung, G., Auge, H. and Brandl. R. 2003. Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. *Oikos* 103: 121–132

Scholes, RJ and Walker, BH. 1993. *An African Savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge

Schulze, ER. 1979. *Climate of South Africa*. Part 8 General Survey. Weather Bureau 158. Pretoria.

Schulze, ED, Mooney, HA, Sala, OE, Jobbágy, E, Buchmann, N, Bauer, G, Canadell, J, Jackson, RB, Loreti, J, Oesterheld, M and Ehleringer, RJ. 1996. Rooting depth,

University of Cape Town

water availability, and vegetation cover along an aridity gradient in *Patagonia. Oecologia* 108: 503-511

Schuurman, G. 2005. Decomposition rates and termite assemblage composition in semi-arid Africa. *Ecology* 86: 1236-1249

Silvertown J, Wells DA, Gillman M, Dodd ME, Robertson H, Lakhani, K.H. 1994. Short-term effects and Long-term after-effects of fertilizer application on the flowering population of green-winged orchid *Orchis morio. Biological Conservation* 69: 191-197

Sing, JS and Gupta, SR. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. *Botanical Review* 43: 449-528

Snyman, HA. 1998. Dynamics and sustainable utilization of the rangeland ecosystem in arid and semi-arid climates of southern Africa. *Journal of Arid Environment* 9 (4): 645-666

Snyman, HA. 1999. Short-term effect of soil-water, defoliation and rangeland condition on productivity of a semi-arid rangeland in South Africa. *Journal of Arid Environment* 43 (1): 47-62

Snyman, HA. 2000. Soil-water utilisation and sustainability in semi-arid grasslands. *Water SA* 26 (3): 333-341

Snyman, HA and Fouche, HJ. 1991. Production and water-use efficiency of semi-arid grasslands of South Africa as affected by veld condition and rainfall. *Water SA* 17 (4): 263-268

Stuwe, J and Parsons, RF. 1977. Themeda australis grasslands on the Basalt Plains, Victoria: floristics and management effects. *Australian Journal of Ecology* 2: 467–476

University of Cape Town

Trollope, WSW. 1984. *Characteristics of fire behaviour in the Kruger National Park.*In Ecological Effects of Fire in Southern African Ecosystems, edited by Booysen, P de V and Tainton, NM. Ecological Studies 48. Springer-Verlag, Berlin

Uys, R, Bond, WJ, and Everson, TM. 2004. The effects of different fire regimes on the plant diversity in southern African grasslands. *Biological Conservation* 118: 489-499

Vogel, J.C., Fuls. A. and Ellis, R.P. 1978. The geographic distribution of kranz grasses in South Africa. *South African Journal of Science* 74: 209-215

Walker, BH. 1985. *Structure and function of savannas: an overview.* In Ecology and Management of World's Savannas edited by Tothill, JC and Mott, JJ, pp 83-91. Canberra: Australian Academy of Science, Australia

Wand, SJE, Midgley, GF, Jones, MH and Curtis, PS. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* 5: 723-741

Wardle, DA, Bonner, KI, Barker, GM, Yeates, GW, Nicholson, KS, Bardgett, RD, Watson, RN, and Ghani, A. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* 69: 535–568

Wardle, DA, Bonner, KI and Barker, GM. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* 16: 585–595

Waring, RH, McDonald, AJS, Larsson, S, Ericsson, T, Wiren, A, Arwidsson, E, Ericsson, A and Lohammer, T. 1985. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. *Oecologia* 66:157-160

University of Cape Town

Watson, PJ. 2005. *Fire frequencies for Western Sydney woodlands: indication from vegetation dynamics*. PhD Thesis. University of Western Sydney, Austaralia

Westoby, M. 1998. The relationship between local and regional diversity: comment. *Ecology* 79: 1825-1827

Whateley, A and Porter. 1983. The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex. *Bothalia* 14: 745-758

Wiegand, T, Snymann, HA and Kellner, K. 2003. From individual scale to population and community scale: Modelling the dynamics of semi-arid grasslands of South Africa. Allsopp, N, Palmer, AR, Milton, SJ, Kirkmann, KP, Kerley, GIH, Hurt, CR and Brown, CJ. International Rangeland Congress, Durban, SA. *Document Transformation Technologies* Volume VII: 37-47

Witkamp, M and Crossley, DA Jr. 1966. The role of micro-arthropods and microflora in breakdown of white oak litter. *Pedobiologia* 6:293-303

Xiao, X, Mellilo, JM, Kicklighter, DW, Pan, Y, McGuire, AD and Helfrich, J. 1998. Primary production of terrestrial ecosystems in China and its equilibrium responses to changes in climate and atmospheric CO2 concentration. *Acta Phytoecologica Sinica* 22: 97-118

Xiong, S and Nilsson, C. 1999. The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology* 87: 984-994

Zucker, WV. 1983. Tannins: does structure determine function? An ecological perspective. *American Naturalist* 121: 335-365

University of Cape Town

In the sun, decomposition rate after 63 days was highest for *U. mosambicensis* followed by *D. australe* and *P. coloratum* and slowest for *S. pyramidalis*, *B. insculpta*, *H. filipendula* and *D. longiflora*. Decomposition over 4 months in the sun showed similar species rankings with highest rates for *U. mosambicensis*, *D. australe* and *P. coloratum*. *B. insculpta* and *T. triandra* had intermediate rates followed by *S. pyramidalis*, *C. excavatus*, *E. curvula* and *H. filipendula*. The species that decomposed the slowest was *D. longiflora* as was the case after two months. It was also evident from the graph (figure 6.1) that decomposition was higher in the first two months but becomes slightly slower towards the end. For example, the fastest decomposing species, *U. mosambicensis,* had a decomposition constant of 0.0034 after two months as compared to 0.0026 after 4 months in the sun.

In the soil, after 63 days of decomposition, the decomposition rate was highest for *D. australe* followed by *U. mosambicensis* and *P. coloratum*. These species were followed by *B. insculpta* and *T. triandra* with slightly lower decomposition rates. *S. pyramidalis*, *D. longiflora* and *H. filipendula* had lower rates with the slowest rates recorded for *C. excavatus* and *E. curvula.* The ranking of species after 124 days were much the same as for the two month period except for the slowest decomposition rates where the ranks changed to *S. pyramidalis*, *C. excavatus*, *E. curvula* and *H. filipendula* with *D. longiflora* showing the least decomposition after 4 months. The rates in the soil were similar for both periods.

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6.4.3.2. Hluhluwe iMfolozi Park Correlations

In the sun, when litterbags were placed vertically, the decomposition rate was only correlated to the decrease in polyphenolic content (Figure 6.1). The H*i*P samples were in the field for only one month. This agrees with the results of the experiment carried out in Cape Town where polyphenolics were one of the most important plant traits at the beginning of decomposition in the sun (see Table 6.3). When litterbags in the sun were placed horizontally the decomposition rate was only slightly correlated to an increase in lignin ($p=0.051$). In the soil, decomposition rate was only correlated with a decrease in C/N ratio (Figure 6.2). The H*i*P samples were quite few due to the fact that only four species were used.

Chimphango, SBM, Musil, CF and Dakora, FD. 2003. Effects of ultraviolet-B radiation on plant growth, symbiotic function and concentration of metabolites in three tropical legumes. *Functional Plant Biology* 30: 309-318

Christie, E.K. 1979. Ecosystem processes in semi-arid grasslands. Litter production, decomposition and nutrient dynamics. *Australian Journal of Agricultural Research* 30: 29-42

Chuyong, GB, Newberry, DM and Songwe, NC. 2004. Rainfall input, throughfall and stemflow of nutrients in a central African rainforest dominated by ectomycorrhizal trees. *Biogeochemistry* 67 (1): 73-91

Coetsee, C. 2003. *Interactions between herbivores, vegetation and nitrogen in Hluhluwe-iMfolozi Park*, South Africa. Masters. Botany Department, University of Cape Town, Cape Town.

Coley, ED. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209-233

Cornelissen, JHC 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84: 573-582

Cornelissen, JHC, Quested, HM, Gwynn-Jones, D, Van Logtestijn, RSP, De Beus, MAH, Kondratchuk, A, Callaghan, TV and Aerts, R. 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology* 18 (6): 779-786

Couteaux, MM, Bottner, P and Berg, B. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution* 10: 63-66

Couteaux, MM, Mousseau, M, Celerier, ML and Bottner, P. 1991. Increased atmospheric CO2 and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos* 61: 54-64

University of Cape Town